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GLASNIK
ZA ŠUMSKE POKUSE

ANNALES
EXPERIMENTIS SILVARUM CULTURAE PROVEHENDIS

37

SVEUČILIŠTE U ZAGREBU
ŠUMARSKI FAKULTET
UNIVERSITAS STUDIORUM ZAGRABIENSIS
FACULTAS FORESTALIS

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Leader: Heinrich Spiecker
Deputies: Robert Rogers, Zoltan Somogyi

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This issue contains the proceedings from the International Conference "OAK 2000 - Improvement of Wood Quality and Genetic Diversity of Oaks", held in Zagreb from 20 to 25 May, 2000 in the organisation of IUFRO and the Faculty of Forestry. The printing of this publication was sponsored by the Ministry of Science and Technology of the Republic of Croatia, the Public Enterprise "Croatian Forests", Zagreb, and Zagrebačka Banka. Circulation 1,000 copies.

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CONTENTS

RIJEČ UREDNIKA

U Zagrebu se od 20. do 25. svibnja 2000. godine održava međunarodni kongres *"OAK 2000 – Improvement of wood quality and genetic diversity of oaks"* (HRAST 2000 – Poboljšanje kakvoće i genetske raznolikosti hrasta). Kongres organiziraju Međunarodna unija znanstvenih institucija u šumarstvu (IUFRO) i Šumarski fakultet Sveučilišta u Zagrebu. Suorganizatori su Ministarstvo znanosti i tehnologije, Ministarstvo poljoprivrede i šumarstva, Javno poduzeće "Hrvatske šume", p.o. Zagreb, Šumarski institut, Jastrebarsko, Akademija šumarskih znanosti i Hrvatsko šumarsko društvo.

Ciljevi su kongresa predstavljanje najnovijih znanstvenih dostignuća u istraživanju ekosustava hrastova s posebnim osvrtom na potrajnost, poboljšanje kakvoće i genetske raznolikosti hrastova te povezivanje znanstvenika koji se bave istraživanjem hrastovih ekosustava. U skladu s tim kongres ima četiri tematske cjeline: poboljšanje kakvoće hrastovine, genetska raznolikost hrastova, gospodarenje hrasticima s ekološkoga i gospodarskoga gledišta te potrajno gospodarenje hrastovim ekosustavima.

U ovom broju GLASNIKA ZA ŠUMSKE POKUSE tiskani su radovi koji su čitani na kongresu. Ukupno je u dva poglavlja tiskano 40 članaka. U prvom su poglavlju članci koji temom pripadaju u IUFRO grupu *1.06.00 – Improvement and silviculture of oaks*, a u drugom su poglavlju članci koji pripadaju u IUFRO grupu *2.08.05 – Genetics of Quercus*. Unutar svakog poglavlja članci su poredani po redoslijedu izlaganja na kongresu.

S obzirom na posebnost ovoga broja GLASNIKA ZA ŠUMSKE POKUSE članci su priređeni za tisak prema posebnim uputama. Tiskani su na engleskom jeziku, bez dvojezičnosti opisu priloga. Na kraju svakoga članka na hrvatskom jeziku tiskan je naslov, sažetak i ključne riječi. Članke su recenzirali inozemni recenzenti, stručnjaci IUFRO-a.

Joso Vukelić
Igor Anić

IUFRO UNIT 1.06.00
IMPROVEMENT AND SILVICULTURE OF OAKS

Leader: Heinrich Spiecker
Deputies: Robert Rogers, Zoltan Somogyi

PREFACE

HEINRICH SPIECKER, ROBERT ROGERS, ZOLTAN SOMOGYI

Oaks are worldwide rather common and economically important tree species. They play a prominent role in timber, cork and forage production, in water conservation, erosion control and recreation. Changing social demands today require a widened scope of sustainable forest management. Besides economic and social considerations environmental issues receive high attention. Society is asking for sustainable forestry emphasizing biodiversity and close to nature forest management. It is of great economic and ecological relevance to know how to manage oak forest ecosystems in order to increase the benefits to society. Knowledge about ecological demands of tree species, about effects of management on wood quality improvement and about management impacts on genetic diversity is needed.

Production aims of oak forest management are changing in time and space. High value of oak wood is economically important for many forest owners as well as for creating jobs in forests and in wood industry. The improvement of wood quality may however conflict with maintaining high diversity in a natural environment. Regeneration, tending and thinning methods as well as harvesting regimes have an impact on the genetic structure of forests. Recent advances in genetic research methods help to get a better understanding of the dynamics of the genetic structure of forests and provide empirical evidence of management effects on genetic diversity of forests.

In recent years the following topics have been discussed in conferences organized by IUFRO 1.06: 'Aspects of Natural Regeneration of Oak', 'Recent Problems in Oak Decline' and 'Advances in Research in Intermediate Oak Stands'. It is the aim of this joint conference of the two IUFRO groups 1.06 *'Improvement and Silviculture of Oaks'* and 2.08.05 *'Genetics of Quercus'* to present research results and their impact on sustainable management of oak ecosystems with special emphasis on high quality timber production and genetic diversity. This special issue contents the papers presented at the international conference 20-25 May 2000 in Zagreb, Croatia. We hope that the papers will provide valuable information for specialists involved in research and management of oak ecosystems: silviculturalists, geneticists, ecologists, managers, and others.

We are aware that knowledge about the ecology and management of oak forest ecosystems as well as knowledge about changing needs of society are important for sustainable forest ecosystem management. Weakening the forest ecosystem will reduce economic and social benefits of forests. It is a political, economic, social and ecological challenge to provide the wonted benefits to society by adequate management regimes.

PREDGOVOR

Hrast je diljem svijeta prilično učestala i gospodarski važna vrsta drveća. On igra važnu ulogu u proizvodnji drva, pluta i krme, u očuvanju voda, sprječavanju erozija i u rekreaciji. Zbog promjena društvenih potreba danas je nužno proširiti opseg potrajnoga gospodarenja šumom. Uz gospodarska i socijalna razmatranja, pitanja okoliša također su u središtu zanimanja. Društvo traži potrajno gospodarenje koje naglašava biološku raznolikost i gospodarenje šumama na prirodan način. U gospodarskom i ekološkom smislu vrlo je važno znati kako upravljati hrastovim šumskim ekosustavima na način da se povećaju opće društveno korisne funkcije šuma. Ovdje je potrebno poznavanje ekoloških zahtjeva vrsta drveća, učinaka gospodarenja na poboljšanje kvalitete drva i učinaka gospodarenja na genetsku raznolikost.

Proizvodni se ciljevi gospodarenja hrastovim šumama mijenjaju u vremenu i prostoru. Za mnoge vlasnike šuma vrhunska vrijednost hrastova drva je ekonomski važna isto kao i otvaranje radnih mjesta u šumskoj i drvnoj industriji. Poboljšanje kvalitete drva, međutim, često je u suprotnosti s očuvanjem raznolikosti u prirodnim okolišima. Načini obnove, njege i prorede, kao i režimi sječe, utječu na genetsku strukturu šuma. Nove, poboljšane metode genetskoga istraživanja omogućavaju bolje razumijevanje dinamike genetske strukture šuma i pružaju empirijski dokaz o učincima gospodarenja na genetski diverzitet šuma.

Posljednjih godina konferencije koje je organizirao IUFRO 1.06 bavile su se ovim temama: "Aspekti prirodne obnove hrasta", "Suvremeni problemi propadanja hrasta" i "Napredak u istraživanju intermedijarnih hrastovih sastojina". Cilj ove zajedničke konferencije dviju IUFRO-ovih grupa 1.06 "*Oplemenjivanje i uzgoj hrasta*" i 2.08.05 "*Genetika hrasta*" jest predstavljanje rezultata istraživanja i njihov učinak na potrajno gospodarenje hrastovim ekosustavima s posebnim naglaskom na vrhunsku kakvoću proizvodnje drva i genetsku raznolikost. Ovo posebno izdanje sadrži radove koji su predstavljeni na međunarodnoj konferenciji održanoj 20–25. svibnja 2000. godine u Zagrebu. Nadamo se da će ovi radovi pružiti vrijedne informacije stručnjacima koji se bave istraživanjem i upravljanjem hrastovim ekosustavima: uzgajateljima, genetičarima, ekolozima, upraviteljima i drugima.

Svjesni smo da su poznavanje ekologije i gospodarenja hrastovim šumskim ekosustavima te svijest o promijenjenim društvenim potrebama važni za potrajno gospodarenje šumskim ekosustavima. Slabljenje šumskoga ekosustava smanjuje gospodarske i društvene funkcije šuma. Osiguravanje traženih općekorisnih funkcija društvu putem odgovarajućih načina gospodarenja politički je, ekonomski, društveni i ekološki izazov.

S. Matić: Oak forests (*Quercus* sp.) in Croatia.
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OAK FORESTS (*Quercus* sp.) IN CROATIA

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This paper describes all oaks that occur naturally and form natural forest communities in Croatia. These are pedunculate oak (*Quercus robur* L.), sessile oak (*Quercus petraea* /Matt./ Liebl.), pubescent oak (*Quercus pubescens* Willd.), live oak (*Quercus virginiana* Ten.), Turkey oak (*Quercus cerris* L.), holm oak (*Quercus ilex* L.), Hungarian oak (*Quercus frainetto* Ten.), and kermes oak (*Quercus coccifera* L.). The most important associations where they occur are described, as well as their principal forest-silvicultural characteristics, area, growing stock, increment, and silvicultural treatments of tending and regeneration. It is emphasised that oak as a species has had a significant effect on Croatian forestry, and that its importance goes beyond the framework of forestry and penetrates all areas of life and customs of the people in Croatia.

Key words: oak, pedunculate oak, sessile oak, pubescent oak, live oak, Turkey oak, holm oak, Hungarian oak, kermes oak

INTRODUCTION

The Republic of Croatia extends over two important vegetative-geographical regions: the Mediterranean and the Euro-Siberian-Northern-American one. Its flora is characterised by a vast diversity of species that include plant representatives ranging from sub-tropical to alpine species. The large number of relict and endemic species and families is the result of the historical development of the plant world and of geological and climatic changes from the Tertiary period up to now. Numerous diverse floral elements, the abundance of relicts and the wealth of endemic species make Croatia a very interesting country in the European framework.

Approximately 4,500 plant species and subspecies have found home in a relatively small area due to Croatia's geographical position and highly diverse synecological conditions. About 50% of them are distributed in the area of forests and their degraded forms (scrub, thickets, maquis and garrigues). Of the total number, there are about 260 autochthonous forest woody species, some sixty of which are interesting from forest-management standpoints (Rauš *et al.* 1992).

Oak forests cover about 30% or 615,000 ha of overall forested area in Croatia (2,078,289 ha) with a growing stock of 89,000,000 or 27.4% of the total growing stock (324,256,000 m^3). The increment is 2,400,000 m^3 annually or 25% of the total annual increment (9,600,000 m^3).

The forests of Croatia contain eight oak species, of which five form autochthonous, coherent, climatogenous forest associations providing important economic and social functions. The remaining three species occur individually or in small, locally-formed forest communities. Their economic function is less significant than their social function and is mainly reflected in the fact that they enhance the biological diversity and stability of the forests in which they occur.

The first group comprises the following oaks: pedunculate oak (*Quercus robur* L.), sessile oak (*Quercus petraea* /Matt./ Liebl.), pubescent oak (*Quercus pubescens* Willd.), live oak (*Quercus virginiana* Ten.) and holm oak (*Quercus ilex* L.).

The second group includes Turkey oak (*Quercus cerris* L.), Hungarian oak (*Quercus fraineto* Ten.) and kermes oak (*Quercus coccifera* L.).

With regard to the fact that oak forests account for 30% of all forests in Croatia, it is important to point out that they occur both in the Mediterranean region and in the Euro-Siberian - Northern-American forest region (European sub-region).

The littoral vegetation belt of the Mediterranean region features holm and kermes oak, which occur in the steno-Mediterranean and eu-Mediterranean vegetation zone. Pubescent oak, live oak, Turkey oak and Hungarian oak occur in the sub-Mediterranean vegetation belt of the same region.

Pubescent, live and Turkey oak occur in the Mediterranean-hilly vegetation belt of the Mediterranean region 400 m above sea level on the islands, 300 m in the Northern Adriatic and 600 m in the southern part.

Depending on ecological and climatic factors in particular, there are lowland areas, low hills, highlands and pre-Alpine belts in the European sub-region of the Euro-Siberian - Northern-American area. Each of these contains several vegetation zones, which contributes to the wealth of forest vegetation in Croatia. Oaks occur in the lowland, hilly and highland areas.

Pedunculate and Turkey oak occur in the lowland vegetation belt, and sessile and Turkey oak in that of the hills and highlands.

In order to obtain a comprehensive picture of all oaks present in the forests of Croatia, each important forest-silvicultural property, that is, the biological characteristics, ecological requirements and economic value of each species will be described.

PEDUNCULATE OAK (*Quercus robur* L.)

Pedunculate oak is the most valuable and best-known economic tree species in Croatian forestry. Thanks to its mechanical, aesthetic and applicable characteristics, it is renowned and valued on all European timber markets. It is most widely distributed in floodplain regions along the rivers Sava, Drava, Danube, Kupa and their tributaries, where, under the name of *Slavonian oak*, it forms forest associations with narrow-leaved ash, lowland elm, common hornbeam and other tree species. Floodplain forests of pedunculate oak, as well as forests on micro-elevations mixed with common hornbeam and numerous other tree species, are characterised by biological diversity, significant productivity and stability.

Pedunculate oak in Croatia covers 10% of the total forested area, or 210,000 ha, with a growing stock of 14% or 44,400,000 m³ of the total growing stock, and an annual increment of 11% or 1,050,000 m³ of the total increment.

Flood and groundwater are the main ecological factors determining the survival and growth of pedunculate oak forests in Croatia. Each disturbance in flood dynamics and groundwater levels causes physiological weakening of especially older and old pedunculate oak stands, allows secondary pest attacks and leads to dieback and degradation.

Forests of pedunculate oak appear in two basic forest associations: those of the floodplain forest of pedunculate oak and *Genisto elata* (*Genisto elatae-Quercetum roboris* Ht. 1938) and the forest of pedunculate oak and common hornbeam (*Carpino betuli-Quercutum roboris* (Anić 1959) emend. Rauš 1969), which grows on micro-elevations. Pedunculate oak is characterised by within-population flushing variability; as a result, there is an early form "*praecox*" and a late form "*tardissima*" (*Quercus robur* var. *tardissima* Sim.). The time difference in the flushing between the early and late oak is about 2-5 weeks.

Forests of pedunculate oak in Croatia form large coherent complexes, such as Spačva (40,000 ha), Lonjsko Polje (30,000 ha), Repaš (5,000 ha), and forest basins in the area of Česma, Donji Miholjac, Našice, Slatina and others.

Pedunculate oak forests are regenerated naturally and sometimes artificially with shelterwood felling in three or two separate cuts (preparatory, seeding and final cut). Tending often begins before the final cut (young growth is tended under the canopy of old trees), and finishes with the last thinning prior to the beginning of the preparatory cut. During tending, all attention is focused on pedunculate oak as the most valuable but silviculturally weakest species in relation to its principal competitors, common hornbeam, narrow-leaved ash, lowland elm and other accompanying pioneer tree species.

SESSILE OAK (*Quercus petraea* Liebl.)

Sessile oak and pedunculate oak are extremely important tree species in Croatian forestry from both economic and social standpoints. In terms of mechanical and aesthetic properties, the value and quality of sessile oakwood is very close to that of Slavonian pedunculate oak.

Forests of sessile oak in Croatia cover the hilly vegetation belt between 150 - 500 m above sea level and the highland vegetation belt up to 700 or 900 m above sea level, depending on the position and macroclimate of the massifs. Sessile oak forests contain a large number of other tree species and shrubs, which makes them biologically diverse and stable.

In Croatia, sessile oak is distributed over 11% or 230,000 ha of the total forested area, with a growing stock of 10% or 32,000,000 m³ and an increment of 1,000,000 m³ or 10% of the total increment.

Sessile oak is a climatogenous tree species forming five different forest communities in the Central-European vegetation zone of acidophilic forests, one forest community in the Central-European zone of thermophilic forests and two communities in the peri-Illyrian vegetation zone.

Of all sessile oak communities in Croatia, special mention should be made of the widely distributed climatic-zonal association of outstanding value - the Illyrian forest of sessile oak and common hornbeam (*Epimedio-Carpinetum betuli* Ht. 1938, Borh. 1963). This forest is characterised by rich floral composition and species that more or less mark the Illyrian floral element. This association grows on acid, loamy and sandy soils poor with lime, as well as on carbonate substrates and eutric soils.

This sessile oak association has high economic and social importance, but is endangered by anthropogenic influences. Areas of sessile oak have been taken over by human settlements, roads, vineyards and other agricultural areas. Synecological conditions of this association are much better suited to sessile oak than to beech; as a result, sessile oak is stronger and more competitive here.

Forests of sessile oak form considerable forest complexes on the hillocks and hills between the rivers Sava and Drava in the north and north-west of Croatia. Similarly, sessile oak forms forest communities in Central Croatia and on suitable positions in the mountains of the Dinaric Alps.

Regeneration of sessile oak forests is similar to that of pedunculate oak forests. Forests are regenerated with shelterwood felling in two or three cuts, depending on the state of a stand and the soil. Compared to pedunculate oak, there are fewer problems relating to natural regeneration due to the fact that changes in site conditions are less conspicuous in sessile stands than in pedunculate ones, while acorn yields are more abundant and more frequent than with the pedunculate oak.

Sessile oak forests are tended in the period of the final cut and during the whole rotation until the beginning of the preparatory or seed cut. In relation to its competitors, common hornbeam and beech, which are more aggressive and silviculturally stronger species than sessile oak, focus is laid on assisting the sessile oak at the expense of its competitors.

PUBESCENT OAK (*Quercus pubenscens* Willd.) AND LIVE OAK (*Quercus virginiana* Ten.)

Climatozonal forests of pubescent oak and live oak occur in the sub-Mediterranean vegetation zone of thermophilic, deciduous and black pine forests. With regard to the fact that the sub-Mediterranean belt of pubescent and live oak forests is relatively high, sometimes reaching heights of 1,200 m above sea level, it is divided into warm, temperate and cold belts according to the presence of various associations.

Apart from other forest associations, the warm belt also encompasses the most widely-distributed mixed forest of pubescent oak and oriental hornbeam (*Querco-Carpinetum orientalis* H-ić 1939).

The temperate belt abounds in several associations, of which the most important is a mixed forest of pubescent oak and hop hornbeam (*Ostryo-Quercetum pubescentis* Ht, Trinajstić 1977) from the standpoint of silviculture and general benefits.

The cold belt of pubescent oak forests is inhabited by the forest of hop hornbeam with autumn rush *(Seslerio-Ostryetum* Ht. and H-ić 1950).

Live oak (*Quercus virginiana* Ten.) occurs in the sub-Mediterranean region from Knin eastwards to the Dubrovnik hinterland, and forms the forest of live oak and oriental hornbeam in the warm belt, and the forest of live oak and hop hornbeam in the temperate belt.

Live oak is more xerothermal than pubescent oak, capable of tolerating drought and heat well, and is a very resistant deciduous tree species.

Forests of pubescent oak and live oak in Croatia cover about 5% or 110,000 ha of forested area, with a growing stock of 1.3 % or 4,300,000 m^3 and an annual increment of 1.3 % or 130,000 m^3.

All the associations mentioned above occur mostly in the degraded stage of scrub and in the low silvicultural form or coppice. Only about 1,000 ha of pubescent and live oak forests are in the high silvicultural form or forest from seed. These stands are often of poor appearance due mostly to the very hard ecological conditions in which they live and to the sites of poor quality.

The main economic product of these forests is fuel wood. In its attempts to preserve these forests and transform them into a higher silvicultural form, the forestry profession is faced with the problem of goat browsing, which is otherwise banned by law. Despite this, a large share of pubescent and live oak forests is in progression. At present, they are left to spontaneous succession, which could be accelerated by providing expert forestry treatments and protection.

The tending of these forests is mostly oriented towards their protection from the negative effects of biotic and abiotic factors (people, cattle and fires). Tending in stands on good sites with favourable structural properties is geared to progressive development towards medium and high silvicultural forms. .

These forests can be regenerated with natural or artificial methods with shelterwood felling in two or three cuts.

Apart from their economic importance, forests of pubescent oak and live oak provide considerable general benefits both from the ecological and social standpoints.

TURKEY OAK (*Quercus cerris* L.)

As a species, Turkey oak appears both in sub-Mediterranean forests of pubescent oak and in continental forests of pedunculate and sessile oak. It occurs more frequently in more xerothermal site conditions where it competes with other oaks. It is less valuable than pedunculate, sessile, pubescent and live oak. However, it has a high forest-silvicultural value and importance in the structure of the forests in which it occurs as it provides biological diversity, survives the most adverse conditions, and repairs the flaws and mistakes in the structure of "parent" stands where it appears.

Its timber is not very valuable economically, at least in Croatian market conditions. It is mostly used as fuel wood, although it has value in building and in some specific products of the timber industry.

Turkey oak occurs largely in the association of pedunculate oak and common hornbeam with Turkey oak (*Carpino betuli-Quercetum roboris quercetosum cerris* Rauš 1969), which represents the most extreme variant of pedunculate-hornbeam forests (Rauš *et al.* 1992). Similarly, Turkey oak forms Hungarian-Turkey oak forests (*Quercetum frainetto-cerris* Rudski 1940, 1949), a climatogenous association that occurs in the transitional area between the steppe and the forest (Vukelić, Rauš 1998).

The growing stock of Turkey oak in the forests of Croatia is 1 % or 3,000,000 m^3 of total growing stock, while the annual increment amounts to 1.2 % or 120,000 m^3.

Silvicultural treatments in the forests in which it occurs are aimed at preserving it in smaller percentages in the interest of favoured oaks. It often yields seeds and regenerates well naturally with shelterwood felling in two or three cuts.

HOLM OAK (*Quercus ilex* L.)

Holm oak is the most valuable and most stable species in the eu-Mediterranean forest region in Croatia. Due to centuries-long exploitation and devastation by both biotic and abiotic factors (man, cattle, fires), the areas where it occurs have decreased. Holm oak has often even disappeared from the associations it originally formed in the region. Today, it occurs mostly in the degraded form of maquis and in the low silvicultural form or coppice forest.

Its timber is highly valued in the shipbuilding industry due to good physical properties. Today, it is largely used as fuel wood.

In the eu-Mediterranean region, holm oak forms two important forest associations. The forest of holm oak with myrtle (*Myrto-Quercetum ilicis* H-ić 1956, Trinajstić 1985) is the most thermophilic forest association in which only evergreen species survive (Trinajstić 1986). The forest of holm oak and manna ash *(Fraxino orni-Quercetum ilicis* H-ić 1956, 1958) is the most widely distributed climatogenous association of the eu-Mediterranean region. It occurs in the areas from Istria over the islands to Zadar, and then along the littoral part and the islands to Prevlaka. It grows in somewhat more favourable temperature and moisture conditions than the previously mentioned association. For this reason, it contains a large number of accompanying species of both an evergreen and deciduous nature, of which manna ash (*Fraxinus ornus* L.) is the most valuable from the forest-silvicultural standpoint.

Holm oak covers 3.5 % or 70,000 ha of the area in Croatia, with a growing stock of 1.6 % or 5,050,000 m³, and an annual increment of 1.3 % or 120,000 m³.

Silvicultural treatments in holm oak forests are divided into treatments in maquis and treatments in coppice forests. In maquis, the treatments are aimed primarily at protection from adverse impacts of biotic and abiotic factors. In the course of time, an excessive number of accompanying species is differentiated and reduced in the interest of holm oak. In this way, maquis is gradually transformed into coppice.

Silvicultural treatments in a coppice include tending and regeneration. Tending that involves cleaning and thinning operations favours holm oak over numerous accompanying species. Regeneration can be done by natural and artificial means, with shelterwood felling in coppice or high forest in two or three cuts.

HUNGARIAN OAK (*Quercus frainetto* Ten.) AND KERMES OAK (*Quercus coccifera* L.)

Hungarian and kermes oak inhabit relatively small areas in Croatia and have no significant economic value, although they are interesting and valuable from the natural-scientific standpoint.

Hungarian oak is a deciduous tree species of the continental part of Croatia. It forms a climatogenous forest association of Hungarian-Turkey oak (*Quercetum frainetto-cerris* Rudski 1940, 1949). It occurs on the slopes of Krndija in the Kutjevo area.

Kermes oak is an evergreen Mediterranean tree species that inhabits a relatively small area of eu-Mediterranean: the islands of Lošinj, Korčula, Mljet, the Pelješac peninsula and the vicinity of Cavtat. It occurs in bush form with a maximal height of about 10m. With manna ash it forms a forest association of kermes oak and manna ash (*Fraxino orni-Quercetum cocciferae* H-ić 1958). There are frequent more of less pure stands of kermes oak in the area of Pelješac, Korčula and Cavtat (Rauš et al. 1992).

CONCLUSION

Oaks, and pedunculate, sessile, Turkey, pubescent, live and holm oaks in particular, are characteristic tree species of Croatian forestry. As such, they have become a symbol of manifold properties appertaining to the Croatian region, people and customs. Their presence marks the living conditions represented by the properties of the soil, water regime and climate. Their influence embraces ecological, social, economic, cultural, national, religious and mythical areas, to which the Croatian man has been adapting for millennia. Oaks carry an outstanding quality of timber reflected in their physical, aesthetic and chemical properties, features belonging only to high-quality tree species.

It is not surprising that the importance of oaks has exceeded the framework of forestry alone. Oaks have become an indelible part of the living styles and customs of the people in these areas, and even feature in the lyrics of the Croatian national anthem, in which they symbolise the permanence and eternal existence of the Croatian people in these regions.

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HRASTOVE ŠUME (*QUERCUS* SP.) U HRVATSKOJ

Članak opisuje sve vrste hrastova koje dolaze od prirode i koje tvore prirodne šumske zajednice u Hrvatskoj. To su hrast lužnjak (*Quercus robur* L.), hrast kitnjak (*Quercus petraea* /Matt./ Liebl.), hrast medunac (*Quercus pubescens* Willd.), dub (*Quercus virginiana* Ten.), cer (*Quercus cerris* L.), crnika (*Quercus ilex* L.), sladun (*Quercus frainetto* Ten.) i oštrika (Q*uercus coccifera* L.). Opisane su najznačajnije šumske zajednice u kojima uspijevaju, njihove temeljne uzgojne značajke, areal, drvna zaliha, prirast i uzgojni postupci njege i pomlađivanja.

Ključne riječi: hrast, hrast lužnjak, hrast kitnjak, hrast medunac, dub, cer, crnika, sladun, oštrika

A. Béky, Z. Somogy: Growth and yield of hornbeam-sessile oak (*Carpinus betulus* L. - *Quercus petraea* /Matt./ Lieb.) stands under optimal management ... Glas. šum. pokuse 37: 15–28, Zagreb, 2000.

UDK 630*221+653+(439) (Quercus petraea Lieb., Carpinus betulus L.)

GROWTH AND YIELD OF HORNBEAM-SESSILE OAK (*Carpinus betulus* L. - *Quercus petraea* /Matt./ Lieb.) STANDS UNDER OPTIMAL MANAGEMENT IN HUNGARY

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In mixed forests, a basic question is what is the optimal ratio of the species with respect to yield As a first attempt in Hungary to address this issue, a yield table for hornbeam-oak forests was developed. This indicated, at a hypothesis level, that mixed hornbeam-oak stands may have around the same yield as unmixed oak stands. In addition to publishing this new yield table, this paper directly addresses the issue of the optimal species ratio by using the data from permanent sample plots established in mixed stands of optimal structure, of too much oak and of too much hornbeam. The optimal ratio is analysed in relation to age and yield class. According to the results, it is best to mix the two species on the best sites and at middle ages; however, on poor sites and at young or old ages, pure oak stands produce the greatest yield. This paper stresses that mixing the two species, as in many other forest types, may also have many ecological and economic advantages.

Key words: sessile oak, hornbeam, mixed stands, yield optimisation, optimal stand structure.

INTRODUCTION

With the expansion of the idea of nature-oriented silviculture, the promoting of the establishment and protection of mixed structures have become key issues in forest management in many countries. In fact, mostly mixed stands would exist under natural conditions in most forests in the world. According to botanists, the number of species in many native forest types under Hungarian site conditions varies between 5-15 (Bartha and Szmorad, 1997, Bartha, 1999, ÁESZ, 1996). In natural hornbeam-sessile oak forest types, usually 8-10 mixing species occur.

In the long run, the area of mixed stands must be much larger than now. In addition to the biological role that the mixing of species can play, and the added economic value they may have, it is usually not worth fighting against naturally emerging species in natural regenerations and elsewhere, and it is also often not profitable to do so. Kerr et al. (1992) present several other benefits of mixtures.

Similar to the uneven-aged stands when compared to the even-aged ones, much less study has been done in mixed stands than in unmixed ones. A practical reason for this is that it is much more difficult to study complex structures than plantation-like, homogeneous structures. This is the case in Hungary, too, where there have only been a few studies conducted in mixed stands (Solymos and Béky, 1995, Solymos, 1998 in stands of indigenous species, and Rédei, 1984, in poplar-Black locust plantation-like stands), although some of these studies were started in the 1960s.

Mixing two or more species and controlling their ratio may be rather difficult. Controlling the species ratio, or, in general, developing an appropriate stand structure, requires the main objective of forest management to be defined. If yield is of greatest importance, the question arises whether the yield of mixed stands is more

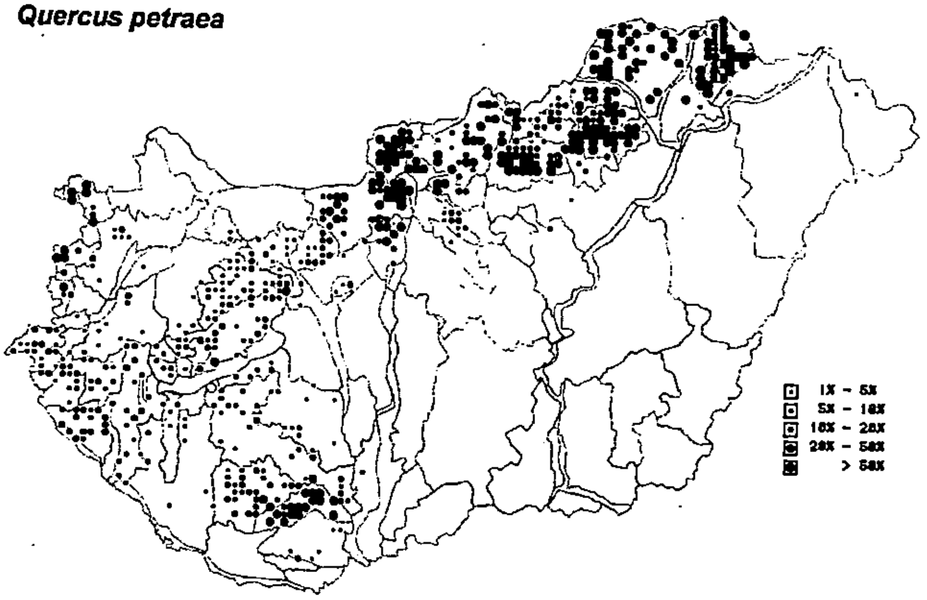
Quercus petraea

Figure 1. The distribution of sessile oak in Hungary (Bartha and Mátyás, 1995)

than that of single species in unmixed stands (the so-called "mixed species effect". Furthermore, if mixed stands seem to perform better, one may need to know what the optimal ratio of the tree species constituting the stand is. One must, of course, bear in mind that, if the amount and value of the yield is not the highest priority of forest management, the optimisation of the species ratio should not be pursued.

The above questions were studied in hornbeam-sessile oak stands in Hungary. These stands occupy large areas in the country: 7.2 % of all forests (ÁESZ, 1996). In fact, hornbeam and oak are the two main components of mixed forests under the conditions of the country. Since their requirements for site are similar, they occur in the same regions (Figure 1 and 2).

Studies on the yield of mixed stands have only been done in hornbeam-sessile oak stands in Hungary (Béky, 1978, Béky, 1986, Béky, 1987, Béky, 1989, Béky, 1997, Béky and Somogyi, 1995). These studies introduced the issues of optimal species ratio, but could not provide substantial evidence on the existence of this ratio. These studies could not even decide whether the mixture of these species could result in a higher yield than any type of unmixed stand forms. This latter issue can be reformulated this way: is it the mixed stand form or the unmixed one that can better utilise a specific site?

By using a purely theoretical approach, mixed stands may perform better. Based on the idea of an ecological niche, every species utilises a partially specific niche, and the sum of the realised niches in a mixed stand is larger than that in unmixed stands. This suggests that the yield of mixed stands is higher. On the other

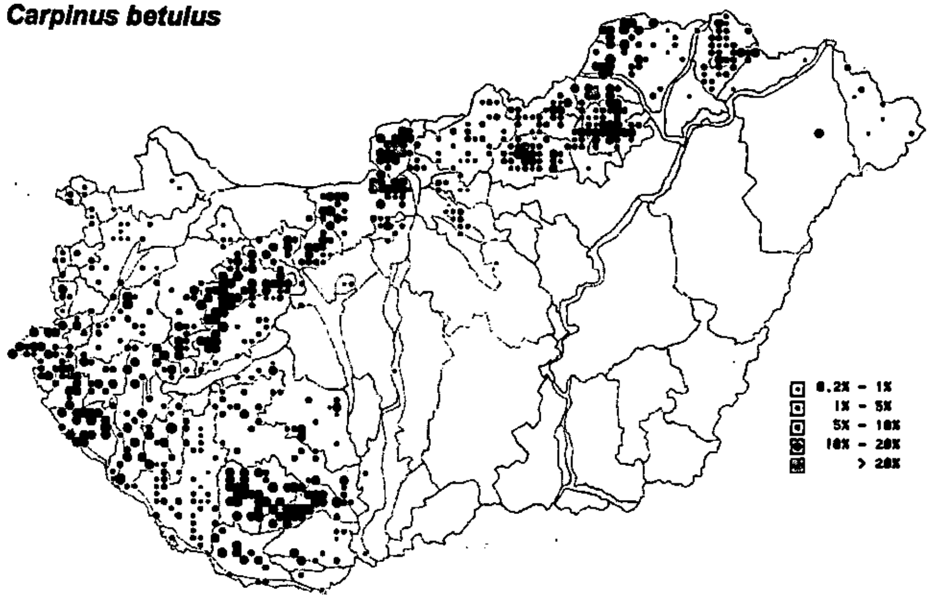

Figure 2. The distribution of hornbeam in Hungary (Bartha and Mátyás, 1995)

hand, the yield of the various species may differ a great deal on the same site, and stand structure modifies the performance of the tree individuals. Since the overall outcome of these effects cannot be theoretically deducted, field studies are required.

According to several studies in other forest types, mixed stands can often outperform unmixed ones in terms of volume. Examples include mixed Scotch pine-beech stands that, if the rotation age is 140 years, produce 20% more than the respective unmixed stands, and Scotch pine-Norway spruce stands with a 15% yield surplus if the rotation age is 120 years (Kramer, 1987). In oak-beech stands, which also occur in Hungary, this surplus accounts for 13. 21 and 27% at the ages 120, 160 and 200 years. A surplus, even if smaller, can also be attained with other mixing species of slower growth. If the mixing species is a fast growing one, such as European larch, the surplus can reach as much as 30% (Karmer, 1987). The results of many more experiences are summarised by Burkhart and Tham (1992). In most of the cases they report on, mixed stands seem to outperform pure stands.

This paper addresses the effect of mixture on the yield of sessile oak and hornbeam. As Burkhart and Tham pointed out, verification of the mixed species effect is rather difficult because it is not easy to obtain reference yields of pure stands of the species of interest, without confounding them with other factors. The results presented in this study were obtained based on data collected in permanent sample plots with a different species ratio. First, the yield table for hornbeam-sessile oak stands (the first of its kind in Hungary) is presented, which is followed by detailed analysis of the data from the parmanent plots. In this analysis, yield is also related to site and age.

MATERIALS AND METHODS

Yield tables were derived from data collected at repeated surveys of 120 permanent sample plots. To study the optimal species ratio, the data of around 100 even-aged stands were selected. All plots were established between 1968 and 1974 by Albert Beky. The size of the plots is 50x50 or 50x40 m. The stands were surveyed every 5(-7-10) consecutive years. The number of increment data per plot ranges from one to five. Data from all subsequent surveys were used, which means that correlations also include autocorrelations.

The plots were established in even-aged stands of an approximately homogenous site where three plots of different species ratios could be established. Although the yield table was made for stands of "optimal" structure, the data of stands of "oak" and "hornbeam" structure were also used. The structure was regarded "optimal" if valuable dominant oak trees that could be grown as future trees were evenly distributed, and all other places were occupied by either oak or hornbeam. The structure is an "oak" one if oak predominates and hornbeam plays an irrelevant role, and a "hornbeam" one if the ratio of oak is too low or if oak is missing in larger patches.

The plots were thinned in a way that was regarded as "optimal", i.e. approximating or maintaining the "optimal" structure. This structure can only be achieved through active silvicultural operations, since in all of the many types of mixtures, hornbeam would suppress oak until about the age of 25-30 years, but die out afterwards. Thinning out strong hornbeam individuals in young stands, as well as protecting good growing ones of good stem quality in older stands, was therefore necessary. The optimal structure can be characterised by the following (Béky, 1987):

- hornbeam is gradually suppressed by oak over time;
- the volume ratio of oak grows from 60% to 80 % over time;
- the stem number ratio of oak varies between 25-40%;
- the horizontal distribution of future oak trees approximates an even structure.

All trees in all plots were identified by specific tree numbers. In each survey, two diameters (to the nearest mm in two perpendicular directions) and total tree height (to the nearest 0.5 m) were measured for each tree. The species of trees and the age of the stands were also recorded. The main crop and thinnings were separately surveyed. Tree volume was calculated by the Király volume function (Király, 1978) which was developed by using the Sopp (1970) volume tables. From these volumes and tree numbers, stand volume, basal area, and growth could be derived for each species, after which species ratio (by number and volume) and growth could be calculated. (Other rarely occurring tree species were recorded as either oak or hornbeam. In some plots, oak disease killed some trees. The slight effects of this disease were corrected where it seemed necessary).

The yield class of mixed stands was defined by the top height of oak and age. The same height-age curves were used as those in the yield table for pure sessile oak stands (Béky, 1981). Although yield class only correlates with site in a non-linear manner, and is not a perfect measure of it, yield class was used in some analyses as a site-related independent variable. (Yield class I indicates best sites, yield class VI the poorest ones).

Age may also be used as an independent explanatory variable. Contrary to yield class, however, age is a continuous variable, which cannot be used in several analyses. Five age groups were created in these cases (Table 1).

Table 1. Five age groups that were used in some analyses

Age (year)	Age group
>30	1
40-59	2
60-79	3
80-99	4
<100	5

The functions of the yield table were developed by graphically fitting them to the data, and simple mathematical functions were then fitted to these graphic lines. The mean height of the two species were developed in the function of the top height of oak. Mean diameters were related to age and D/H values. The number of stems in the main stand was developed by the method of Reinecke (1933). Finally, volume was calculated by using form height estimated from mean height. From these data all other data in the yield table could be calculated by using standard growth and yield functions.

Data evaluation to explore the effect of mixture on yield was done by drawing graphs and by using regression analysis. Depending on the number and distribution of the data, linear, logarithmic, as well as negative exponentially-weighted fitting (NEGEXP) was used. Statistical analyses were done by the STATISTICA (StatSoft, Inc., 1998) software.

RESULTS AND DISCUSSION

YIELD OF HORNBEAM-SESSILE OAK STANDS

Yield table for hornbeam-sessile oak stands

General data

Data must be calculated for the end of 5-year intervals by functions. The main functions of the yield table are as follows (all totals are for 1 ha):

YG = yield grade; top height of sessile oak at the age of 100 years (m)

yield class	yield grade
I	32
II	29
III	26
IV	23
V	20

A = age (yr)

H_t (top height of sessile oak) =

$$= (a + b \cdot \lg(A) + c \cdot \lg(A)^2 + d \cdot \lg(A)^3 + e \cdot \lg(A)^4 + f \cdot \lg(A)^5) \cdot YG / 100$$

a = -154.958
b = 629.7612
c = -935.3223
d = 644.2674
e = -186.7059
f = 17.8086

Data for the main crop (denoted by m in the index)

H_{gm} (basal area weighted mean height, m) $= a + b \cdot H_t$

sessile oak	*hornbeam*
a = -0.25	-0.42
b = 0.98334	0.694

D_{gm} (diameter from the mean basal area, cm) $= H_{gm} \cdot (a + b \cdot A)$

sessile oak	*hornbeam*
a = 0.6425	0.545875
b = 0.011225	0.006456

G_m (basal area, m^2) $= D_{gm}{}^2 \cdot \pi / 40000 \cdot N_m$

V_m (volume, m^3) $= G_m \cdot (a + b \cdot \lg(H_{gm}) + c \cdot \lg(H_{gm})^2 + d \cdot \lg(H_{gm})^3)$

sessile oak	*hornbeam*
a = 2.2394	-8.16148
b = 16.2606	48.89907
c = -29.1697	-64.4873
d = 17.0736	30.00008

N_m (number of stems) $= 10^{a + b \cdot \lg(D_{gm})}$

sessile oak	*hornbeam*
a = 4.775232	4.68307
b = -1.62601	-1.73569

Thinnings (denoted by t in the index)

$H_{gt} = a + b \cdot H_t$

sessile oak	*hornbeam*
a = -1.545	-2.79
b = 0.9665	0.79

$D_{gt} = (a + b \cdot A) \cdot H_{gt}$

sessile oak	*hornbeam*
a = 0.418857	0.472071
b = 0.011771	0.006964

$G_t = D_{gt}{}^2 \cdot \pi / 40000 \cdot N_t$

Because of the self-thinning phenomenon in young stands, the timber of which cannot be utilised, the basal area of the oak portion of the young stands must be reduced (the diameter, height and tree number are for all trees). The basal area estimated above must be divided by gdiv between the ages of 10 and 40 years, where

$gdiv = 10^{a + b * A}$
$a = 0.763394$
$b = -0.01908$

$V_t = G_t \cdot (a + b \cdot \lg(H_{gt}) + c \cdot \lg(H_{gt})^2 + d \cdot \lg(H_{gt})^3)$
a, b, c, d are the same as for the main crop.

$N_t = N_{mA} - N_{m(A-5)}$.

Data for the whole stand (denoted by w in the index):

$H_w = (H_{gm} \cdot G_m + H_{gt} \cdot G_t) / (G_m + G_t)$
$D_w = (G_w / N_w \cdot 40000 / \pi)^{1/2}$
$G_w = G_m + G_t$
$V_w = V_m + V_t$
$N_w = N_m + N_t$

Growth and yield:

ΣV_t (total thinnings, m^3) = sum of all thinnings (V_t) up to A
$V_{t\%}$ (%) = $\Sigma V_t / V_y \cdot 100$
V_y (yield, m^3) = $V_m + \Sigma V_t$

MAI (mean annual increment, m^3/yr) = V_y/A.
PMAI (periodic mean annual increment, m^3/yr) = $(V_{yA} - V_{y(A-5)})/5$.

Analysis of possible yield surplus by means of yield tables

A possible yield surplus in hornbeam-sessile oak stands, relative to either pure hornbeam or pure sessile oak stands, can be studied by comparing yield levels at approximately similar site conditions. This, however, is not at all easy if only yield class can be used for site estimation. Although no correct comparison is possible between the performance of oak and hornbeam by using yield tables, it can be stated that oak generally has a substantially higher production capacity than hornbeam. Such a comparison is not possible between pure oak stands and mixed hornbeam-oak stands because the yield level of the two stand forms is too similar and yield tables cannot provide the flexibility that would be necessary to explore any surplus.

YIELD OF MIXED STANDS COMPARED TO UNMIXED ONES - AN ANALYSIS BASED ON DATA OF PERMANENT SAMPLE PLOTS

In this analysis, the data of 296 surveys were used (Table 2), of which 129, 84 and 83 were done in stands of “optimal”, “oak” and “hornbeam” structures respectively.

Table 2. Frequency of surveys by age group and yield class

Yield class	age group					Total
	1	2	3	4	5	
I	9	9				18
II	2	35	29	19	9	94
III	7	24	16	21	12	80
IV	15	62	14	3		94
V	2	8				10
Total	9	85	124	54	24	296

The role of the two species in the stand is, of course, not the same. Oak is a species of continuous growth in the top storey which is usually shown by the number and the size of the tree individuals. The thinnings are usually also done in favour of oak. It is no wonder then that the relative current annual increment (CAI), calculated for each survey independently from age and site, is equal for the two species if the ratio of hornbeam is 0.6. This ratio changes over time and yield class. The ratio of hornbeam in yield class II changes from 72 to 78%, in yield class III from 68 to 72%, and in yield class IV from 75 to 70% over the 30 year period of observations. In stands of "optimal" structure, hornbeam ratios grew from 73 to 80%, in stands of "hornbeam" structure from 53 to 55%, but in stands of "oak" structure it decreased from 90 to 86%.

The yield of oak usually decreases with an increasing ratio of hornbeam (Figure 3). No species ratio can be found that could be regarded as optimal for oak with respect to yield, but, especially on better sites, the yield of oak only slightly decreases as long as the ratio of hornbeam is less than 10-15%. This decrease is more intensive at younger ages.

The issue of optimal species ratio can be studied if total CAI is graphed over species ratio (Figure 4). The surfaces show that there are only a few cases when a surplus can be achieved in hornbeam-sessile oak stands as compared to pure oak ones. It is the better sites and over 60 years of age where a surplus is obvious, but the maximal rate of this surplus is 10%. In yield class 3, the highest yield is reached in pure oak stands, and even a minimum can be found in yield class four. (In this analysis, the NEGEXP fitting was used.)

Concerning the existence of a yield optimum, there may be no single combination of the two species, not even in yield class II, where yield is at its maximum. Instead, a wide range of species ratio of approximately between 0 and 50% appears to be in this yield class at ages over 60 years where one does not have to count with yield decrease compared to pure oak stands. In yield class III, this range is only between 0 and 20%. In general, it seems important to stress that mixing species may result, at worst, in a moderate yield loss, even if one species grows relatively slowly, which may well be offset by the increase of value of the timber of the whole stand.

The reasons why there is no general yield surplus in hornbeam-sessile oak stands are severalfold. One reason is that, as was pointed out above, hornbeam in pure stands usually grows more slowly than oak. Hornbeam grows faster than oak on better sites until about the age of 30 years, after which oak outperforms hornbeam whose growth slows down substantially with age. All other species that were mentioned in the introduction keep growing fast at older ages, too. Another reason is that hornbeam is overtopped by oak in middle age, after which hornbeam does not get full sunshine, which further suppresses its growth. Because of its slower growth rate, as well as the lower value of hornbeam timber, hornbeam is also thinned out in the upper canopy layers to favour oak, which even further decreases its growth potential. In the case where beech, a fast growing species, is mixed with oak, both oak and beech are left to grow in the upper canopy layer, and the two species together can outperform pure stands.

Why is it, then, that there are cases of yield surplus in hornbeam-sessile oak stands? The explanation is, again, both biological and silvicultural. On one hand, the two species utilise partially different niches, thus making better use of the potentials of the site. On the other hand, oak individuals in mixed stands do not have to compete so much with each other, because co-dominant, intermediate and suppressed oak trees in pure oak stands are replaced by hornbeam trees in the mixed stand that partially use different resources. However, this is only true on better sites. On poorer sites, where it is the amount of available water that limits grow,

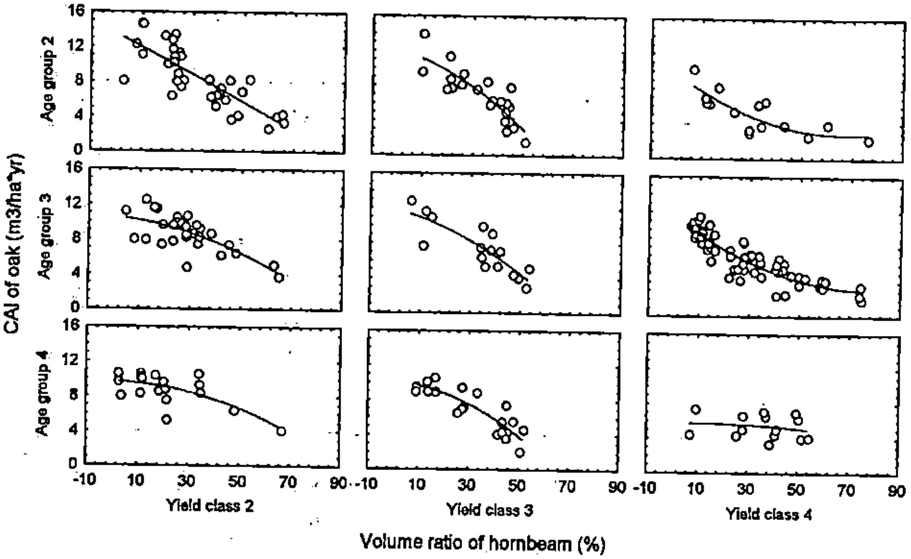

Figure 3. Current annual increment of sessile oak (CAI of oak) over volume ratio of hornbeam by yield class and age group. (The figure shows all data in those yield classes and age groups where the number of data were sufficient for a simple regression analysis)

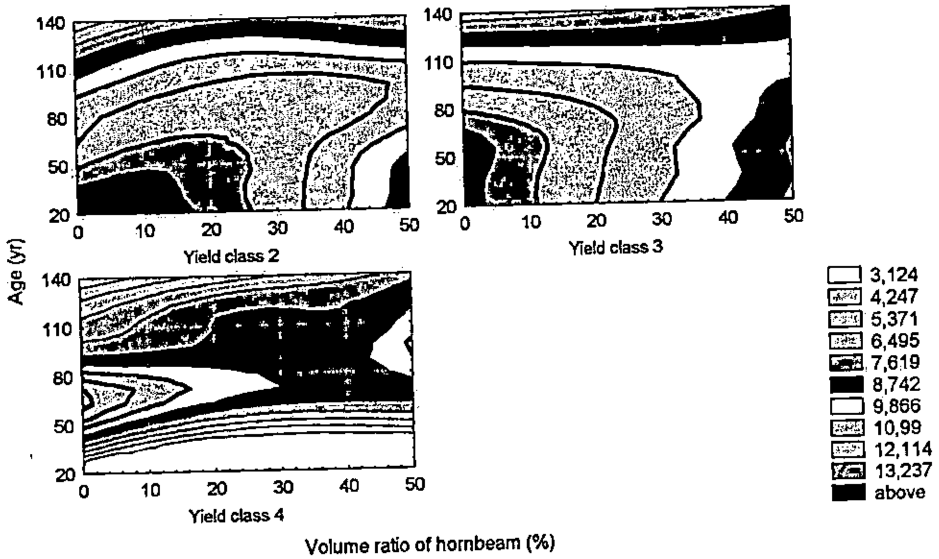

Figure 4. Total current annual increment (Total CAI) over volume ratio of hornbeam by age and in yield class II-IV. Increment categories between 9.866, 10.99, 12.114, 13.237 m3/ha and above are denoted by thick lines, whereas those below are denoted by thin lines. (This figure allows a more detailed analysis of the effect of age on the optimal species ratio, too, since here age is used as a continuous variable. Although total yield increases with age in all higher yield classes, it definitely decreases with an increasing hornbeam ratio, however small this ratio is.)

hornbeam, which less efficiently utilises water than oak, prevents oak from accessing enough water, which results in slower growth of oak, too.

It follows from the analysis above that it is worth mixing the two species, at least on better sites, purely from the point of view of yield and maximising yield. The value of mixing hornbeam with oak is, however, more than that. Oak bole of high value can better be grown if hornbeam is present than if there are only oak individuals in the stand. Therefore, a balance must be established so that hornbeam can help oaks grow timber of high quality without decreasing yield too much. It is important to stress this because, at least in some regions in Hungary, there is a tendency to suppress hornbeam too much, and thin it out well before the end of the rotation period. If high value oak timber is to be grown in subsequent rotations, hornbeam - and other mixing species - must be tended at ages when oak grows faster, and even several fast growing hornbeam individuals of good stem form must be kept in the dominant-codominant layer as long as they can compete with oak. This must be done by cutting out oak individuals of slower growth and poor stem quality (Béky, 1997).

Quite naturally, ratios of species change over time. In order to form and maintain an optimal structure, silvicultural interventions must continuously be applied. This ideal structure and its change can be well seen in Figure 5. This illustrates

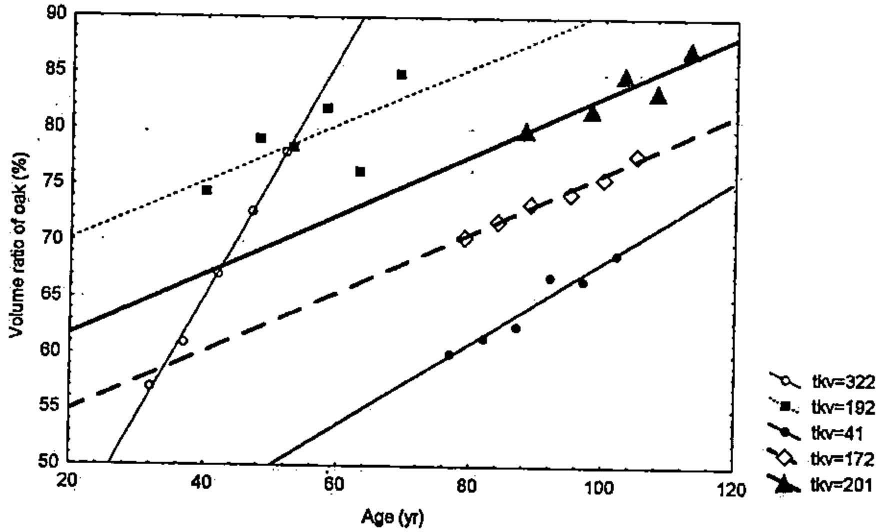

Figure 5. Ratio of oak main crop by volume over age in five hornbeam-oak stands of optimal structure. (The stands are marked by their respective registry number (tkv). Yield classes of the stands: tkv=322: III; tkv=192: I; tkv=41: IV; tkv=172: III; tkv=201: II.)

that, after having reached the optimal stand structure, the volume of oak must (and can) be increased by 7-10% in three decades. The trees in plot No. 322 were young, the yield class was III, and the volume ratio of oak was only 57% at the beginning of the surveys, therefore, heavier thinnings had to be done in favour of oak which was the reason for the more intensive increase of the oak ratio over time. On the other hand, in stands of higher oak ratio this increase is slower.

Finally, it must be emphasised that optimal stand structure, thus maximal yield production, can only be achieved if oak individuals of high growth potential can be found in a density that approximates a good even density of future trees. It is impossible to develop a good structure from a patchy stand structure. Too much hornbeam or too patchy a stand structure cannot be controlled in one rotation period.

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RAST I PRIRAST SASTOJINA GRABA I HRASTA KITNJAKA (*CARPINUS BETULUS* L. - *QUERCUS PETRAEA* /MATT./ LIEB.) U UVJETIMA OPTIMALNOGA GOSPODARENJA U MAĐARSKOJ

Temeljno pitanje u mješovitim šumama odnosi se na problem optimalnoga odnosa vrsta s obzirom na prirast. Pri prvom pokušaju da se u Mađarskoj pozabavimo ovim pitanjem napravljena je prirasno-prihodna tablica za grabove i hrastove šume. Na hipotetskoj se razini pokazalo da mješovite grabovo-hrastove sastojine daju po prilici isti prirast kao i nemješovite hrastove sastojine. Uz objavljivanje ove nove prirasno-prihodne tablice ovaj se rad izravno bavi problemom optimalnoga odnosa vrsta rabeći podatke iz trajnih eksperimentalnih ploha koje su osnovane u mješovitim sastojinama optimalne strukture s prevelikim brojem hrastova i prevelikim brojem grabova. Analiziran je optimalni odnos u pogledu dobi i boniteta. Rezultati pokazuju da je najbolje miješati te dvije vrste na najboljim staništima u srednjoj dobi; međutim, na slabim staništima i u mladoj ili staroj dobi najbolji prirast daju čiste hrastove sastojine. U ovom se radu naglašava da miješanje dviju vrsta, kao u mnogim drugim tipovima šuma, ima i mnogobrojne ekološke i gospodarske prednosti.

Ključne riječi: hrast kitnjak, mješovite sastojine, optimalizacija prirasta, optimalna struktura sastojine

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UDK 630*222+288+(510) (Quercus sp.)

MANAGEMENT TO SUSTAINABLE UTILIZATION ON TUSSAH-FEEDING OAK FORESTS IN NE CHINA

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Tussah-feeding oak forests in northeastern China are valuable natural resources in developing the economy and improving the environment of the region. Problems in growth decline and soil deterioration can be solved through the intensive management of the forest ecosystem. Rotational coppicing, pruning, cleaning out undergrowth and fertilising are plausible measures. Shaping the crown of the oak tree into a "Stair" form by coppicing and pruning can produce the highest leaf biomass and make better use of solar energy compared to the "Tree" and "Shrub" forms. Nutrient loss can occur through larvae removal, and nitrogen fertilizer should be applied to the soil before the subsequent growing season starts. Introducing nursing species such as N_2-fixing plants into oak forests can also increase nitrogen nutrients to the soil. A well-planned rotation of coppicing practice may be the cheapest way to sustain the production of tussah cocoons, as well as dividing the forests into sections and letting each section have a turn at being off limits for a rejuvenation period of 7-10 years.

Key words: oak forest, tussah, silkworm, coppicing, sustainable utilisation

INTRODUCTION

Northern China contains the largest total area of forests in the country, much of it being secondary forests in which oaks are one of the dominant species. Oak forests are developed from the destroyed virgin forest, covering approximately 28 million hectares in northeastern China. The mountainous oak forests play an important role not only in preserving soil and water in the region, but also in producing forest side-products, including tussah cocoons and nutrition-rich and edible tussah larvae.

Silkworm culturing was brought to China approximately 300 years ago. Culturing silkworms by feeding on oak-tree leaves is a unique practical system of utilising oak forests, being a profitable and important industry in the four provinces of northeastern China. At present, approximately 400,000 hectares of coppice oak forests are used for silkworm production. Mainly there are six oak species in northeastern China, which are *Quercus mongolica* Fisch. Ex Turcz, *Q. liaotungensis* Koidz, *Q. acutissima Carr*, *Q. variabilis Blume*, *Q. dentata* Thunb and *Q. acutidentata* Koidz. Due to improper use and the lack of good management, the oak forest resource is now facing a serious problem in soil deterioration and growth decline. To find a way of sustainable use of the resources, a series of research studies has been carried out in the past ten years. A technical system for management has also been established. The purpose of this paper is to summarise the results from the research and suggest alternative options for future oak forest management.

SITES AND METHODS

The research sites are situated at a latitude of 40°30'N and a longitude of 124°E, in the eastern mountain areas of Liaoning province. The altitude is about 400m above sea level. Annual precipitation ranges from 500 to 900mm with an annual mean temperature of 5~8 °C. The main tree species in the stands are *Quercus mongolica*, *Q. liaotungensis* and *Q. accuttissima* with an undergrowth mainly of *Lespedeza bicolor*, *Amorpha fruticosa*, *Corylus heterophylla*, *Rubus parvivolius*, *Indigofera kirilowii* and *Sophora flavescens*.

Experiments that have been conducted include canopy structure reforming, nutrient cycling, the introduction of N_2-fixing plants as undergrowth, standardising coppicing, and controlling the feeding rates. During the experiments, related measurements and tests were carried out. Leaf biomass, canopy structure and light interception were measured at the different layers of the stratified tree crowns. In each layer, light intensities were measured on the points along 2 crossed lines at 10 cm intervals. A photometer was calibrated with a quantum sensor. Leaf areas were measured using a portable leaf area meter (Li-3000). Models of light distribution, cumulative leaf area and leaf area density in different canopy structures were established through data processing by microcomputer. The elements N. P. K. contained in tussah silkworm, cocoons, trees and soil at different stages of feeding were analysed with routine chemical analysis methods in laboratories, and the rates of N_2-fixation produced by the introduced undergrowth plants were tested using a method of acetylene reduction.

RESULTS AND DISCUSSION

CANOPY STRUCTURE AND LEAF BIOMASS

The tussah-feeding oak forest is a unique coppiced forest ecosystem. Over a long period of management, different canopy forms have been artificially established. Three types of canopy forms exist. The traditional structure of tussah-feeding oak stands was a single layer with a crown form, named "Shrub". To increase the efficiency of solar energy use, crowns were reformed into "Tree" and "Stair" forms. The latter consists of two layers in the canopy. The characteristics of the three forms were analysed. Table 1 shows that the "Stair" crown form presents the highest value in leaf area index (LAI), canopy height and leaf density.

Table 1. Comparison of Leaf Area Index in 3 Crown Forms

	Q. liaotungensis			*Q. mongolica*		
	"Stair"	"Tree"	"Shrub"	"Stair"	"Tree"	"Shrub"
LAI	5.16	2.50	2.44	4.06	3.68	3.57
Height (m)	2.60	2.10	1.90	2.50	2.40	1.80
Leaf Density	2.06	0.97	1.22	1.60	1.48	1.79

The radiation measurements show that the light intensity decreased rapidly with an increase in cumulative leaf area index. Measurements on light intensity indicate that the "Stair" crown form also presents the highest values in solar energy interception.

Since oak leaves are an important food source for silkworms, management practice should be focused on promoting the production of the leaf biomass of oak forests, especially new leaf growth. Table 2 shows the leaf biomass of closed stands in three canopy types.

Table 2. Estimation of leaf biomass (t/ha) of closed stands in three canopy types

Canopy types	*Q. liaotungensis*			*Q.mongolica*			*Q. acutissima*		
	"Stair"	"Tree"	"Shrub"	"Stair"	"Tree"	"Shrub"	"Stair"	"Tree"	"Shrub"
Dw	5.705	2.765	2.697	4.421	4.085	3.936	3.446	2.019	2.315
Fw.	9.225	4.470	4.362	8.699	7.982	7.743	6.888	4.215	4.626

Shaping the crown of the oak tree in the "Stair" form can produce the highest leaf biomass compared with the "Tree "and "Shrub" forms.

NUTRIENT CYCLING IN THE SECONDARY PRODUCTION OF THE TUSSAH-FEEDING FOREST

The production process of the tussah-feeding forest is the change from primary production to secondary production. Background investigations show a deterioration in tussah-feeding forests related to an absence of balance between primary production and secondary production. Excessive output due to long-term over-grazing has brought about a decline in the stand situation and a decrease in leaf production. Primary production cannot be restored for a lack of accumulation, while the decease in nutrient storage in the trees is the main cause of the decease in their productivity.

Secondary production is mainly the yields of tussah cocoons. Cocoon production in practice depends on the primary production of the biomass of vegetation, mainly leaf biomass. Leaf consumption by silkworms is not only the key point of secondary production, but also an important factor affecting the vitality of forest growth, thus influencing the productivity of the forest stand. Understanding the nutrient cycling pattern in the process of secondary production is necessary to balance the relation between tree growth and secondary production. Table 3 gives the results of the analysis of nitrogen cycling.

Table 3. Nitrogen cycling in secondary production of tussah-feeding plantation ($kg^{-1}.ha^{-1}.yr^{-1}$)

Species	Consumption	Return			N output
	Total	drops	dead larvae	total	cocoon
Q.liaotungensis	17.22	8.51	1.18	9.69	7.47
Q.mongolica	19.10	9.06	1.35	10.41	8.60

Studies on two species of oak indicate that in the condition of 50% of total leaf biomass consumed, nitrogen consumption by tussah larvae reached 17.22~19.10kg per hectare. The total output of nitrogen contained in cocoons was only 7.27~8.60 kg per hectare. The remainder was returned to the ground by larvae drops.

To stabilise the productivity of such a stand at the production level mentioned above, it is necessary to give an input of nitrogen of at least 8kg yearly per hectare for nutrient compensation.

TECHNICAL SYSTEM FOR INTENSIVE MANAGEMENT

Due to traditional extensive management, the tussah-feeding forests have deteriorated. Intensive management is the only way to preserve oak resources. Noticeable affects have been produced by serial sets of technology. Putting this effective technology into production, good results have clearly been achieved. According to statistics in three counties, leaf biomass has increased by 40-50%. Cocoon products have improved by 20%. Water loss and soil erosion have been controlled.

1) Improving stand structure through introduced plants

Introducing N_2-fixation plant species as undergrowth to oak stands has been conducted during a long-term experiment. Four species were selected. In the third year of seeding, root nodule weight and N_2-fixation rates were investigated and tested. Table 4 shows the estimation of nitrogen fixation by the four plant species.

Since these four species are perennial in root, the root nodules increase yearly with growth and with development of the root system. Although the fixed nitrogen can be taken by the oak only after the nodules and plant tissues have decomposed, the long-term use of biological means in nitrogen input is of superior value both economically and environmentally.

Introducing shade-tolerant trees can also improve the ability to preserve the soil.

Table 4. Annual N_2-fixation by introduced undergrowth

Species	Value of nodules $g.indiv^{-1}$	Rate of N_2-fixation $mgN.g^{-1}h^{-1}$	Annual N_2-fixation $kg.ha^{-1}a^{-1}$
Indigoferra Kirilowii	0.24	0.0183	1.53
Sophora flavescens	0.28	0.0245	1.55
Amorpha fruticosa	0.38	0.0208	0.89
Lespedeza bicolar	0.30	0.0200	0.68
Total			4.65

2) Control of coppicing interval

The tussah-feeding oak stand is generally coppiced every 3~4 years. Although oak trees possess a higher ability in sprouted regeneration, too frequent coppicing reduces the growth vitality in subsequent years. In many cases, people probably shortened the interval period, often to 2 or 3 years, so that they could obtain much more fuel wood from coppicing. This increased tremendously the output of nutrients from the ecosystem. To reduce the disturbance, prolonging the period between two coppice operations was beneficial to stabilise the forest stand. Nevertheless, coppicing is needed to promote sprouting and to obtain more tender leaf biomass. A well-planned rotation of coppicing practice may be the cheapest way to sustain the production of tussah cocoons. Table 5 shows the nutrient output in the coppicing operation of plantations from coppicing.

Table 5. Nutrient output in coppicing operations of tussah-feeding plantations (kg/ha)

Coppicing cycle	Dry weight of coppicing	Biomass losses	Nutrient losses kg/ha.yr		
	kg/ha	kg/yr	N	P	K
6	8000	1000	4.70	3.00	6.00
5	5500	1100	5.17	3.30	6.60
4	5000	1250	5.88	3.75	7.50
3	4500	1500	7.05	4.50	9.00
2	4000	2000	9.40	6.00	12.00

Annual nutrient losses increased while the coppicing cycle shortened. Intervals of 5-6 years were recommended.

CONCLUSION

Tussah-feeding oak forests in northeastern China are valuable natural resources in developing the economy and improving the environment of the region. Problems in growth decline and soil deterioration can be solved through intensive management of the forest ecosystem. By understanding the nutrient cycling process and the pattern of solar energy use in the stand, a technical system for intensive management has been established in the regulation and control of primary and secondary production. The main control measures include:

1) Shaping the crown of the oak tree into the "Stair" form by coppicing and pruning, which can produce he highest leaf biomass and obtain better use of solar energy.
2) Introducing nursing species such as N_2-fixing plants into oak forests, which can increase nitrogen nutrients in the soil. Nitrogen fertilizer should be applied to the soil before the subsequent growing season starts.
3) Prolonging the coppicing interval period in order to reduce nutrient loss from the ecosystem and balance the input and output of nutrients.
4) Dividing the forests into sections and letting each section have a turn at being off limits for a rejuvenation period of 7-10 years.

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GOSPODARENJE KOJE VODI POTRAJNOM ISKORIŠTAVANJU HRASTOVIH ŠUMA ZA UZGOJ HRASTOVA JAPANSKOGA PRELCA U SJEVEROISTOČNOJ KINI

Hrastove su šume za uzgoj hrastova japanskog prelca u sjeveroistočnoj Kini vrijedni prirodni resursi u razvoju gospodarstva i poboljšanju okoliša regije. Problemi smanjenoga rasta i pogoršanja tla mogu se riješiti intenzivnim gospodarenjem šumskim ekosustavom. Dobri postupci obuhvaćaju gospodarenje panjačama, obrezivanje, čišćenje podrasta i gnojenje. Oblikovanjem krošnje hrastova stabla u stupnjevit oblik sječama na panj i obrezivanjem može se proizvesti najveća lisna biomasa i postići bolja upotreba solarne energije u usporedbi sa stablimičnim i grmastim oblicima. Odstranjenje larvi može dovesti do gubitka hraniva, pa tlu treba dodati dušikovo gnojivo prije početka sljedećega vegetacijskoga razdoblja. Uvođenje rasadničkih vrsta u hrastove šume, na primjer biljke koje vežu N_2, također povećavaju dušikova hraniva u tlu. Dobro planirano gospodarenje panjačama najjeftiniji je način za održavanje proizvodnje čahura svilca, dijeljenje šume u odjeljke i omogućavanje obnove svakoga odjeljka u razdoblja od 7 do 10 godina.

Ključne riječi: hrastova šuma, hrastov japanski prelac, svilac, sječa panjača, potrajno iskorištavanje

L. Nutto, H. Spiecker: Production of valuable wood: a software aided decision tool for managing oak stands (*Quercus petraea* Liebl. *and Q. robur* L.)... Glas. šum. pokuse 37: 37–49, Zagreb, 2000.

UDK 630*531+535+583+(430) (Qurcus petraea Liebl., Q. robur L.)

PRODUCTION OF VALUABLE WOOD: A SOFTWARE AIDED DECISION TOOL FOR MANAGING OAK STANDS (*QUERCUS PETRAEA* LIEBL. *AND Q. ROBUR* L.) IN EUROPE

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Oak is an important indigenous species of very variable quality and, consequently, value production in Europe. To produce high-quality wood, management regimes are required based on information on the effects of inter-tree competition on crown development and stem diameter growth and their impact on timber quality. Since these parameters are very complex and can occur in a large number of combinations, new decision tools like simulation software should be provided in order to enable the user to simulate various management regimes and their impact on wood quality.

For this study, more than 3300 oaks from differently managed stands in Germany, France, Poland, Denmark, Austria and Hungary were measured. The age of the oaks ranged between 10 and 350 years. With stem and crown distribution maps for each sample unit, inter-tree competition was described and evaluated. From several trees, stem disks were taken and the radial growth was reconstructed in cross sections in order to quantify the influence of competition on radial growth.

The aim of the study was the development of generally valid growth models for oak at all ages, and a wide range of sites and management practices in order to program a simulator that is able to predict growth and quality for different management regimes.

Key words: oak, management, wood quality, simulation software, growth modelling

INTRODUCTION

The change from volume increment orientated forestry in pure stands without pronounced structure to high value timber production and close-to-nature forestry in Europe requires new ways of forest management. New decision tools for forestry practitioners should also take into account biological explanative patterns. Modelling in growth and yield science should be based on single tree characteristics in order to make them applicable in richly structured pure and mixed stands and to allow for management regimes focused on the high value timber production of a few future crop-trees.

Oak, especially, is a very important indigenous species for high quality and, consequently, high value wood production in Europe. In addition, the positive ecological impact and the high stability of oak stands and the reduction of risks in forest management should be considered. However, the regeneration and management of oak stands in Europe is rather expensive. The common opinion is that intensive forestry input is necessary to produce high-quality wood. In order to rationalise work input and to reduce costs, information about crown development, inter-tree competition and their effects on tree growth and timber quality is needed. If these interactions are known better, forest management can profit by including natural processes like self differentiation and pruning as “biological automatisation“.

Growth and quality of trees are closely linked. Not all quality aspects can be influenced by management, but one of the most important of these, the dimension of the knotty core, can. Modern decision tools should be able to predict not only growth, but also the resulting quality of a management regime. Today, this can be realised if growth models with a good estimation of the important parameters are implemented in modern technologies like computer-aided management tools.

MATERIAL AND METHODS

The data for parameterising simulation models have been collected in differently-treated oak stands in several parts of Germany, France, Denmark, Poland, Hungary and Austria. The criteria for plot selection were:

- all available forms of natural and artificial regeneration and the different resulting initial stand densities should be included
- to evaluate as many management regimes as possible
- to include differences between sessile and pedunculate oaks (*Q. petraea* and *Q. robur)* if there are any
- to cover a wide range of site quality.

The differences in species, site and management considered in the study allow a better understanding of how oak reacts to various ecological and management factors. The research was focused on the development and architecture of crowns as a result of the actual and past competition situation. Overall, more than 3,150 sessile and pedunculate oaks (*Q. petraea (Matt.) Liebl.* and *Q. robur L.*) in 108 temporary sample plots were included in this study. The material ranged from:

- average annual air temperature from 6.5 to 10°C
- average annual rainfall from 450 to 1000 mm
- very fertile sites (loess and brown earth) to poor and relatively dry sites
- initial densities from 4,000 to 120,000 plants /hectare
- geographical coordinates from 1° - 18° east and 46° to 55° north
- elevation from 50 to 550m above sea level

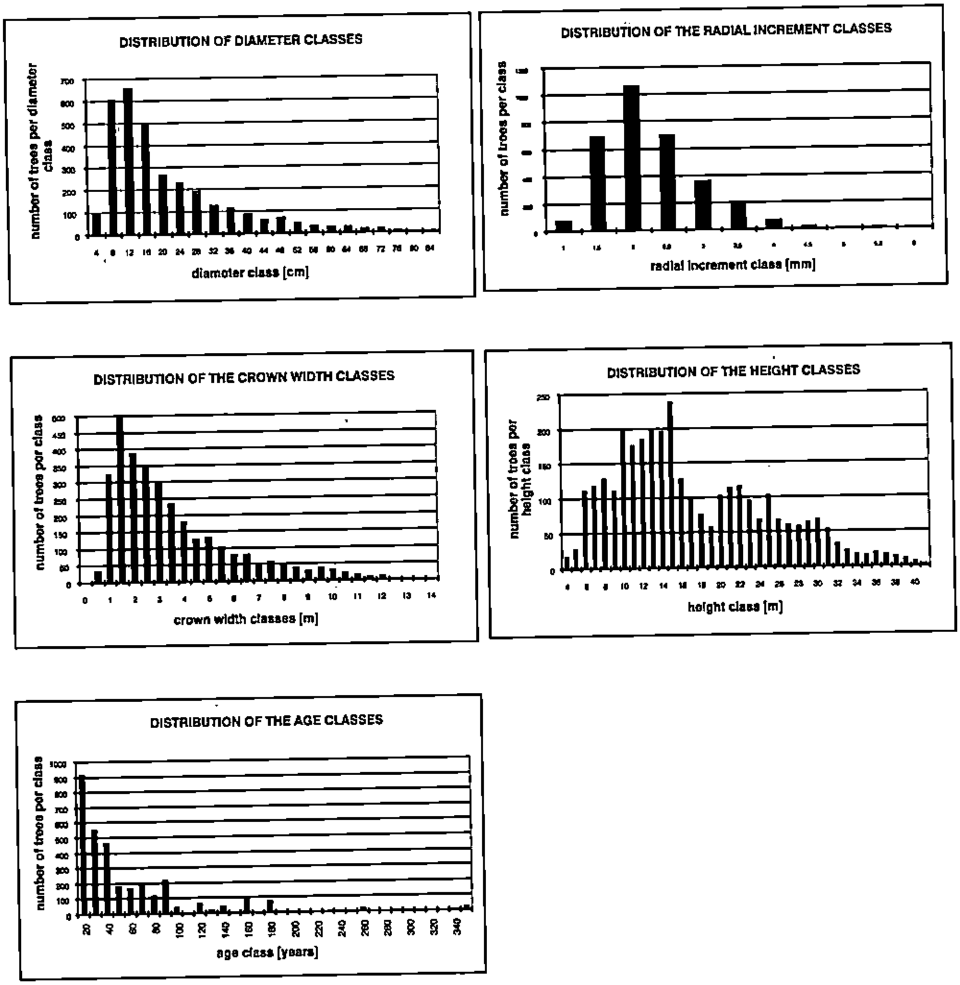


Fig. 1. Overview of the material used for modelling

This shows that the material covers a wide range of growth-relevant conditions and is therefore valid for several management regimes and site conditions in Europe.

The method used in this study is *ex-post facto*, i.e. an observational research approach based on an explorative data analysis of temporary sample plots. In 108 sample units, data were collected based on single trees. About 68 of these plots are or were already research plots of other institutions, so that additional information and further data could be obtained. In each sample plot the coordinates of the trees and tree stumps were measured. In addition, the parameters

- height of the lowest dead primary branch at the stem
- height of the first living primary branch (crown base)
- total tree height
- diameter at 1.30 m height of the stem and
- the crown projection area

of the dominant and co-dominant oaks were measured. Using stem distribution and crown area projection maps including information on dead and cut trees, the actual and past inter-tree competition could be described and evaluated for each tree in a sample unit. From several trees, stem disks were taken and the radial growth was reconstructed on cross sections in order to quantify the influence of competition on radial growth.

RESULTS AND CONCLUSIONS

THE CROWN WIDTH MODEL - A GROWTH MODEL FOR OAKS

Important criteria for wood quality are stem diameter and branches. For practical forest management it is very important to have a decision tool for estimating the dimension and the internal wood quality of the possible future crop trees.

The energy-converting area of a tree is the crown. Oak is classified as a rather light-demanding tree species. A hypothesis can be made that the exposed crown area is an important factor for the productivity of a tree. It can be expected that by managing tree competition the crown size and the diameter growth of the trees can be controlled. Crown width is a very good estimator for diameter growth and is closely related with the parameters diameter at 1.30m and the age of a tree.

This hypothesis was able to be proved in earlier studies by authors of several European countries (Hochbichler & Krapfenbauer 1988, Nutto 1997, Mayer 1958, Spiecker 1983 and 1991, Szappanos 1984). For sessile and pedunculate oaks (*Q. petraea* (Matt.) Liebl. and *Q. robur* L.) measured in this study, the model (Fig. 2) is

$$cw = 0.23 + 0.20 * d_{1..3} - 0.015 * age \qquad (n = 3183,\ R^2 = 0.92,\ p < 0.001)$$

(where cw = crown width, $d_{1..3}$ = diameter at 1.30m.)

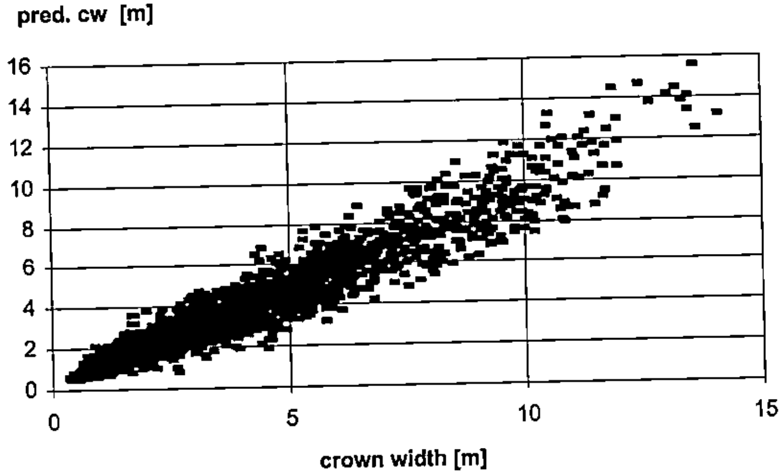


Fig. 2. Crown width as a function of diameter at breast height and age

With this model, the area of the crown needed to make sure of a certain diameter increment can be predicted.

The model shows a constant linear relation between the dependent variable cw and the independent variables $d_{1.3}$ and age. Age in this equation is less important in even-aged stands with the same treatment, but it becomes more important in cases where extreme management regimes have been applied or where younger and older oak stands are compared. Age explains part of the existing variation if uneven-aged trees are compared. In addition, it is very important for management to include the factor time in order to be able to predict the growing space needed to reach a certain dimension in a given time.

This model was tested for sessile and pedunculate oaks (*Q. petraea* (Matt.) Liebl. and *Q. robur* L.) and shows no significant differences between the two oaks. The advantage of using the crown projection area is that the growing space required by a single tree for a certain diameter growth can be calculated. Considering that the growing parameters are no longer mean values of the whole stand, the development of a subject tree and competitors can be defined and predicted. Knowing the interactions between growing space and growth, decision tools based on distant-dependent models are easily available. With this model, crown development, growing space, thinning regimes and radial growth of trees can be assessed (Spiecker 1983).

The crown width model shows no effects on changes in site quality. For the same crown width reached in a certain age, the same dbh can be expected. But site quality has an effect on the maximum crown expansion that can be reached in a certain time. The better the site conditions, the better the tree crown can develop and therefore a higher radial increment can be reached. For the material used in this study, a relationship between the maximum radial increment and the site con-

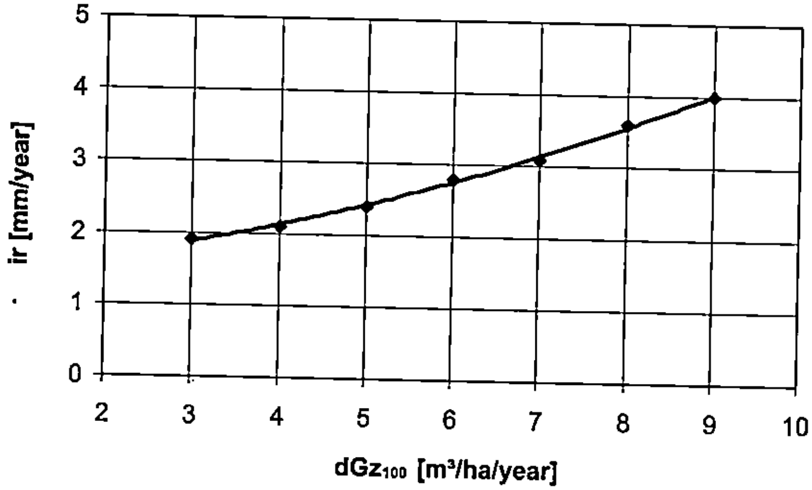


Fig. 3. Maximum average annual radial increment (ir) at an age of 35 years for site conditions according to the yield table of Jüttner (1955).

dition could be found. To classify different site indexes, the yield tables of Jüttner (1955) were used.

The influence of the site quality to the maximum possible crown expansion can be described in the following equation:

$$dGz_{100} = 0.0179 * ir^2 + 0.1464 * ir + 1.2643$$

(where ir = radial increment)

Fig. 3 shows the maximum radial increment (mean value of the most open grown trees per site unit) is closely related to the site quality.

THE CROWN BASE MODEL AND MODEL OF THE LOWEST DEAD BRANCH

However, not only are the diameter growth and the dimension of a tree important for the production of valuable wood, but also the dimension of the knotty core. For high quality, branch-free wood is essential. A very important factor of quality production is the estimation of the crown base recession, i.e., the dynamic of self-pruning. Therefore, a model for estimating the base of the living crown (Fig. 4) was developed.

$$cb = -0.84 + 0.77 * height - 0.20 * d_{1.3} + 0.025 * age \quad (n=3184, R^2= 0.89)$$

where cb = crown base [m], $d_{1..3}$ = diameter at 1.30m [cm],
age = total age [years].

For describing the quality and dynamic of the self-pruning of oak, not only is the height of the crown base important, but also the height of the lowest dead

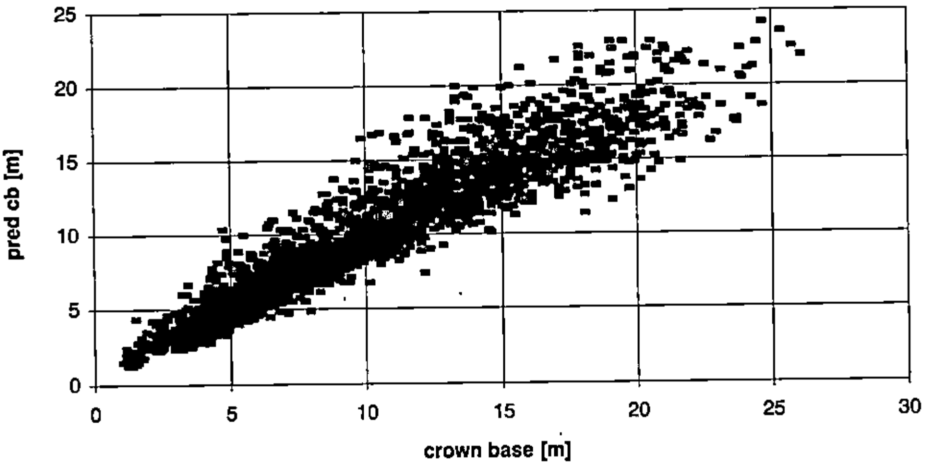


Fig. 4. Crown base recession model (pred cb = predicted crown base)

branch which is a good indicator for describing the branches within the stem. A model based on the same parameters like the crown base model could be found:

$$ldb = -3.03 + 0.68*height - 0.16*d_{1.3} + 0.025*age$$

(where ldb = lowest dead branch, $d_{1.3}$ = diameter at 1.30m [cm], age = total age [years]).

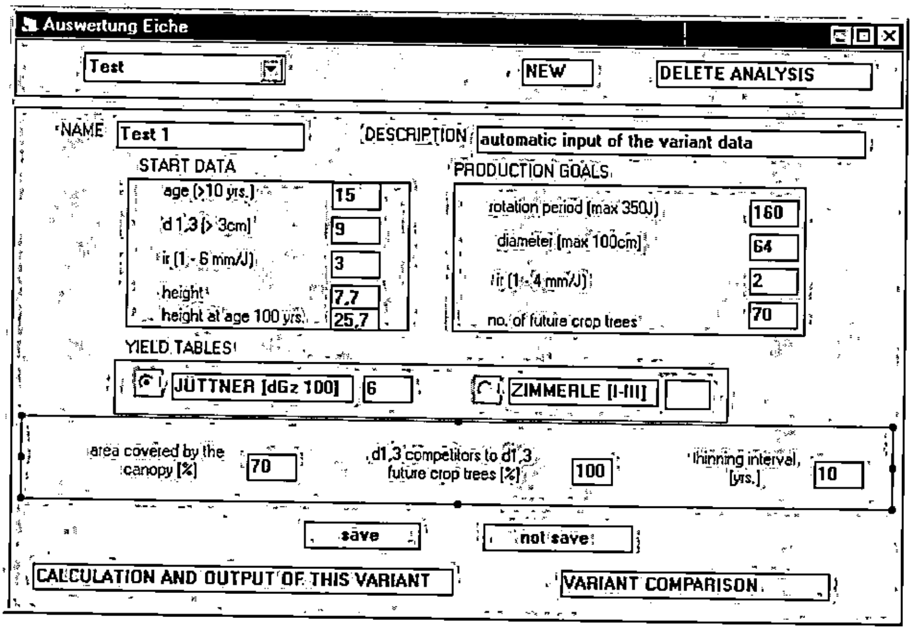
It can be assumed that the crown width model and the self-pruning models are closely linked. The crown width model allows the diameter increment to be managed by regulating the growing space, i.e. the competition. The dynamic and quality of self-pruning, according to the crown base model and the model of the lowest dead branch, depend on two factors: the diameter increment, i.e. the diameter reached at a given age and the site quality, because this parameter influences height growth (Spiecker 1991). It can be concluded that the timber quality on the one hand is determined by the diameter increment, which can easily be influenced by silvicultural management, but also by site quality, which cannot be changed without cost-intensive human input.

Therefore, the production of high-value oak timber should focus on the regulation of competition by tending and thinning. For modelling internal wood quality, the site conditions must be taken into account, because height growth influences the dynamic of self-pruning.

THE OAK SIMULATION SOFTWARE *IWW_Eiche 1.0*

The models described above can vary in very many ways: the thinning regimes, thinning interval, site quality, area covered by canopy and more. To give the forestry practitioner a decision tool adaptable to his personal resources and production goals, many combinations have to be considered. The growth and quality simulator for oak *IWW_Eiche 1.0* tries to do so. In an easy and user-friendly way, a starting situation for a stand or for single trees can be described, as well as the production goal.

In Fig. 5, the starting mask of the software is shown. As mentioned before, the starting situation can be described by defining a site index (or height at a given age) and a radial increment (or diameter at a given age). The production goal can be defined by the diameter of a given number of crop trees, by the diameter at the end of the rotation period or the radial increment over the rotation period. In addition, some parameters influencing growth and management like area covered by the canopy, thinning intervals or the relation between future crop trees and competitors can be defined by the user.



Test

NAME: Test 1

DESCRIPTION: automatic input of the variant data

START DATA
age (>10 yrs.) 15
d 1,3 (> 3cm) 9
ir (1 - 6 mm/J) 3
height 7,7
height at age 100 yrs. 25,7

PRODUCTION GOALS
rotation period (max 350J) 160
diameter (max 100cm) 64
ir (1-4 mm/J) 2
no. of future crop trees 70

YIELD TABLES
● JÜTTNER [dGz 100] 6
○ ZIMMERLE [I-III]

area covered by the canopy [%] 70
d1,3 competitors to d1,3 future crop trees [%] 100
thinning interval [yrs.] 10

Fig. 5. Starting window of the simulation software *IWW_Eiche 1.0*

The values typed in the start window are checked for plausibility and are automatically corrected according to the models presented above. Figure 6 shows the redundancy of these values and how they are checked for plausibility in between the growing parameters of the collected material. Values depending on each other are automatically calculated. If, for instance, age and diameter at breast height ($d_{1.3}$) are typed in, the radial increment is calculated. The same procedure is done for the site index, when information about height at a given age is available. The height curves of the yield tables of Jüttner (1955) and Zimmerle (1930) are included in the program as functions. If starting values are changed, all other parameters are checked again and recalculated if necessary.

In the part of the window where the production goal is defined, the number of future crop trees can be chosen. This value is determined by the age at the time of harvest and the diameter reached at this time. Based on these two values, the needed crown projection area of each tree for a given radial increment is calculated by the crown model. The user also has the option to choose the number of crop trees and the diameter he wants at the age at the time of harvest. The number of crop trees is a very important parameter because all the thinning calculations are based on this information.

Another important parameter is the area covered by the canopy. In the study this value ranged in all plots between 62 and 80 %, the mean value was 70 %. The standard in the program was set to the mean value, but an option is offered to change it. This should be done very carefully because the number of trees per hec-

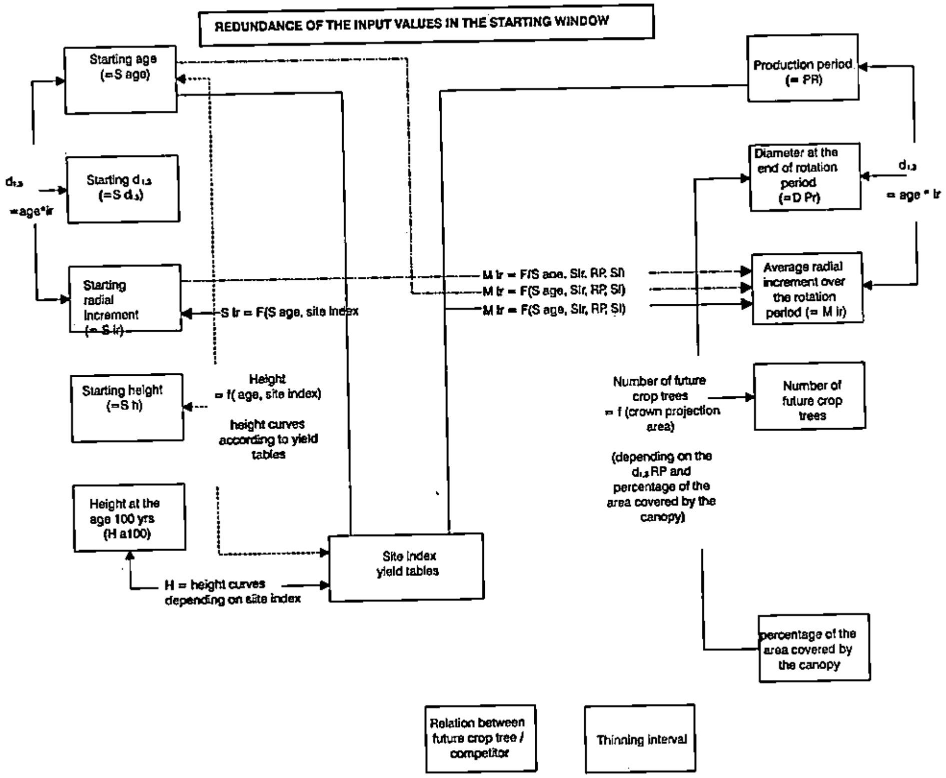
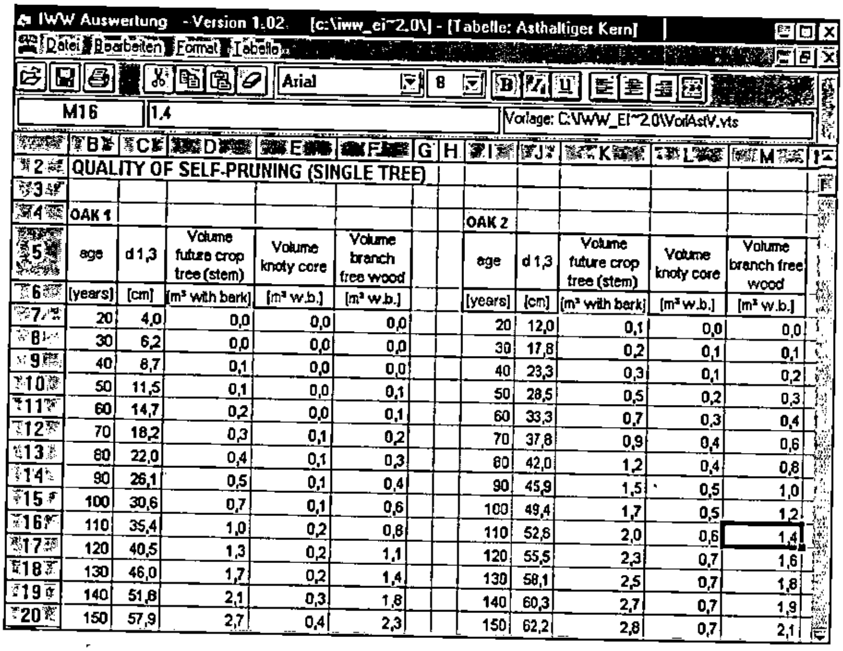


Fig. 6. Redundant values of the input window



	B	C	D	E	F	G	H	I	J	K	L	M
2	QUALITY OF SELF-PRUNING (SINGLE TREE)											
3												
4	OAK 1							OAK 2				
5	age	d 1,3	Volume future crop tree (stem)	Volume knoty core	Volume branch free wood			age	d 1,3	Volume future crop tree (stem)	Volume knoty core	Volume branch free wood
6	[years]	[cm]	[m³ with bark]	[m³ w.b.]	[m³ w.b.]			[years]	[cm]	[m³ with bark]	[m³ w.b.]	[m³ w.b.]
7	20	4,0	0,0	0,0	0,0			20	12,0	0,1	0,0	0,0
8	30	6,2	0,0	0,0	0,0			30	17,8	0,2	0,1	0,1
9	40	8,7	0,1	0,0	0,0			40	23,3	0,3	0,1	0,2
10	50	11,5	0,1	0,0	0,1			50	28,5	0,5	0,2	0,3
11	60	14,7	0,2	0,0	0,1			60	33,3	0,7	0,3	0,4
12	70	18,2	0,3	0,1	0,2			70	37,8	0,9	0,4	0,6
13	80	22,0	0,4	0,1	0,3			80	42,0	1,2	0,4	0,8
14	90	26,1	0,5	0,1	0,4			90	45,9	1,5	0,5	1,0
15	100	30,6	0,7	0,1	0,6			100	49,4	1,7	0,5	1,2
16	110	35,4	1,0	0,2	0,8			110	52,6	2,0	0,6	1,4
17	120	40,5	1,3	0,2	1,1			120	55,5	2,3	0,7	1,6
18	130	46,0	1,7	0,2	1,4			130	58,1	2,5	0,7	1,8
19	140	51,8	2,1	0,3	1,8			140	60,3	2,7	0,7	1,9
20	150	57,9	2,7	0,4	2,3			150	62,2	2,8	0,7	2,1

Fig. 7. Table for the variant comparison of the internal wood quality

tare is calculated by the crown projection area each tree needs for a given diameter growth.

A possibility to give a kind of structure to the simulated stand is the option to define the relation of the $d_{1.3}$ of the future crop tree to the $d_{1.3}$ of the competitors. Usually, trees of high vitality and quality are selected as future crop trees. The thinnings are calculated by the additional crown area a tree needs to keep the wanted diameter increment in the period between two thinnings (Spiecker 1983). The number of competitors that have to be removed in the thinning is based on this calculation. If the diameter of these trees is lower, more of them have to be taken out to obtain the required growing space for the future crop tree.

After finishing the data input, the user at least may define the thinning period he wants. After saving the data he will get all relevant data about growth, volume and quality in a table. Information is available for the single tree, for the whole stand and the competitors that have to be cut in each thinning period from the starting age until the end of the rotation period. The difference to the common yield tables is the additional information about the single future crop tree and competitor, the dynamic of self-pruning and the details about the internal wood quality like the dimension of the knotty core and the dimension of the clear bole.

At least the user can compare the most important parameters of two variants in graphs and tables. For the forestry practitioner, the development of the volume of the future crop trees is very important. The program shows how the volume in-

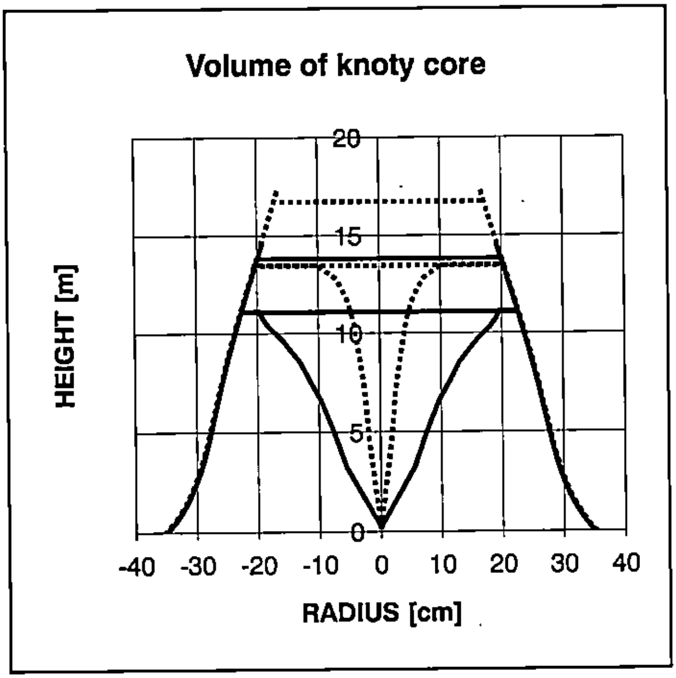


Fig. 8. Comparison of the knoty core of two different production variants (oak1=dots, oak2=lines) with the same rotation period.

crement can be concentrated on the future crop trees. The tables offered give information about how the volume of the tree in which diameter class is distributed in the stem and how much of it is branch-free wood. The same can be done for the trees that have to be cut in each thinning interval. The third option is to compare the development of the basal area of both the future crop trees and the thinning trees.

Another option is the comparison of the dynamic of self-pruning which gives information on the internal wood quality that can be expected. Based on the height curves, the development of the total height, crown base and lowest dead branch are shown. This is an important tool to evaluate the management of the diameter growth or the influence of the site quality.

The last option is the comparison of the volumes of the stem, the knotty core and branch-free wood, as shown in Fig. 7. The internal wood quality can be influenced by management if the interactions between diameter growth, self-pruning and site quality are known (Spiecker 1991). With the models included in the program, growth and quality can be predicted. The model to predict the internal wood quality was validated within a project where 30 oaks were cut into boles and the number, location and diameters of the dead branches were investigated (Metzger 1999, Nutto 1999).

The tables created by the tool *FORMULA ONE®* (Fig. 7) enable the user to save them in the *Microsoft EXCEL 4.0®* format. The graphs are generated by the tool *VISUAL CHARTS®* and can be easily modified in this program. There is also an option available to save them in the Windows-Metafile-Format (wmf) or as a simple bitmap-file (bmp). All graphs and tables can be copied and pasted in other *WINDOWS®* applications.

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PROIZVODNJA VRIJEDNOGA DRVA: SOFTVERSKA PODRŠKA PRI ODLUČIVANJU U GOSPODARENJU HRASTOVIM SASTOJINAMA (*QUERCUS PETRAEA* LIEBL. I *Q. ROBUR* L.) U EUROPI

Hrast je važna autohtona vrsta vrlo varijabilne kvalitete i prema tomu proizvodna vrijednost u Europi. Za proizvodnju drva vrhunske kakvoće potrebno je gospodarenje koje se zasniva na informacijama o učincima konkurencije među stablima na razvoj krošnje i rast promjera debla i njihov utjecaj na kakvoću drva. Budući da su ti parametri vrlo složeni i da se mogu pojaviti u velikom broju kombinacija, pri odlučivanju je potreban nov alat, kao što je simulacijski softver, koji će omogućiti korisniku da simulira razne režime gospodarenja i njihov utjecaj na kakvoću drva.

Za ovu je studiju izmjereno više od 3300 hrastova iz sastojina kojima se različito gospodarilo u Njemačkoj, Francuskoj, Poljskoj, Danskoj, Austriji i u Mađarskoj. Njihova se dob kretala od 10 do 350 godina. Konkurencija je među stablima opisana i procijenjena pomoću karata rasprostranjenosti debla i krošnje za svaku jedinicu. Uzeti su diskovi iz nekoliko debala i rekonstruiran je radijalni rast u presjecima kako bi se kvantificirao utjecaj konkurencije na radijalni rast.

Studija je za cilj imala razvoj općega vrijednosnoga modela rasta za hrastove svih dobi, na velikom broju staništa i uz razne gospodarske postupke kako bi se programirao simulator kojim se može predvidjeti rast i kakvoća u različitim režimima gospodarenja.

Ključne riječi: hrast, gospodarenje, kvaliteta drva, simulacijski softver, model rasta

E. Hochbichler, W. Ruhm, H. Schönauer: Management of oak forests in Austria
Glas. šum. pokuse 37: 51–68, Zagreb, 2000.

UDK 630*232+242+228+(436) (Quercus sp.)

MANAGEMENT OF OAK FORESTS IN AUSTRIA

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In Austria, oak stands cover about 4% of the total forest area or 130,000 ha (high forest and coppices with standards). Potentially natural oak-forest communities cover an area of about 430,000 ha. The intention to manage suitable areas for oak has apparently grown over the last three decades. Due to the still very high costs for establishing and tending oak stands, it has become necessary to reconsider traditional stand establishing methods and also to test new concepts. The experiences and results of on-going investigations in the field of plot-culture and tending models (open-stand model and a high-forest model) for high-class timber production on middle forest stands (coppice with standards) will be discussed in this paper. Species-rich and well-structured oak stands can be achieved by plot culture, especially if natural succession on the site is considered. In addition to the ecological benefits, this type of cultivation provides more flexibility and is less costly. In 1996, the Austrian Federal Forest Centre established an experimental series of oak nest plantings and oak cluster plantings. After three vegetation periods, self-differentiation of the oaks in the centre of the nest plantings and a positive impact on growth could be observed. The use of different tending methods as well as browsing affected the growth of oaks on the unfenced control plots.
The effects of thinning treatments according to the two different thinning models on stand structure and biomass relationships are also discussed.

Key words: *Quercus*, plot culture, thinning, stand structure, biomass

INTRODUCTION

At present, the share of oak in Austria in production forests (high-forests) is about 2 % (70,000ha) and in coppice forests is around 60 % (60,000 ha). Potentially natural oak-forest communities cover an area of approximately 430,000 ha, which is 12 % of the total forest area. Oak-hornbeam forests comprise approximately 300,000 ha. Oak forests on acidic soils occupy approximately 40,000 ha and on thermophile soils 30,000 ha, while pine-pedunculate oak forests cover an area of 50,000 ha. At present, approximately one third of potential oak-forest sites are occupied by pure coniferous forests (forest inventory 1992 – 96).

OAK MANAGEMENT – STATUS – TRENDS

Up to the mid-eighties, it was quite common to emphasise the conversion of hornbeam and common hazel (field maple) dominated stands and/or the conversion of middle-forest stands with a poor upper storey into high-forest stands with oak in order to take advantage of the financial yield potential of the site (Lang 1979; Hochbichler 1993, Weinfurter 1991, etc.).

The average plant number at the moment of the establishment of the stand was in the range between 4,000 and 6,000 plants per hectare (3,500 – 5,000 oaks; 2,000 – 3,500 hornbeam/lime trees). Secondary species were planted on soils where stumps had previously been removed. Spacing varied between 2.2m*0.5 (0.7) m (Vienna Woods) and 3-4m*0.5 (0.7)m (stands in middle forests).

Due to the high costs (fencing and tending amounting to over 180,000 ATS/ha) and management considerations, these activities were reduced during the following years by emphasising at the same time the natural regeneration of old growth forest. Natural regeneration takes place by using the compartment method in the high-forest and the middle-forest cut in the composite forest system (coppice with standards system), whereby a trend towards small-scale regeneration methods (selection cutting) can be noticed.

Depending on the original stands (artificial or natural regeneration), the cultivation and conservation of admixed tree species (mixture regulation) through positive selection is recommended for young growth and thicket stages whereby at the beginning negative selection occurs in the dominant stand (wolf trees) and early transition (5-7m) in order to encourage valuable stand elements (by pruning if needed). An early transition for the selective promotion of plus trees is less costly than tending operations carried out schematically. However, a regulated encouragement of plus trees in this tending stage has not been made so far in all cases.

The thinning of future high-class oak stands depends on the principle of selection thinning (selection and preference of plus trees) which is aimed at regulating crown development and annual ring growth (radial increment) by the conservation of the secondary stand. This is put in practice to a great extent.

In 1990/91 a severe storm damaged a number of stands on mixed oak sites in the foothills of the Alps, where coniferous forests dominate. Increasing problems with the health of secondary coniferous stands and concerns in connection with the continuous vitality loss by the oak in the middle forest region have led to the discussion of "new", less costly strategies for the conversion of forests on potential mixed oak forest stands (Weilharter 1991; Ruhm 1996; Tiefenbacher 1996, etc....).

Due to still very high costs for establishing and tending oak stands, it has become necessary to reconsider traditional stand establishing methods and to test new concepts.

In addition to the reduction of the plant numbers in the case of the stand establishment to 2,000 oaks and 700 hornbeams per hectare (Lang 1991), variants of "plot-cultures" (cluster-nest plantings, wide spacing (7-10m*2-3m) with the inclusion of existing natural regeneration (pioneer crops; Müller 1995) and even non-influenced natural regeneration (secondary succession) are being discussed and implemented. In this case, costs may be reduced from 130,000 ATS/ha to 50-70,000 ATS/ha (Exenberger and Hochbichler 1999).

These concepts have in common the fact that the growth and a desired natural pruning in young growth and at the thicket stage are monitored by self-differentiation and interspecific competition (soft broadleaved species, pioneer species). This approach is not only advantageous from the silvicultural and ecological points of view, but it is also economically justified (Leder 1992, Leder 1996; Görlitz and Leder 1994).

We still need to improve our knowledge regarding the planting stock (provenance issues), the specific growth of the different tree species, the competition behaviour and the quality development of such mixed broadleaved stands with a high share of nurse crop tree species (birch, European aspen) in order to be able to apply target-oriented regeneration methods and tending operations (intervention intensity and timing). It is important to find out to what extent steering interventions would be necessary in order to keep oaks competitive in comparison with soft broadleaved species and to ensure the desired pruning effect. In addition, the question arises on how far pioneer species growing abundantly on many sites may influence the production target ("nurse crop" – birch stand).

The following chapters describe the experience and results of the on-going investigations in the field of plot-culture (Ruhm 1996) and tending models for high-class timber production on middle-forest stands (coppice with standards) (Krissl und Müller 1989; Hochbichler and Krapfenbauer 1987).

PLOT CULTURES

For broadleaved species these models are based on the idea that a plot as small as possible should be used for mixtures of the same type which are planted only on parts of the planting site, in a more or less final crop oriented distribution of clusters, groups or nests (Gockel 1994; Johann 1994; Krissl & Müller 1990; Müller 1998; Szymanski 1986, 1994; Koss 1992, 1993, 1995).

By planting more or less dense oak groups only on parts of the planting site, it should be possible to reduce not only planting costs but also avoid costly tending operations during the pre-thicket and thicket stage. Stand establishment does not take place any more on the whole site but in the range of the final crop trees. This allows the best possible distribution of plus trees, while the available planting site can be used in the best possible way (Gockel 1994). This method can be used to establish both pure stands and mixed stands; in the form of temporary mixtures (e.g. cherry, Douglas fir) or permanent mixtures (e.g. beech, noble hardwood species, larch) they may contribute to increasing yield regulation by area, minimising the management risk at the same time.

NEST PLANTING

For nest plantings, 21 oaks are planted on $1m^2$ with a square spacing of 25 cm. This method was introduced in German-speaking countries by Szymanski (1986, 1994) under the term "Nest planting". The high density in the collective allows for mutual protection of the plants, similar to spruce groups at the sub-alpine level. As a consequence, the competing vegetation is displaced from the inner part of the nest towards the borders. However, this should also have a self-tending effect. Oak planting in dense groups favours the development of better stem types and quicker self-pruning compared to row plantings (Szymanski 1986, 1994).

CLUSTER-PLANTINGS

This method also abandons traditional row planting. It is based on the idea of the most favourable number of trees in the final crop which is the objective to be aimed at. (Gockel 1994). In cluster-plantings, 19 oaks are planted on a surface of approx. $12m^2$. Around one central oak, one ring consisting of 6 oaks and a second one consisting of 12 trees are planted. One more ring consisting of a nursing shade tree species may be planted in addition, provided that no natural regeneration is to be expected. The spacing of the different rings in the cluster as well as the trees on the ring are one metre each, the spacing of the cluster trees corresponds to the desired final crop tree spacing.

PROVISIONAL RESULTS

The following section provides the first results of the experimental plot "St. Kathrein" after three vegetation periods. The results achieved so far reflect the trends of a long-term experiment. Detailed comments can only be made after several measuring periods and statistical data interpretation.

The experimental plot is located in the hilly country of East Styria and Southern Burgenland. The average annual temperature is 9.5°C, the average rainfall is 726 mm. The old growth, a 85-years-old spruce stand on brown earth with stagnant water was clear-cut following a bark beetle outbreak in 1995. Most of the collective oak plantings (nests, clusters) were established with 10 metre square spacing. The planting stock consisted of two-year-old pedunculate oak seedlings. The experimental design was divided into four variants with three different tending models in order to study the impact of browsing by game and vegetation competition.

Variant 1: Oak-nests behind a fence, chemical treatment by systemic leaf herbicides on a one-metre strip around the nest. There was no application of herbicide in the nests themselves.

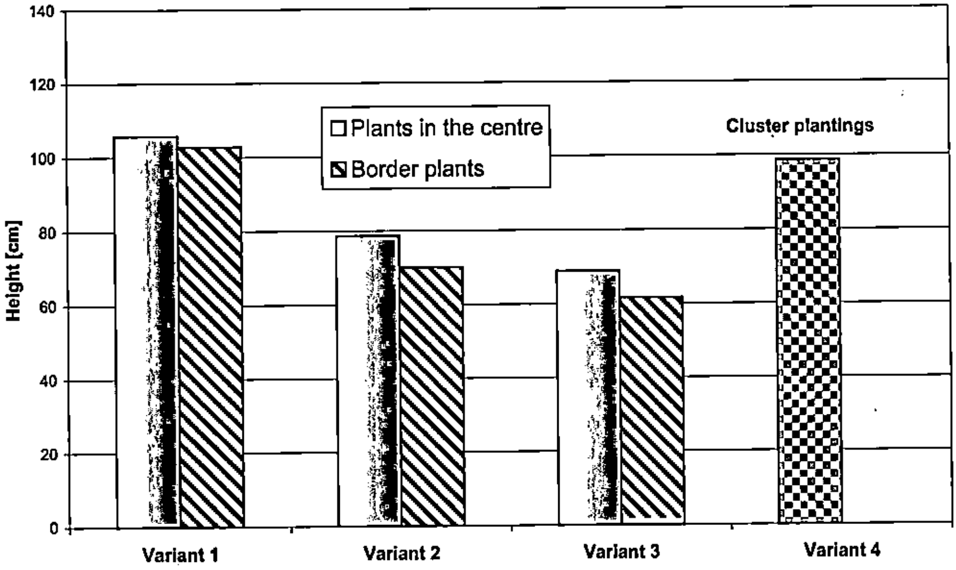
Variant 2: Oak-nests protected individually (Polyethylene-net on four pickets around the nest); Mechanical tending operation by scythe once a year.

Variant 3: Oak-nests without fencing or tending.

Variant 4: Oak-clusters behind a fence; chemical treatment by systemic leaf herbicides on a one-metre strip around the cluster.

What is striking is the small difference between variant 2 and 3 as regards the tending effect. The main competitive factor, a very aggressive growth type of *Rubus frukticosus*, cannot be eliminated on a sustainable basis by mechanical tending

Figure 1. Experimental plot St. Kathrein. Average height of oaks in nest plantings (differentiated according to their position in the nest) and clusters after three vegetation periods and different tending operations.



operations once a year. Within the same tending model (Variants 1 and 4), differences are not so obvious. The chemical treatment in variants 1 and 4 which is much more efficient has a favourable and sustainable impact on height growth in comparison with the other variants.

An early differentiation process within the nests can be noted in all three variants. While in variant 1 the upcoming differentiation may be explained by strong competition within the same species in the nest and thus by the "driving" force caused thereby, variants 2 and 3 have to cope with the increased competition at the borders of the nest. This additional factor probably determines the bigger difference in height between border and centre trees of both variants. According to Szymanski (1986, 1994), the self-differentiation and quality improvement of oaks within the nests is an essential advantage of nest plantings. Koss (1995) also observed a strong differentiation within the nests, but he presumes that the canopy cover of a pine stand has intensified this effect. In his study of nine-year-old nest plantings, Guericke (1996) noticed strong differentiation but no quality improvement of the oaks in the centre. A similar result was reported by Nutto (1998). His study of Polish nest plantations of 1952 showed that in most of the cases the trees at the border of the nest survived but not those in the centre of the nest.

Fencing has an influence on the number, quantity and height development of species in natural regeneration. In particular, tree species of commercial value such as cherry and sessile oak are almost completely missing in the unfenced plot. Also hornbeam is likely to be very sensitive to the "site factor red deer". Soft broadleaved species are abundant, fulfilling their function as filler on the intermediate plots also within the unfenced variant. Browsing by game leads to retarded height growth and reduces the competition pressure on oak collectives.

When planting approximately one hundred nests per hectare, sufficient self-pruning and quality improvement of nest oaks will depend to a great extent on the competition among the trees between the nests.

Plot-culture is not intended to replace proven row concepts but should become an additional possibility to reach the goal of high-class oak wood, at the lowest expense possible. Rationalisations in the field of stand establishment and tending

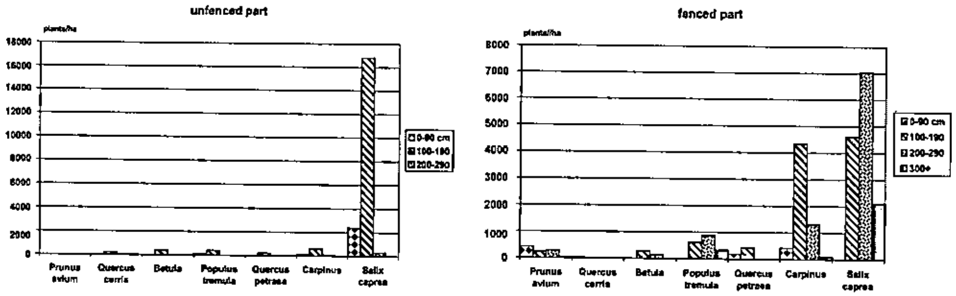


Figure 2. Experimental plot St. Kathrein. Height distribution and number/ha of the natural regeneration on the surfaces between the oak plot culture under fenced and unfenced conditions.

favour not only cost reduction but also increase the diversity of species in young growth.

THINNING

This chapter deals with experience in connection with the implementation of two management models, the opening up thinning model according to Krissl and Müller (1989) and the high-forest model ("hochwaldartig") according to Hochbichler and Krapfenbauer (1987). Both models have been developed to grow high-class oak timber (rotation period of 110-130 years; target diameter 60 cm; branch-free stem length 5-7m) on vigorous middle forest stands in the dry, summer warm East of Austria.

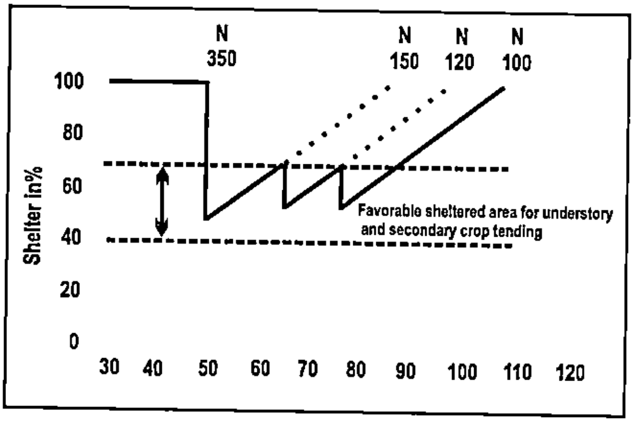
The dominating forest vegetation type in the main growth zone "Sommerwarmer Osten" (Killian, Müller and Starlinger, 1994) is the warmth loving Oak-Hornbeam forest type. The average rainfall is 450 to 600 mm, where most of the rainfall occurs during the summer and there is a dryer period that occurs in spring and autumn. The average annual temperature is 9.3 °C, the January average is -3.0 °C and the average July temperature is 19.6 °C. Coppice with standards and coppicing still dominate.

OPEN-STAND SYSTEMS FOR OAKS

MODEL

After reaching the desired branchless part of the stems, the oak crowns develop without interference thanks to radical liberation cutting. Because of the intensive thinning operations, it is of major ecological importance to plant or foster understoreys, which is important to get straight stems. The precondition is to provide necessary shelter conditions. According to local experience obtained from existing stands, the sheltered area must be between 40 and 70%, under which the hornbeam understorey develops without additional interventions. If the indicated range is exceeded or not reached at all, the result may be extinction or a too vigorous development with subsequent oppression of the main trees. In order to be able to derive the corresponding stem numbers for the shelter percentages necessary, it is important to know about the development of the crown volume of the individual trees which are characteristic for an open-stand system on different sites. For this purpose, crown diameters of oaks from coppices with standards were measured under the assumption that the development conditions for such oaks are comparable to those of an open-stand system. Accordingly, the crown volume of single trees with widely unhindered crown development which is typical for oaks from coppices with standards and for the open-stand system was approximately derived for the individual age classes.

Figure 3. Stem number development



The open-stand system should obtain a stem number of about 350 oaks/hectare at the age of 50 (this corresponds to a dominant quality class of 20 m and a mean height of the co-dominants of 16 m). It is important that the pruning operations conducted to reach the desired branchless stem length of the plus trees are finalised by then. In the case of high densities (e.g. natural regeneration), this can be achieved by fostering natural pruning, and in progressive cultivation concepts with low tree numbers through shaping and pruning. At the age of 50, the stem number will be reduced by selective thinning to reach 150 stems/ha. If a secondary stand is desired but not yet existing, the time is ready for the understorey fostering the development. According to the model to develop an upper limit of favourable sheltered area (70 %), this can be reached after 15 years if a stem number of 150/ha is observed. Otherwise, a further stem number reduction by 30 trees will be necessary at the age 65 to reach 120 n/ha (reduction of the shelter to 55 %). At the age of 75, a final stem number reduction by 20 trees will be necessary to reach 100 n/ha. After the age of 75, no more interventions take place until canopy closure is reached. According to the provision of the model at 100 n/ha, the upper limit will be exceeded to guarantee good light conditions for the understorey at a stand age of oaks between 85 and 90 optimal years. The understorey has a time period of about 40 years for the best possible development and could fulfil its function for stem and soil protection. Canopy closure takes place after 20 more years at an age of 110 years approximately. Taking into account a rotation period of 120 years for the next 10 years, no further enlargement of the crown cover takes place. (In a longer rotation period, an additional stem number reduction - at the age of 90 - to 80 n/ha, and thus a subsequent delay of canopy closure may be conceivable). The applicability of these model calculations has been studied by selecting an experimental plot with 50-year-old oaks in “Mollmannsdorf”.

RESULTS

The stem number in a 50-year-old (virgin original) stand was, at 1035 n/ha, very high. The crown diameter development remained far behind that of isolated oaks from coppices with standards The average crown cover of the individual tree was only 13.6 m^2. In order to reach the starting point, which corresponds to the model for the projected open-stand system, the crown cover of the stand was reduced to 40 % by the simultaneous planting of hornbeam as an understorey. The small crown volume of the individual trees resulted in a significantly greater number of stems compared to the model where the open-stand system had been prepared by good crown tending. Thus, the stem number on the experimental plot was reduced to 425 trees/ha, creating a sheltered area of 45 %. The planted hornbeam understorey is developing very well. The shelter was 80% before the thinning operation. Epicormic sprouts which developed partly on plus trees were eliminated manually. The stem number was reduced from 425 /ha to 200 /ha to reach a shelter of 40 % after the intervention.

Table 1. Mean values of the plus tree collective

	1985		1999	Oaks from coppice with standards
Branchless stem length:	9,3m		9,3m	
Diameter breast high:	24,5cm		31cm	31cm
Height:	17m		19m	
Crown cover:	13,6m^2		31m^2	38m^2
Crown length percentage:	46%		49%	60%
Year ring width 85 – 99:		2,2mm		
Shelter icrement:		17,4m^2		
Height increment:		2m		

EXPERIMENTAL PLOTS HOHENRIEDSTEIG

The experimental plots Hohenriedsteig 1 (HR1; 1600 m^2) and Hohenriedsteig 2 (HR2; 1000m^2) were established artificially (from seed) in the year 1968/69 with a low plant density (row spacing 4 to 5 m; within the row 0.5*0.7m). The experimental plots were established in winter/spring of 1996/97.

Classified after Hartmann (1949), the stands are at a moist location (HR1) and in a less moist area on mildly sloped areas (HR2).

Mechanised tending was carried out in the study areas up to 1983/1984. After 1984, machine-based clearing was carried out between the rows of the hard and soft

Figure 4. Stem number development

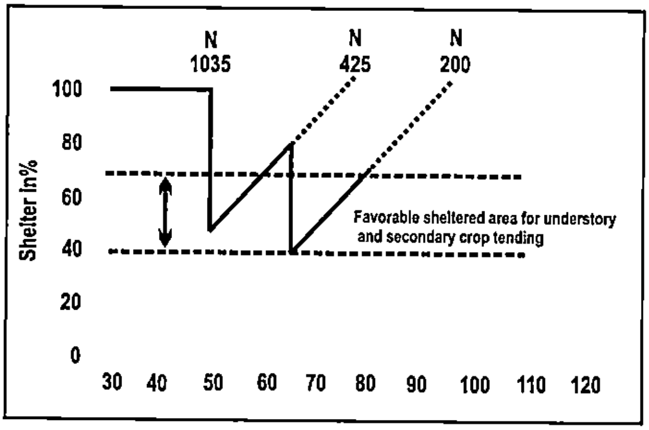


Figure 5. Crown-projection of the oaks on experimental plot "Mollmansdorf"

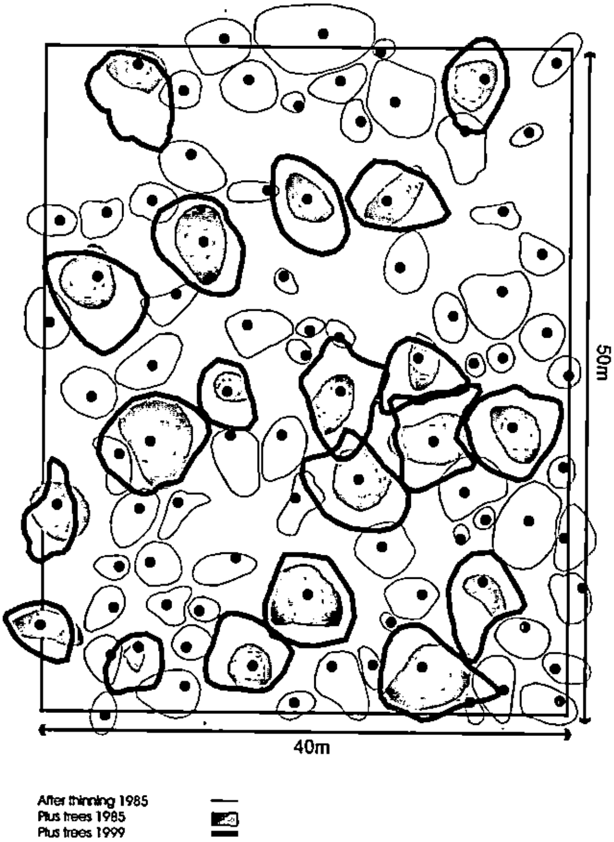


Table 2. Stem number (stems/ha), d.b.h.($\bar{x}$ in cm), height($\bar{x}$ in m) and crown height($\bar{x}$ in m) of the potential plus trees and comparison trees, percentage of trees of high and poor quality on the basis of branchiness (poor quality: trees with diameter (dm) of green and/or dead branches and/or dead branch stubs > 3cm) and percentage of the trees with epicormics up to a stem height of 5 m (Hochbichler 1997)

		Potential plus tree		Comparison tree	
		HR1	HR2	HR1	HR2
	Stem (stem/ha)	10 (60/ha)	7 (70/ha)	10 (60/ha)	7 (70/ha)
	d.b.h. ($\bar{x}$ in cm)	18.6	16.2	18.8	14.9
	Height ($\bar{x}$ in m)	13.6	11.9	13.2	11.8
	Crown height ($\bar{x}$ in cm)	5.9	5.3	4.2	4.1
Quality	High	80	100	0	0
	Poor	20	0	100	100
Epicormic	None	30	86	20	42
	-5	40	14	0	29
	5-35	30	0	80	29

deciduous trees with varied intensity (in study area 1, only between every second row; in area 2, no tending). The understorey is approximately 18 years of age.

In 1984, the first pruning was carried out according to the single-tree tending model of Krapfenbauer (1983). Further pruning was carried out to achieve the goal to obtain 5 to 6m of branch-free stems and 60 to 70 future crop trees per hectare (Hochbichler and Krapfenbauer, 1987). Through this operation a sufficient number of potential plus trees with the desired distribution and quality could be achieved (Table 2).

In the winter of 1999, initial thinning operations took place on both experimental plots. According to considerations concerning the management type and based on studies on the relationship d.b.h.- crown width and shelter of the dominant stand of 70 %, after reaching a branch-free stem length of about 5-7m, a consequent, selective promotion of plus trees (60-70 trees/ha=number of final crop trees) was foreseen by harvesting 2-3 oppressing species. The impact of these interventions is described using stand characteristics and biomass distributions (leaf area indices), which are successively gaining more importance from an ecological point of view.

SURVEY METHOD

Forest inventory and biomass inventory

The present paper characterises components of dominant and secondary stands as follows:

Dominant stand – oak (complete survey): Oak, d.b.h. ($>=$ 7cm), height, living/dead

Secondary stand (4 basal areas with 25m^2 in the centre of every quadrant: tree (shrub) species, d.b.h. (oak, d.b.h. $<$ 7cm), height

Single tree biomass components (dry weight, 24h drying at 105°C) were calculated by means of regression analysis (Pellinen 1986; Freedman et al. 1982; Meyer 1941; etc.).

In addition to our own studies, data were used from 13 oaks (d.b.h.-range 3cm – 19cm), recorded by Glück (1996) directly in the investigated area and from 15 "oaks from coppice with standards" (d.b.h.-range 15cm-60cm), made available by Pertlik (1982). The calculation of biomass components of the secondary stand (hornbeam, common hazel, dogwood) is based on the experiences of Bellos (2000).

For the calculated assessment functions for the different biomass components of oaks (wood and bark), see Table 3.

Table 3. Assessment functions for the calculation of the biomass components such as stem, branches, twigs, dead branches, and foliage (samples, regression coefficient, coefficient for determination)

(a)	stem (wood+bark; $>=$7cm, 7-2cm): $\ln W\,(kg) = -6{,}146 + 2{,}046 * \ln BHD(cm) + 1{,}943 * \ln H(m)$	(n=13; r^2=0.95)
(b)	branches (wood+bark, stem 2-1cm, branches 7-1cm): $\ln W(kg) = -6{,}643 + 3{,}299 * \ln BHD$	(n=13; r^2=0.73)
(c)	twigs (wood+bark, $<=$ 1cm): $\ln W = -8{,}915 + 1{,}309 * \ln BHD + 2{,}684 * \ln H$	(n=13; r^2=0.90)
(d)	dead branches (wood+bark) : $W = -0{,}447 + 0{,}141 * BHD$	(n=13; r^2=0.43)
(e)	foliage: $\ln W(kg) = -5{,}320 + 1{,}517 * \ln BHD + 0{,}798 * \ln H$	(n= 28; r^2=0.95)

The leaf area index (LAI; unilateral projected leaf area in m^2/m^2) was calculated for the tree and shrub species taking the specific leaf area (SLA, cm^2/g) and foliage. The mean specific leaf areas used can be seen in Table 4.

The mean specific leaf area of oak with 120 cm^2/g is below the specific leaf area found by Möller (1945) in thinned oak stands. At a dry weight for 100 leafs of 27-30 g he mentions a specific leaf area of 138-177 cm^2/g. In Hungarian mixed sessile oak-Turkey oak stands, Jakucs (1987) found a specific leaf area of 90-170 cm^2/g of sessile oak depending on the season, the year of survey and the crown position (light and shade leafs). Similar interactions were observed by Leuschner (1994).

The single tree biomass of each tree was calculated using the recorded comparison functions projected on the basis of the represented stem number per hectare to receive the stand values.

Table 4. Number of samples (N), dry weight for 100 leafs (TBLG100; $\bar{x}$ in g) and specific leaf area (SLA; $\bar{x}$ in cm²/g) and standard deviation (+-s.d.) separated according to tree and shrub species

Tree species	N	TBLG100 (g)		SLA (cm²/g)	
		$\bar{x}$	+-s.d.	$\bar{x}$	+-s.d.
Pedunculate oak	10	32.2	7.52	119.9	23.4
Hornbeam	12	13.1	1.63	217.0	33.8
Common hazel (BELLOS, 2000)	15	31.6	11.5	200.4	19.5
Dogwood (BELLOS, 2000)	17	17.0	5.9	144.2	33.2

RESULTS - COMPARISON OF STAND CHARACTERISTICS AND BIOMASS RELATIONSHIPS

The stand characteristics before and after the thinning operation can be seen in Table 5.

Before the thinning operation at the experimental plot, the numbers of the dominant stand were 944 per hectare on experimental plot HR1 and 1010 on experimental plot HR2. The share of standing dead trees was16 % and 2 % respectively. During thinning operations, around 35% of the stem number on experimental plot HR1 and 37% on experimental plot HR2 representing 36% and 28% of the growing stock (50 and 32 m^3o.b./ha) were harvested. The basal areas were reduced to 12m²/ha by a reduction of the sheltering percentage to 45 % and 40 %.

The stem numbers of the secondary stand (hornbeam, common hazel, dogwood and other broadleaved trees) which had been maintained in the framework of tending operations, reflect the varying tending intensities. On experimental plot HR2, the stem number was, at 7650 trees/ha, 2.7 times higher than on experimental plot HR1. The understorey covering the whole area reached a height between 3 and 5 m on both plots.

Before the ongoing operation, the total aboveground timber biomass of the dominant oak stand was 127.4 t/ha on experimental plot HR1, whereas it was 88.6 t/ha on experimental plot HR2. The stem wood had a share of 83%, the branch biomass was 12 %, the twig biomass was approximately 4.5% and the dead branches biomass had a share of approximately 1.0%.

The dry weight of foliage was, at 2.6 t/ha on experimental plot HR1, slightly higher than on experimental plot HR2 where it was 2.1 t/ha. This signifies a share of 2.0% and 2.3% respectively of aboveground biomass.

The timber and shrub biomass of the secondary stand differs significantly, accounting for 7.5 t/ha on experimental plot HR1 and 22.8 t/ha on experimental plot HR2. Foliage varies between 0.3 t/ha and 1.1 t/ha. The standing dead biomass was 3.5 t/ha and 0.8 t/ha.

Table 5. Stand characteristics (stem number (N/ha), d.b.h., height, basal area (b.a.; m²/ha), growing stock (v.; m³/ha), sheltering percentage (s.p.; %) and biomass components (t/ha; stem, branches, twigs, dead branches, foliage) and leaf area indices (LAI; m²/m²) of experimental plots HR1 and HR2 before (STb) and after (STa) thinning, divided into dominant (DST) and secondary stand (SST) (oak=QURO, hornbeam=CABE, hazel=COVA, dogwood=COSP, o.d.tree= =other deciduous trees)

		Tree species	N/ha	d.b.h/ height	b.a./v.per ha	s.p.	stem	bran-ches	twigs	dead-branches	total	Fo-liage	LAI
				cm/m	m²/Vfm	%	biomass(t/ha)						m²/m²
HR1													
D	STb	QURO	944	16,4/14,0	20/135	70	105,9	14,0	5,7	1,7	127,4	2,6	3,1
S	TH		331	--	7/50	25	39,3	5,1	2,1	0,6	47,2	0,9	1,1
T	Sta		613	16,3/13,9	13/85	45	66,7	8,9	3,6	1,1	80,2	1,7	2,0
S		CABE	1700	3,3/5,9							5,9	0,2	0,4
S		COVA	900	1,7/3,1							1,6	0,1	0,2
T		COSP	200	1,5/3,3									
		QURO	20	5,2/5,6									
		Total	2820								7,5	0,3	0,7
Dead standing tree			150	10,5/8,3							3,5		
HR2													
D	STb	QURO	1010	13,9/12,9	17/103	60	72,8	10,3	3,9	1,6	88,6	2,1	2,5
S	TH		340	--	6/32	20	21,8	3,2	1,2	0,5	26,7	0,7	0,8
T	STa		670	14,7/12,9	11/71	40	50,7	7,0	2,7	1,0	61,4	1,4	1,7
S		COVA	6600	3,0/5,3							16,8	0,9	1,8
S		CABE	600	2,3/4,8							5,6	0,2	0,2
T		COSP	300	1,7/2,9									
		o.d.tree	150	9,4/11,0									
		Total	7650								22,8	1,1	1,9
Dead standing tree			20	7,1/7,0							0,8		

According to the time, before the thinning operation, timber biomass without standing dead trees was approximately 134.9 t/ha and 111.4 t/ha. Leaf biomass showed values of 2.9 t/ha and 3.1 t/ha respectively. With a reduced biomass on the experimental plot HR2 of about 18%, leaf biomass was respectively higher by approximately 8%.

Papp (1978) found in a 60 to 75-year-old mixed sessile oak-Turkey oak stand an aboveground standing biomass of 181.8 t/ha (stem percentage of around 70 %)

for the dominant stand and a foliage of about 4.3 t/ha. This is 2.3 % of the total aboveground biomass. To this biomass, 3.8 t/ha of wood-biomass and 0.5 t/ha foliage of the secondary stand have to be added.

For the experimental plots, leaf area indices (m^2/m^2) of 3.1 (HR1) and 2.5 (HR2) without the secondary stand and 3.8 and 4.4 with the secondary stand were calculated.

Jakucs (1987) found for the mixed oak forest mentioned above an index of leaf area of 6.6 for the dominant stand, 1.4 for the shrub layer and 0.3 for the ground vegetation.

Berger (1991) indicates for a coppice with standards of oak stands with an understorey by foliage weight of 3.3 to 3.5 t/ha, leaf area indices are from 5.3 to 6.6, while Haupolter (1991) shows they are 4.6 for coppices with standards of oak with an understorey, and 1.6 in those without an understorey.

The thinning operation yielded 39.3 t/ha stem wood over bark on experimental plot HR1 and 21.8 t/ha stem wood over bark on experimental plot HR2. With a stem biomass above 7 cm diameter of about 90% of the stem wood, 20 - 35 t/ha biomass was harvested, while the residual biomass components remained in the stand and contributed to the external biomass cycle. After the thinning operation, a reduction of leaf area indices of 1.7 and 2.0 was calculated for the dominant stand with a foliage mass of 1.7t/ha on experimental plot HR1 and 1.4t/ha on experimental plot HR2.

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GOSPODARENJE HRASTOVIM ŠUMAMA U AUSTRIJI

U Austriji se hrastove sastojine prostiru na oko 4 % ukupne šumske površine ili na 130 000 ha (visoke šume i panjače s pričuvcima). Potencijalno prirodne zajednice hrastovih šuma prostiru se na približno 430 000 ha. U posljednja tri desetljeća sve je snažnija namjera da se bolje gospodari hrastovim područjem. Kako su troškovi podizanja i njege hrastovih sastojina još uvijek vrlo visoki, pojavila se potreba za ponovnim razmatranjem tradicionalnih metoda osnivanja sastojina, ali i za testiranjem novih metoda. U ovom se radu govori o iskustvima i rezultatima trenutnih israživanja u području kulture ploha i modela njege (model otvorene sastojine i model visoke šume) za proizvodnju visokokvalitetnoga drva u srednjim šumskim sastojinama (panjače s pričuvcima). Bogate i dobro strukturirane hrastove sastojine mogu se dobiti pomoću kulture ploha, osobito ako se uzme u obzir prirodna selekcija na staništu. Uz ekološke prednosti ovaj tip kultivacije omogućuje veću fleksibilnost uz manje troškove. U 1996. je Austrijski savezni šumski centar postavio pokusnu seriju sadnje hrasta u gnijezda i sadnje u krpe. Nakon tri vegetacijska razdoblja primijećena je autodiferencijacija hrastova u središtu sadnje u gnijezda i pozitivni učinci na rast. Na rast hrastova u neograđenim kontrolnim plohama utjecali su primjena različitih načina njege i brst.

U radu se razmatraju učinci prorede na strukturu sastojine i odnosa biomase prema dvama različitim modelima prorede.

Ključne riječi: kultura ploha, proreda, struktura sastojine, biomasa

S. Matić, et al.: The number of plants and sites as important factors in the growth of young stands of pedunculate oak (*Quercus robur* L.). Glas. šum. pokuse 37: 69–81, Zagreb, 2000.

UDK 630*232.4+236+114.5+522 (Quercus robur L.)

THE NUMBER OF PLANTS AND SITES AS IMPORTANT FACTORS IN THE GROWTH OF YOUNG STANDS OF PEDUNCULATE OAK (*QUERCUS ROBUR* L.)

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The paper presents the results of research of 11 years in two forest cultures of pedunculate oak established in two different sites (forest soil, non-forest pastureland) with six different planting spaces and different number of plants (3,000, 5,000, 7,000, 10,000, 15,000, and 20,000 plants per ha) with three repetitions. An increased tree quality and a higher number of plants per ha have been achieved in both sites. A trend of increased quality is particularly evident with 10,000 to 20,000 plants /ha. The smallest number of low-quality trees and the highest number of medium-quality trees were obtained on forest soils, while the largest number of bad-quality trees and the lowest number of quality trees occurred on non-forest pastureland. Significant differences in tree quality were obtained in the two sites with all planting distances. Aggressive expansion of common hornbeam and the occurrence of natural young sprouts of pedunculate oak were noted in the cultures established on forest soils.

A higher number of plants per surface unit are accompanied with increased tree heights. On average, absolute height values are 25 cm higher in the cultures on forest soils. In the last 6 years heights have been reduced in the cultures with 20,000 plants/ha due to competition among pedunculate oaks and the formation of lower storeys. In such cases cleaning is necessary. It is recommended that the cultures of pedunculate oak with at least 10,000 plants per ha, as well as natural stands, be raised only on forest soils.

Key words: pedunculate oak, forest cultures, planting spacing, forest soil, non-forest soil, tree quality, tree height.

INTRODUCTION

Natural regeneration of a mature forest stand is a natural manifestation of a good quality stand in terms of its structure and site, as well as of professional silvicultural treatments during a stand's life (Matić 1993, 1994). This type of regeneration reduces stresses occurring in the site and in the young stand during the "death" of the old and the birth of the young stand.

The problems that may aggravate or even undermine natural regeneration of pedunculate oak stands can be divided into three groups. These are:

- absence or impossibility of a good quality seed crop
- regeneration made difficult due to weeds, waterlogging, drying and degradation of forest soil,
- disturbed structural relations in a site caused by tree dieback or improper management procedures during exploitation, tending or regeneration of a stand.

Forest soils that have not been degraded (by waterlogging, weeds, etc.) should be subjected to artificial regeneration by planting seedlings or planting or sowing seeds of pedunculate oak and shelterwood cutting.

Degraded soils or areas to be afforested such as meadows, plough land or pastureland are not afforested with pedunculate oaks but with adequate pioneering tree species (narrow-leaved ash, black alder, willows, poplars and others) (Matić 1999). During one rotation, these species will create forest soil of good quality and conditions conducive to pedunculate oak.

THE PROBLEM, AREA AND RESEARCH METHOD

For successful growth of young pedunculate oak stands, an adequate, optimal number of plants per surface unit is needed. This will ensure good stand conditions, microclimate, competition among trees, good growth and increment, good quality trees and other factors.

Research dealing with an optimal number of plants and impacts of site on the growth of young stands of pedunculate oak was done in two areas within the natural areal of pedunculate oak with 6 different planting spaces or plant numbers (3,000, 5,000, 7,000, 10,000, 15,000 and 20,000 per ha).

The experiment was set up in the autumn of 1987 in the Forest Office Vrbovec in the central part of Croatia on good quality forest soil, and in the Forest Office Stošinci in eastern Croatia on former pastureland. Each experiment was done in six randomly distributed variants (planting spaces) with three repetitions.

During the 11-year period the success of planting was monitored, as well as height and diameter growth and increment, growth of weed vegetation and the succession of autochthonous vegetation. The quality of trees was assessed as good (0), medium (1) and poor (2), and the soil was pedologically analysed.

The experiment in the Vrbovec area was established in the site of a stand of pedunculate oak and common hornbeam, where a coppice of common hornbeam growing on good quality forest soil was converted. The experiment is located within the natural areal of pedunculate oak forests in the Forest Administration Bjelovar, the Forest Office Vrbovec and Management Unit Novakuša, Compartment 1, forest region Seljansko, in the seed district of forests of lowland Posavina and seed zone of Upper Posavina and Pokuplje.

The soil is podzoluvisol, dystric, deep (Haplic planosol). Up to 100 cm in depth the soil is loam to clayey loam in structure, with very acid to acid reaction, very rich in humus and total nitrogen in the surface horizon.

The experiment in the area of Strošinci was established on non-forest soil of former pastures. It is located in the area managed by the Forest Administration Vinkovci, Forest Office Strošinci, Management Unit Debrinja, Compartment 88, over 40,000 ha of an unbroken complex of pedunculate oak forests "Spačva" in the seed district of lowland forests of Posavina, seed zone Lower Posavina.

The soil is mollic gleysol, carbonate vertic, clayey (Calci-mollic Gleysol), clayey in structure (light clay), neutral (in the surface part) to medium alkali reaction, moderately rich in humus and rich in total nitrogen in the surface horizon. It should be pointed out that this soil has very large reserves of humus and total nitrogen in the humus-accumulative horizon: 324,000kg/ha humus and 19,500kg/ha nitrogen. G-horizon occurs at a depth of 45 cm.

RESEARCH RESULTS AND DISCUSSION

Research on structural properties of young stands of pedunculate oak aged 3 to 10 years has shown that at this age, an average of about 40,000 plants of woody tree species per hectare are found in these stands (Matić 1993, 1994, 1996, 1999). The association of pedunculate oak and common hornbeam is a climatogenous association containing other tree species apart from pedunculate oak. These are primarily common hornbeam and other pioneering tree species (lime, maple, narrow-leaved ash, fruit trees and others).

During stand regeneration, the number of accompanying species depends mostly on the number of pedunculate oaks, that is, on the success of its natural or artificial regeneration. Of the total of 40,000 plants/ha, the standing space per plant is 0.25 m^2. In regeneration, this space is at the disposal of both pedunculate oak and other tree species. If the space is taken predominantly by the pedunculate oak, then, with proper tending, it has realistic conditions for a permanent stay in the stand. In a natural stand of pedunculate oak, an optimal mixture ratio is 80% of pedunculate oak (about 30,000 plants/ha) and 20% of other tree species (about 10,000 plants/ha). A pedunculate oak stand of such a structure is stable, productive, biologically diverse and sustainable.

This paper will present some measurement results of 11-year-old experimental plots in the area of Seljansko (forest soil) and Strošinac (non-forest soil), as well as the results of previous measurements and some published papers on this problem matter.

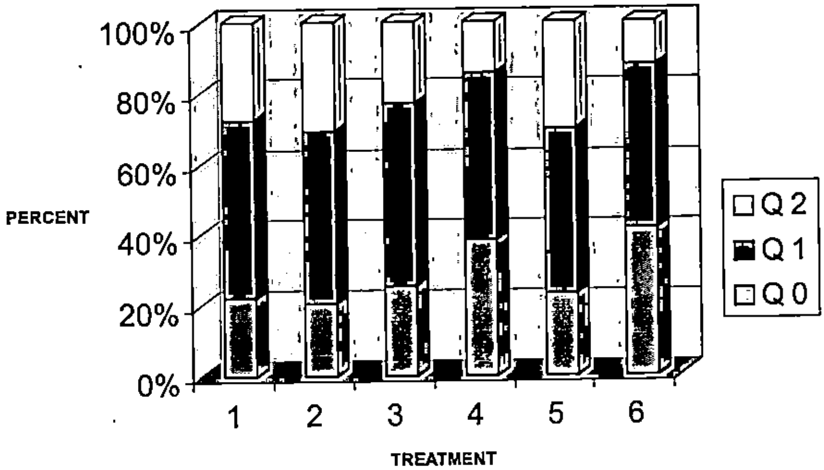
Special attention will be paid to the influence of site and planting spacing (plant number) on the quality and height growth and increment of pedunculate oaks in a stand.

IMPACTS ON THE QUALITY OF TREES

Table 1 presents the results of measurements in experimental plots established on quality forest soil during the conversion of a hornbeam coppice into a pedunculate oak stand in the area of Seljansko. The number of plants in the area of each repetition (400 m^2), the condition in the spring of 1999, planting spacing, and height and quality per number of plants and per percentage are shown. Graph 1 gives a graphic representation of the impact of planting distance on the quality percentage of pedunculate oak plants for the same area. Data from the Table and the Graph show that the percentage of best-quality trees (o) rises with smaller planting distances, that is, with increased number of plants per surface unit. A growth in the trend of good quality trees is noted at 10,000, 15,000 and 20,000 plants per ha. According to the data, trees of medium quality (1) are the most numerous, while those of the poorest quality (2) are the least numerous.

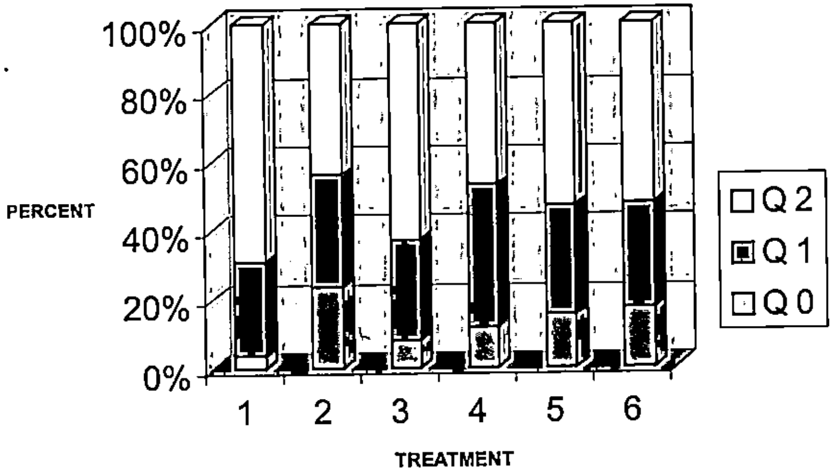
Table 1. Number, heights and quality of pedunculate oak plants at different planting spacing on forest soil of the Seljansko area

Tret-ment	Distance		Height	Quality			Quality		
	m	piece	cm	0	1	2	0	1	2
					piece			%	
I/1	1.8x1.8	91	273	14	54	23	15.38	59.34	25.27
II/1		96	178	25	48	23	26.04	50.00	23.96
III/1		85	229	20	37	28	23.53	43.53	32.94
Mean		91	227	20	46	25	21.65	50.96	27.39
I/2	1.4x1.4	125	316	22	67	36	17.60	53.60	28.80
II/2		99	244	25	43	31	25.25	43.43	31.31
III/2		133	203	23	68	42	17.29	51.13	31.58
Mean		119	254	23	59	36	20.05	49.39	30.56
I/3	1.2x1.2	147	267	42	78	27	28.57	53.06	18.37
II/3		89	240	19	43	27	21.35	48.31	30.34
III/3		142	199	36	78	28	25.35	54.93	19.72
Mean		126	235	32	66	27	25.09	52.10	22.81
I/4	1.0x1.0	187	265	57	101	29	30.48	54.01	15.51
II/4		138	339	72	44	22	52.17	31.88	15.94
III/4		185	232	60	104	21	32.43	56.22	11.35
Mean		170	279	63	83	24	38.36	47.37	14.27
I/5	0.8x0.8	215	276	43	102	70	20.00	47.44	32.56
II/5		308	278	72	137	99	23.38	44.48	32.14
III/5		227	305	57	112	58	25.11	49.34	25.55
Mean		250	286	57	117	76	22.83	47.09	30.08
I/6	0.7x0.7	311	233	80	158	73	25.72	50.80	23.47
II/6		259	267	96	142	21	37.07	54.83	8.11
III/6		269	256	168	92	9	62.45	34.20	5.36
Mean		280	252	115	131	34	41.75	46.61	12.31



Graph 1. The impact of planting spacing on the quality percentage of pedunculate oak plants on forest soils of the Seljansko area

Similar data relating to oak cultures established on pastureland in the area of Strošinci are shown in Table 2 and Graph 2. Like in Table 1 and Graph 1, it is evident that the percentage of the best quality trees rises with more plants per surface unit. A trend of an increased quality of trees is notable with planting 10,000, 15,000 and 20,000 plants per hectare. Under these site conditions the same trend is noted with medium-quality trees (1), where the percentage of these trees is higher than that of best quality trees (0), but lower than that of poorest quality trees (2), whose number is the highest.



Graph 2. The impact of planting spacing on the quality percentage of pedunculate oak plants on non-forest soils of the Strošinci are

Table 2. Number, height and quality of pedunculate oak plants at different planting spacing on non-forest soil in the Strošinci area

Tret-ment	distance m	piece	Height cm	Quality			Quality		
				0	1	2	0	1	2
				piece			%		
I/1	1.8x1.8	109	243	2	45	62	1.83	41.28	56.88
II/1		107	159	9	21	77	8.41	19.63	71.96
III/1		105	198	1	22	82	0.95	20.95	78.10
Mean		107	200	4	29	74	3.73	27.29	68.98
I/2	1.4x1.4	182	271	80	55	47	43.96	30.22	25.82
II/2		193	214	44	74	75	22.80	38.34	38.86
III/2		183	176	7	52	124	3.83	28.42	67.76
Mean		186	220	44	60	82	23.53	32.33	44.15
I/3	1.2x1.2	246	228	2	79	165	0.81	32.11	67.07
II/3		257	203	44	69	144	17.12	26.85	56.03
III/3		680	177	45	184	451	6.62	27.06	66.32
Mean		394	203	30	111	253	8.18	28.67	63.14
I/4	1.0x1.0	382	228	43	166	173	11.26	43.46	45.29
II/4		349	282	44	131	174	12.61	37.54	49.86
IIII/4		375	202	44	156	174	11.73	41.60	46.40
Mean		369	237	44	151	174	11.87	40.87	47.18
I/5	0.8x0.8	601	240	77	209	315	12.81	34.78	52.41
II/5		601	235	44	177	380	7.32	29.45	63.23
III/5		559	263	142	174	243	25.40	31.13	43.47
Mean		587	246	88	187	313	15.18	31.79	53.04
I/6	0.7x0.7	627	197	100	168	359	15.95	26.79	57.26
II/6		629	230	148	165	316	23.53	26.23	50.24
III/6		737	221	102	271	364	13.84	36.77	49.39
Mean		664	216	117	201	346	17.77	29.93	52.30

The data above suggest that the quality of pedunculate oak increases with a larger number of plants per surface unit. Likewise, forest cultures established on forest soils of good quality have a higher participation of good and medium quality trees in relation to the cultures established on former pastureland. This can be particularly seen from the data in Table 3, where cultures on the forest soil in the area of Seljansko contain 28.3% of good quality (0), 40% of medium quality (1) and 22.8% of poor-quality trees in relation to the forest cultures established on pastureland of Strošinci, where only 13.4% of good quality (0) trees, 31.8% of medium-quality (1) trees and 54.8% of poor-quality (2) trees occur.

Table 3. Participation percentage per quality (0, 1, and 2) of pedunculate oak seedlings on forest (Seljansko) and non-forest soil (Strošinci)

LOCATION	QUOLITY 0	QUOLITY 1	QUOLITY 2
		%	
Seljansko	28.28	48.91	22.79
Strošinci	13.37	31.81	54.80

If we compare the quality of trees at all planting distances in Seljansko (forest soil) and Strošinci (pastureland), then we can conclude from Table 4 that there is a significant difference in the quality of trees at all planting spacing in these two areas. The smallest variability in the thickness occurs with poor-quality trees (2) and the highest with best-quality trees (0).

Table 4. Significant difference in the quality of seedlings between the locations of Seljansko and Strošinci

	Sum of squares	df	mean square	F	
Effect	0.312444	1	0.312444	3,948.104	p-level
Error	0.079138	10	0.007914		9.10E-05

Table 5. Significant difference between the planting density for all qualities (0, 1 and 2) in the locations of Seljansko and Strošinci

Quality 2				
	df	Mean square	F	p-level
Blocks	2	216.0556		
Treatment	5	1150.322	3.984183	0.030024
Error	10	288.7222		
Quality 1				
	df	Mean square	F	p-level
Blocks	2	459.0555		
Treatment	5	3364.089	5.845958	0.009073
Error	10	575.4556		
Quality 0				
	df	Mean square	F	p-level
Blocks	2	468.3889		
Treatment	5	3798.056	8.722028	0.002057
Error	10	435.4556		

Measurements done in the experimental plots of Seljansko in the spring of 1999 clearly show that cultures of pedunculate oak with different planting spacing are intensively and aggressively invaded by common hornbeam. A certain degree of spontaneous natural expansion of pedunculate oak with seeds (birds, rodents and others) was also noted. All this indicates gradual increase in biological diversity in the stands established on forest soils of good quality.

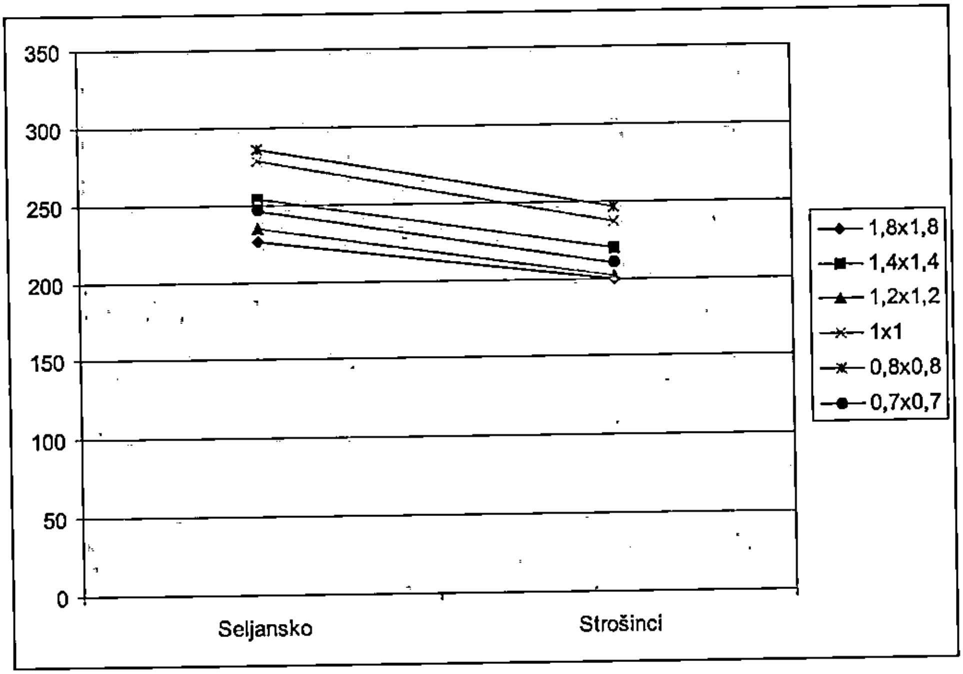
An expansion of common hornbeam and pedunculate oak was not detected in the area of Strošinci.

IMPACTS ON THE HEIGHT OF TREES

Table 6 shows mean heights of pedunculate oak trees for six planting distances in the forest culture of pedunculate oak raised on forest soils in the Seljansko area and the same data for the forest cultures raised on pastureland in the Strošinci area. The same data are also shown graphically in Graph 3. According to the data, the heights of trees at all six planting distances in the Seljansko area exceed the heights measured in the same experiment in the Strošinci area. It is important to mention that the best heights (287.7cm) were measured in the cultures with 15,000 plants/ha in Seljansko. This is followed by cultures with 10,000 plants/ha (287.7cm), then by those with 5,000 plants/ha (254.3cm), 20,000 plants/ha (252.0cm), 7,000 plants/ha (235.3cm) and 3,000 plants/ha (226.7cm). The same phenomena, but with different and lower absolute height values was noted in the Strošinci area.

Table 6. Mean heights of pedunculate oak for six planting spacing on forest (Seljansko) and non-forest site (Strošinci)

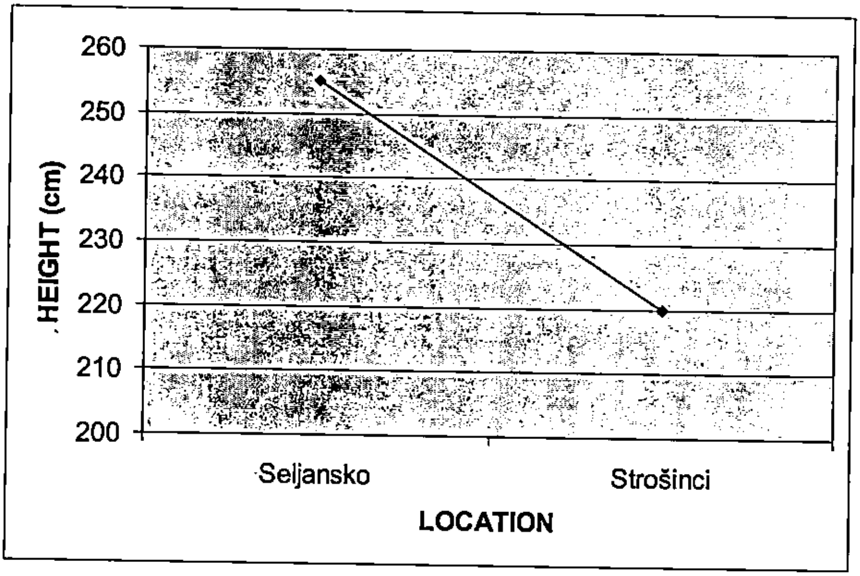
LOCATION	TREATMENT	HEIGHT (cm)
Seljansko	1	226
Seljansko	2	254
Seljansko	3	235
Seljansko	4	278
Seljansko	5	286
Seljansko	6	252
Strošinci	1	200
Strošinci	2	220
Strošinci	3	202
Strošinci	4	237
Strošinci	5	246
Strošinci	6	216



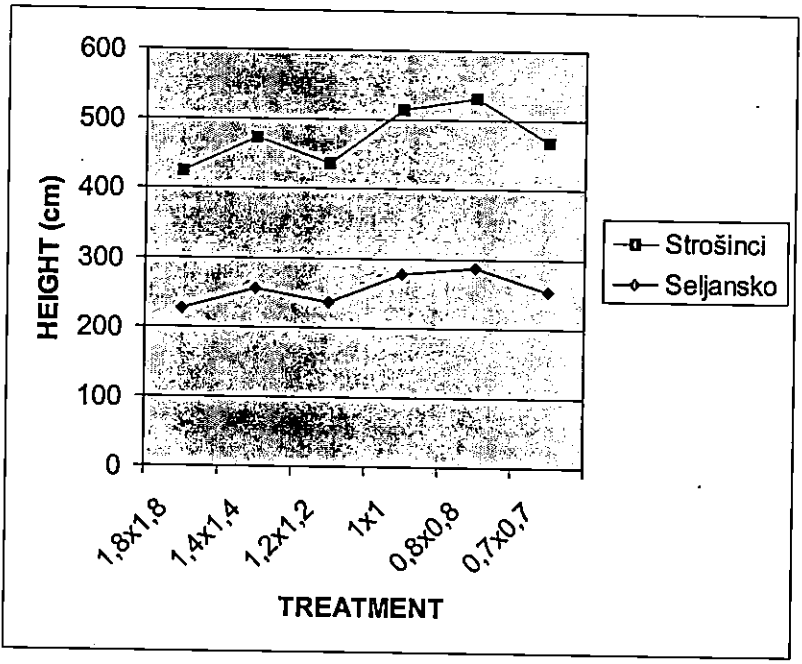
Graph 3. Graphic representation of mean heights for different planting spacing in Seljansko (forest soil) and Strošinci (non-forest soil)

The mean tree height in the Seljansko area (255.1cm) and that in the Strošinci area (221.1cm) are given in Graph 4. These data clearly indicate that the site has an important role in the development of tree heights in establishing forest cultures of pedunculate oak. In the 11 years of stand development, the difference in the mean height is 25 cm in favour of the trees growing on forest soils.

Graph 5 shows frequency distribution of mean heights for various planting spacing for pedunculate oak in the area of Seljansko and Strošinci. A trend can be seen of height development in individual areas, already shown in Table 6 and Graph 3. In this case, a drop in the height for the plots with 20,000 plants/ha is interesting in relation to the results obtained in earlier years (Matić 1993). After five years of the stand's development in the Seljansko area, the best heights were achieved in the plots with 20,000 plants/ha (175.3cm), followed by those with 15,000 plants/ha (161.2cm), 5,000 plants/ha (159.1cm), 10,000 plants/ha (156.8cm), 3000 plants/ha (155.3cm) and 7,000 plants/ha /148.2cm). Although the results did not differ significantly, a trend in increased plant heights was noted with 10,000 plants to 20,000 plants/ha. The most densely planted area, that with 20,000 plants/ha, dropped from the first to the fourth place in the six years of growth, which can be explained by mutual competition among trees and the formation of lower storeys. The trees in lower storeys visibly lag behind in their growth, espe-



Graph 4. Mean heights of pedunculate oak in the area of Seljansko (forest soil) and Strošinci (non-forest soil)



Graph 5. Frequency distribution of mean heights for various planting spacing for pedunculate oak in the area of Seljansko (forest soil) and Strošinci (non-forest soil)

cially in comparison to the trees in the dominant storey that have secured the space above the soil and in the soil. This is the reason why average height values in the thickest stand are falling although dominant future trees are higher than the trees in the stands with a smaller number of plants. Similarly, it is also a proof of very intense processes and changes occurring in young stands of pedunculate oak. Cleaning is necessary in the thickest stands in order to remove trees of poor quality.

On the basis of these data it can be concluded that the quality of a site and number of plants per surface unit (planting spacing) have a significant impact on the height of pedunculate oak trees. Stands erected on good quality forest soil have better heights than those established on agricultural, pasture, non-forest or degraded forest soil.

When forest cultures are formed or artificial regeneration following the principles of natural regeneration is conducted, stands of pedunculate oak should be established on forest soils of good quality. Plants should be planted or seeds sown in such a way as to ensure at least 10,000 plants/ha to the future stand.

CONCLUSIONS

In order to study the influence of planting spacing and site quality on the growth of young stands of pedunculate oak, experimental plots were established on good quality forest soils in the forest area of Seljansko in Forest Office Vrbovec and on the pastureland in the area of Strošinci.

Each plot consists of 18 smaller plots (400m² area), where oak was planted with six different planting spacing and plant numbers per hectare (3,000, 5,000, 7,000, 10,000, 15,000 and 20,000 plants/ha). Each variant has three repetitions.

After 11 years of research on the experimental plots, the following conclusions can be drawn:

1. In the stands of pedunculate oak established on good quality forest soils (Seljansko) the percentage of best-quality trees (0) increases with smaller planting spacing, that is, a larger number of plants per surface unit. A rising trend is noted in good quality trees at plant numbers of 10,000, 15,000 and 20,000 per ha. Trees of medium quality (1) are the most numerous, while those of the poorest quality (2) the least numerous.
2. In the stands established on non forest pastureland (Strošinci) the percentage of best quality trees increases with a larger number of plants per surface unit. A rising trend in the quality of trees at 10,000, 15,000 and 20,000 plants per hectare is evident. The percentage of best trees (0) is the lowest, those of medium quality (1) is higher, while those of the poorest quality (2) is the highest.
3. There are significant differences in the quality of trees at all planting spacing and numbers of pedunculate oaks between the locations in Seljansko (forest soil) and Strošinci (non forest pastureland).

4. The cultures on the forest soil have 28.3% good quality (0), 49% of medium-quality (1) and 22.8% of poor-quality trees, while the cultures established on pastureland have 13.4% of good-quality (0), 31.8% of medium-quality (1) and 54.8% of poor-quality (2) trees.
5. Cultures of pedunculate oak on forest soils at all planting spacing are intensively and aggressively invaded by common hornbeam. Natural expansion of pedunculate oak with seeds (birds, rodents and others) was also noted. This phenomenon was not detected in forest cultures of pedunculate oak raised on non-forest soils. All this indicates a gradual increase in biological diversity of stands established on forest soils of good quality.
6. Mean tree heights at all six planting spacing in the area of Seljansko (forest soil) are higher than those measured in the same experiment in Strošinci (non-forest soil). In the period of 11 years, the difference in the mean height is 25 cm in favour of the trees growing on forest soils.
7. With a larger number of trees/ha, heights display a rising trend in growth and increment both on forest soils and non-forest soils. The difference is that absolute values of tree heights are bigger in the cultures established on forest soils at all planting spacing.
8. Plots with the largest number of plants/ha (20,000) suffered mutual competition and selection into lower storeys. The trees in lower storeys display notably weaker growth, particularly if compared with those trees in the dominant storey that have secured their place above the soil and in the soil. For this reason, average height values in the thickest stand have dropped in the last 6 years, so that they fell from the first place in the 5th year to the 4th place in the eleventh year of development. Cleaning aimed at removing poor quality trees from the stand and thus lessen the competition for future trees is the necessary silvicultural treatment to be undertaken in the most densely populated stands.
9. Forest cultures should be established or artificial regeneration conducted according to the principles of natural regeneration on forest soils of good quality, and plants should be planted or seeds sown in such a way that at least 10,000 plants/ha are ensured to the future stand.

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BROJ BILJAKA I STANIŠTE KAO ZNAČAJNI ČIMBENICI USPIJEVANJA MLADIH SASTOJINA HRASTA LUŽNJAKA (*Quercus robur* L.)

Prikazani su rezultati 11-godišnjih istraživanja u dvjema šumskima kulturama hrasta lužnjaka podignutim na dvama različitim staništima (šumsko tlo, nešumsko pašnjačko tlo) u šest različitih razmaka sadnje i broja biljaka (3000, 5000, 7000, 10 000, 15 000, 20 000 kom./ha) u tri ponavljanja. Trend povećanja kvalitete osobito je uočljiv od 10000 do 20000 biljaka/ha. Na šumskim tlima najmanje je nekvalitetnih, a najviše srednje kvalitetnih, dok je na nešumskim pašnjačkim tlima najviše nekvalitetnih, a najmanje kvalitetnih stabala. Dobiveni su signifikantni rezultati razlike kvalitete stabala na dvama različitim staništima kod svih razmaka sadnje. U kulturama podignutim na šumskim tlima uočeno je agresivno širenje običnoga graba te pojava prirodnoga pomlatka hrasta lužnjaka.

Povećanjem broja biljaka po jedinici površine povećavaju se i visine stabala s tim da su apsolutne vrijednosti visina veće u kulturama na šumskim tlima u prosjeku za 25 cm. U kulturama s 20 000 biljaka/ha u posljednjih se 6 godina smanjuju visine zbog međusobne konkurencije lužnjakovih stabala i izlučivanja u donjec etaže. U takvim slučajevima nužna je njega čišćenjem. Preporuka je da se kulture hrasta lužnjaka kao i prirodne sastojine mogu podizati samo na šumskim tlima i s brojem biljaka od najmanje 10 000 kom./ha.

Ključne riječi: hrast lužnjak, šumske kulture, razmak sadnje, šumsko tlo, nešumsko tlo, kvaliteta stabala, visine stabala

J. Čavlović, M. Božić, N. Lukić: Trends in forest and timberland values in the dynamic system of an even-aged forest of pedunculate oak ... Glas. šum. pokuse 37: 83–93, Zagreb, 2000.

UDK 630*613+652 (Quercus robur L.)

TRENDS IN FOREST AND TIMBERLAND VALUES IN THE DYNAMIC SYSTEM OF AN EVEN-AGED FOREST OF PEDUNCULATE OAK IN THE MANAGEMENT UNIT "JOSIP KOZARAC"

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In terms of multiple functions, the value of a forest varies dramatically over time and depends on a large number of influences and relationships. Some of the most important factors that influence trends in the timberland value of an even-aged forest within its economic function are the rotation period and trends in the age structure. The aim of this paper is to study the relations in forest value, forest rent and interest percentage over time as a consequence of variations in the rotation and age class area.

The subject of the research is the forest of pedunculate oak in the first site class with a total area of 3894.29 ha. The forest contains a surplus of mature understocked stands, and the management is based on a 140-year rotation period.

The value of forest land and stands has been determined using accepted methods, while trends in the entire forest and timberland value have been obtained using the SD model of even-aged forest management.

The relationship of forest value trends, forest rent and interest percentage has yielded the following result: the value of pedunculate oak forest would increase by 5-7 monetary units (6%) if the rotation period were lengthened from 140 to 160 years.

Key words: pedunculate oak, forest timberland value, age class distribution, income, costs

INTRODUCTION

Forests and forest land as specific renewable resources are goods of special social importance. This renewable natural resource is a goods that cannot be enlarged, at least not infinitely. Therefore, it has a monopolistic importance, and its value increases with the increase of population. The importance and role of forests can be estimated on the basis of various criteria, of which the most significant are physical, economic and social ones (Klepac 1963). According to these criteria, forest functions are classified into protective, economic and social ones. Present day forest management is directed solely at the production of two basic products: non-market forest services and timber. However, it is difficult to differentiate between forests that yield only generally useful benefits and those that serve exclusively for the production of wood. These two functions are mutually intertwined and, depending on a situation, have different relationships. Not all forests have economic functions, while the function of general benefit is present to a lesser or higher degree in all forests.

AIM OF RESEARCH

The value of a forest is a function that changes over time and depends on a large number of influences and relationships. The value of generally useful forest functions depends on several factors: the degree of demand for these functions, the awareness of people about the role of forests in maintaining ecological stability, the wealth of a society, willingness to invest into services provided by the non-market values of a forest, and others. The value of generally useful forest functions is very high and is constant for all forests that are managed in a proper and sustainable manner. As it is difficult to evaluate exactly the value of forest functions of general benefit, the value of forest stands, forests and forest land is assessed on the basis of timber value.

The value of an economic forest, viewed solely in the light of timber production, is a function that changes over time and is dependent on a series of factors. These include supply and demand for raw wood material, development of timber processing technology, costs of forest production, structure and quality of wood assortments, age ratio and condition of stands. Forest managers can directly or indirectly influence the last three elements. In recent times, extensive research has been done in pedunculate oak forests (Dekanić 1962, 1975; Klepac 1964, 1971, 1982, 1988; Pranjić 1970; Prpić 1974; Pranjić et al. 1988; Meštrović 1989; Meštrović at al. 1996; Matić and Skenderović 1993; Mayer 1993; Prpić et al. 1997), although trends in the values of these forests have been studied in far less detail. The aim of this paper is to study trends in forests values, forest rent and the rate of interest in the function of time and of changed management with even-aged forest (varied rotation periods) on the example of the management unit "Josip Kozarac". Trends in values, that is, in the receipts and expenditures over time as a consequence of trends in age class areas are also worth studying.

THE OBJECT OF RESEARCH

The research was targeted at the management class of pedunculate oak in the management unit “Josip Kozarac”. The management class consists of pedunculate oak stands in the first quality site class. The total area of the management class is 3,894.29 ha, the total growing stock is 1,327,407 m^3 and the measured annual increment is 30,633 m^3 (8.62 m^3/ha). Compared to the normal age class distribution, there is a surplus of mature understocked stands (the last two age clases) (Table 1)

Table 1. Data of real forest of even-aged stands (Management class of pedunculate oak-Management unit "Josip Kozarac").

	AGE CLASS							Total
	0-20	21-40	41-60	61-80	81-100	101-120	121-140	
	years							
Actual area	341.37	257.63	126.61	327.03	544.4	1398.57	898.68	3894.29
Normal area	556.32	556.32	556.33	556.33	556.33	556.33	556.33	3894.29
Actual growing (m^3)	-	40087	28001	121163	233656	579036	325464	1327407
stock (m^3/ha)	-	156	221	370	429	414	362	341
Norm. growing (m^3)	-	79554	156885	223088	266482	295411	313214	1334634
stock (m^3/ha)	-	143	282	401	479	531	563	343

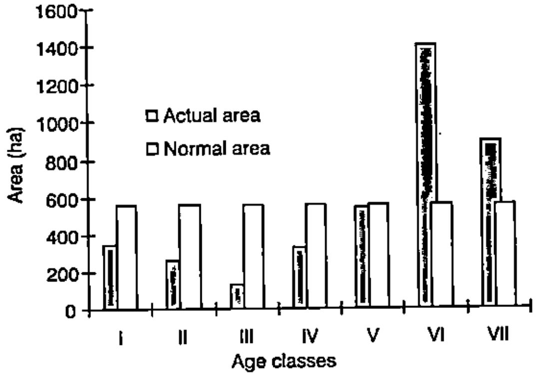

Figure 1. Age class distribution per area

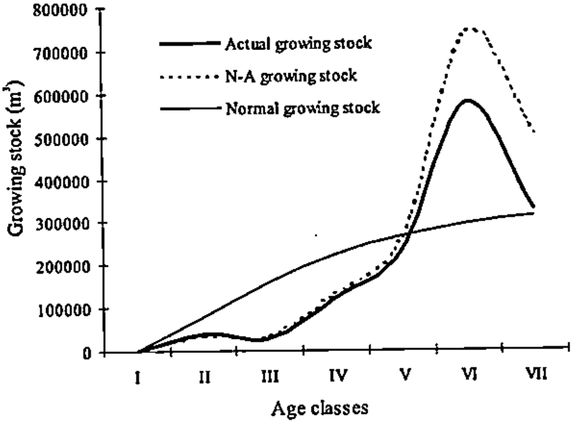

Figure 2. Age class distribution per growing stock

The surveyed and classified data present the initial states in the course of simulation research on the behaviour of the given even-aged forest system.

METHOD OF WORK

As the aim of this paper was to study the value of an even-aged forest as a changeable dynamic system, the research was based on the dynamic processing model of management with an even-aged forest (Čavlović 1995, 1996; Čavlović and Benko 1998). This model gives the condition of an even-aged forest (stand ratio according to age structure) at every point of time with assumed management. Almost every regular forest is characterised by an irregular initial age structure, and the same is true for the forest "Josip Kozarac". Assuming that an even-aged forest is managed regularly, the normal condition will be gradually achieved through qualitative and quantitative changes in the age structure, growing stock and increment of a stand.

The value of a forest is determined on the basis of:

a) estimating the average value per hectare of an individual age class,

b) capitalised value of permanent forest rent of a forest over time.

ESTIMATING THE AVERAGE VALUE OF AN INDIVIDUAL AGE CLASS PER HECTARE

A method of stand cost (Sabadi 1992) to calculate a stand value has proved to be the most adequate for stands of up to 30 years of age. For this reason, the average value per hectare in the first age class has been determined using the cost method for 10-year-old stands, and the value of the second age class has been determined using the same method for a 30-year-old stand.

The evaluation of the average stand value per ha in the I age class is shown in the following example:

Assuming that a 10-year-old stand has no timber yield, the estimated costs of the stand represent its cost value.

If the establishment cost is $c^*=2431.4$ m.u. (monetary units)/ha; cultural improvement cost is $c_{1-20}=347.3$ m.u./ha; annual costs of administration, protection, taxes $v= 22.4$ m.u. /ha; purchase cost of land $r = 131.42$ m.u./ha, with interest $p = 1.75\%$, the total costs of a stand can be calculated:

$$C.V._{10} = 2431.4*1.0175^{10} + \left(347.3*\frac{1.0175^{10}-1}{1.0175-1}*1.0175\right) + \left(22.4*\frac{1.0175^{10}-1}{1.0175-1}\right) +$$

$$+\left(131.42*\frac{1.0175^{10}-1}{1.0175-1}\right) = C.V._{10} = 8382.69 \text{ n.j.}$$

For stands over 30 years of age, the expected value method or the yield value method was applied. The same method was used to estimate the average value of the III, IV, V, ... X age class (average stand age 30, 50, ..., 190 years).

The felling value of expected intermediate standing yields and mature standing yields has been determined for the mentioned stands using yield tables for pedunculate oak in the first site class (Špiranec 1975), the assortment structure table, and unit prices of timber assortments.

The estimate of a 50-year-old stand value is as follows:

Expected stand value = expected discounted receipts-expected discounted expenditures

$$E.V._{50} = \frac{(D_{60} * 1.0175^{80} + D_{70} * 1.0175^{70} + ... + D_{130} * 1.0175^{10} + A140) - ((B_u + V) * (1.0175^{90} - 1))}{1.0175^{90}}$$

$E.V._{50} = 22075.29$ n.j., where:

$D_{60}, D_{70}, \ldots, D_{130}$ – net value of thinnings

A_{140} – value of major harvest cut at rotation age

Bu – income land value

V – capitalised value of annual costs (administration, protection, taxes)

At any moment, the total value of an even-aged forest of pedunculate oak is calculated in the model using the formula:

$$T.V._F = ((a_I * C.V._{10}) + (a_{II} * C.V._{30}) + (a_{III} * E.V._{50}) + ... + (a_N * E.V._{u-10}))$$

where:

$a_I, a_{II}; \ldots a_N$ – the area of the first, second, ..., last age class at a given moment

$C.V._{10}, C.V._{30}, \ldots, E.V._{u-10}$ – average value per ha of the first, second, ... last age class at a given moment

CAPITALISED VALUE OF A PERMANENT FOREST RENT OF A FOREST OVER TIME

The value of a forest is a function that depends on the permanent forest rent that a given forest yields annually at a defined interest rate. The rent depends on the size of the receipts and expenditures in the forest. When only the yields from timber and the improvement costs, costs of administration, protection, and taxes, and purchase cost of land are assumed, it can be said that the forest rent will depend on the age structure of stands in a real even-aged forest at a given moment. When a normal age structure in an even-aged forest is achieved, constant receipts and expenditures can be expected within the forest surrounding.

Since the mentioned model can show trends in age structures over time within a longer period for assumed management with a real even-aged forest, trends in forest rent, that is, forest value over time, can be monitored by inserting the value of wood material and costs into the model.

The establishment (regeneration) costs of stands will depend on the annual surface cut of the main yield, the improvement costs of young stands will depend on the area of the first age class, while the costs of administration and protection, as well as the purchase cost of land for the total forest area, will be more or less constant (assuming that the forest surface does not change).

Starting from these assumptions, the net annual income in the model has been calculated using the formulae:

Year expenditures$=(c^{*}*\text{I.F.})+(c_{1\text{-}20}*a_{I})+(v*a_{T})+(r_{b}*\ a_{T})$

Year receipts$=(a_{II}*D_{30})+(a_{III}*D_{50})+\ldots+(a_{n\text{-}1}*D_{u\text{-}30}))/10)+\ \text{I.F.}*A_{u\text{-}10}$

where:

I.F. - annual surface cut of the main yield (ha/year)

RESEARCH RESULTS

The average value of stands in a given age class under management with rotation periods of 60, 80, 100, ... 200 years has been calculated using the method described above. These values, shown in Table 2, were used as input data in the SD model.

Table 2. Value per hectare of even-aged pedunculate oak stands in first quality site class in relation to the rotations

Rotation	Timberland value of an even-aged stand in age (monetary unit/ha)									
	10	30	50	70	90	110	130	150	170	190 year
60	8590	17115	23585							
80	8882	18169	25716	33935						
100	8740	17657	24680	32157	41004					
120	8543	16946	23243	29692	37084	45808				
140	8383	16369	22075	27689	33901	40953	49018			
160	8271	15964	21258	26287	31671	37554	43963	51029		
180	8180	15640	20601	25160	29879	34821	39900	45083	51147	
200	8122	15428	17196	21549	25976	30505	34999	39355	44250	50701

As was said earlier, the trend in age class distribution with regard to management with 60 to 200-year rotation periods (Figure 3) has a direct impact on the trend of the overall value of the studied forest.

The value of a forest equals the sum values of all stands (age classes) over time. Likewise, the value of a forest represents the capitalised value of the net annual income. The question remains what rate of interest will be applied in the process of capitalisation. The SD model searched for the rate of interest at which the capitalised value of the forest rent would be equal to the value of all stands at the moment the normal age structure is achieved. Figure 4 shows the ratio between the forest rate of interest obtained in this manner and the rotation.

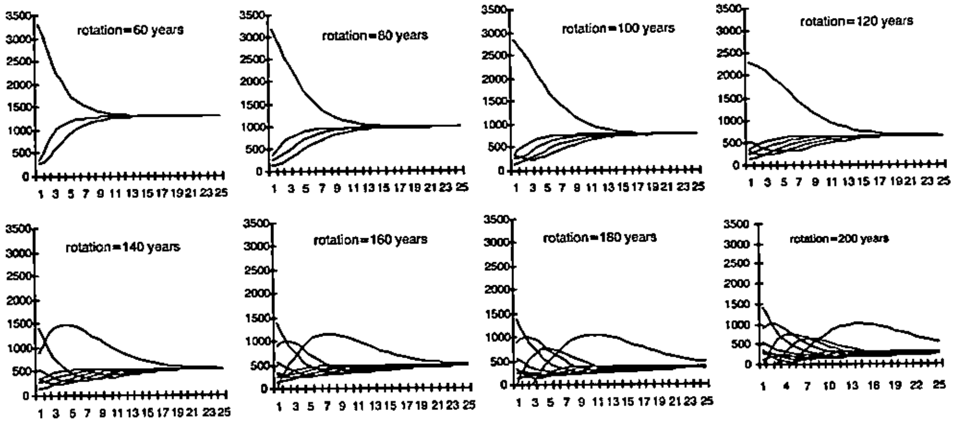

Figure 3. Trends in age class distribution per area under different rotation

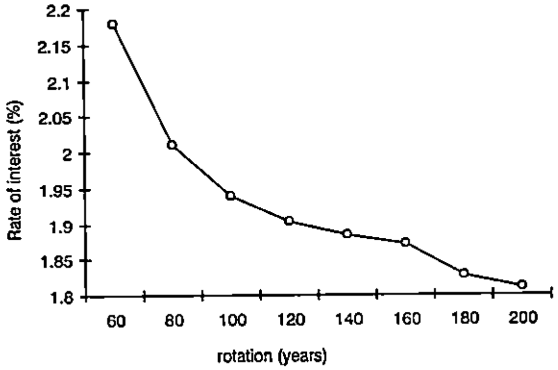

Figure 4. Relationship between the forest rate of interest and rotations

A trend in the value of a pedunculate oak forest as the sum values of all stands (age classes), and as the capitalised value of a permanent forest rent is seen in Figure 5.

Figure 6 shows the total value trends of a forest of even-aged pedunculate oak stands under eight different rotation periods.

With rotation periods of 120 years or less, the value of a forest quickly decreases, so that in the first part of the simulation period it achieves a constant amount at a low level in relation to a 140-year rotation period. The shorter the rotation period, the lower the level is. With a 140-year rotation period normally applied in this forest, the value gradually decreases from the initial 138 million to 111 million monetary units. By prolonging the rotation period to 160 years, the value of the forest is increased by 5-7 million monetary units in relation to a 140-year rotation during the entire simulation period. The timberland value of the forest will decrease if the rotation is prolonged to over 160 years.

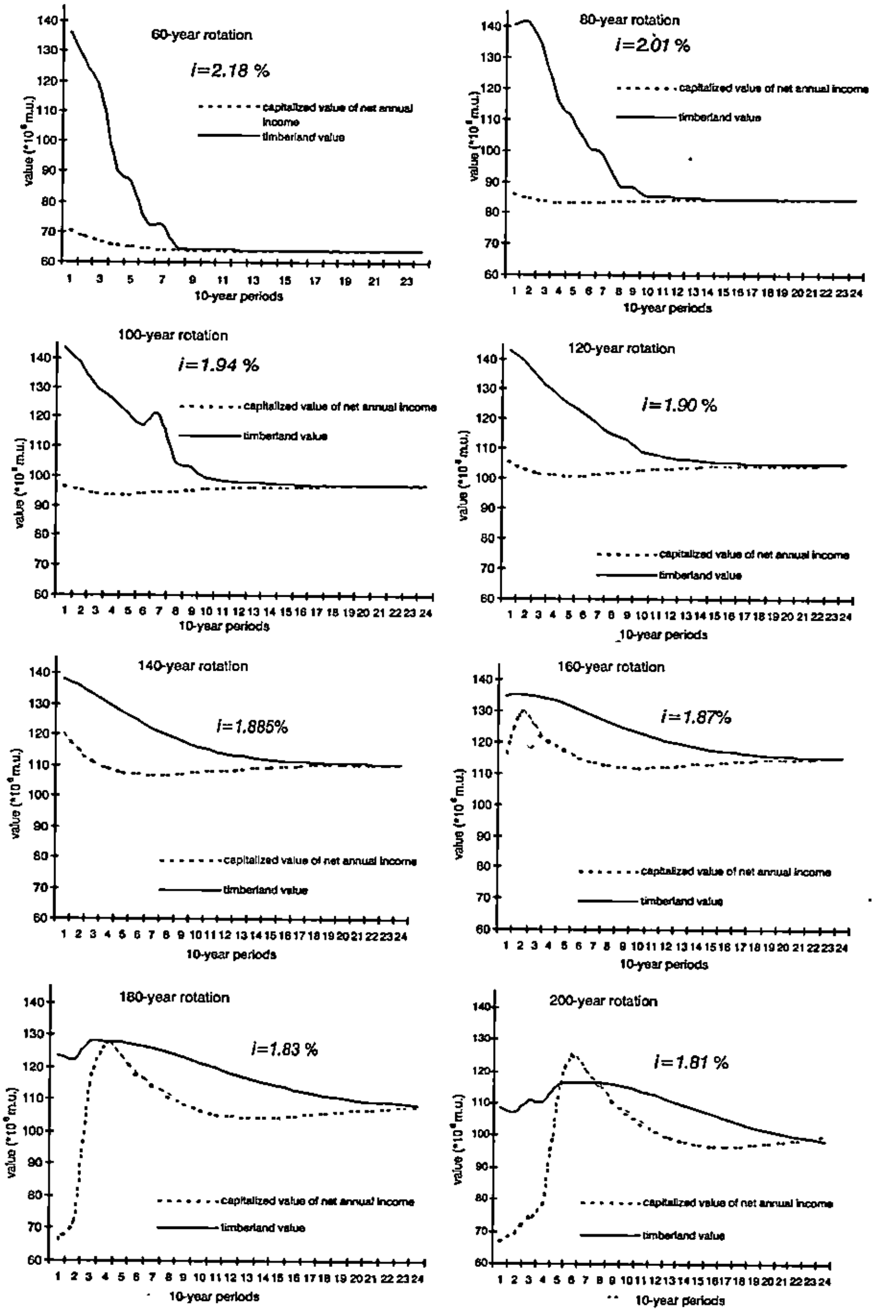

Figure 5. Trends in the values (capitalized v. of net annual income, timberland value) of a pedenculateoak forest under diferent rotations

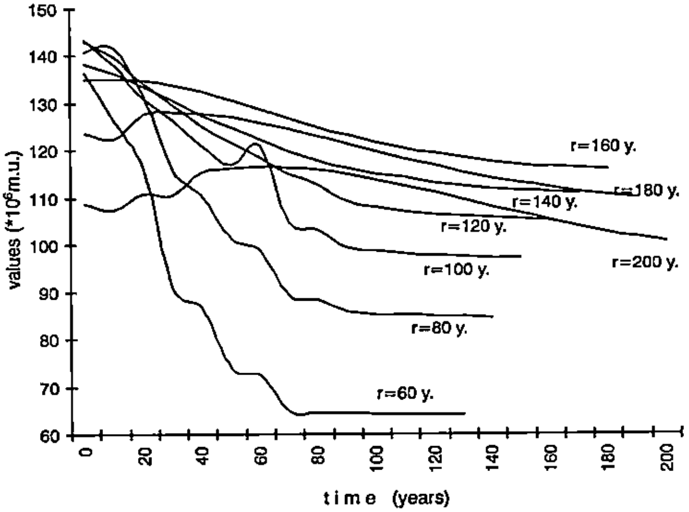

Figure 6. Trends of timberland value under different rotations

CONCLUSION

The value of an economic forest, when only the production of timber is taken into account, is a function that changes over time. One of the important factors affecting the trend in values of an even-aged forest is the trend in age class distribution under management with different rotation periods.

The forest of pedunculate oak in the management unit "Josip Kozarac" has an irregular age structure with a surplus of mature understocked stands.

During a given rotation period, the value of the forest changes (decreases) until it reaches a normal age structure, when it becomes constant. Other factors that might influence the value of the forest and forest land are assumed to be excluded.

The forest rate of interest is obtained by equalising the value of the forest as the sum values of all stands and the capitalised forest rent after the moment the normal age structure has been reached. This rate ranges from 2.18% for the 60-year rotation period to 1.82% for the 200-year rotation period.

Shortening the rotation period to below 140 years (the period used today) would decrease the *timberland value,* while lengthening the rotation period to 160 years would increase the *timberland value* by 5-7 million monetary units (6%). However, further lengthening of the rotation to over 160 years would again lower the *timberland value.*

The next important step involves introducing other forest functions and influential factors into the dynamic model for determining trends in forest and timberland values.

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KRETANJA VRIJEDNOSTI ŠUMA I ŠUMSKOGA TLA U DINAMIČNOM SUSTAVU JEDNODOBNE ŠUME HRASTA LUŽNJAKA U GOSPODARSKOJ JEDINICI "JOSIP KOZARAC"

S obzirom na višestruke funkcije vrijednost šume značajno varira kroz vrijeme i ovisi o velikom broju utjecaja i o raznim odnosima. Neki od najvažnijih čimbenika koji utječu na kretanje vrijednosti šumskoga tla jednodobne šume u njezinoj ekonomskoj funkciji jesu ophodnja i promjene u dobnoj strukturi. Cilj je ovoga rada proučavanje odnosa vrijednosti šume, šumske rente i postotka kamata tijekom vremena kao posljedica promjena u ophodnji i dobnom razredu.

Predmet je izučavanja šuma hrasta lužnjaka u prvom bonitetu ukupne površine 3894,29 ha. Šuma sadrži višak zrelih nedovoljno popunjenih sastojina, a gospodarenje se temelji na ophodnji od 140 godina.

Vrijednost šumskoga zemljišta i sastojina određena je upotrebom prihvaćenih metoda, dok su kretanja u vrijednostima cijele šume i šumskoga tla dobivena pomoću SD modela gospodarenja jednodobnom šumom.

Iz odnosa kretanja vrijednost šume, šumske rente i postotka kamata dobiven je sljedeći rezultat: vrijednost bi se šume hrasta lužnjaka povećala za 5–7 novčanih jedinica (6 %) ako bi se razdoblje ophodnje povećalo sa 140 na 160 godina.

Ključne riječi: hrast lužnjak, vrijednost šumskoga tla, distribucija dobnih razreda, dohodak, troškovi

N.-V. Nicolescu, et al.: Research on establishment and maintenance of network of access racks opened in young sessile-oak stands subject ... Glas. šum. pokuse 37: 95–106, Zagreb, 2000.

UDK 630*243+236.1+686+(498) (Quercus petraea Liebl.)

RESEARCH ON ESTABLISHMENT AND MAINTENANCE OF NETWORK OF ACCESS RACKS OPENED IN YOUNG SESSILE-OAK STANDS SUBJECT TO WEEDINGS AND CLEANINGS

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Sessile oaks (*Quercus petraea*, *Quercus dalechampii*, and *Quercus polycarpa*) are some of the most valuable forest species in Romania, covering about 672,000 ha (10 per cent of national forestland). Usually, they are naturally regenerated by using the group shelterwood system and young stands are pure, extremely dense and impenetrable.

Taking into account some of their main characteristics (e.g., relative intolerance of shade; danger of epicormic branching; quite slow height growth at young ages), the tending models traditionally applied in the Romanian young sessile oak stand before the first commercial thinning include low-moderate intensity weedings and cleanings, and reducing canopy cover to about 80 per cent.

Based on research work started in 1992, a new approach is proposed and includes:

- Opening and maintenance of access racks, 1.0-1.5m wide (seedling stage) up to 1.5-2.5m wide (thicket stage), established at intervals also depending on stages of development (12-15m in seedling stage and 25-40m in thicket stage).
- Weedings and cleanings (low, of negative selection type) of high intensity in very dense stands, non-tended from the very beginning.

Key words: sessile oak, access racks, weedings, cleanings.

INTRODUCTION

In comparison with our continent where, according to Savill and Kanowski (1993), 27 species of oaks are found, in Romania there are only 9 species, as follows: *Quercus petraea*, *Q. dalechampii*, *Q. polycarpa*, *Q. robur*, *Q. cerris*, *Q. frainetto*, *Q. pubescens*, *Q. pedunculiflora*, and *Q. virgiliana*.

At present they cover about 1.128 million ha (18.2 percent of the forestland) and account for about 14 per cent of the standing volume. The three sessile oak species (Q. petraea, Q. dalechampii, and Q. polycarpa, sometimes considered as subspecies of the species Q. petraea), which are the dominant oaks, cover over 672,000 ha (Daia 1998, Stanescu et al. 1997, xxx 1999).

All of them usually inhabit the hills, but their altitudinal range extends between the lower ramifications of the Carpathians (maximum elevation = 800-1,000m above sea level in the Transylvanian Alps but reaching, in small stands or as scattered species, even 1,300m on their northern slopes) and, quite seldom, the southern plain regions. They show their best growth on moist, well-drained and fertile soils, being intolerant of flooding. Sessile oaks do better than pedunculate oak on more acid soils such as acid brown earths but avoid the heavy clay soils (Haralamb 1967, Negulescu and Stanescu 1964, Negulescu and Savulescu 1965, Stanescu 1979, Stanescu et al. 1997).

Differently from other European countries where sessile oak (*Q. petraea*) is especially regenerated by planting (Austria - Hochbichler 1993; Belgium - Bary-Lenger et al. 1988, Boudru 1989, 1992; Hungary - Solymos 1993; Great Britain - Hart 1994, Kerr and Evans 1993, Savill 1991; Ireland - Joyce et al. 1998; Switzerland - Schutz 1993) or by artificial seeding under shelter (Germany - Martinot-Lagarde 1970, Kenk 1993), in Romania it is mostly naturally regenerated. Good seed years occur quite frequently (every 4-6 years) and, owing to its tolerance to shade up to the thicket stage (even being a light-demander, but more tolerant than pedunculate oak), sessile oak is regenerated by using the group shelterwood system, which has been considered in Romania, for a long time, as the most suitable for oak stands. Usually, three to five fellings (preparatory, if necessary, seeding, secondary, and final) are performed and the regeneration period is usually no longer than 10 years (between 5 and 7 years) (Antonesco 1911, Ciumac 1967, Damaceanu 1984, Purcelean and Ciumac 1965).

In general, Romanian sessile oak regenerations are ± pure and uniform, without or with very low proportions of understorey species (beech, hornbeam, lime) or shrubs and its saplings and thickets are very compact, dense, with tall, slender and small-crowned trees. Obviously, as also stated in other European countries (Kenk 1993, Schutz 1993), the late and heavy snowfalls easily curve such trees in an irreversible manner.

Taking into account this reality, as well as other facts (sessile oak, unlike most strong light-demanders, is rather slow growing at young ages; it has a medium ability to natural pruning but is prone to the development of epicormic branches), Romanian literature recommends the application of the following tending interventions before the first thinning:

- *Weedings* (in seedling and sapling stages) - of low-moderate intensity (canopy cover after intervention at least 80 per cent) and 1-3 years rotation.

They aim at eliminating undesired species such as pioneers (goat willow, aspen), also reducing, if necessary, the proportion of understorey species or density of too dense groups of sessile-oak trees.

- *Cleanings* (in thicket stage) - also of low-moderate intensity (the same canopy cover after intervention) and 3-5 years rotation. They focus on eliminating low quality stems of different species and favouring the development of symmetrical and regular crowns of sessile-oak trees. At the same time, cleanings are designed to protect the understorey species and shrubs of extreme importance in the natural pruning of sessile-oak trees as well as in soil protection against invasive herbs or shrubs (Constantinescu 1976, Negulescu and Savulescu 1965, Petrescu 1971, xxx 1956, xxx 1986).

Unfortunately, for different reasons, many Romanian young sessile-oak stands are left untended during the first stages of development (sapling and thicket stage, up to 10-15 years of age). In such circumstances, during the first interventions, two very unpleasant problems are encountered:

Very high stand densities that make access into the young stands almost impossible;

The problem of stem curvature, which affects the majority of too dense groups of trees.

Taking into account these facts, the paper focuses on two aspects:

1. The opening and maintenance of a network of access racks (tending trails). Such racks were first used in Romania in Norway spruce (1957-1965) and mixed broadleaved stands of Dobrudja (1962-1967) (Papadopol et al. 1965, Petrescu et al. 1967, Petrescu 1968, Petrescu and Dragomir 1969, all in Daia 1998), even before the publication of the well-known *Le cloisonnement* of CERAFER in 1971.

Since then, almost nothing has happened in the field and only at the beginning of the 1990s was the first introduction to the practical application of this system in France published in Romania (Nicolescu et al. 1992).

2. The silvicultural interventions to be carried out in previously untended stands before the first commercial thinning.

MATERIALS AND METHODS

Fieldwork was carried out in the south east of the Getic Hills (Hulubesti Forest District, IV Rincaciov Working unit, sub-compartment 71E, surface area 6.7 ha). The local climate is, according to Koppen's climatic classification, of the D.f.b.x type, with average annual temperature of 9.9°C and average annual rainfall of 688mm (de Martonne index = 35).

The main characteristics of the sub-compartment are as follows:

Site: elevation = 290m; gentle slope ($< 10^0$); Soil: brown podzol, with mull flora. Potential fertility: high for pure sessile-oak stands.

Stand (data in 1996): Species composition = 100 per cent sessile oak; mean age = 15 (between 10 and 20) years, owing to the application of group shelterwood system. Mean dbh = 4 cm, mean height = 6 m. Canopy closure = 100 percent (but many stems are curved, owing to late heavy snowfalls in previous years). Production objective = sawlog timber (dbh = at least 48cm); rotation = 130 years. Interventions proposed: beating up (the gaps where canopy is still open), weedings and cleanings.

In 1996, a large network of parallel access racks (16 trails, amounting to 2.495m), 1.0, 1.5, 2.0, and 2.5m wide, at 12, 22, 32 and 42m intervals between axes was opened using topographic devices and portable chainsaws. After opening the network, eight plots of different sizes (but especially 100sq.m. large) were established, half of them being subject to silvicultural interventions (weedings or cleanings, depending on development stage), the other half being left untended. In all plots a complete inventory was performed, a sufficient number of individual tree heights also being measured in each plot. After the inventory, trees to be removed were marked, ground cut and stacked along the trails.

No maintenance intervention has been carried out along the access network since their opening in 1996 and the second inventory took place in the same plots in 1999, being combined with the evaluation of the density and measurement of the height of all stump shoots developed within some of the racks of various widths. At the same time, after inventorying the initial and final trees, cleanings were performed in the additional plot no. 5. Here, owing to the obvious differentiation of trees in terms of social status and quality, some potential final crop trees were also chosen.

RESULTS AND DISCUSSION

OPENING AND MAINTENANCE OF NETWORK OF ACCESS RACKS

To assess the overall efficiency of the network of access racks, some aspects (cost of their opening and maintenance; time consumed for the transport of cut trees to the racks; duration of canopy closure and, in connection, the duration of the maintenance of the access) were taken into consideration.

According to this assessment, in the seedling stage, the best results are provided by racks 1.0-1.5 m wide, at 12-15m intervals, whereas in the thicket stage, racks of 1.5-2.0m at 25-30m intervals, or 1.5-2.5m wide, at 25-40m intervals, are the best solution. In comparison with other recommendations (Bary-Lenger and Nebout 1993, Buffet 1978 and 1980, Dubois 1988, Duplat 1992, Jarret et al. 1996, Lafouge 1990, Lanier 1986 and 1988), the proposed racks are similar in terms of width (1-2m) but more spaced (most frequent value of intervals in French sessile-oak stands = 6m).

Racks are best opened in the seedling stage whenever in the year (but avoiding the beginning of a new growing season, when edge trees are easily wounded during the extraction of felled trees). In thicket-stage stands, racks are best opened in autumn, due to the better illumination and visibility within the stand after the leaf fall.

When they are narrower than 1.5m, the canopy (above racks) closes after 1-2 years, this period being prolonged up to 2-3 years when racks are 1.5-2.0 m wide or even 3.5 years when their width reaches 2.5m. This means that the duration of maintenance works is more or less equal to that necessary for canopy closure and extends no longer than 3 years.

At the same time, the density and height of the stump shoots developed within the racks are positively correlated with the width of the racks. If shoot density is considered as 100% in 2.5m wide racks it reduces down to 56% in 2.0m wide racks and only 33% in 1.5m wide racks. In terms of shoot height, if this is 100% in 2.5 m wide racks, it represents 72% in 2.0m wide racks and only 62% in 1.5m wide racks. Height is more homogenous in wider racks and varies between 80 and 160cm in 2.5m wide racks, 40 and 120 cm in 2.0m wide racks and between 30 and 110 cm in 1.5m wide racks.

SILVICULTURAL INTERVENTIONS CARRIED OUT IN PREVIOUSLY UNTENDED STANDS

As previously stated, weedings and cleanings were performed in four different-sized plots (P1, 2, 3, and 4) in 1996 and one plot (P5) in 1999. The results of the two inventories carried out in some of the above plots in 1996 (before (b) and after (a) intervention) and 1999, as well as in plot P2 (left untended), are shown in Table 1.

Table 1. Main characteristics of some plots in 1996 and 1999

Plot no.	Species composition (%)			Number of trees per hectare			Basal area (sq.m ha-1)			Sessile oak dbh. (cm)		
	1996 (b)	1996 (a)	1999	1996 (b)	1996 (a)	1999	1996 (b)	1996 (a)	1999	1996 (b)	1996 (a)	1999
P2	90SO10OS	84SO16OS	83SO17OS	15400	4900	4700	21.2	10.4	13.1	5.00	5.84	7.30
P2a	95SO5OS	-	92SO8OS	16500	-	15600	15.0	-	14.4	4.29	-	5.88
P3	98SO2OS	97SO3OS	95SO5OS	12800	4100	4100	15.2	8.8	13.6	4.81	5.50	7.03
P4	94SO6OS	96SO4OS	100SO	12400	5300	4900	14.0	9.6	14.2	4.87	5.19	7.60

Legend: SO = sessile oak; OS = other broadleaved species (e.g., beech, hornbeam, wild cherry, field maple, Norway maple, aspen, goat willow)

As shown in Table 1, stand 71E was extremely dense, its initial density being in all plots higher than 15,000 stems per hectare (in plot 1, which is not included in the above-mentioned table, initial stand density was even higher, reaching 22,300 stems per hectare).

Compared with the Romanian production tables for the same species composition, production class (II) and age (15 years), where stand density is only 5,000 stems ha^{-1} (Giurgiu et al. 1972), the initial density in all plots is at least double. In such conditions, trees were very tall, with high-value slenderness indices (h/d), as shown in Figure 1 (trees individually measured (heights and diameters) and extracted from plot no. 5 in 1999).

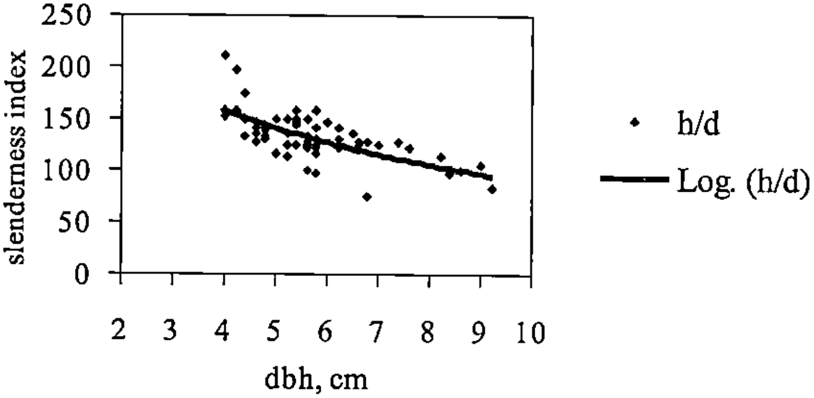

Figure 1. Distribution of slenderness index by dbh classes in plot 5

Even this trend is a normal one, and the individual values (the majority of them higher than 100 and reaching in the case of many trees more than 150) are extremely high and show the susceptibility of such a stand to late and heavy snowfalls as already happened in the recent past.

At the same time, owing to the same reason (non-execution of silvicultural interventions in the early stages), the initial basal area in all plots (between 14.0 and 21.2 sq.m ha^{-1}) is higher than the target value from the production tables (12.0 sq.m ha^{-1}).

In such circumstances, cleanings performed in plots nos. 1-4 in 1996 had a much higher intensity than the Romanian guidelines (low-moderate, up to 15 per cent of number of trees) for similar stands reaching a very high intensity level (over 55 per cent per number of trees and over 30 per cent per basal area) as shown in Table 2.

Table 2. Intensity of weedings and cleanings performed in plots no. 1-4

Plot	Intensity of interventions (%)	
	per number of trees	per basal area
P1	60.5	33.1
P2	68.2	50.9
P3	68.1	42.1
P4	57.3	31.4

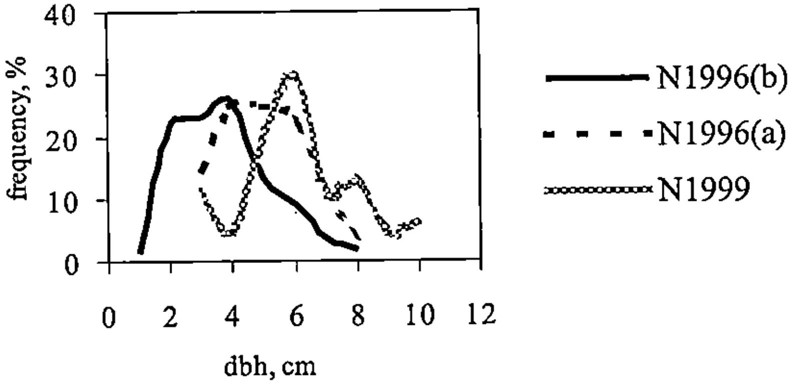

Figure 2. Distribution of trees by dbh classes in plot 2

But, since starting with very high stand densities, the remaining densities, as well as basal areas, were quite high and approached those recommended by the production tables or other Romanian papers dealing with young sessile oak silviculture (Ciumac 1975, Nitescu and Achimescu 1979).

According to Table 1 and Figure 2, owing to the presence of many low-diameter, intermediate and suppressed trees, cleanings were of the negative selection type (removal of the low quality and inferior Kraft class trees of different species).

They had a low effect on mean dbh after intervention, which had increased quite slowly but differently in all plots. After three years, the effect of cleaning was obvious and the mean dbh had increased consistently and reached in some of the plots over 7cm. But, even the majority of trees, despite their dbh, had grown at least 1cm between 1996 and 1999, the tallest (predominant and dominant) trees, especially those with dbhs over 7cm in 1996, showing the most significant diameter growth. Considering this fact as well as the trend of diameter growth of trees in

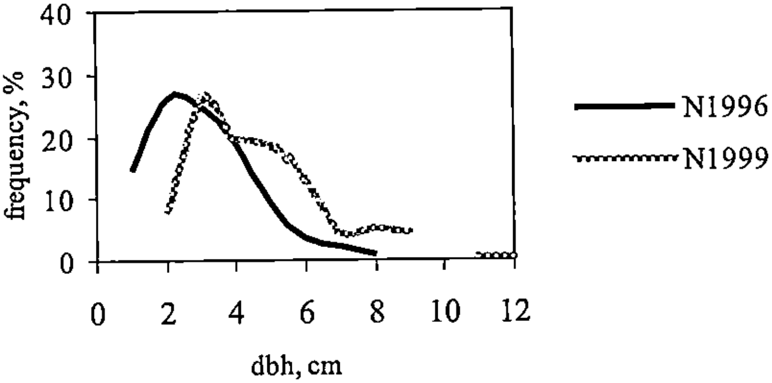

Figure 3. Distribution of trees by dbh classes in plot 2a

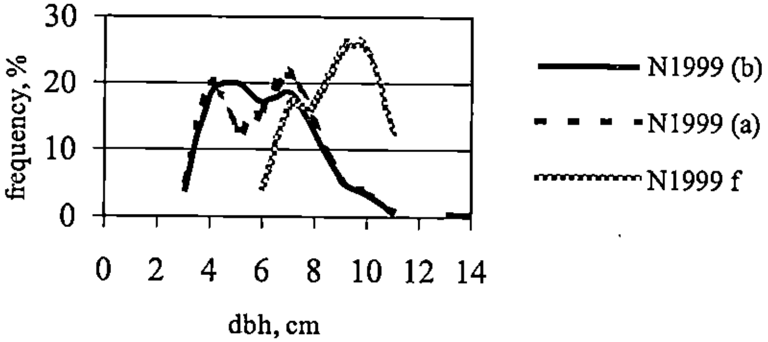

Figure 4. Distribution of trees by dbh classes in plot 5

untended plot 2a (Figure 3), we suppose that the diameter growth of young sessile-oak trees up to this stage is more dependent on site and genetic potential rather than on stocking and tending interventions. Of course, such a conclusion is a provisional one, due to the short period of research and the quite low number of plots and trees used.

After three years, despite the high intensity of low cleanings, affecting only the lower storey, sessile-oak trees in plot nos. 1-4 do not show any special problems with epicormic branches, while the stem curvatures of trees affected by heavy snowfalls prior to 1996 and left in the stand after intervention have not recovered yet. We suppose that such trees will not recover in the future and the curved trees will be gradually removed during the following interventions.

In plot no. 5, intermediate cleanings of much lower intensity (25.2 per cent per number of trees and 22.1 per cent per basal area) were performed in 1999, initial (b) and final (a) mean dbh being 7.01cm and 7.27cm respectively. After the intervention, about 500 "candidate" final crop trees per hectare were chosen (Figure 4).

As shown in the figure, these trees (N1999 f) are the largest (predominant and dominant) trees, as evenly spaced as possible, with regular and large crowns (but without being included in the *wolf* category) and slenderness indices around 100. The early choice (positive selection) of such candidates, as already recommended by Boudru 1989, Kenk 1993, Lanier 1986, Petrescu 1971, is possible and advisable for the following interventions owing to the early and obvious social differentiation of sessile-oak trees as already stated by Leibundgut (1945, 1976, in Schutz and Badoux 1979).

CONCLUSIONS AND RECOMMENDATIONS

Our paper focused on some aspects related to the opening and maintenance of a network of access racks, as well as on silvicultural interventions applied to non-treated young sessile-oak stands.

Taking into account the first aspect, it is obvious that, although expensive and time-consuming, the opening and maintaining of such a network is beneficial from all viewpoints (it provides a better access into the stand, can be used for the extraction of felled timber and the surveillance of workers, for hunting activities etc). If opened at early stages, racks do not reduce significantly the production surface of the stands. They account for only 6-8 per cent of the surface area when 1.5-2.5m wide in both sapling and thicket stage and reach a maximum of 12 per cent of the same area when 1.0-1.5m wide racks are opened in the sapling stage. Indeed, in the long-term, no production surface is lost if we take into account the initial (tens of thousands of trees per hectare) and final (hundreds of trees per hectare) stocking of the stand. In addition, if the racks are narrow enough and opened at early stages, trees along the racks do not bend and few epicormic branches develop.

Regarding the silvicultural interventions, it is also quite obvious that high intensity interventions in previously non-tended stands are possible. When done properly, they remove only low quality and dead and dying small trees from the lower storey, as well as some co-dominant and wolf trees. The increase of average quality stems after intervention is quite spectacular, the obvious differentiation of predominant and dominant high-quality stems making possible and advisable the early selection of "candidate" final crop trees even at early ages, just before the beginning of the pole stage.

In such stands located in the ecological optimum of the sessile oak natural range, understorey species such as beech, hornbeam or linden are missing or are very rare. Unfortunately, nothing can be done at this early stage, except for their promotion where they already exist. Later introduction by planting under the shelter of these species in our pure sessile-oak stands, even though sometimes advised in Romania (Negulescu and Savulescu 1965) or abroad (Duplat 1992, Joyce et al. 1998, Schutz and Badoux 1979), has never been used and, for economic reasons especially, it is not going to be proposed and applied on a large scale in the future.

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ISTRAŽIVANJE NAČINA POSTAVLJANJA I ODRŽAVANJA MREŽE ŠLJUKARICA U MLADIM SASTOJINAMA HRASTA KITNJAKA U KOJIMA SE PROVODI ČIŠĆENJE KOROVA I NJEGA MLADIKA

Hrast kitnjak (*Quercus petraea*, *Quercus dalechámpii* i *Quercus polycarpa*) pripada među najvrednije šumske vrste u Rumunjskoj. Rasprostire se na približno 672 000 ha (10 posto nacionalne šumske površine). Šume se obično obnavljaju prirodnim putem grupimičnom sječom, a mlade se sastojine čiste jer su izrazito guste i neprohodne.

Uzevši u obzir neka od najvažnijih kitnjakovih obilježja (npr. slabo podnošenje zasjene, opasnost od epikormusnoga grananja, prilično polagan visinski rast u mladoj dobi), modeli njege koji se tradicionalno upotrebljavaju u rumunjskim mladim hrastovim sastojinama prije prve komercijalne prorede obuhvaćaju slabo do umjereno čišćenje od korova, čime se sklop smanjuje na oko 80 posto.

Na temelju istraživanja, koje je započelo 1992. godine, predlaže se nov pristup koji obuhvaća:

– otvaranje i održavanje šljukarica, širine 1,0 – 1,5 m (stadij mladika) do 1,5 – 2,5 m (stadij koljika), koje se postavljaju u razmacima ovisno o razvojnim stadijima (12 – 15 m u stadiju mladika i 25 – 40 m u stadiju koljika)

– čišćenje i njega (niskoga intenziteta, negativnoga selekcijskoga tipa) visokoga intenziteta u vrlo gustim sastojinama, koje su od početka nenjegovane.

Ključne riječi: hrast kitnjak, šljukarice, čišćenje, njega

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UDK 630*232+561+(438) (Quercus robur L., Q. petraea Liebl.)

INITIAL SPACING AND MORPHOLOGY OF OAK TREES (*QUERCUS ROBUR* L. AND *QUERCUS PETRAEA* /Matt./ Liebl.) IN UNTENDED OAK SAPLINGS AT THE AGE OF 17 YEARS

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The influence of the initial spacing on the morphology of trees of common oak and sessile oak (*Quercus robur* L. – 1.5 x 0.4; 1.2 x 0.8; 1.0 x 1.0; 1.5 x 0.8; 1.2 x 1.3; 1.5 x 1.5; 2.0 x 2.0 and *Quercus petraea* (Matt.) Liebl. – 1.5 x 0.4; 1.2 x 1.3; 1.5 x 1.5) was investigated in oak saplings at the age of 17 years. The experimental plot is located in the south-western part of Poland. The following characteristics were measured: the total tree height, breast height diameter (DBH), the height of the dead-branch zone, the length and the width of the crown, the number and diameter of branches up to a height of 2 m. The biosocial position of trees was also taken into consideration.

The gathered data were subjected to a typical analysis of variance. The linear correlation with the initial growing place was estimated and the structures of the examined features were compared by using the Kolmogorov-Smirnov test.

A distinct relationship with initial spacing was ascertained only for DBH and for the maximum diameter of branches. The influence of the initial spacing on the remaining characteristics was less significant or negligible. The morphology of oaks from the dominant stand (I, II and III Kraft's classes) was characterised by stronger dependence on the initial spacing than the morphology of trees from the dominated stand.

Qualitative features indicate that the initial growing place of oak cultures should not be greater than 1.5 m^2.

Key words: Poland, oak, spacing, trees morphology

INTRODUCTION

The initial spacing of young stands (initial density) is very significant for the process of self-thinning and self-pruning in the juvenile stage of the stand. It also affects the quantitative and qualitative features of trees, their morphology and anatomy. Knowledge of the influence of the initial spacing on the growth of trees in the juvenile stage is useful for the creation of tending models which allow for the control of the diameter increment or for the self-pruning of trees (Spiecker 1991, Nutto 1999).

The influence of the initial spacing is significant for the tree species where the quality of wood is especially important. Such species are, among others, common oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). The importance of the initial spacing results from the high costs of the establishment and tending of such stands (Ceitel 1995).

A large variety of forest culture types is known as far as artificial reviving is concerned (Krahl-Urban 1959, Szymański 1966, 1983). The most popular culture is planting "in rows" using different sizes of plants.

Nowadays in Central Europe (Czech Republic, Slovakia, Germany, Poland) the initial density for oak stands (*Q. robur* and *Q. petraea*) generally amounts to a quantity of 5 up to 15 thousand plants per hectare with a distance of 1.5 to 2.0 m between rows (Otto, 1985, Spellmann et al. 1988, Ceitel 1995). On account of the qualitative features of trees, the threshold distance between rows is 3 m (Nutto 1999). Only in some methods of the establishment of oak stands may the density be lower (Renner et al. 1988, Anonim 1991, Hochbichler et al 1990) or higher (Fleder 1981).

The initial density for both oak species in Poland varies from 6 to 12 thousand plants per hectare and the maximum distance between rows is 1.5 m (Ceitel 1995).

Most recommendations concerning the choice of density and initial spacing in Europe derive mainly from practice (Kramer 1960, Spellmann et al. 1988). The first experiments from our part of Europe date from the 70s and from the beginning of the 80s and were located mostly in Germany for sessile oak (Spellmann et al. 1988, Struck et al. 1998, Schmaltz et al. 1997, Gaul et al. 1996). The experiment presented in this paper concerns the initial spacing of common and sessile oak in Poland at comes from the same period (Ceitel et al. 1984).

The influence of the initial spacing on some morphological characteristics of trees, regarding their biosocial position in untended oak saplings, is presented.

MATERIALS AND METHODS

Data were collected from the experimental plot established in the experimental forests of the Faculty of Forestry of the Agricultural University in Poznań (Experimental Forest District Siemianice, forest compartment 25 h). The altitude of the plot is 190 m. The annual average temperature is about 8 °C and during the vegetation season it is 15.5 °C. The annual average precipitation is 601 mm (334 mm for the average temperature of the vegetation period). Soils are described as postagricultural brown soils and the forest site was described as fresh mixed broadleaved forest with some fragments of fresh mixed coniferous forest (in accordance with the Polish classification).

The experimental plot was established on the surface after clear-cutting (after removal of the pine stand and full cultivation) in three replications using 2-year-old oak plants of local provenance. 7 different spacings were applied for common oak: 1.5 x 0.4; 1.2 x 0.8; 1.0 x 1.0; 1.5 x 0.8; 1.2 x 1.3; 1.5 x 1.5 and 2.0 x 2.0 and 4 spacings for sessile oak: 1.5 x 0.4; 1.2 x 1.3; 1.5 x 1.5 and 2.0 x 2.0 - differentiating density from 2500 to 16666 plants per hectare. No tending operations were carried out on that experimental plot, except for the removal of pine self-sowing. The survival of oaks and the age of stand closure are presented in Table 1.

Table 1. The survival (%) and the age of stand closure of oaks depending on the initial spacing

Spacing m x m	Number of plants per hectare	Age of crown closure	Survival at the age of 17
	Quercus robur		
1.5 x 0.4	16600	13 (15)	86.1
1.2 x 0.8	10400	11 (13)	66.7
1.0 x 1.0	10000	10 (12)	80.0
1.5 x 0.8	8300	12 (14)	84.2
1.2 x 1.3	6400	11 (13)	80.7
1.5 x 1.5	4400	11 (13)	75.5
2.0 x 2.0	2500	13 (15)	82.0
	Quercus petraea		
1.5 x 0.4	16600	14 (16)	80.9
1.2 x 1.3	6400	11 (13)	59.4
1.5 x 1.5	4400	13 (15)	75.5

Explanation: 13 (15) - age of forest culture (real age of tree)

Data were collected from 10 m x 10 m sample plots situated at the centre of each replication. The following morphological characteristics were taken into consideration: the total tree height (H), breast height diameter (DBH - $D_{1,3}$), the height of the dead-branches zone (H_d), the width of the crowns (W_c) - along and across the crowns, the number (N_b) and diameter of branches up to a height of 2 m. - in this paper only the maximum branch diameter (d_{max}) is presented. The length of the crowns (L_c) results from the difference between total tree height and the height of the crown base. The biosocial position of each tree according to Kraft's classification was estimated.

On account of the different numbers of initial spacings, the experiment was treated as two separate trials in a randomised complete block design - separate for common oak and sessile oak. Large differences in survival made us resign some replications or even spacings (in the case of sessile oak) during statistical elaboration.

This is why the analysis of variance for common oak was done for a completely random design, and for sessile oak for a completely randomised block design. Due to a large variety of analysed characteristics (high V value), the conclusions were based additionally on the linear correlation of mean values with the initial growing place and on a comparison of the structures of the investigated features by using the Kolmogarov-Smirnov test (λ).

RESULTS

BIOSOCIAL STRUCTURE OF SAPLINGS

The biosocial structure of untended oak saplings (common oak and sessile oak) at the age of 17 years, stated according to Kraft's classification, is diversified. It does not show dependence on the initial spacing (Fig. 1). The culmination of tree share occurs in different Kraft classes. The share of the dominant stand (I - III Kraft's classes) and lower story (IV and V Kraft's classes) is similar at all investigated spacings in the case of common oak and is ca. 50%. In the case of sessile oak, the share of the lower story is slightly higher.

THE HEIGHT AND DIAMETER OF OAKS

The height of both species is differentiated. The mean values show some dependence on the spacing. The highest trees are at the loosest densities and the

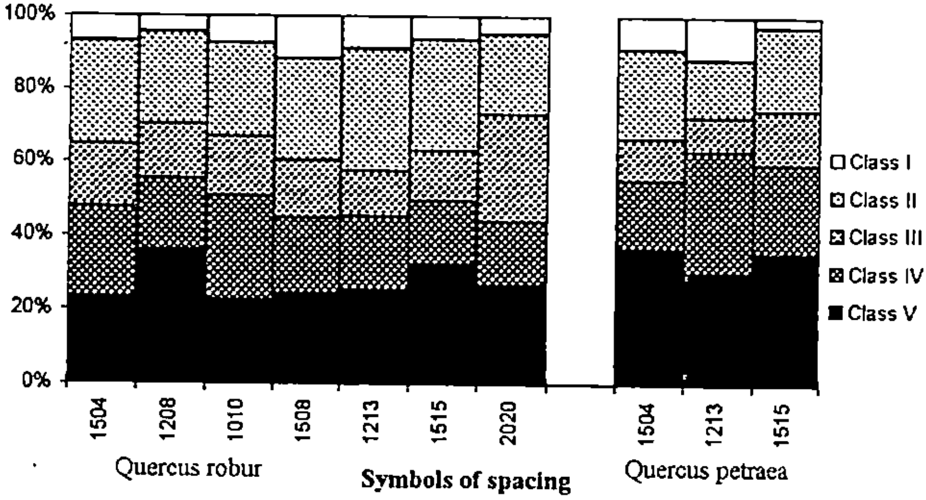

Fig. 1. Biosocial structure (Kraft's classes) of the oak atands at the age of 17-years depending on the initial spacing

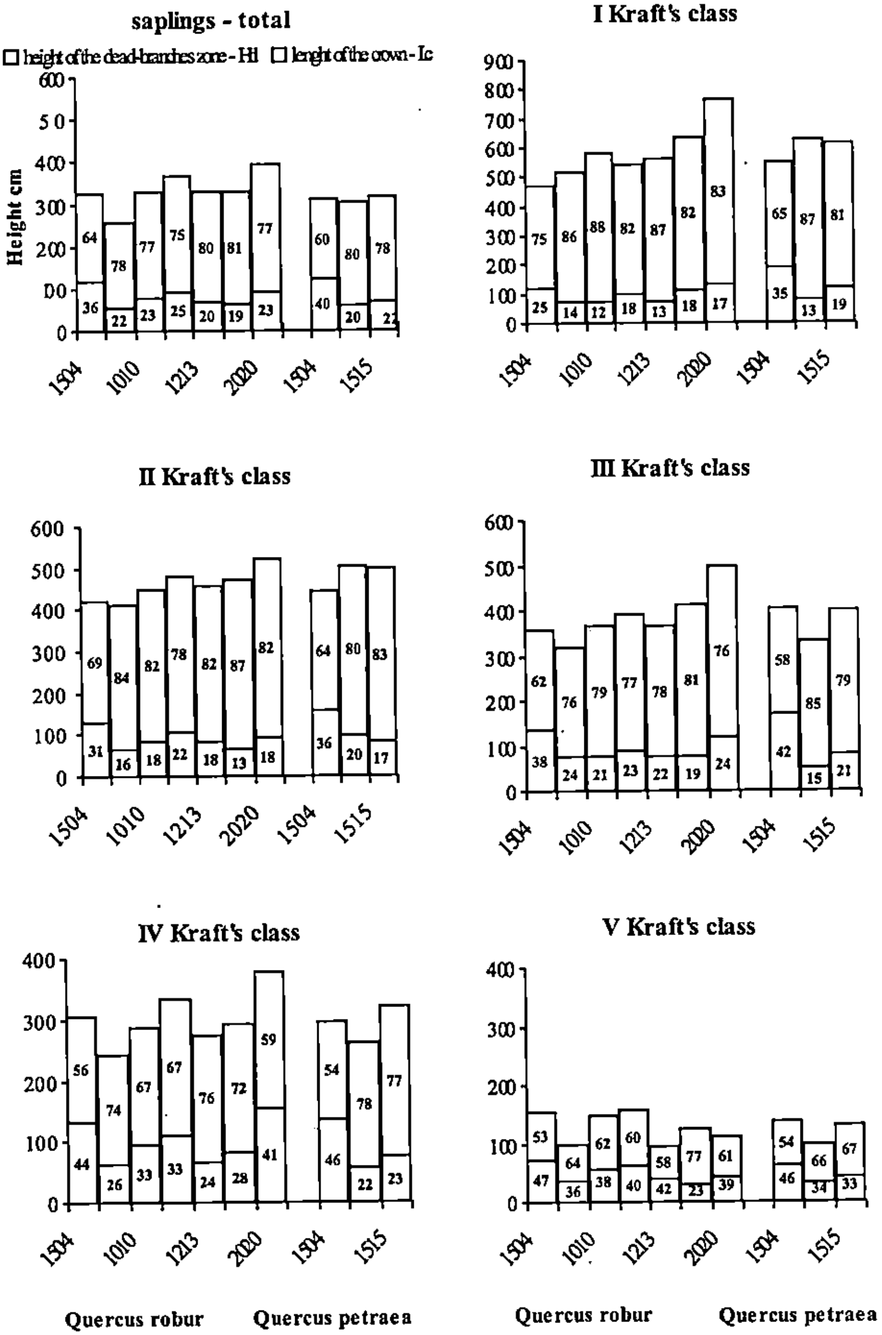
saplings - total
☐ height of the dead-branches zone - Hl ☐ lenght of the crown - lc
Height cm
600
5 0
400
300
200
DO
0
64 36
78 22
77 23
75 25
80 20
81 19
77 23
60 40
80 20
78 2
1504
1010
1213
2020
1504
1515
I Kraft's class
900
800
700
600
500
400
300
200
100
0
75 25
86 14
88 12
82 18
87 13
82 18
83 17
65 35
87 13
81 19
1504
1010
1213
2020
1504
1515
II Kraft's class
600
500
400
300
200
100
0
69 31
84 16
82 18
78 22
82 18
87 13
82 18
64 36
80 20
83 17
1504
1010
1213
2020
1504
1515
III Kraft's class
600
500
400
300
200
100
0
62 38
76 24
79 21
77 23
78 22
81 19
76 24
58 42
85 15
79 21
1504
1010
1213
2020
1504
1515
IV Kraft's class
400
300
200
100
0
56 44
74 26
67 33
67 33
76 24
72 28
59 41
54 46
78 22
77 23
1504
1010
1213
2020
1504
1515
V Kraft's class
400
300
200
100
0
53 47
64 36
62 38
60 40
58 42
77 23
61 39
54 46
66 34
67 33
1504
1010
1213
2020
1504
1515
Quercus robur
Quercus petraea
Quercus robur
Quercus petraea

Fig. 2.

Table 2. Results of the analysis of variance (value of probability P) for the different morphological characteristics of oaks depending on the initial spacing

Morphological features	Kraft's class					Total
	I	II	III	IV	V	I -V
			Quercus robur			
H	0.7769	0.6130	0.7470	0.6223	0.8575	0.8004
$D_{1,3}$	0.0640	0.0346^{x}	0.0007^{xx}	0.0156^{x}	0.3790	0.0177^{x}
L_c	-	-	-	-	-	0.7031
W_c						0.1414
H_d	0.2371	0.0604	0.3138	0.4419	0.6376	0.2165
N_b	-	-	-	-	-	0.6551
d_{max}	0.2933	0.0246^{x}	0.0015^{xx}	0.0755	0.9934	0.0013^{xx}
			Quercus petraea			
H	0.0909	0.0618	0.2321	0.8597	0.5271	0.9931
$D_{1,3}$	0.5305	0.8351	0.9143	0.8294	0.9368	0.4785
L_c	-	-	-	-	-	0.3244
W_c	-	-	-	-	-	0.1350
H_d	0.3227	0.4758	0.4654	0.4967	0.4909	0.4879
N_b	-	-	-	-	-	0.5705
d_{max}	0.0175^{x}	0.0472^{x}	0.1005	0.1915	-	0.1118

smallest ones are at the highest densities (Fig. 2). Detailed structures of this characteristic indicate considerably large variability (from 50 to 650(750) cm) in saplings (total) and in Kraft's classes.

The performed analysis of variance (Table 2) did not prove significant influence of the initial spacing on this characteristic. The linear correlation of mean tree height with initial growing place (Table 3) proved that the height of predominating (I Kraft's class), dominating (II Kraft's class) and codominant (III Kraft's class) trees increases with a loosening of the spacing in the case of common oak and that the relationship is strong (minimum $\alpha = 0.05$). The correlation in the case of sessile oak has not been proved. The comparison of height structures in saplings (total) of both species using the Kolmogorov-Smirnov test shows that there are three groups of spacings for common oak: 1)1.2 x 0.8; 2) 2.0 x 2.0; and 3) remaining spacings. In the case of sessile oak, only one group is presented. The lack of dependence of the height of trees on the initial spacing was proved.

The breast height diameter (DBH) of oaks varies between 5-125 mm depending on the spacing and species. The average values point to the influence of the initial spacing and biosocial position on this feature (Table 4). This influence is more distinct in the case of common oak and it was proved by analysis of variance (Table 2). A distinct lack of influence of spacing on the DBH was observed only for the common oak and trees from V Kraft's class (Table 2). The application of Duncan's test allowed groups of similar average values to be distinguished (Table 4).

Table 3. Values of the linear correlation index for different morphological characteristics of oaks depending on the initial spacing

Morphological features	Kraft's class					Total I -V
	I	II	III	IV	V	
Quercus robur						
H	0.967^{xxx}	0.869^{x}	0.931^{xx}	0.683^{ns}	0.371^{ns}	0.646^{ns}
$D_{1,3}$	0.948^{xx}	0.984^{xxx}	0.993^{xxx}	0.803^{x}	0.886^{xx}	0.978^{xxx}
L_c	0.891^{xx}	0.834^{x}	0.904^{xx}	0.645^{ns}	-0.165^{ns}	0.786^{x}
W_c	0.789^{x}	0.952^{xxx}	0.984^{xxx}	0.869^{x}	0.104^{ns}	0.936^{xx}
H_d	-0.009^{ns}	-0.630^{ns}	-0.109^{ns}	-0.118^{ns}	-0.552^{ns}	-0.345^{ns}
N_b	-0.718^{ns}	0.141^{ns}	0.064^{ns}	0.402^{ns}	0.105^{ns}	0.290^{ns}
d_{max}	0.388^{ns}	0.919^{xx}	0.971^{xxx}	0.945^{xx}	0.306^{ns}	0.968^{xxx}
Quercus petraea						
H	0.810^{ns}	0.864^{ns}	-0.149^{ns}	0.343^{ns}	-0.221^{ns}	0.277^{ns}
$D_{1,3}$	0.755^{ns}	0.810^{ns}	0.767^{ns}	0.981^{ns}	0.281^{ns}	0.768^{ns}
L_c	0.761^{ns}	0.935^{ns}	0.999^{x}	0.996^{ns}	0.491^{ns}	0.939^{ns}
W_c	0.952^{ns}	0.774^{ns}	0.998^{x}	0.980^{ns}	0.657^{ns}	0.869^{ns}
H_d	-0.755^{ns}	-0.957^{ns}	-0.785^{ns}	-0.836^{ns}	-0.750^{ns}	-0.870^{ns}
N_b	-0.895^{ns}	0.309^{ns}	0.284^{ns}	0.721^{ns}	-	0.773^{ns}
d_{max}	0.977^{ns}	0.555^{ns}	0.976^{ns}	0.939^{ns}	-	0.646^{ns}

Table 4. Average breast height diameter (DBH - mm) of oaks depending on the initial spacing and biosocial position

Spacing	Kraft's class					Total I-V
m x m	I	II	III	IV	V	
Quercus robur						
1.5 x 0.4	42.3	34.7 A	25.3 A	18.7 A	8.5	25.0 A
1.2 x 0.8	58.3	42.2 AB	27.9 A	17.0 A	6.9	28.2 A
1.0 x 1.0	67.2	45.6 AB	28.1 A	18.9 A	10.1	30.6 AB
1.5 x 0.8	60.6	44.5 AB	31.9 AB	22.2 AB	10.4	33.5 AB
1.2 x 1.3	63.6	49.0 AB	31.3 AB	18.9 A	7.3	36.5 ABC
1.5 x 1.5	79.3	55.0 CB	41.0 B	27.1 B	12.3	41.6 BC
2.0 x 2.0	100.0	71.7 C	56.7 C	26.4 B	17.0	51.3 C
Quercus petraea						
1.5 x 0.4	51.4	36.6	27.8	17.5	8.9	26.4
1.2 x 1.3	91.7	65.0	26.4	20.6	7.2	38.2
1.5 x 1.5	80.0	59.1	42.3	25.0	10.0	35.0

Explanation: The same letter indicates the lack of significant differences

The correlation of average values of diameter with the initial growing place indicates that the dependence is significant and direct (Table 3). The settlement of spacings with regard to the structure of the breast height diameter on the base of the λ-statistic allowed 4 groups of spacings to be distinguished: 1) 1.5 x 0.4; 2) 1.2 x 0.8 and 1.0 x 1.0; 3) from 1.5 x 0.8 to 1.5 x 1.5 and 4) 2.0 x 2.0. The sequence of the spacings proves their influence on this characteristic.

In the case of sessile oak, the dependence of the breast height diameter (DBH) on the initial spacing was not proved either by analysis of variance (Table 2) or by linear correlation with the initial growing place (Table 3). The settlement of the spacings - using the λ-statistic - proves that the structure of the DBH of untended saplings grown at the initial spacing of 1.5 x 0.4 differs from the remaining initial spacing: 1.2 x 1.3 and 1.5 x 1.5.

Sessile oak reaches slightly higher mean values of the breast height diameter (DBH) at the same initial spacing in comparison to the values for common oak (Table 4).

The value of the slenderness index ($H/D_{1,3}$ - m/cm) increases together with the increase of density and with aggravation of the biosocial position (Table 5). Trees from I and II Kraft's classes may be approved as more stable in the case of both examined species, except for 1.5 x 0.4 spacing.

Table 5. The slenderness of oaks ($H / D_{1,3}$ - m/cm) depending on the initial spacing and biosocial position

Spacing	Kraft's class					Total
m x m	I	II	III	IV	V	I-V
			Quercus robur			
1.5 x 0.4	1.10	1.21	1.41	1.63	1.80	1.29
1.2 x 0.8	0.89	0.97	1.14	1.42	1.42	0.91
1.0 x1.0	0.86	0.98	1.30	1.51	1.45	1.08
1.5 x 0.8	0.89	1.07	1.22	1.50	1.52	1.09
1.2 x 1.3	0.88	0.93	1.17	1.46	1.31	0.90
1.5 x 1.5	0.79	0.86	1.01	1.07	1.02	0.80
2.0 x 2.0	0.76	0.73	0.88	1.43	0.66	0.76
			Quercus petraea			
1.5 x 0.4	1.07	1.22	1.45	1.69	1.54	1.17
1.2 x 1.3	0.69	0.78	1.26	1.27	1.36	0.79
1.5 x 1.5	0.77	0.84	0.94	1.29	1.33	0.90

THE SIZE OF OAK CROWNS

The crowns of oaks were characterised by their length (Fig. 2) and their width (Table 6). For both of the species, the length as well as the width of crowns increases with the improvement of the biosocial position of trees and with decreasing density. The average length of crowns of saplings is between 200 and 300 cm and the width of crowns is between 100 and 200 cm. The asymmetry of crowns does not exceed 20% in the case of the most irregular spacing of 1.5 x 0.4, so the crowns are rather symmetric.

Table 6. The average width of the crowns (cm) of oaks depending on the initial spacing and biosocial position

Spacing	Kraft's class					Total I-V
m x m	I	II	III	IV	V	
Quercus robur						
1.5 x 0.4	168.0	148.0	127.6	103.9	63.5	115.9
1.2 x 0.8	239.4	204.4	157.1	122.0	42.5	124.7
1.0 x 1.0	299.7	204.4	156.7	115.8	62.5	147.1
1.5 x 0.8	242.9	195.0	162.2	123.5	65.9	149.5
1.2 x 1.3	269.6	225.2	175.3	120.8	47.7	157.3
1.5 x 1.5	295.7	239.6	197.0	157.4	61.9	165.7
2.0 x 2.0	342.5	305.6	243.8	155.7	60.0	197.6
Quercus petraea						
1.5 x 0.4	172.2	148.4	122.2	102.3	56.4	104.0
1.2 x 1.3	313.9	266.7	156.4	129.8	53.3	152.7
1.5 x 1.5	335.0	235.6	187.3	138.3	66.3	147.9

The relative length of the crowns of common oak and sessile oak keeps at a level of ca. 75-80% (Fig. 2). The lower values are only in the case of 1.5 x 0.4 spacing and in the case of oaks from the dominated storey.

The dependence of the length of crowns for common oak on the initial spacing was not proved by analysis of variance (Table 2). A comparison of the structures of that characteristic (Kolmogorov-Smirnov test) did not show a clear dependence on the initial spacing for common oak despite the existence of some differences. The spacings do not fall into the expected sequence according to the growing place. However, in the case of sessile oak, the influence of the initial spacing on the length of crowns is more distinct. Enlargement of the growing place causes an increment in crown length, which was indicated by the linear correlation. In the case of common oak, the influence is significant, especially for trees from the dominant stand.

The influence of the initial spacing on the width of the crowns of both species was not proved by analysis of variance (Table 2). However, the dependence is more distinct than in the case of the length of crowns (lower error). The value of the linear correlation index indicates that the width of the crowns of common oak increases together with the enlargement of the plant growing place. That dependence is direct and significant for trees from I, II, III and IV Kraft's classes (Table 3). A similar situation applies in the case of sessile oak, but the significance was not proved.

SELF-PRUNING OF OAKS

Differentiation in the rate of decay of branches is expressed in the height of the dead-branches zone. This height is, for both species, weakly differentiated by the initial spacing and more so by the biosocial position of trees (Fig. 2). Only the oaks at an extreme spacing show clear differences concerning the height of the dead-branches zone. The differentiation of this feature in saplings is very considerable because the index of variability for average values is from 50 to 80%. The longest average length of such a zone (ca. 120 cm) was ascertained in the case of 1.5 x 0.4 spacing. The dependence of the height of the dead-branches zone on the initial spacing was not proved either by analysis of variance (Table 2) or by linear correlation with the initial growing place (Table 3). The share of this zone in the total tree height is ca. 20-25%, except for the 1.5 x 0.4 spacing.

The number of branches up to the stem height of 2 m for common oak and sessile oak is considerable and varies from 14 to 20 per tree (Table 7). These branches are mostly alive, except for the 1.5 x 0.4 spacing. A great number of these branches (ca. 40-50%) are very thin (to 5 mm) and they are grown up of dormant buds. The dependence of the number of branches on the initial spacing for both species of oaks was not proved either by analysis of variance (Table 2) or by linear correlation with the growing place (Table 3).

Table 7. The number of branches up to the stem height of 2 m depending on the initial spacing and biosocial position

Spacing	Kraft's class					Total
m x m	I	II	III	IV	V	I-V
			Quercus robur			
1.5 x 0.4	18.4	16.7	17.3	14.9	13.9	16.2
1.2 x 0.8	19.9	20.3	22.0	24.4	14.2	20.2
1.0 x 1.0	16.3	20.1	17.7	21.0	20.2	19.6
1.5 x 0.8	18.3	16.1	16.7	15.5	15.5	16.2
1.2 x 1.3	16.9	16.6	19.9	20.2	14.5	17.7
1.5 x 1.5	18.4	16.9	17.1	24.5	16.3	18.4
2.0 x 2.0	14.5	19.3	19.2	21.9	-	19.2
			Quercus petraea			
1.5 x 0.4	16.9	16.6	14.8	12.2	8.5	14.0
1.2 x 1.3	16.5	15.4	20.7	23.8	-	19.3
1.5 x 1.5	14.5	17.4	16.0	19.9	27.9	17.9

The main importance on quality is shown by the thickest branches up to a stem height of 2 m. The mean values of the number of the thickest branches (Table 8) indicate a clear dependence on the initial spacing and on the biosocial position of trees (Table 2 and Table 3). The dependence of the number of such branches is stronger in the case of common oak. Oaks from extreme spacings clearly differ from each other (Table 8). Variability of the maximum diameter of branches is large (V - 30-50%), and hence the structure of such branches is very important. Trees with very thick branches (over 30 mm) are predominant at the spacing with a growing place of more than 1.5 m^2. Among oaks from I and II Kraft's classes (growing place above 1.5 m^2), more than 80 % have at least one branch thicker than 20 mm (Fig. 3).

Table 8. The maximum diameter of branches (mm) to the height of 2 m depending on the initial spacing and biosocial position

Spacing	Kraft's class					Total
m x m	I	II	III	IV	V	I - V
			Quercus robur			
1.5 x 0.4	18.7	17.8 A	14.1 A	13.0	12.8	15.1 A
1.2 x 0.8	24.9	24.8 AB	21.3 AB	16.4	11.3	20.8 AB
1.0 x 1.0	37.2	24.0 AB	20.5 AB	15.6	12.7	20.9 AB
1.5 x 0.8	27.6	22.4 AB	18.7 A	16.3	12.4	20.4 AB
1.2 x 1.3	28.9	29.2 CB	22.0 AB	16.5	10.4	23.7 B
1.5 x 1.5	33.1	30.3 CB	26.4 CB	20.3	14.2	25.6 B
2.0 x 2.0	31.0	36.1 C	36.9 C	22.5	-	32.9 C
			Quercus petraea			
1.5 x 0.4	17.5 A	17.5 A	14.6	13.5	10.7	15.8
1.2 x 1.3	34.4 B	33.3 B	22.4	17.5	-	25.3
1.5 x 1.5	36.5 B	25.0 AB	24.6	17.9	10.9	21.2

Explanation: see Table 4

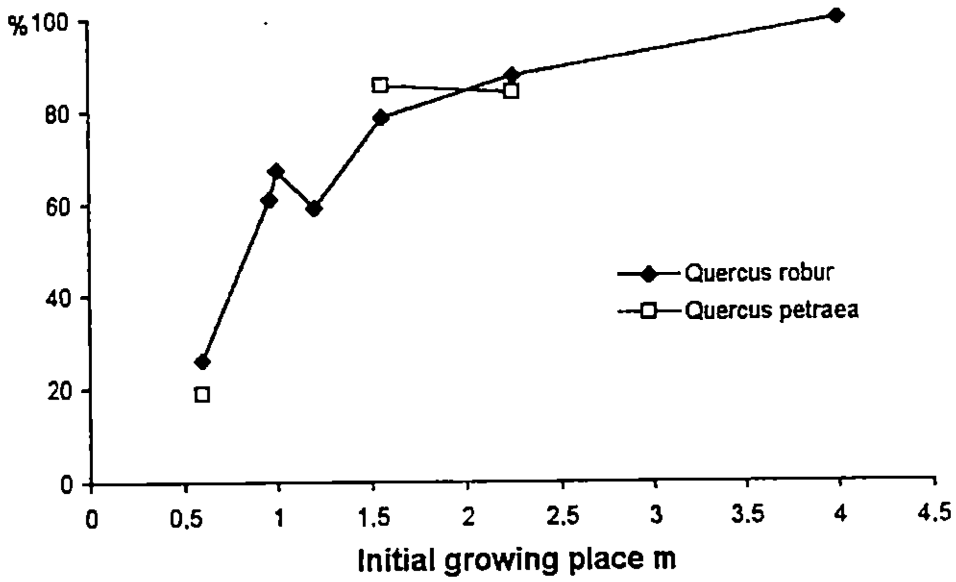

Fig. 3. Percentage of oaks from I and II Kraft's clesses with maximum thicknes of branches over 20 mm in the lower 2m section of trunk depending on the initial growing place

DISCUSSION

The variability of morphological characteristics higher than 20% causes some difficulties in the interpretation of the results of analysis of variance and - in the case of sessile oak - in the interpretation of correlations. Ascertained forest site variation is a kind of fault too.

The ability to survive in the case of both oaks was not related to the initial spacing. The mortality of plants up to the age of 17 did not exceed 25%, except for the 1.2 x 1.3 spacing. These values are in accordance with values in other literature (Spellmann et al. 1988, Gault et al. 1996, Schmaltz et al. 1997, Struck et al. 1998). Also, the biosocial differentiation (as well) in common oak and sessile oak saplings does not show any dependence on the initial spacing, a fact which has also been stated by Renner et al. (1988). The similar survival and the lack of significant differentiation of biosocial structure on the initial spacing proves a weak intensity of self-thinning.

The average height of oaks is not dependent on the initial spacing. The increase in height with the increase in density was ascertained only for trees from a dominant stand. The results of research on this account are diverse. One study does not show any influence of spacing (Savina et al. 1978), others show an inverse influence (Spellmann et al. 1988, Schmaltz et al. 1997) or a direct influence (Gaul et al. 1996). The range of the investigated spacing (Gaul et al. 1996) as well as age, differentiation of height and biosocial class influence the results.

The breast height diameter (DBH) shows a strong and clear dependence on the initial spacing, especially for common oak and trees from a dominant stand. This dependence was ascertained in other research, too (Savina et al. 1978, Schmaltz et al. 1997, Strauch et al. 1998, Gaul et al. 1999). The dependence is not always statistical significant (Spellmann et al. 1988, Schmaltz et al. 1997).

The slenderness index depends on the initial growing place (Spellmann et al. 1988, Gaul et al. 1999) and on the biosocial position of the trees. It is more advantageous at a looser spacing and with a better biosocial position. The value of this index in the case of trees from a dominant stand is lower than the critical one published by Leibundgut (1976, cited after Gaul et al. 1996).

Together with decreasing density, the increase in the length and width of crowns is observed in the case of both species of oak. The influence on the width is more significant. Decreasing density causes a delay in the natural self-pruning of trees (Spellmann et al. 1988, Gürth et al. 1991). However, the influence of the initial spacing on the height of the dead-branches zone for both species was not proved.

The influence of the initial spacing on the number of branches up to a stem height of 2 m was not ascertained. The thickness of the thickest branches in that zone as well as the structure of those kinds of branches clearly correlate with the initial spacing in the shape of direct dependence (prosta zale–nośæ). This is in accordance with the research of Gaul et al. (1996). Schmaltz et al. (1997) ascertained the significant influence of the spacing on the number of branches, although they did not ascertain it for the maximum diameter of branches.

From the investigated morphological characteristics, only the breast height diameter (DBH) and maximum diameter of branches are most clearly dependent on the initial spacing. This refers to both oak species at the age of 17 years as untended saplings. On account of growth increment and the stability of the stand, spacings with growing place of more than 1.0 m^2 are more profitable. Taking into consideration the thickness of branches it seems that the initial spacings in the case of both species of oak should not exceed a growing place over 1.5 m^2.

CONCLUSIONS

The results of our experiment on the initial spacing for common oak and sessile oak established in Poland allow us to draw the following conclusions:

1. The breast height diameter and the maximum diameter of branches in the lower section of the trunk show a significant and direct dependence on the initial spacing. The dimensions of oak crowns and total tree height are less dependent on the initial spacing. No influence of the initial spacing was ascertained on the height of the dead-branches zone and the number of branches.
2. Generally, a stronger influence of the initial growing place on the morphology of trees was ascertained for oaks from a dominant stand (I, II and III Kraft's classes).
3. Taking into consideration only one quality feature, namely the maximum diameter of branches in the lower 2 m section of the trunk, we may suppose that the initial spacings in the case of both species of oak should not exceed 1.5 m^2 growing place. This limit should guarantee a satisfactory quality of wood.

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POČETNI RAZMAK PRI SADNJI I MORFOLOGIJA HRASTOVIH STABALA (*QUERCUS ROBUR* L. I *QUERCUS PETRAEA* /MATT./ LIEBL.) U NENJEGOVANIM HRASTOVIM KOLJICIMA U DOBI OD 17 GODINA

Proučavan je utjecaj početnoga razmaka pri sadnji na morfologiju stabala hrasta lužnjaka i hrasta kitnjaka (*Quercus robur* L. – 1,5 x 0,4; 1,2 x 0,8; 1,0 x 1,0; 1,5 x 0,8; 1,2 x 1,3; 1,5 x 1,5; 2,0 x 2,0 i *Quercus petraea* /Matt./ Liebl. – 1,5 x 0,4; 1,2 x 1,3; 1,5 x 1,5) u sedamnaestogodišnjim hrastovim mladicima. Pokusna je ploha smještena u jugozapadnom dijelu Poljske. Izmjerena su ova svojstva: ukupna visina stabla, promjer prsne debljine, visina zone mrtvih grana, visina i širina krošnje, broj i promjer grana do visine od 2 metra. U obzir je uzet i biosocijalni položaj stabala.

Prikupljeni su podaci podvrgnuti tipičnoj eksperimentalnoj shematskoj analizi varijance. Procijenjena je linearna korelacija s početnim mjestom rasta, a strukture ispitanih svojstava uspoređene su pomoću Kolmogor-Smirnova testa.

Izraziti odnos s početnim razmakom utvrđen je samo za promjer prsne debljine i za maksimalni promjer grana. Utjecaj početnoga razmaka na ostala svojstva bio je manje važan ili zanemarljiv. Morfologija hrastova iz dominantne sastojine (I, II i III Kraftove klase) obilježena je jačom ovisnošću o početnom razmaku od morfologije stabala iz nedominantne sastojine.

Kvalitativna svojstva pokazuju da početno mjesto sadnje hrastovih kultura ne treba biti veće od 1,5 m².

Ključne riječi: Poljska, hrast, razmak, morfologija stabala

V. Topić, O. Antonić, Ž. Španjol, Ž. Vrdoljak: Regression models for estimating biomass of resprouted pubescent oak ... Glas. šum. pokuse 37: 123–131, Zagreb, 2000.

UDK 630*222+537+(4-015) (Quercus pubescens Willd., Q. frainetto Ten., Q. ilex L.)

REGRESSION MODELS FOR ESTIMATING BIOMASS OF RESPROUTED PUBESCENT OAK (*QUERCUS PUBESCENS* WILLD.), ITALIAN OAK (*QUERCUS FRAINETTO* TEN.) AND HOLM OAK (*QUERCUS ILEX* L.)

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The development of models for the quick biomass estimation of dominant Mediterranean tree and shrub species is an important part of long-term research on competition between forestry and livestock grazing in Croatia. This paper introduces regression models for estimating biomass above the ground in the second growth forest that were developed for pubescent oak (*Quercus pubescens* Willd.), Italian oak (*Quercus frainetto* Ten.) and the holm oak (*Quercus ilex* L.). Samples were collected in Dalmatia, Croatia. Foliage and wood biomass was independently measured as weight and volume. Independent estimators were crown diameter, height and number of stems. General linear modelling was used for model development. The yielded models are appropriate for the quick and confident estimation of the population biomass (foliage and/or wood) of the examined oak species in second growth forests.

Key words: foliage volume and weight, Mediterranean oaks, second growth forest, wood volume and weight

INTRODUCTION

The biomass of trees and its components is a parameter which is hard to measure but is of utmost importance for forest management (Attiwill and Ovington, 1968). Consequently, the building of models for tree biomass estimation as a function of easily measurable dendrometric variables (see e.g. Baskerwille, 1965, Whittaker and Woodwell, 1968, Cunia, 1986 or Lukić and Kružić, 1996) is an important subject of forest research.

Pubescent oak (*Quercus pubescens* Willd.), Italian oak (*Quercus frainetto* Ten.) and holm oak (*Quercus ilex* L.) belong to the major tree species of the Croatian Adriatic coast and islands. The first two are sub-Mediterranean species and the third is an eu-Mediterranean species. The natural areas of spread of these species are significantly reduced, basically due to constant human impact during history. Their stands in Croatia, as well as elsewhere in the Mediterranean region, are mainly second growth forests, resprouted after repetitive cutting for firewood. Forests from seeds are rare, basically due to the negative impact of goat and sheep grazing which can also often endanger the resprouting of the existing second growth forest.

Competition between forestry and livestock grazing in Mediterranean forests and related cost-benefit analyses are the objects of long-term research in Croatia (e.g. Topić and \upe, 1996). An important part of this research comprises the development of models for the quick biomass estimation of dominant trees and shrubs that are being grazed by livestock. The basic aim of this paper was the building and optimisation of multivariate regression models for the estimating of the biomass of the three mentioned oak species as a function of easily measurable dendrometric variables.

MATERIAL AND METHODS

Samples were collected on the typical second-growth stands for each oak species, located in Dalmatia, Croatia. Pubescent and Italian oak were analysed on an individual tree basis and holm oak was analyzed on a stem basis (due to the usually large number of stems in one individual tree). In total, 129 individuals of pubescent oak, 176 individuals of Italian oak and 162 stems (44 individuals) of holm oak were sampled for foliage volume and weight, wood volume and weight, height and crown diameter. Weights were measured in kg, volumes were measured in m^3, heights were measured in decimeters and crown diameters were measured in centimeters.

Foliage volume and weight, wood volume and weight, and also total volume and weight (derived as the sum of foliage and wood) were examined as separate dependent variables in terms of height, crown diameter and number of stems as independent variables. The reason for the inclusion of a number of stems as an independent variable is different for the holm oak in relation to the other two oak species. For the holm oak, this variable could describe competition between stems of the same individual (an increasing number of stems decreases the biomass of a particular stem). For the other two oak species, this variable could be a multiplier (an increasing number of stems increases individual biomass). The basic statistics of the sampled independent variables are shown in Table 1.

Table 1.Basic statistics of the sampled independent variables. N – number of observations, AVR – average, MED – median, MIN – minimum, MAX – maximum, LQU – lower quartile, UQU – upper quartile, STD – standard deviation.

	N	AVR	MED	MIN	MAX	LQU	UQU	STD
pubescent oak (*Quercus pubescens*)								
number of stems	129	1.83	1	1	8	1	2	1.19
plant height (m)	129	2.85	2.9	0.5	4.7	2.3	3.5	0.93
crown diameter (m)	129	1.69	1.75	0.50	3.25	1.35	2.00	0.53
Italian oak (*Quercus frainetto*)								
number of stems	176	2.74	2	1	11	1	4	1.88
plant height (m)	176	2.70	2.5	1	5.7	2.1	3.3	0.88
crown diameter (m)	176	1.70	1.75	0.30	4.00	1.20	2.10	0.75
holm oak (*Quercus ilex*)								
number of stems	44	3.68	2	1	12	1	5	3.14
stem height (m)	162	3.55	3.6	1.8	5.6	3.1	4.2	0.80
crown diameter (m)	162	0.65	0.50	0.10	1.90	0.30	1.00	0.46

Multivariate regression models for estimating biomass variables as a function of the mentioned three independent variables were derived using a general linear modelling procedure (Ott, 1993). The model was generally defined as:

$$y = b_0 + S\, b_{ij} x_i^j \quad 1)$$

where y is a biomass variable (foliage volume, foliage weight, wood volume, wood weight, total volume or total weight), x_i is an independent variable (number of stems, height or crown diameter, i = 1 to 3), j is 1 or 2 (linear or quadratic term) and b_0 and b_{ij} are empirical parameters. Each included term was examined as a separate regressor in the general linear model. An optimal model for each oak species and for each biomass variable was found by using a backward stepwise procedure (Ott, 1993). The significance of the predictive power of the regressors was tested using t-test (Ott, 1993).

RESULTS AND DISCUSSION

The statistics and empirical parameters of the optimised regression models are presented in Table 2 for pubescent oak, in Table 3 for Italian oak and in Table 4 for holm oak. The relations between estimated and observed values are shown in Fig. 1.

Summarising the results presented in Tables 2, 3 and 4, the following can be concluded:

1. All regressors selected by the backward stepwise procedure are significant according to the t-test at a probability level of $p=0.05$
2. The set of selected regressors is different for the particular oak species and for the particular biomass variable.

Fig. 1. Scatterplots of observed values (y-axis= of biomass variables versus respective values predicted by regression models in terms of independent variables (x-axis). 1^{st} row - foliage weight, 2^{nd} row - wood weight, 3^{rd} row - total weight. 1^{st} column - pubescent oak (Quercus pubescense), 2^{nd} column - italian oak (Quercus frainetto), 3^{rd} column - holm total volume are the same, but differently scaled.

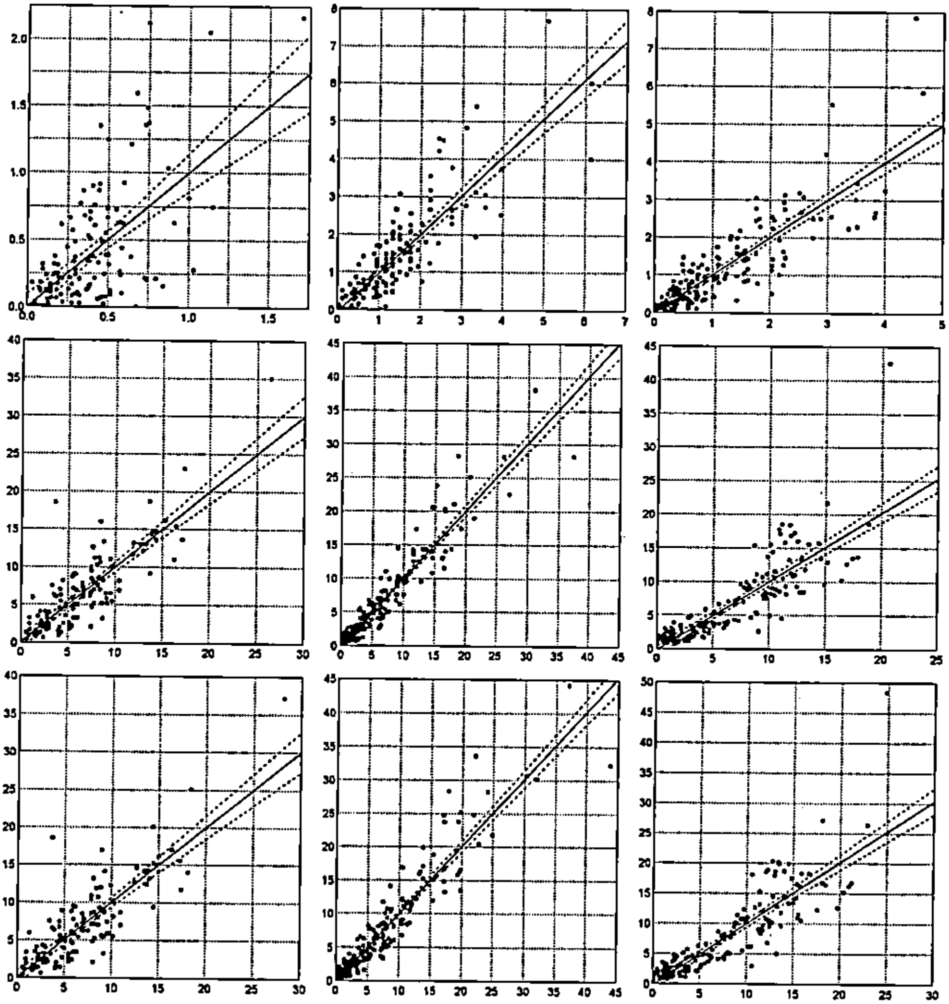

Table 2. Regression models for estimating biomass variables of pubescent oak (*Quercus pubescens*). General linear model follows equation $y = b_0 + \Sigma\, b_{ij} x_i^j$, $i = 1$ to 3, $j = 1$ to 2, where y is a biomass variable (foliage, wood or total weight or volume) b_0 and b_{ij} are empirical parameters, x_i is an independent variable, ns is number of stems, h is height (m), cd is crown diameter (m) and 2 indicates quadratic term. Weights are in kg and volumes are in m^3. R is regression coefficient. F is the ratio between regression mean square and residual mean square and p(F) is respective probability. SE(b) is standard error of respective empirical parameter (b). The t-value and respective p-value are used to test the hypothesis that respective empirical parameter (b) is equal to zero. Underlining indicates insignificance of the respective regressor after the model optimisation using the backward stepwise method.

	model statistics			intercept	ns	ns2	h	h2	cd	cd2
foliage weight	R	0.6544	b	0.3381390	–	–	–	0.0240438	-0.6402174	0.2863598
	F	31.199	SE(b)	0.2114261	–	–	–	0.0064921	0.2618475	0.0743543
	p(F)	0.0000	t	1.5993245	–	–	–	3.7035617	-2.4450007	3.8512877
			p(t)	0.1122731	–	–	–	0.0003177	0.0158787	0.0001866
wood weight	R	0.8404	b	6.3705735	1.0559999	–	-3.4959148	1.1960273	-7.4580808	3.1943473
	F	59.149	SE(b)	2.4714032	0.2559427	–	1.4921459	0.2570105	2.4419461	0.6894039
	p(F)	0.0000	t	2.5777151	4.1259236	–	-2.3428774	4.6536135	-3.0541545	4.6334920
			p(t)	0.0111252	0.0000675	–	0.0207411	0.0000083	0.0027674	0.0000090
foliage volume	R	0.6442	b	0.0004913	–	–	–	0.0000331	-0.0009164	0.0003981
	F	29.562	SE(b)	0.0002916	–	–	–	0.0000090	0.0003611	0.0001025
	p(F)	0.0000	t	1.6851724	–	–	–	3.6973855	-2.5378671	3.8826676
			p(t)	0.0944503	–	–	–	0.0003247	0.0123818	0.0001664
wood volume	R	0.8316	b	0.0064957	0.0009087	–	-0.0041145	0.0012610	-0.0062173	0.0027665
	F	55.152	SE(b)	0.0023720	0.0002457	–	0.0014321	0.0002467	0.0023437	0.0006617
	p(F)	0.0000	t	2.7384572	3.6991338	–	-2.8729616	5.1119101	-2.6527215	4.1810809
			p(t)	0.0070899	0.0003247	–	0.0047914	0.0000012	0.0090377	0.0000546
total weight	R	0.8430	b	6.5410384	1.0988442	–	-3.4300505	1.2134589	-8.0974650	3.4678587
	F	60.408	SE(b)	2.5962058	0.2688674	–	1.5674972	0.2699891	2.5652612	0.7242178
	p(F)	0.0000	t	2.5194607	4.0869366	–	-2.1882338	4.4944729	-3.1565850	4.7884192
			p(t)	0.0130353	0.0000783	–	0.0305421	0.0000159	0.0020078	0.0000047
total volume	R	0.8348	b	0.0068134	0.0009587	–	-0.0040640	0.0012909	-0.0071195	0.0031464
	F	56.563	SE(b)	0.0025496	0.0002640	–	0.0015394	0.0002651	0.0025193	0.0007112
	p(F)	0.0000	t	2.6722716	3.6309335	–	-2.6399893	4.8686992	-2.8260377	4.4238682
			p(t)	0.0085552	0.0004128	–	0.0093650	0.0000034	0.0055017	0.0000211

3. The estimation of the foliage biomass variables is less reliable than the estimation of the wood and total biomass variables for all three oak species.
4. The best models were yielded for Italian oak and the worst models were yielded for pubescent oak.
5. All models are applicable for the quick and confident estimation of the population biomass (foliage, wood and total) of examined oak species in second growth forests, but not for the estimation of individual tree biomass.

Table 3.Regression models for estimating biomass variables of Italian oak (*Quercus frainetto*). General linear model follows equation $y = b_0 + \Sigma\, b_{ij} x_i^j$, i = 1 to 3, j = 1 to 2, where y is biomass variable (foliage, wood or total weight or volume) b_0 and b_{ij} are empirical parameters, x_i is independent variable. ns is number of stems, h is height (m), cd is crown diameter (m) and 2 indicates quadratic term. Weights are in kg and volumes are in m^3. R is regression coefficient. F is the ratio between regression mean square and residual mean square and p(F) is respective probability. SE(b) is standard error of respective empirical parameter (b). The t-value and respective p-value are used to test the hypothesis that respective empirical parameter (b) is equal to zero. Underlining indicates insignificance of the respective regressor after the model optimisation using the backward stepwise method.

	model statistics			intercept	ns	ns2	h	h2	cd	cd2
foliage weight	R	0.8732	b	-0.2655202	–	–	–	–	–	0.4004902
	F	558.32	SE(b)	0.0758318	–	–	–	–	–	0.0169493
	p(F)	0.0000	t	-3.5014341	–	–	–	–	–	23.6287363
			p(t)	0.0005880	–	–	–	–	–	0.0000000
wood weight	R	0.9420	b	-0.9009434	0.7215554	-0.0644158	–	0.4078357	-3.7703674	2.6047109
	F	268.06	SE(b)	0.8756470	0.2785582	0.0317769	–	0.0454533	0.8181532	0.2176649
	p(F)	0.0000	t	-1.0288888	2.5903215	-2.0271283	–	8.9726230	-4.6083881	11.9666117
			p(t)	0.3049936	0.0104210	0.0442114	–	0.0000000	0.0000079	0.0000000
foliage volume	R	0.8421	b	-0.0003422	–	–	–	–	–	0.0005689
	F	424.13	SE(b)	0.0001236	–	–	–	–	–	0.0000276
	p(F)	0.0000	t	-2.7688509	–	–	–	–	–	20.5943873
			p(t)	0.0062354	–	–	–	–	–	0.0000000
wood volume	R	0.9308	b	0.0004642	–	–	–	0.0003308	-0.0033874	0.0024183
	F	371.52	SE(b)	0.0007246	–	–	–	0.0000416	0.0008142	0.0002179
	p(F)	0.0000	t	0.6405384	–	–	–	7.9587065	-4.1603364	11.0982873
			p(t)	0.5226750	–	–	–	0.0000000	0.0000501	0.0000000
total weight	R	0.9418	b	-1.2920462	0.8487995	-0.0812481	–	0.4281081	-3.9142891	3.0179155
	F	266.73	SE(b)	1.0345319	0.3291022	0.0375427	–	0.0537008	0.9666060	0.2571599
	p(F)	0.0000	t	-1.2489187	2.5791363	-2.1641501	–	7.9721010	-4.0495189	11.7355622
			p(t)	0.2134119	0.0107511	0.0318482	–	0.0000000	0.0000779	0.0000000
total volume	R	0.9354	b	-0.0014801	0.0009017	-0.0000844	–	0.0003996	-0.0036713	0.0029846
	F	237.85	SE(b)	0.0010883	0.0003462	0.0000395	–	0.0000565	0.0010169	0.0002705
	p(F)	0.0000	t	-1.3599907	2.6044517	-2.1364602	–	7.0725727	-3.6104252	11.0323729
			p(t)	0.1756337	0.0100170	0.0340725	–	0.0000000	0.0004020	0.0000000

Table 4. Regression models for estimating biomass variables of holm oak (*Quercus ilex*). General linear model follows equation $y = b_0 + \Sigma\, b_{ij} x_i^j$, $i = 1$ to 3, $j = 1$ to 2, where y is biomass variable (foliage, wood or total weight or volume) b_0 and b_{ij} are empirical parameters, x_i is independent variable. ns is number of stems, h is height (m), cd is crown diameter (m) and 2 indicates quadratic term. Weights are in kg and volumes are in m^3. R is regression coefficient. F is the ratio between regression mean square and residual mean square and p(F) is respective probability. SE(b) is standard error of respective empirical parameter (b). The t-value and respective p-value are used to test the hypothesis that respective empirical parameter (b) is equal to zero. Underlining indicates insignificance of the respective regressor after the model optimisation using the backward stepwise method.

	model statistics			intercept	ns	ns2	h	h2	cd	cd2
foliage weight	R	0.8596	b	0.7907485	-0.2551758	0.0172938	–	–	1.0962462	0.6127596
	F	111.12	SE(b)	0.2118195	0.0607074	0.0046453	–	–	0.3855214	0.2166722
	p(F)	0.0000	t	3.7331252	-4.2033724	3.7228201	–	–	2.8435417	2.8280488
			p(t)	0.0002640	0.0000440	0.0002741			0.0050556	0.0052942
wood weight	R	0.8551	b	1.6876990	-2.1318486	0.1676267	–	0.2918539	8.5565468	–
	F	106.79	SE(b)	1.0297446	0.3098426	0.0237578	–	0.0491038	0.6343839	–
	p(F)	0.0000	t	1.6389491	-6.8804242	7.0556646	–	5.9436119	13.4879634	–
			p(t)	0.1032263	0.0000000	0.0000000		0.0000000	0.0000000	
foliage volume	R	0.8599	b	0.9156739	-0.2960958	0.0200528	–	–	1.2675272	0.7167410
	F	111.4	SE(b)	0.2460426	0.0705157	0.0053959	–	–	0.4478092	0.2516794
	p(F)	0.0000	t	3.7216072	-4.1990030	3.7163134	–	–	2.8305075	2.8478333
			p(t)	0.0002753	0.0000448	0.0002807			0.0052556	0.0049913
wood volume	R	0.8521	b	1.5622983	-1.9074992	0.1496515	–	0.2645198	7.6061093	–
	F	104.01	SE(b)	0.9327242	0.2806499	0.0215193	–	0.0444773	0.5746136	–
	p(F)	0.0000	t	1.6749842	-6.7967216	6.9542784	–	5.9472932	13.2369119	–
			p(t)	0.0959280	0.0000000	0.0000000		0.0000000	0.0000000	
total weight	R	0.8690	b	2.0428597	-2.3677672	0.1836296	–	0.3016420	10.6363190	–
	F	121.08	SE(b)	1.1494962	0.3458750	0.0265206	–	0.0548142	0.7081580	–
	p(F)	0.0000	t	1.7771783	-6.8457312	6.9240342	–	5.5029898	15.0196978	–
			p(t)	0.0774751	0.0000000	0.0000000		0.0000001	0.0000000	
total volume	R	0.8689	b	1.9698692	-2.1811567	0.1682015	–	0.2758336	10.0249328	–
	F	120.93	SE(b)	1.0776346	0.3242524	0.0248626	–	0.0513875	0.6638870	–
	p(F)	0.0000	t	1.8279565	-6.7267257	6.7652283	–	5.3677231	15.1003603	–
			p(t)	0.0694543	0.0000000	0.0000000		0.0000003	0.0000000	

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REGRESIJSKI MODELI PROCJENE BIOMASE HRASTA MEDUNCA (*QUERCUS PUBESCENS* WILLD.), HRASTA SLADUNA (*QUERCUS FRAINETTO* TEN.) I HRASTA CRNIKE (*QUERCUS ILEX* L.) U PANJAČAMA

Razvoj modela za brzu procjenu biomase dominantnih mediteranskih vrsta drveća i grmlja važan je dio dugoročnoga istraživanja kompeticije između šumarstva i stočarstva u Hrvatskoj. Ovaj rad uvodi regresijske modele za procjenu biomase iznad površine tla u panjačama, razvijene za hrast medunac (*Quercus pubescens* Will.), hrast sladun (*Quercus frainetto* Ten.) i hrast crniku (*Quercus ilex* L.). Uzorci su prikupljeni u Dalamciji. Biomasa lišća i drveta je odvojeno mjerena kao težina i volumen. Nezavisni procjenitelji bili su promjer krošnje te visina i broj izbojaka iz panja. Generalno linearno modeliranje korišteno je za razvoj modela. Dobiveni su modeli prikladni za brzu i pouzdanu procjenu biomase populacije (lisnu i/ili drvenastu) u panjačama.

Ključne riječi: volumen i težina lišća, mediteranski hrastovi, panjača, volumen i težina drveta

D. Barčić, Ž. Španjol, O. Antonić: Vegetation succession on permanent plots in holm-oak (*Quercus ilex* L.) forests in Croatia. Glas. šum. pokuse 37: 133–143, Zagreb, 2000.

UDK 630*228+521+561+(4-015) (Quercus ilex L.)

VEGETATION SUCCESSION ON PERMANENT PLOTS IN HOLM-OAK (*Quercus ilex* L.) FORESTS IN CROATIA

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The aim of this research was to compare the forest structure of the permanent plots of holm-oak forests in Croatia. These plots are included in the UNESCO program "Man and Biosphere" (MAB). The plots have an area of 1 ha and are situated along the Adriatic coast: on the island of Rab (sampled in 1983 and 1993), the island of Mljet (sampled in 1981 and 1995) and on the island of Brijuni (sampled in 1988). These five samples cover different development stages; i.e. differently aged holm-oak stands. The sampling comprised the measurement of diameter at breast height (DBH) for holm oaks and for other woody species on the plot. A regression model was constructed to describe changes in DBH distributions over time. Model testing suggests high model reliability and the possibility to estimate unknown forest age. Holm oak has unimodal DBH distributions in all development stages (excluding maquis), while other woody species have decreasing DBH distributions in all stages, which illustrates the dominance of the holm oak.

Key words: forest structure, general linear model, macquis, woody species density

INTRODUCTION

The Republic of Croatia established one hundred permanent "Man and Biosphere" (MAB) plots (UNESCO programme) in the period between 1977 and 1990. MAB plots are squares measuring 100 by 100 m (1 ha). The net of these permanently protected areas covers all areas protected by law within the Republic of Croatia (National Parks, nature reserves, etc.), as well as other important natural areas, aimed at the main terrestrial and aquatic ecosystem types (Ilijanić & Meštrov 1975, Rauš 1984, 1995, Rauš et al. 1994). The research conducted on these plots is directed at monitoring the changes in abiotic and biotic factors and the changes in the structure of each ecosystem. Each plot has been included in the registry and permanently outlined in the field. Research methods used to study these plots are in line with the mentioned UNESCO programme.

The Mediterranean vegetation in the Republic of Croatia comprises thermophilic evergreen and deciduous forests of the Adriatic region divided into two separate zones: 1) Mediterranean littoral zone and 2) Mediterranean mountainous zone (Trinajstić 1986 and Rauš et al. 1992). Among the forests of the Mediterranean littoral zone, the most represented phytocoenosis (forest type) is *Fraxino orni - Quercetum ilicis* H-ić 1956, 1958 in which holm oak (*Quercus ilex*) is the dominant species. Holm oak is also one of the most important tree species in the Mediterranean and is consequently the object of frequent research (see, for example Lieth, 1992).

The data analysed in this work was collected on the permanent plots that are within the previously mentioned phytocoenosis. The basic aim of this research was to analyse changes in the diameter at breast height (DBH) distributions for all woody species over time. The specific aim of the research was the construction and testing of the model which estimates DBH distributions of holm oak for a given age, or the age of a holm-oak forest for a given DBH distribution, both on the assumption of undisturbed even-aged stands.

MATERIAL AND METHODS

Three permanent plots with known DBH distributions, i.e. number of stems in 2 cm wide diameter classes for the holm oak and other woody species, were examined in this study.

The first plot is situated on the western part of Rab island in the northern Adriatic (Fig. 1). This part of the island (the Kalifrant peninsula) has the best forest cover and contains one of the most preserved holm-oak forests in the Mediterranean (Španjol, 1995). The climate of the island is between Mediterranean and inland climate types (Seletković & Katušin 1992). This is illustrated by the climatic data recorded at the meteorological station Rab (see Fig. 2). The plot is situated on a flat terrain without topoclimatic influence. The soil type of the plot is cambisol over limestone. The plot has been established within the area that was clear-felled in 1945. Since then, there have been no treatments or any other humanly-caused disturbances. Measurements of DBH were undertaken in 1983 and 1993.

The second plot is situated on the western part of the island Mljet in the southern Adriatic (Fig. 1). This is one of the most forested islands in the Adriatic (Matić 1995, Trinajstić 1995). The climate of the island is typically Mediterranean (see Penzar & Penzar 1995) which is illustrated by the data recorded at the nearby meteorological station Goveđari (see Fig. 2). The climate of the plot is somewhat colder and more humid due to the northern exposure of the terrain. The soil type

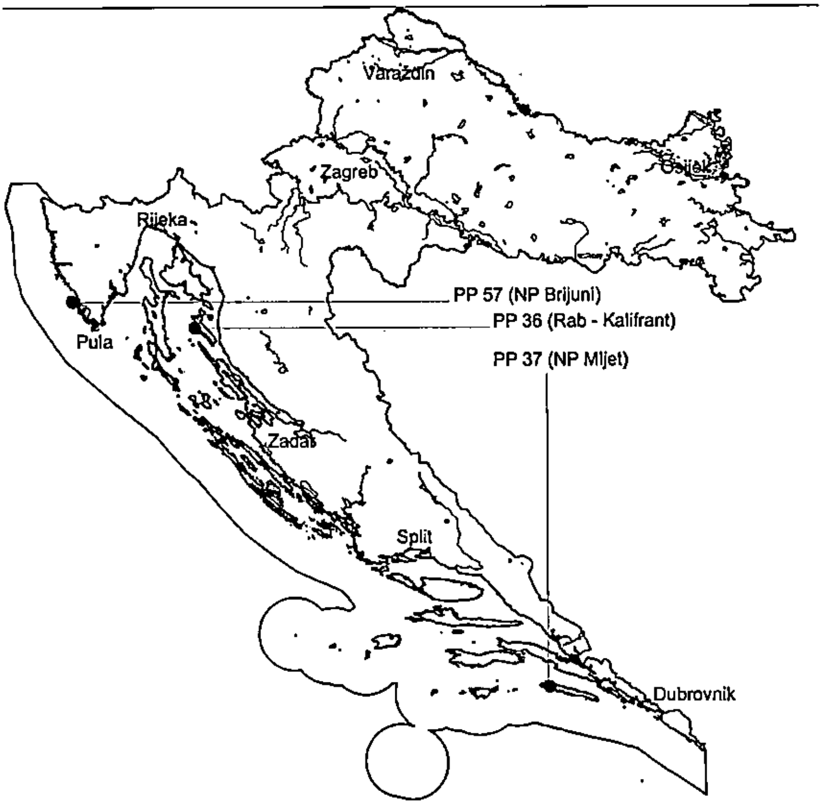

Fig. 1. Location of holm-oak permanent plots in the Republic of Croatia.

on the plot is cambisol over dolomite. The plot has been established within the area disturbed by wildfire in 1917. Since then, there have been no treatments or any other humanly-caused disturbance. Measurements of DBH were undertaken in 1981 and 1995.

The third plot is situated on the island Veli Brijun which belongs to the Brijuni archipelago in the northern Adriatic (Fig. 1). The plot climate can be illustrated (Fig. 2) by an estimation based on the macroclimatic model presented in Antonić et al. (in print). The plot is situated on flat terrain and is not influenced topoclimatically. The soil type on the plot is a mosaic of terra rossa and cambisol over limestone. The plot has been established in the old growth holm-oak forest of unknown age. Over the last hundred years there have been no treatments or any other humanly-caused disturbances in this forest. Measurements of DBH were undertaken in the year 1987 only.

In total, five samples of DBH distributions were available for this research. These five samples cover different development stages, from maquis (Rab plot in

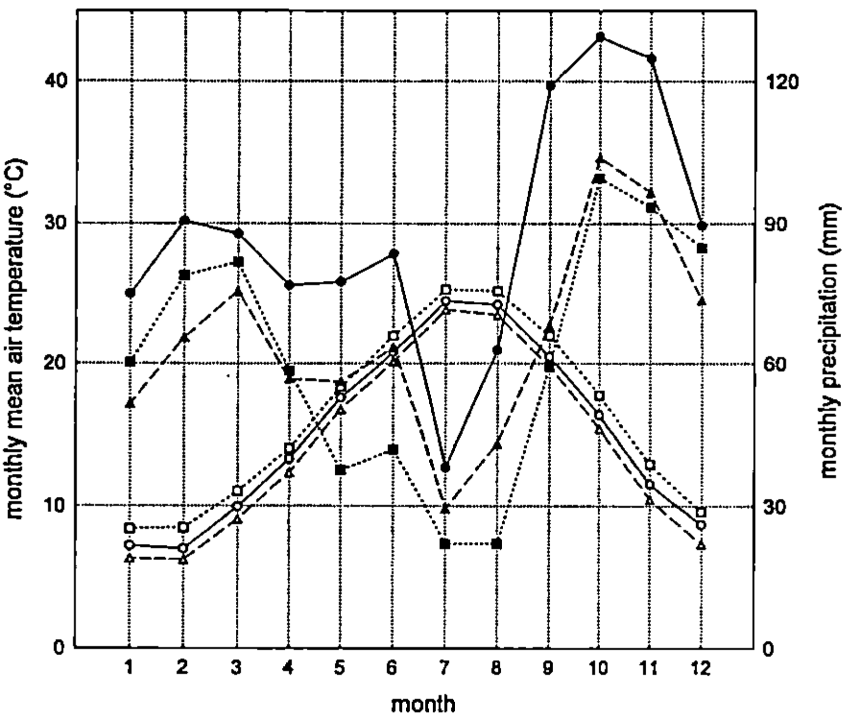

Fig. 2. Monthly mean air temperature (open symbols) and monthly precipitation (full symbols), both averaged for the period of 1981-1992, for the meteorological station Rab (circles), for the meteorological station Govedari on the island Mljet (squares) and the model estimation for the island Veli Brijun (triangles).

1983) to the old holm-oak forest (Brijuni plot), including differently-aged forests (Rab plot in 1993 and Mljet plot in both years).

Data from DBH distributions of holm oak, recorded on the Rab plot in the years 1983 and 1993 and on the Mljet plot in the years 1981 and 1995, were used for the construction of the regression model. The model estimates the number of stems for each diameter class as a function of the forest age. The following expression was used:

$$Y = a\, DBH^{\,b}\, e^{-c\, DBH} \qquad 1)$$

where Y is the number of stems per ha, DBH is diameter at breast height in cm, and a, b, c are parameters. With the aim of using a general linear modelling procedure (Ott, 1993) which enables model optimisation and estimation of parameter errors, expression 1) was linearised using logarithmic transformation to the form:

$$\ln Y = \ln a + b \ln DBH - c\, DBH \qquad 2)$$

and parameters were expressed as a function of forest age in years:

$$\ln a = k_0 + k_1 t + k_2 t^2 \qquad 3)$$

$$b = k_3 + k_4 t + k_5 t^2 \qquad 4)$$

$$c = k_6 + k_7 t + k_8 t^2 \qquad 5)$$

where t is the forest age in years and k_i is empirical parameter obtained by the general linear modelling ($i = 0, 1, 2, \ldots, 8$). The full, nine-parameter model arising from expressions 2) to 5) was optimised using the backward stepwise procedure (Ott, 1993). The significance of the predictive power of the regressors was tested using the t-test (Ott, 1993). Data recorded on the Brijuni plot were used for model testing, and for the estimation of the forest age of this plot. This was done by non-linear regression using expressions 1), 3), 4) and 5), where Y was the number of stems of holm oak on this plot, k_i was the constant (respective parameter yielded by the general linear model described above) and t was estimated as an empirical parameter.

The distributions of the number of stems of the other woody species were compared only qualitatively, because the small number of plots did not provide a data sample sufficient for the building of similar species-specific models as for the holm oak, or for the use of more exact numerical methods for the comparison of species composition on different plots (e.g. following Legendre & Legendre, 1998).

RESULTS AND DISCUSSION

All observed distributions of the number of stems of holm oak are presented in Fig. 3. The optimised regression model and related statistics are presented in Table 1. The level of explained variability is very high (Table 1, Fig. 4 and 5). The testing of the model on the independent sample of the Brijuni plot suggests high model reliability (Fig. 6). The application of the model on the data from the Brijuni plot also enables the estimation of primarily unknown forest age (104 years in the year 1987).

These results suggest that the presented model could probably be widely applied in the prediction of the development of holm-oak maquis or forests as well as for the estimation of the age of the holm-oak forest. At this moment, the model is applicable only on undisturbed even-aged stands which belong to the *Fraxino orni - Quercetum ilicis* forest type. These constraints could probably be overcome using the larger sample, covering other holm-oak forest types and appropriate independent variables which describe the influence of forest management. This will be the object of future research.

DBH distributions for other woody species are shown in Table 2. These distributions are mostly decreasing in all development stages, while holm oak has uni-

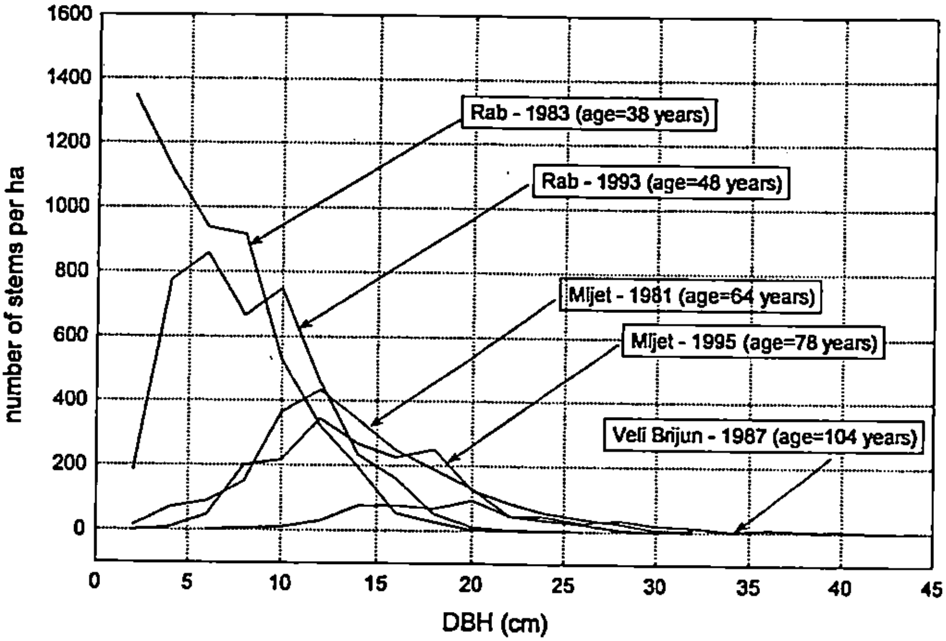

Fig. 3: Diameter at breast height (DBH) distributions of holm oak recorded for different plots and ages.

modal DBH distributions in all stages (excluding maquis) which illustrates the dominance of holm oak in these forests. It is obvious and expected that the total number of stems of all species decrease from maquis (Rab plot in year 1983), through the young forest (Rab plot in 1993) to the mature forest (Mljet plots in 1981

Table 1. Regression model for estimating logarithm of a number of stems per ha for holm oak (*Quercus ilex*). General linear model follows expressions 2) to 5). Regression coefficient is R=0.979. Ratio between regression mean square and residual mean square is F=176.44, with respective probability of p(F)=0.000. The t-value and respective p-value were used to test the hypothesis that the respective empirical parameter (k_i) is equal to zero. Model was optimised using backward stepwise method and parameters of insignificant regressors were omitted.

parameter	value	st. error	t	p(t)
k_0	9.766383	0.74083	13.18	0.000
k_2	-0.002539	0.00022	-11.47	0.000
k_3	1.446154	0.57153	2.53	0.000
k_5	0.000940	0.00015	6.07	0.000
k_6	0.987612	0.09676	10.21	0.000
k_7	-0.012664	0.00252	-5.03	0.000
k_8	0.000089	0.00002	3.98	0.000

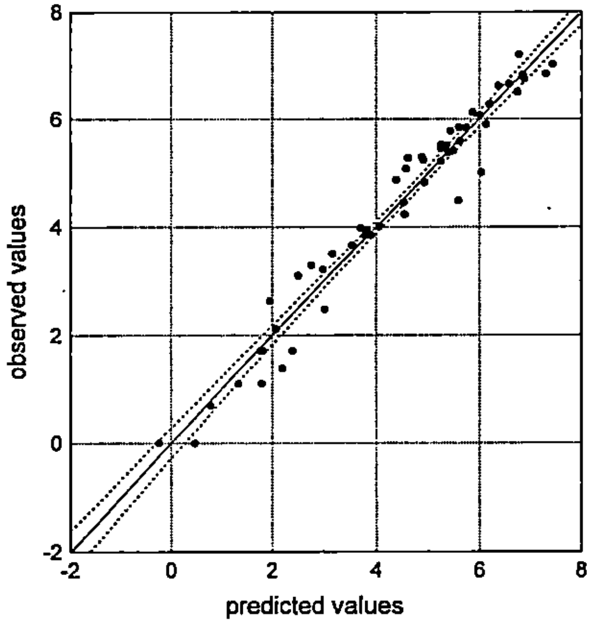

Fig. 4. Logarithm of the number of holm-oak stems: relation between predicted and observed values. Further explanation in the text.

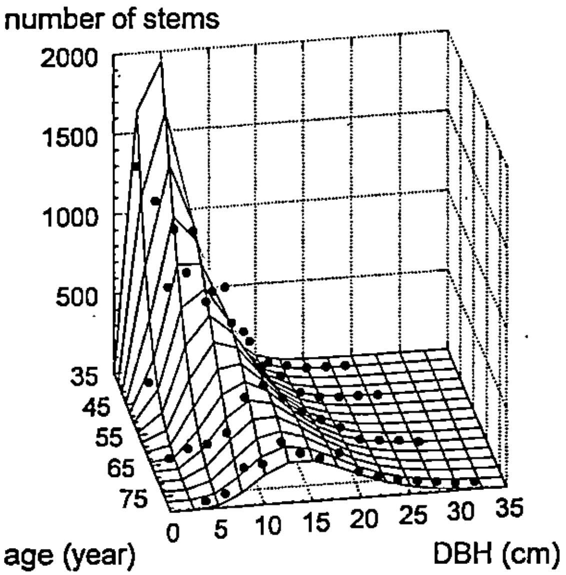

Fig. 5. Relation between the number of holm-oak stems, diameter at breast height (DBH) and stand age. Points represent observed values at the Rab plot (1983 and 1993) and the Mljet plot (1981 and 1985) fitted by the regression surface.

Table 2: Diameter at breast height (DBH) distributions of the other woody species on the studied plots. (*) for Brijuni plot data relate to *Phillyrea latifolia* (*Phillyrea media* is not present).

	Phillyrea media*					Vibumum tinus					Arbutus unedo					Fraxinus ornus				
DBH (cm)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)
2	1901	947	33	28		5895	2223	50	28		858	313	3			537	203			
4	668	696	86	44	106	565	645	156	17	49	424	491	14		8	128	161		3	74
6	119	109	22	14	71	28	25	106		21	320	301	3	3	40	39	95			53
8	13	11		6	35	8	3	14		3	89	132	6		54	18	39			45
10	1	2		6	28	2	3			1	15	33	3		59	2	19			33
12					19		1				1	2	3		50	1	1			23
14					14										38		1			26
16					8										41					19
18					4										23					13
20					3										24					5
22					1										8					3
24															5					
26															5					
28																				5

	Erica arborea					Pistacia lentiscus					other woody species					total				
DBH (cm)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)	RAB (1983)	RAB (1993)	MLJET (1981)	MLJET (1995)	BRIJUNI (1987)
2	1776	786				18	7				7					10992	4479	86	56	
4	544	652			9	12	5			4	4	1			376	2345	2651	256	64	626
6	107	105			1					4		10			226	613	645	131	17	416
8	10	24										1			159	138	210	19	6	296
10	3	6													123	23	63	3	6	244
12															46	2	4	3		138
14												1			36		2			114
16															11					79
18																				40
20																				32
22																				12
24																				5
26																				5
28																				5

and 1995). For the holm oak, this is the consequence of intra-species competition. For other species, this illustrates the impact of the closed holm-oak canopies which strongly reduce the light available for the understorey in mature forests in relation to the maquis. Contrary to this trend, the old forest of the Brijuni plot has a large density of other woody species (see Table 2). This plot has evident gaps in the holm-oak canopies, but it is not clear if this is the consequence of forest age or some locally specific unknown environmental influence.

The basic constraint of this research was the limited number of comparable plots representing undisturbed holm-oak forests, because they are relatively rare, due to strong and diverse human pressure. This fact additionally extends the scientific value of the permanently preserved plots in the Mediterranean area and points to the need for international collaboration.

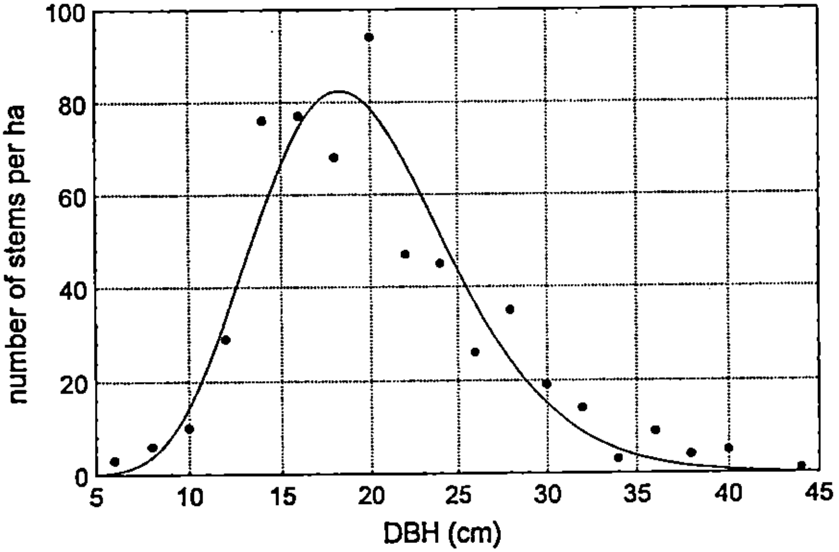

Fig. 6. Number of stems per ha for different diameter classes for the Brijuni plot. Points – observed data, line – predicted by the model based on data from the Rab plot and the Mljet plot.

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SUKCESIJA VEGETACIJE NA TRAJNIM PLOHAMA U ŠUMI HRASTA CRNIKE (*Quercus ilex* L.) U HRVATSKOJ

Cilj je ovog istraživanja bila usporedba sastojinaske strukture na trajnim plohama u sastojinama hrasta crnike u Hrvatskoj. Te plohe pripadaju UNESCO-ovu programu "Čovjek i biosfera" (MAB). Plohe imaju površinu od 1 ha i nalaze se uzduž jadranske obale: na otoku Rabu (uzorkovane 1983. i 1993), na otoku Mljetu (uzorkovane 1981. i 1995) i na Brijunima (uzorkovane 1988). Tih pet uzoraka pokriva različite razvojne stadije, odnosno sastojine hrasta crnike različite dobi. Uzorkovanje je obuhvatilo mjerenje prsnoga promjera jedinki hrasta crnike i drugih drvenastih vrsta na plohi. Izrađen je regresijski model koji opisuje promjenu distribucije prsnoga promjera kroz vrijeme. Testiranje modela upućuje na njegovu visoku pouzdanost, kao i na mogućnost procjene dobi sastojine kada ona nije poznata. Hrast crnika ima unimodalnu distribuciju prsnih promjera u svim razvojnim stadijima (isključujući makiju), dok druge drvenaste vrste imaju padajuće distribucije prsnih promjera u svim stadijima, što pokazuje dimnansnost hrasta crnike.

Ključne riječi: šumska struktura, generalni linearni model, makija, gustoća drvenastih vrsta

H. Guttenberger: Anatomy of *Quercus* x *viridis* Trin., an oak of unknown origin in Croatia
Glas. šum. pokuse 37: 145–159, Zagreb, 2000.

UDK 630*811+168+(4-015) (Quercus viridis Trin.)

ANATOMY OF *QUERCUS* x *VIRIDIS* TRIN., AN OAK OF UNKNOWN ORIGIN IN CROATIA

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Near Zadar, Croatia, grows an oak which is different from other local oak species in the neighborhood: *Q. x viridis* Trin., called "green oak". To clarify the origin of this tree we investigated the anatomy of wood and leaves (in particular, the hairs and epidermis cells were examined). The investigations were done with different methods: light and scanning electron microscopic (high vacuum and ESEM) techniques combined with digital image analysis. We compared the results of the wood anatomy with the results of *Q. cerris, Q. ilex* and *Q. pubescens* in the neighborhood and in literature. *Q. cerris, Q. ilex* and *Q. pubescens* are supposed to be the ancestors of *Q. x viridis*. Investigations of the leaves were done with *Q. x viridis, Q. cerris*, and *Q. ilex*. A number of measurements and histochemical reactions were done with the epidermis, hair, and root meristem-cells. EDX was used to determine the elements in the hairs, and the DNA-content of the nuclei was measured using Feulgen-reaction in combination with a densitometric method.

The woods of *Q. x viridis, Q. cerris*, and *Q. pubescens* are ring-porous, *Q. ilex* is diffuse-porous. Of the whole rays the anatomy of *Q. x viridis* and *Q. cerris* is very similar, triangular ray cells were only seen in preparations of these trees. *Q. x viridis* has five different types of hairs, the other investigated oaks only four. *Q. x viridis* and *Q. cerris* have a similar number of hairs on the adaxial surface of the leaves. The numbers of hairs on the abaxial surface are different, *Q. x viridis* has less hairs. The sizes of the hairs of *Q. x viridis* and *Q. cerris* are similar. We found lipoids and cuticle in all hairs, only the cell walls of the hairs of *Q. x viridis* are slightly woody. EDX analysis shows no flint or lime. DNA measurements show contents of 1.2 pg for 2 C nuclei of Q. x viridis, *Q. ilex* has 1.4 pg (root meristem). The majority of the nuclei of hair cells have a DNA content of 2 C (all investigated oaks), some of them 4 C and 8 C (*Q. cerris*). The Nuclei of epidermis cells have DNA contents up to 16 C.

The results of this investigation and the origin of the "Green oak" will be discussed.

Key words: anatomy, *Quercus*, image analysis, electron microscopy, nuc-DNA-content

INTRODUCTION

Quercus x viridis is a single tree growing on a plateau in Ravni Kotari (Islam Latinski) in the neighborhood of Zadar, Croatia. The tree is more than 20 m high, the leaves are green deep into the winter. Trinajstić (1974) compared this tree with *Q. cerris* and *Q. ilex* and came to the result that this tree is a hybrid between *Q. ilex* and *Q. cerris*: *Q. x viridis* Trinajstić, hybr. nov, = ? *Quercus cerris L f. austriaca x Quercus ilex* L. Some difficulties appeared: hybrids between oaks whose acorns mature in a single season with oaks whose acorns mature in two seasons are seldom possible by artificial pollination (Cottam et al. 1982), but are not seen in nature. Our own measurements of the leaves did not show the same results as Trinajstić´s measurements. In the winters of the years 94 to 97 the tree lost its leaves.

Borzan and Pfeifhofer (1998) investigated the volatile compounds of the "green oak". They came to the conclusion that this oak could be a hybrid between *Q. cerris* and *Q. suber* or a variety of *Q. cerris*. Investigations of the hairs of *Q. cerris* and *Q. ilex* were made by Safou and Saint-Martin (1989), Llamas et al. (1995), Penas et al. (1997), Westerkamp and Demmelmeyer (1997), and Aas (1998). The anatomy of the wood, leaves, and hairs of the "green oak" has not been described till now, and the DNA-content of the "green oak" had not been determined. We thought, that the determination of these elements and a comparison with other oaks would be useful in the discussion on the origin of the "green oak".

MATERIALS AND METHODS

PLANT MATERIALS

The "Green Oak", *Quercus x viridis* Trin., grows 15 km northeast of Zadar, Croatia, in Ravni Kotari (Islam Latinski, 44° 12´ north, 15° 26´ east). Two-years-old branches were sampled in May 1996 (the tree is protected, therefore it was not allowed to harvest older twigs). Probes of *Quercus ilex* L., *Quercus cerris* L., and *Quercus pubescens* Willd. were sampled in Posedarje (44° 13' north, 15° 27' east), 20 km northeast of Zadar. Green leaves were harvested and cooled transported to Graz. Fixation or preparation was done within two days.

LIGHT MICROSCOPY

Light microscopic investigations were done with an Axioskop microscope (Zeiss Inc.) equipped with a DXC 930 P videocamera (Sony Inc.). The camera was connected with a framegrabber 3M-V equipped with a variable scan module

AM-VS-VP and a color module AM-CLR-VP (Image Technology Inc.). This equipment was built-in in a personal computer (R+R Inc.). The image analysis software used was Optimas 5.2 (Media Cybernetics Inc.). The probes were fixed in ethanol (75 %). Parts of the wood were macerated, modified after Gerlach 1969: after removing the bark, the untreated wood was cut into small pieces and cooked in nitric acid (53 %) for 5-6 min. Then samples were washed in tap water and kept in diluted ethanol. Other pieces of the wood were rinsed in glycerol for 24 hours. Cross-, radial-, and tangential-sections were done with a rotation-microtome HM 335 E (Micron Inc.). The sections were about 5 μm thick. Using a pipette (for the macerated wood) or a brush (for the sections) the objects were put on a slide in a drop of warmed Kaiser´s glycerol gelatin (Merck Inc.). To estimate the dimensions of the wood cells, 150 cells of *Q. x viridis* and 50 cells of the *per* other Quercus species were measured.

Histochemical staining of the hairs: the cuticle was stained with Sudan III and Nil-blue, wood reaction with phloroglucine-HCl.

Quantitative DNA-determination: the samples were fixed in ethanol:acetic acid 3:1 (v:v), determination was done after Feulgen reaction with image analysis equipment. *Allium cepa* root tips were used as an internal standard.

SCANNING ELECTRON MICROSCOPY

Scanning electron microscopic investigations were done with a XL 30 ESEM microscope (Philips Inc.). The macerated probes or leaf cuttings were air dried and mounted on stubs. They were investigated in high or low vacuum (ESEM®). Analysis of elements was done with EDX.

EVALUATION AND STATISTICS

The evaluation of the data was done with Excel 7.0 (Microsoft Inc.), statistics (ANO-VA/MANOVA, analysis of variance using LSD-test) and graphs with Origin 4.2 (Microcal Inc.) and Statistica (StatSoft Inc.). Figures were made with Corel Draw 7.0 (Corel Inc.).

RESULTS

WOOD ANATOMY

In the woods of *Q. x viridis*, *Q. cerris* and *Q. pubescens* the largest vessels are localised in the early woods (transections): the wood is therefore ring-porous (see

Fig. 1a, c, and d). *Q. ilex* has vessels with essentially equal diameters and are uniformly distributed through a growth ring: the wood is diffuse-porous (Fig. 1b). This result is confirmed by the measurements of the vessels of wood macerates: only *Q. ilex* has vessels with relative small diameters and a low standard deviation (Tab. 1). The anatomy of the rays of *Q. x viridis* and *Q. cerris* is very similar (Fig. 1a, c). The rays are one cell wide and 3 to 20 cells high. Triangular ray parenchyma cells were only seen in preparations of these two trees species.

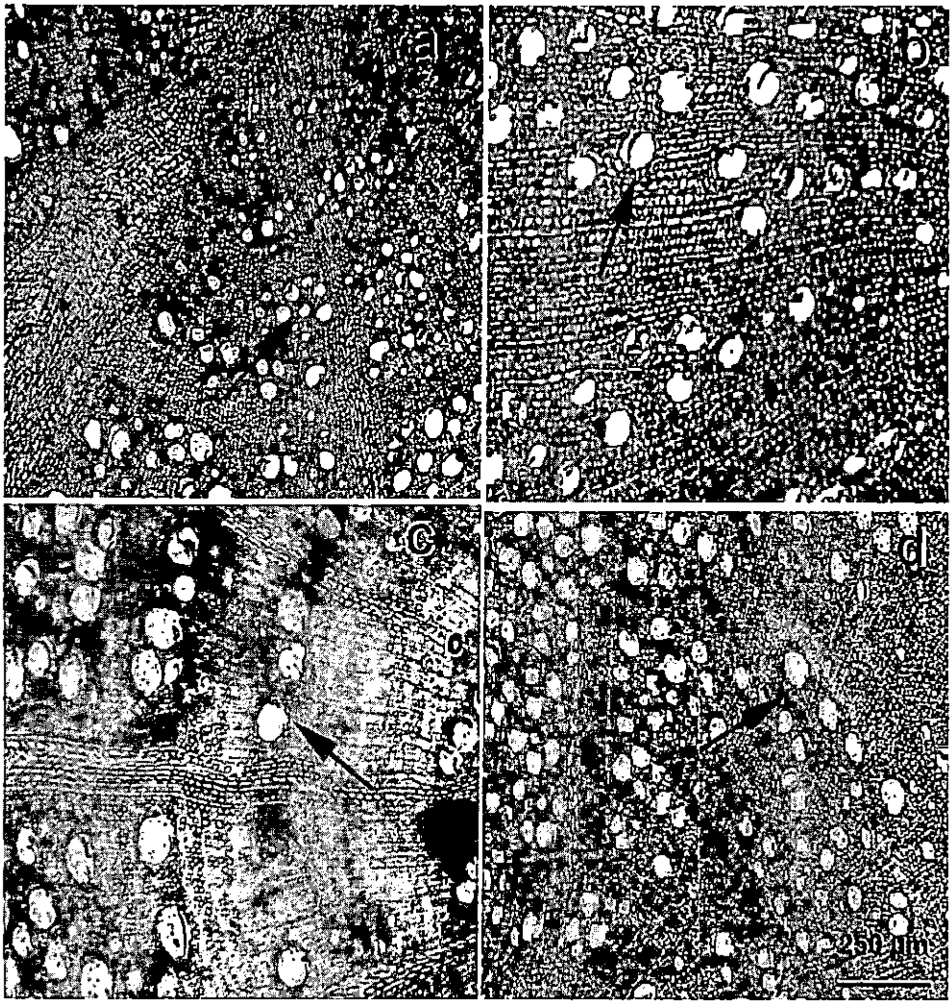

Fig. 1. Transverse section of the wood. a) *Q. x viridis*, b) *Q. ilex*, c) *Q. cerris*, d) *Q. pubescens*. Arrows are indicating large vessels.

Table 1. Average (i) and standard deviation (ii) of different cell types of the wood (macerated) of four *Quercus* species. * : significant difference. Areas in μm^2, all other values in μm.

	libriform fibers			vessels		axial xylem parenchyma		ray parenchyma	
	area	diameter	length	length	diameter	length	diameter	length	diameter
	Q. x viridis								
i	5428.77	37.8	524.9	195.6	55.2	72.6	12.3	20.7	20.4
ii	2262.3	15.9	167.9	49.0	22.2	16.0	2.5	3.5	3.3
	Quercus ilex								
i	5997.7	51.4	560.2	194.8	39.8 *	77.1	14.3	23.0	23.2
ii	1910.0	30.1	85.3	74.45	12.6	19.6	2.7	5.6	4.6
	Quercus cerris								
i	7583.8 *	57.7	696.9 *	250.3 *	68.3	76.2	12.5	29.1 *	19.9
ii	2309.7	30.8	124.3	50.9	24.9	17.9	2.2	7.4	3.5
	Quercus pubescens								
i	6467,48	58,18	607,30	197,79	66,34	73,03	12,19	19,16	19,16
ii	1746.2	41.0	110.2	50.1	17.5	19.9	2.5	4.0	4.1

LEAVES AND HAIRS

The investigation of the leaves showed that all leaves were dorsiventral and had several adaxial layers of palisade parenchyma cells. Spongy parenchyma was loose, the epidermis cells of Q. *ilex* were much bigger and showed a positive wood reaction in their cell walls.

Table 2. Kinds of glandular hairs found within the leaves in different oak species:

	simple uniserate hairs	*glandular hairs with head*
Q. cerris	*AD:* missing *AB:* fragments, near and on the midvein	near and on the midvein *AD*: seldom *AB*: very seldom
Q. ilex	*AD:* missing *AB:* missing	on the veins or between *AD*: often *AB*: seldom
Q. x viridis	near and on the midvein *OS:* mssing *US:* seldom	near and on the midvein *AD*: seldom *AB*: very seldom
AD: adaxial, upper epidermis *AB: abaxial, lower epidermis*		

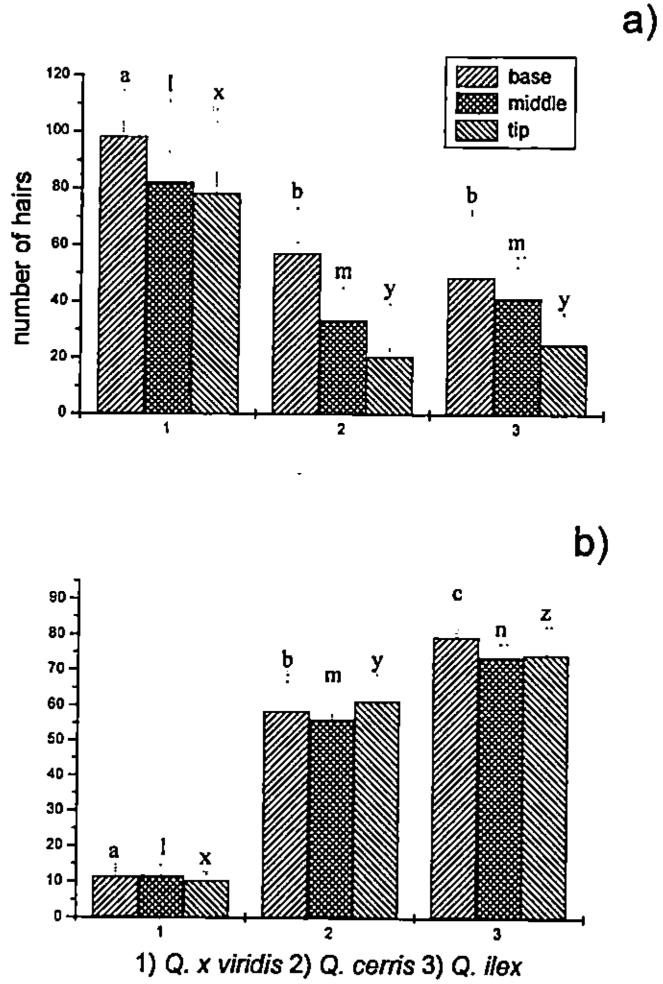

Fig. 2. Number of hairs on the leaves of 3 oak species (base, middle, and tip of the leaves). Different letters within one region of the leaves: significant difference. a) adaxial, b) abaxial surface.

Q. x viridis has five different types of hairs, the other investigated oaks only four. *Q. x viridis* and *Q. cerris* have a similar number of hairs on the adaxial surface of the leaves. The numbers of hairs on the abaxial surface are different: *Q. x viridis* has fewer hairs. On the adaxial surfsace the density of hairs is higher *in Q. x v*iridis than in the other investigated species (Fig. 2). The sizes of the hairs of *Q. x viridis* and *Q. cerris* are similar. We found lipoids and cuticles in all hairs, *only the cell walls* of the hairs of *Q. x viridis* are slightly woody. EDX analysis shows no flint or lime (Fig. 6). DNA measurements show contents of 1.2 pg for 2 C nuclei of *Q. x viridis*; *Q. ilex* has 1.4 pg (root meristem). The majority of the nuclei of the hair head

Fig. 3. Scanning electron microscopic images of different kinds of hairs of *Quercus cerris* leaves: a) glandular hair with head b) glandular hair with head (ESEM modus); c) ordinary hair d) stellate hair e) stellate hair ESEM f) stellate hairs.

cells have a DNA content of 2 C (all investigated oaks), some of them 4 C and 8 C (*Q. cerris*). The Nuclei of the upper epidermis cells have DNA contents up to 16 C (Fig. 7).

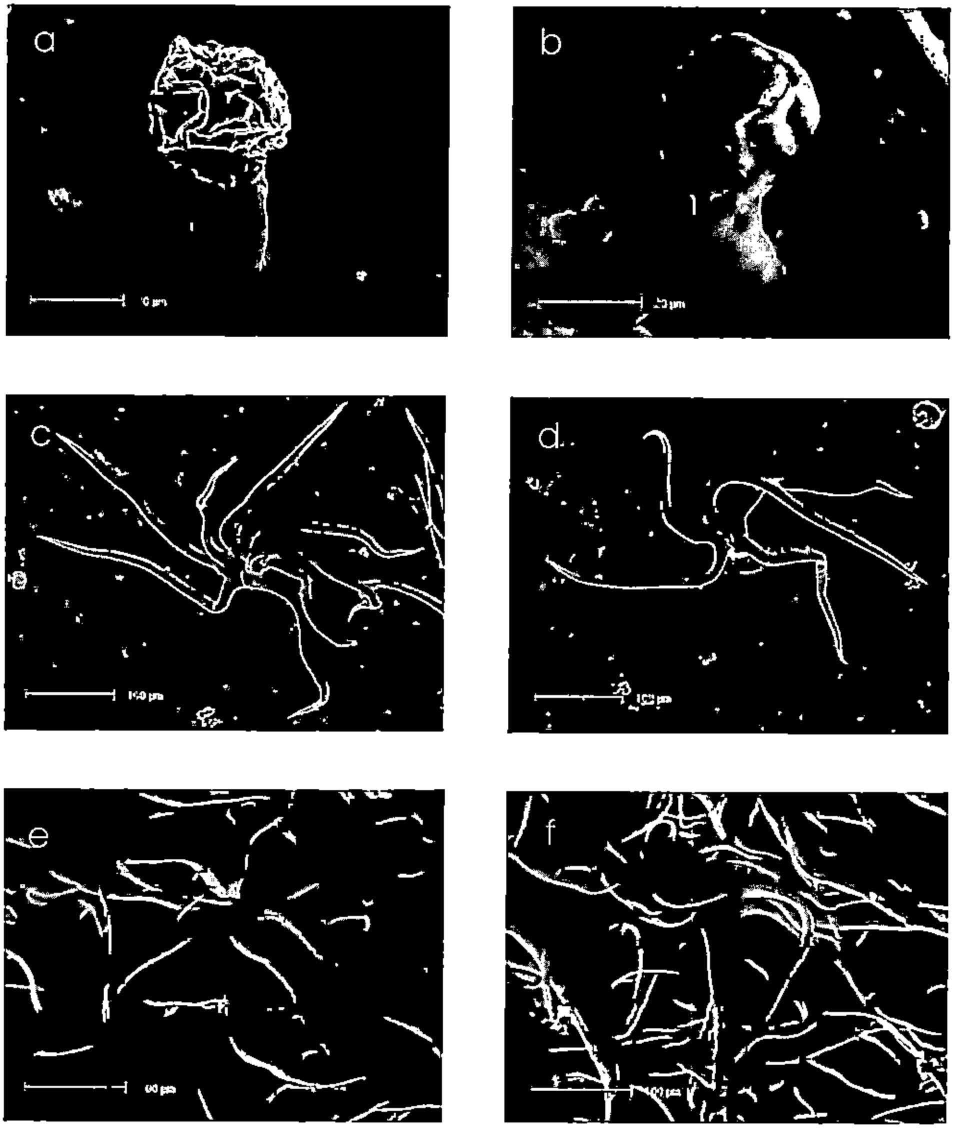

Fig. 4. Scanning electron microscopic images of different kinds of hairs of *Quercus ilex* leaves; a), b) and f): upper epidermis, all others: lower epidermis. a) glandular hair with head b) glandular hair with head (ESEM modus); c) and d) stallate hair e) and f) stellate hair (ESEM modus).

The glandular trichomes with heads of the investigated oaks are similar (Fig. 3 to 5).

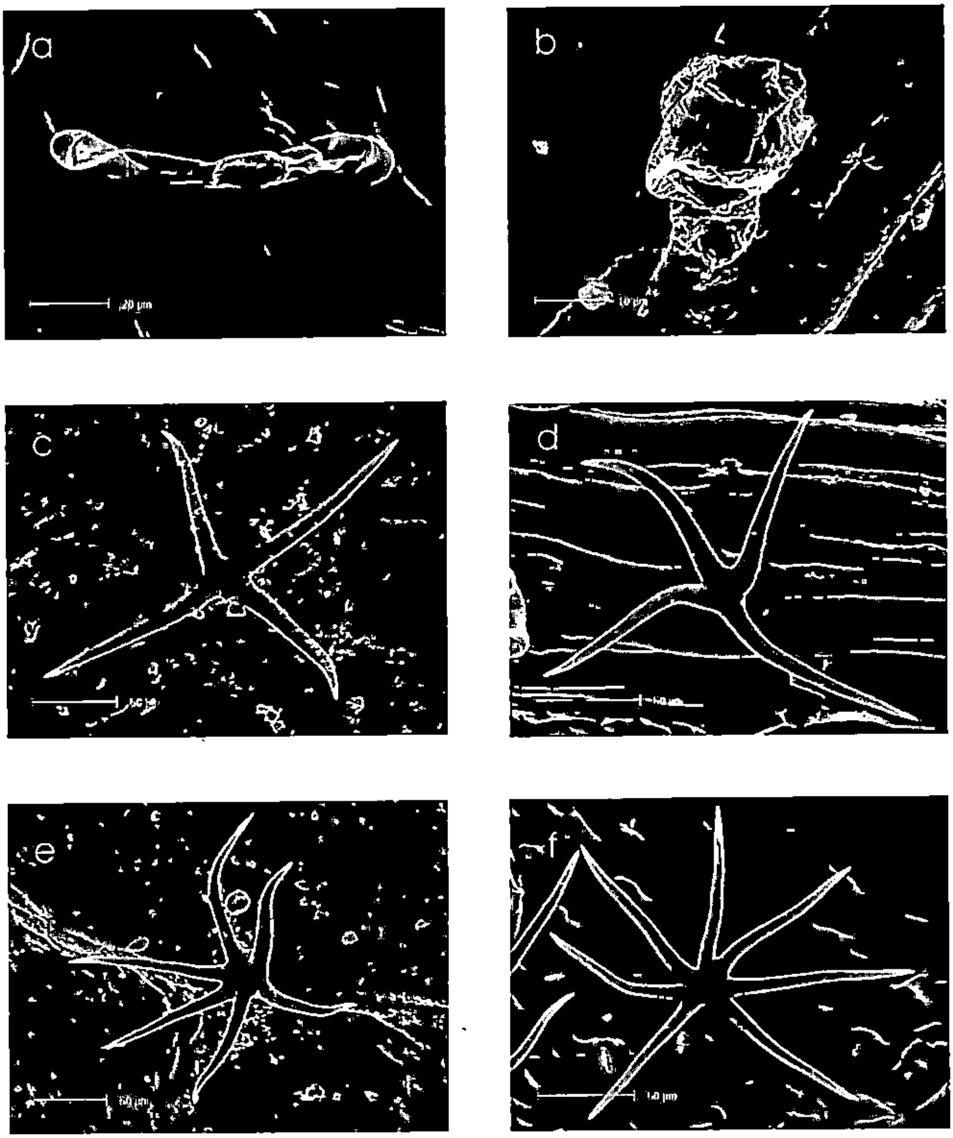

Fig. 5. Scanning electron microscopic images of different kinds of hairs of *Quercus x viridis* leaves. a), f): lower epidermis, all others: upper epidermis. a) glandular uniserate hair b) glandular hair with head (ESEM modus); c) and d) stallate hair e) and f) stellate hair (ESEM modus).

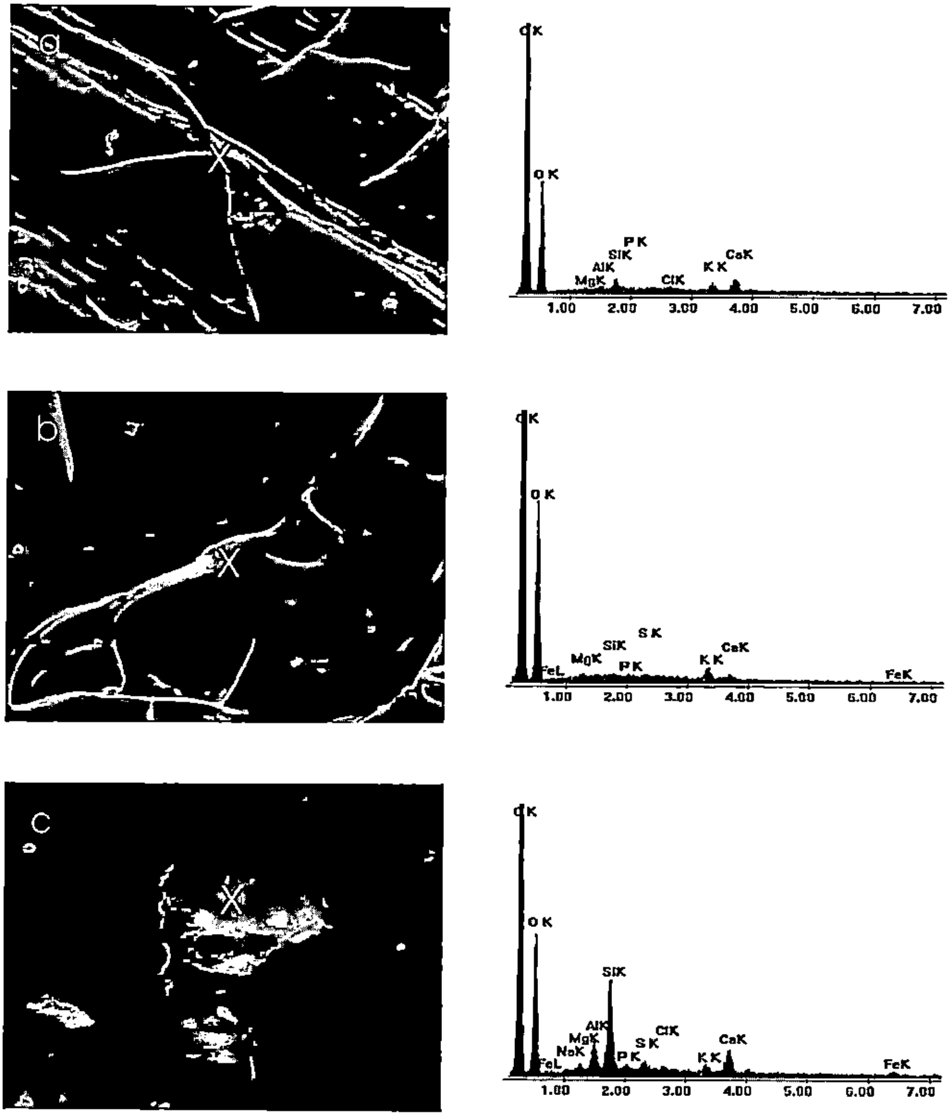

Fig. 6. EDX- analysis. a), b) Stellate hair of *Q. x viridis*; c) glandular hair with head from *Q. cerris*. X: where the analysis was done.

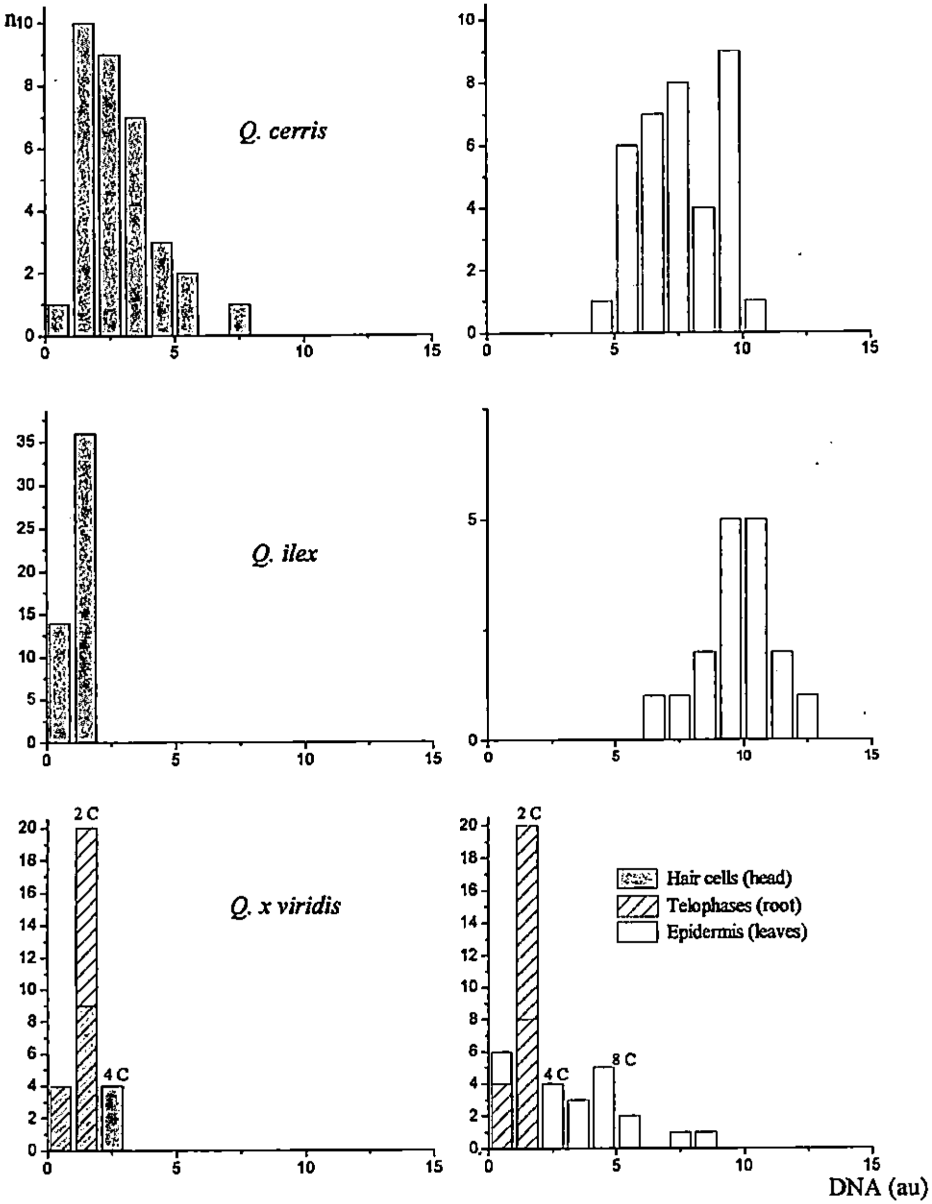

Fig. 7. DNA content in arbitrary units (au) of the nuclei of different kinds of cells of *Q. ilex*, *Q. cerris*, and *Q. x viridis*. n = number of nuclei.

DISCUSSION

Twigs were used for the investigation of the wood anatomy. The anatomy and dimensions of the twigs and the stem are very similar (Bosshard 1974). The results of Greguss (1959) and Huber and Rouschal (1954) were confirmed by our findings: the woods of *Q. cerris*, and *Q. pubescens* are ring-porous (see Fig. 1c, and d). The wood of *Q. ilex* is diffuse-porous (Fig. 1b). These results are confirmed by the measurements of the vessels of wood macerates: only *Q. ilex* has vessels with relative by small diameters and a low standard deviation (Table 1). *Q. x viridis* has not been described yet and has ring-porous wood (Fig. 1a). Tyloses were not found in our preparations, although the are typical for *Quercus* (Wagenführ and Scheiber 1989). The reason is that our wood had not developed heartwood because tyloses are found mainly in the transition between sapwood and heartwood (Wagenführ 1989). The area of the libriform fibers of *Q. x viridis* are smaller than those of the other investigated *Quercus* species: the fibers are shorter, but the diameters are nearly the same (Table 1). Greguss (1959) found triangular ray parenchyma cells in the wood of *Q. cerris,* while we found such cells in Q. *cerris* and *Q. x viridis*. The tangential face of the wood showed that *Q. cerris* and *Q. x viridis* have many rays only one cell broad and three to twenty cells high. To sum up the results of the investigation of the wood, the similarity of Q. x *viridis* and Q. *cerris* is evident, although there are some differences.

The investigation of the leaves showed that all had several layers of palisade parenchyma cells: we had collected sun leaves (Jurzitza 1987). Spongy parenchyma was loose, this means that we had adult leaves (Esau 1969). The epidermis cells of *Q. ilex* were much bigger and showed a positive wood reaction in their cell walls, therefore *Q. ilex* has xeromorphic leaves (Larcher 1994).

Simple uniserate hairs are very common in the genus *Quercus* (Hardin 1976). We found these hairs abaxial near the veins in *Q. x viridis.* and fragments also in *Q. cerris* leaves. In *Q. ilex* leaves these kinds of hairs were missing (see Table 1). Llamas et al. (1995), Penas (1997) also did not find these kind of hairs in Q. *ilex*. Westerkamp and Demmelmeyer (1997) found hairs with heads, uniserate hairs and peltate hairs in *Q. cerris* leaves, and uniserate hairs which were only adaxial.

The DNA-contents show that our measurements accord well with the results in literature: we found in telophases of *Q. x viridis* 1.20 ± 0.26 pg.; in 2 C nuclei of *Q. petraea* 1.8 pg (Benett and Leitch 1995, Greilhuber 1988), 1.58 pg (Ohri and Ahuja 1990), and 1.87 pg were found (Favre and Brown 1996), in *Q. robur* 2C = 1.59 pg (Ohri and Ahuja 1990), 1.84 pg (Favre and Brown 1996). Olszewska and Osiecka (1984) found in *Q. sessilis* 2C = 1.0 pg. Also the DNA-contents of the nuclei of the head cells of the trichomes of *Q. x viridis* (1.53 pg ± 0.68) and *Q. ilex* (1.40 pg ± 0.42) are within these values.

In conclusion, *Q. x viridis* the most similarities to *Q. cerris*. *Q. ilex* seems not to be one of the ancestors of this tree. Further investigation should be done clerify more details of this interesting tree.

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ANATOMIJA *QUERCUS* X *VIRIDIS* TRIN., HRASTA NEPOZNATOGA PORIJEKLA U HRVATSKOJ

Blizu Zadra, u Hrvatskoj, raste hrast koji se razlikuje od ostalih lokalnih hrastovih vrsta u okolici: *Quercus* x *viridis* Trin., zvani "zeleni hrast". Kako bismo razjasnili porijeklo ove vrste, istražili smo anatomiju drva i lišća (posebno smo istražili dlake i epidermske stanice). Istraživanje je provedeno različitim metodama: tehnikom svjetlosnoga i elektronskoga mikroskopskoga skeniranja (visoki vakuum i ESEM) u kombinaciji s digitalnom analizom slike. Usporedili smo rezultate anatomije drva s rezultatima *Q. cerris*, *Q. ilex* i *Q. pubescens* iz okolice i literature. *Q. cerris, Q. ilex* i *Q. pubescens* trebali bi biti preci *Q.* x *viridis*. Ispitivani su listovi *Q.* x *viridis, Q. cerris* i *Q. ilex*. Obavljena su brojna mjerenja i histokemijske reakcije sa stanicama epiderme, dlake i korijenskoga meristema. Za određivanje elemenata u dlaci korišten je EDX, a sadržaj DNA u jezgrama je izmjeren pomoću reakcije Fuelgen u kombinaciji s denzitometrijskom metodom.

Stabla *Q.* x *viridis, Q. cerris* i *Q. pubescens* prstenasto su porozna, *Q. ilex* je difuzno porozan. što se tiče sržnih traka, anatomija *Q.* x *viridis* i *Q. cerris* vrlo je slična, a trokutaste stanice traka su pronađene samo u preparatima tih stabala. *Q.* x *viridis* ima pet različitih tipova dlaka, a ostali istraživani hrastovi samo četiri. *Q.* x *viridis* i *Q. cerris* imaju vrlo sličan broj dlaka na adaksijalnoj površini lista. Broj dlaka na adaksijalnoj površini je različit, *Q.* x *viridis* ima manje dlaka. Veličina dlaka kod *Q.* x *viridis* i *Q. cerris* je slična. U svim su dlakama pronađeni lipidi i kutikule, samo su stanični zidovi dlaka *Q.* x *viridis* neznatno drvenasti. Analiza EDX nije pokazala prisutnost kremena ili vapna. Mjerenje DNA je pokazalo sadržaj od 1,2 pg za 2 C jezgre *Q.* x *viridis*, *Q. ilex* ima 1,4 pg (korijenski meristem). Većina jezgri stanica dlaka ima sadržaj DNA od 2 C (svi istraženi hrastovi), neki od njih 4 C i 8 C (*Q. cerris*). Jezgre stanica epiderme imaju sadržaj DNA do 16 C.

U ovom se radu razmatraju rezultati ovoga istraživanja i porijeklo "zelenoga hrasta".

Ključne riječi: anatomija, *Quercus,* analiza slike, elektronska mikroskopija, sadržaj DNA u jezgri

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žUDK 630*811+165+(44)

HOMOGENISATION: A MATHEMATICAL TECHNIQUE USED TO PREDICT THE SHRINKAGE OF OAK AS A RESULT OF THE ANNUAL RING MORPHOLOGY AND THE MICROSCOPIC PROPERTIES OF TISSUES

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As a result of its plant origin, wood is a very complex material which is heterogeneous and highly variable. Homogenisation techniques are used in this work to propose a deterministic approach to oak properties. The latter requires two kinds of information:
- the morphology that describes the spatial distribution of the components
- the intrinsic properties of each anatomical component.

From these pieces of information, the macroscopic properties are calculated by homogenisation. This paper is devoted to mechanical and shrinkage properties.

The microscopic properties have been measured with the help of specific experimental devices previously developed in our laboratory.

A new numerical X-ray imaging system is presented. It generates numerical images of the annual ring structure. After the separation of different components by image processing, a Finite Element mesh is built. Finally, a specifically developed computational tool, *MorphoPore*, solves four homogenisation problems. This software calculates the macroscopic properties of the complete annual ring.

Two examples are proposed which show how the morphology of the annual ring can be taken into account for the prediction of mechanical and shrinkage properties.

The first example proves that the proposed approach is capable of quantifying the influence of morphological variations using virtual structures.

The second example deals with two successive actual annual rings: the first one is thin and the second one is large. The influence of morphological changes due to the growth rate of the tree becomes obvious.

The most innovative aspect of this tool is that the influences of parameters due to genetic and growth conditions of the tree can be distinguished.

Key words: shrinkage properties, mechanical properties model, morphology, homogenisation

INTRODUCTION

Oak is a high valued species. Unfortunately, it is also renowned for being very difficult to dry. Among several reasons that can explain this behaviour, shrinkage values in the transverse plane are commonly involved when cracks or warping occur.

As a result of the biologic activity of the tree, wood is a material with high varying properties, both within a tree and from one tree to another. This variability is controlled both by the genetic origin of the tree and by its growth conditions, from which results the anatomical structure of wood. The observation of this structure reveals that wood is a complex composite material. It is generally composed of layers of early wood and late wood made up of highly elongated cells in the longitudinal direction. In the case of oak, the different kinds of cells are grouped and form zones that can be distinguished according to their density, form or orientation in the transverse plane. The diversity of these components, their intrinsic properties and their spatial organisation are parameters that must be taken into consideration to investigate its shrinkage and mechanical properties (Kollman and Coté 1984, Gibson and Ashby 1988, Watanabe 1998). However, it is very difficult to evaluate quantitatively the structural organisation of wood and microscopic properties of its components.

Different ways are possible to understand the properties of wood. In the present study, we opted for a deterministic approach. Several scales of observation are conceivable. For example, at the cell level, the arrangement of the cells is an important parameter for the understanding of the mechanical properties (Koponen 1991, Farruggia 1998). In this paper we show how the spatial distribution of the different tissue zones of one annual ring of oak can be taken into account to determine its shrinkage and mechanical properties. The homogenisation techniques are highly appropriate for the study of heterogeneous materials. Figure 1 shows that this deterministic approach requires two types of data:

- the morphology, that is, the definition of the different structural elements of the composite and their spatial distribution in the material,
- the microscopic properties: the modelling of shrinkage implies that the mechanical and the shrinkage properties of each constituent of the heterogeneous material be known.

This paper is divided in 3 parts:

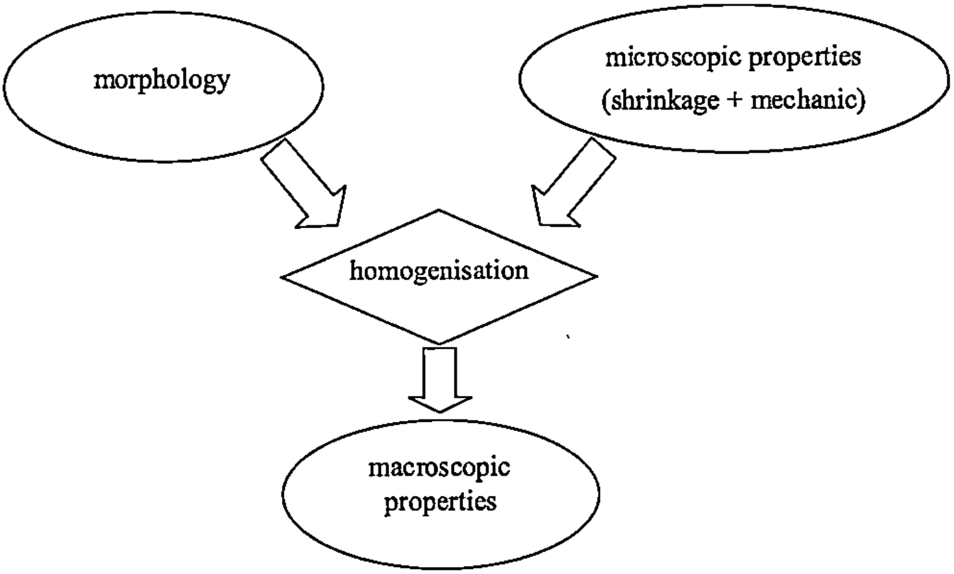

Fig. 1. Principle of the determinist approach. Assuming that the spatial distribution and the microscopic properties of the components are determined, the homogenisation techniques permit calculation of the macroscopic properties of the composite material.

- description of the material structure. A new numerical X-ray imaging device has been specially developed in order to describe the wood morphology at the annual ring level,
- construction of a numerical finite element mesh from the previous image,
- calculation of the macroscopic properties with the help of a specific numerical tool, *MorphoPore* (Perré 1998), which uses homogenisation techniques. Two examples are presented. At first, a virtual oak structure is used to modify and control morphology parameters. Then, the method is applied to real structures in order to predict the influence of growth conditions on the morphology changes.

DESCRIPTION OF THE MATERIAL STRUCTURE

The determinist approach requires morphological information of the actual structure of the material. At the annual ring scale, wood is almost a bi-dimensional material. That explains why the principle of X-ray projection is highly appropriate for its study (Polge 1966). Because materials absorb X-ray according to their density, X-ray techniques are commonly used in wood sciences in order to get information on the internal structure. For our description objective, the main idea is that the different tissues of an annual ring absorb differently the X-ray beam.

We developed a new numerical X-ray imaging system based on these principles: attenuation and bi-dimensional projection. The device is mainly composed of:

- a microfocus X-ray source. Its specificity is the very small size of its spot (Ø ≈ 8 μm). This characteristic allows X-ray magnification without detrimental fuzziness. The voltage can vary from 10 kV to 80 kV and the source intensity from 0 to 100 μA,
- a scintillator. This element is a converter. It absorbs the energy of the X-ray beam and re-emits it into visible light,
- a 2D detector. The detector is a coded CCD camera. The low temperature (-35°C) allows long acquire time with very low noise. This specific characteristic is required because of the very low photon flux of the microfocus X-ray source. The CCD is made of 1317× 1035 small pixels (6.8×6.8 μm^2 each). A computer drives the camera and records the image.

The physical principle is as follows: the sample absorbs a part of the incident X-ray beam. The scintillator converts the residual beam into visible light, which is deviated by a prism in order to protect the CCD camera from the X-photons. (Figure 2).

The X-ray magnification is determined by the position of the sample support. Figure 2 shows the device with an adjustment for a magnification around ×3. In this configuration, the spatial resolution, determined according to relevant methods (Kaftandjian 1996), corresponds to 25μm.

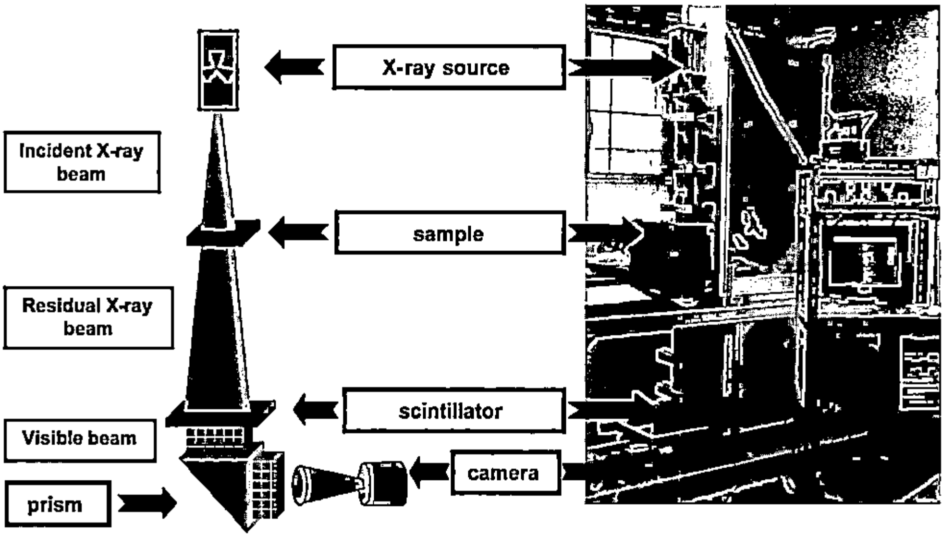

Fig. 2. General setup of the numerical X-ray imaging device. The energy of residual X-ray beam (after the sample) is converted into visible light that is detected by a cooled CCD camera.

The grey level recorded on the image (I_R) is proportional to the number of photons transmitted through the sample. Specific image processing permits us to obtain the attenuation ratio I/I_0 (I_0: intensity of the incident beam; I: intensity of the residual beam).

At first, a complementary image is acquired without X-ray illumination. This allows the offset of the camera and the mean noise level to be evaluated and corrected as the real intensity I_R - I_B. In addition, another image permits the intensity of the incident X-ray beam to be measured. This final image, calculated pixel by pixel, is free of spatial non-uniformity. This third image is called "Flatfield". Finally, the grey level of each pixel is calculated as follows:

$$G(i,j)=\frac{I_R\,(i,j)-I_B\,(i,j)}{I_F\,(i,j)}$$

i,j : coordinates of the pixel on the image

I : intensity of the pixel

G is in a theoretical range from 0 to 1 and can be directly interpreted as the physical ratio I/I_0, which can be calculated (for a polychromatic X-ray beam) as follows:

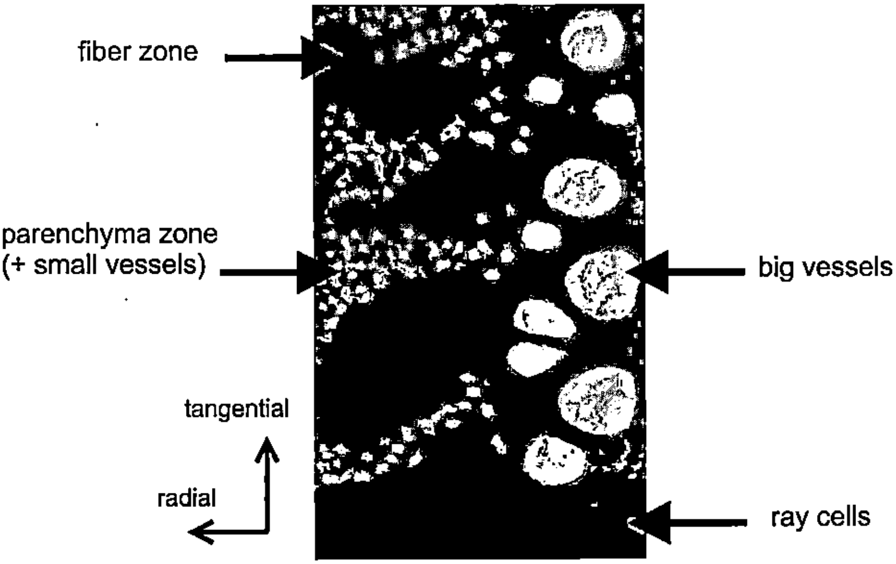

Fig. 3. X-ray image of a cross section of oak. The spatial resolution permits us to distinguish details as small vessels in the late wood. The observation shows that the main components are: the big vessels (early wood), the ray cells, the fiber zone and the parenchyma zone.

$$\frac{I}{I_o}=\frac{\int_0^\infty I_0(\lambda)e^{-\mu_m(\lambda)\rho x}d\lambda}{\int_0^\infty I_0(\lambda)d\lambda}$$

λ: wavelength
I: intensity
μ: attenuation coefficient
ρ: density

A specific study permitted us to define the best exposure parameters. The best resolution for the ratio Signal/Noise requires high voltage in order to increase the X-ray photon flux. With such conditions (70 kV), an accuracy of 1 % can be reached within 30 min. Figure 3 depicts an example performed with an X-ray magnification ×3. The four main components of an annual ring of oak become evident: the big vessels in the early wood, the ray cells and the late wood that is composed of fiber and parenchyma zones. The grey levels in the vessels are equal to 1 (100 % of the intensity of X-ray beam is transmitted). The darkest part corresponds to dense tissues as fiber (G<1).

FROM THE X-RAY IMAGE TO THE FINITE ELEMENT MESH.

The X-ray image is the basis for the construction of a Finite Element mesh, which represents the actual structure of the material. According to their intrinsic X-ray attenuation properties, the different components of the annual ring are separated. This operation is performed with the help of an image analysis system (VISILOG). Then, the boundaries of the different zones are extracted, smoothed

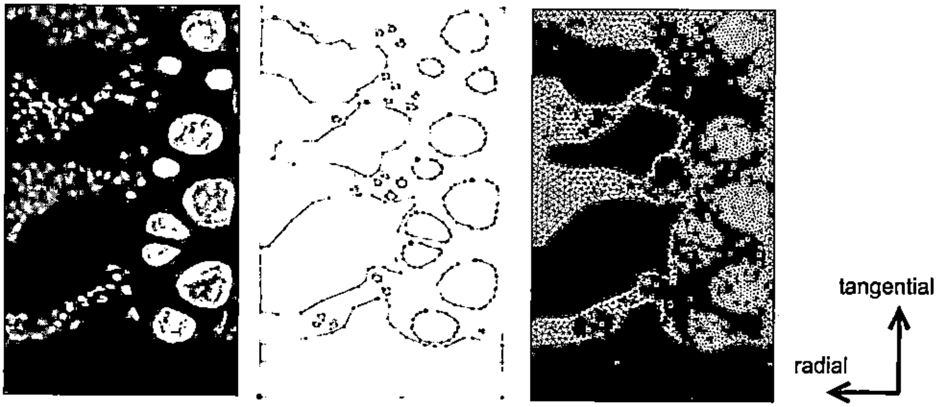

Fig. 4. From the X-ray image to the triangular Finite Element mesh. The different tissues are separated, their boundaries detected, vectorized and the numerical mesh is built.

and vectorised. The size of the segments, which define the contours of the different zones, is chosen for each type of tissue. In this study, we distinguish the big vessels, the fiber zone, the parenchyma zone and the ray cells. Finally, specific software, Easymesh (Niceno 1996) generates the F.E. mesh using triangular elements, which permit us to fit the boundaries of the complex forms. Figure 4 shows different steps from the image to the final F.E. mesh.

CALCULATION AND EXAMPLES

Homogenisation techniques are highly appropriate for the study of heterogeneous material (Suquet 1985). Assuming that the described annual ring is a representative cell of the periodic material, specific software "MorphoPore" specially developed for this study (Perré 1998) calculates the macroscopic (or homogenised) properties. It solves four different problems (1for shrinkage and 3 for mechanical problems) according to the microscopic properties of the different components. These come from specific experimental studies (Badel 1999, Badel and Perré 1999). The main microscopic properties in the transverse plane are:

– rays cells: high rigidity and low shrinkage,

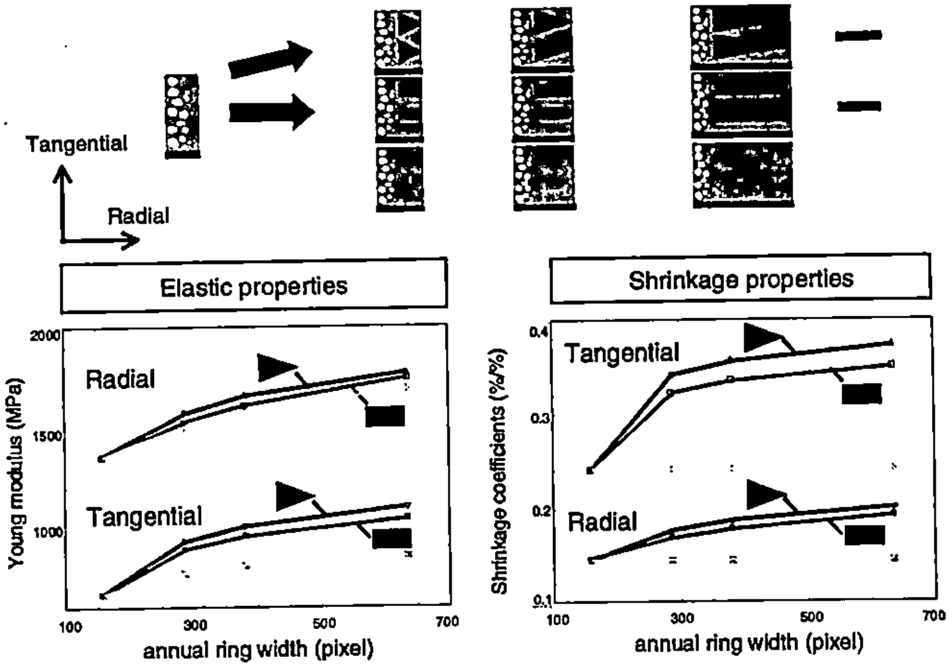

Fig. 5. Effect of annual ring width increase and fiber zones form on elastic and shrinkage properties of oak in the radial-tangential plane (virtual annual rings)

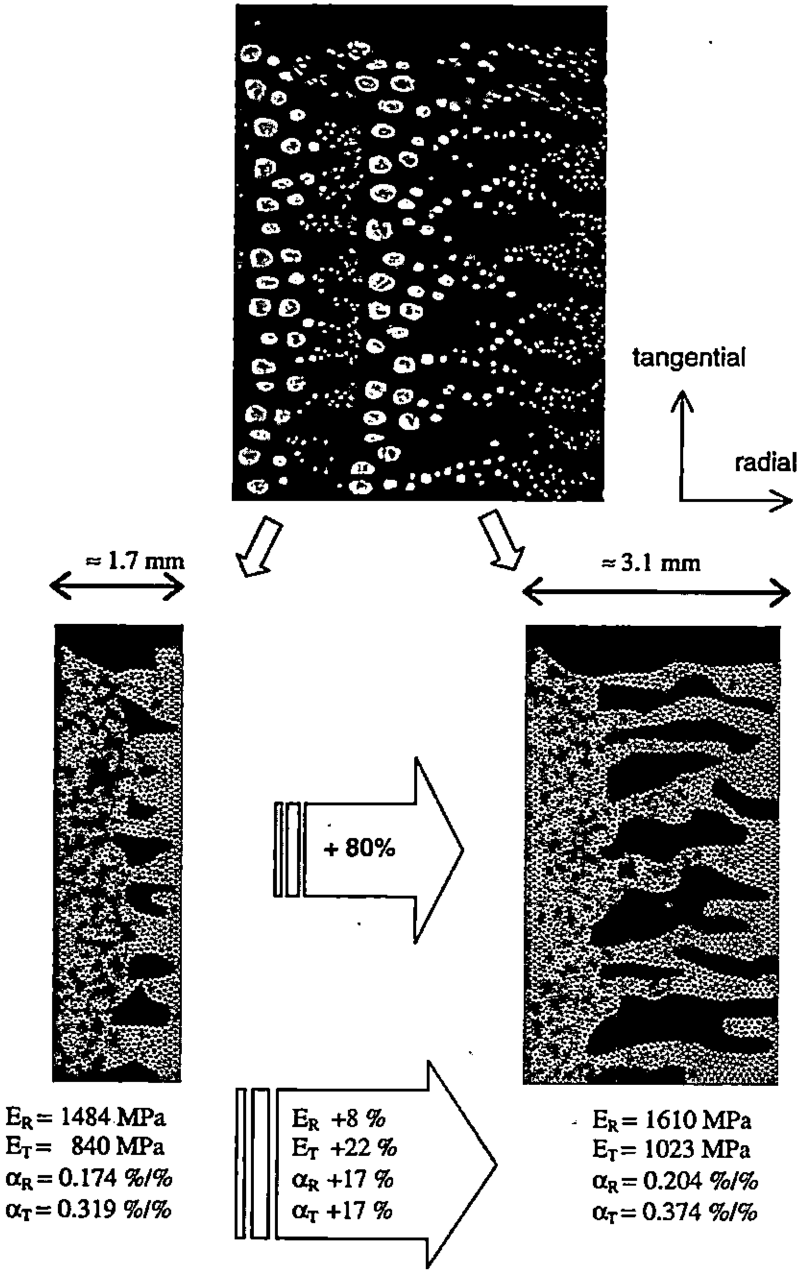

Fig. 6. Effect of growth width and fiber pattern on elastic and shrinkage properties of oak in the radial-tangential plane (actual annual rings). The microscopic properties of each tissue are supposed to be identical in the two configurations.

- fiber: high rigidity and high shrinkage (specially in tangential direction),
- parenchyma: medium rigidity (with high anisotropy : E_R/E_T č 2) and medium shrinkage (with high anisotropy : $\alpha_R/\alpha_T \approx 0.5$).

The first example uses an actual image of the oak's structure that has been modified in order to control morphology parameters. The annual ring width has been virtually increased. The early wood (real structure) does not change, whereas the late wood has been increased (virtual structure).

Three configurations have been tested:
- late wood without fiber zone
- late wood with rectangular fiber zone
- late wood with triangular fiber zone

The fibre proportion is exactly the same in the two last configurations. Figure 5 represents the evolution of the macroscopic properties of these three cases as a function of the annual ring width.

First, we observe that all properties (shrinkage and Young moduli) increase with the annual ring width. However, the evolution is different according to the direction and/or the late wood structure. The increase is the most important in the case of the triangular fiber zone and very low in the case of late wood without fiber. As the variations are not the same in the two directions, the anisotropy of the properties (well known to be an important factor for drying stresses) is modified. Note that the macroscopic shrinkage values do not vary if fiber is absent in late wood.

This example shows that it is possible to quantify the effect of morphological variations. In particular, we can now separate the influence of genetic parameters from other parameters due to the growth conditions of the tree.

The second example uses only actual morphology. It compares two successive annual rings (Fig. 6). The first has a very low width (1.7 mm) whereas the second has a very large width (3.1 mm). This configuration (a very important increase in annual ring width) is certainly due to a strong thinning resulting from silvicultural action. As already observed in the previous example, all the properties increase. The shrinkage coefficient increases by the same amount in the two directions (+ 17 %), whereas the Young moduli increase differently, inducing a modification of the anisotropy ratio.

This example shows the possibility to study actual morphology and to quantify the effect of parameters due exclusively to the growth conditions of the tree. In this case, the tool gives predictive answers to foresters who want to know the consequences of silvicultural actions.

CONCLUSION

A comprehensive tool chain is now operational for the determination of the elastic and shrinkage properties in the transverse plane of oak according to its microscopic characteristics. Using microscopic properties and a structural description obtained with the help of specific experimental devices developed in the laboratory, the numerical tool *MorphoPore* applied homogenisation techniques in order to calculate the macroscopic properties of the complex structure described by a Finite Element mesh.

Two applications are presented which work with virtual or actual morphologies. They permit us to underscore that the effect of genetic and growth parameters can be separated and quantified. This tool can be used in order to understand the role of the different parameters and, on the other hand, it can be employed as a predictive tool to quantify the effects of a change in growth conditions.

Note that a new version of MorphoPore is now available. It computes the microscopic stress field due to shrinkage. These new output possibilities display the zones of the annual ring where the stress is the most important according to the spatial distribution of the anatomical constituents.

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HOMOGENIZACIJA: MATEMATIČKA TEHNIKA ZA PREDVIĐANJE UTEZANJA HRASTA KAO REZULTAT MORFOLOGIJE GODOVA I MIKROSKOPSKIH SVOJSTAVA TKIVA

Zbog svojega biljnoga porijekla drvo je vrlo kompleksan, heterogen i varijabilan materijal. U ovom se radu primjenjuju tehnike homogenizacije radi predlaganja determinističkoga pristupa svojstvima hrasta. Za to su potrebne dvije vrste podataka:

- morfologija koja opisuje prostornu distribuciju komponenata
- urođena svojstva svake anatomske komponente.

Iz tih se podataka homogenizacijom izračunavaju makroskopska svojstva. Ovaj je rad posvećen mehaničkim svojstvima i svojstvu utezanja. Mikroskopska su svojstva izmjerena pomoću posebnih eksperimentalnih naprava koje smo prije razvili u našem laboratoriju.

Predstavljen je novi numerički rentgenski slikovni sustav. On daje numeričke slike strukture godova. Nakon odvajanja različitih komponenata obradom slike dobiva se mreža finitnih elemenata *(Finite Element mesh)*. Na kraju posebno razvijen računalni program, *MorphoPore*, rješava četiri problema homogenizacije. Taj softver izračunava makroskopska svojstva kompletnoga goda.

Predložena su dva uzorka koja pokazuju kako se morfologija godova može uzeti u obzir za predviđanje mehaničkih svojstava i svojstava utezanja. Prvi primjer dokazuje da se predloženim pristupom može kvantificirati utjecaj morfoloških varijacija korištenjem virtualne strukture. Drugi se primjer bavi dvama sukcesivnim stvarnim godovima: prvi je tanak, a drugi je velik. Utjecaj morfoloških promjena zbog brzine rasta stabla postaje očigledan.

Najinovativniji aspekt ovoga programa sastoji se u tome što može razlučiti utjecaje parametara koji nastaju zbog genetskih uvjeta i uvjeta rasta stabla.

Ključne riječi: značajke utezanja, mehaničke značajke, model, morfologija, homogenizacija

J. Hansen: Dendroecological analysis of vessels on cross sections of european oak
Glas. šum. pokuse 37: 173–187, Zagreb, 2000.

UDK 630*811+186+453+(430) (Quercus robur L.)

DENDROECOLOGICAL ANALYSIS OF VESSELS ON CROSS SECTIONS OF EUROPEAN OAK

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Changing environmental conditions that have an impact on growth, such as climate and weather, competition, insect defoliation etc., induce varying cell structures within tree rings. On the basis of cell characteristics and the location of cells on the tree ring, this structural variation can be transformed into quantitative data. A novel method for the preparation of samples for high-resolution reflected-light microscopy in combination with a finely tuned system for cell structure analysis provide the prerequisites for a continuous microscopic analysis without patching or sub-sectioning. Corresponding measurement series for vessel parameters have been performed for several oak collectives felled in the South-West of Germany. By describing the interannual and intraannual distribution of earlywood vessels across entire disc radii or disc diameters, the author examines the anatomical patterns of the samples against weather records. In addition, the investigation took the phenomenon of oak decline and the impact exerted by the gypsy moth calamities of 1993/94 into account. The results produced in the course of these investigations are introduced and evaluated against the long-term goal of the description and forecasting of the growth reaction of oak to various environmental phenomena.

Keywords: earlywood vessels, growth reactions, oak decline, gypsy moth, defoliation

INTRODUCTION

Over recent years, dendroecological research based on tree-ring characteristics has gained in significance. In addition to the macroscopic properties of tree rings, such as tree-ring width, parameters in the microscopic range have now become of interest (e.g. Eckstein and Frisse 1982, Merkel 1984, Woodcock 1989, Vaganov 1990, v. Wilpert 1991, Saß and Eckstein 1995, Astrade and Begin 1997). By matching these tree-ring properties with well-known environmental events, models explaining and predicting the growth reactions to these events can be developed. Such environmental events include a variety of factors, such as insect defoliation, climate and weather. Both recent and (sub-) fossil cross sections can be used for retrospective identification and research on these environmental changes, their development, and dynamics. Such information can cover remarkably large time spans. Cell structure analysis within the individual tree rings allows for a more detailed examination of the relationships between forest growth and environmental influences. Its advantage over other analytical approaches, such as analysis of density or isotopes, is that the latter are less detailed because they often integrate across several cells. Until recently, extensive research projects were not possible due to the enormous amount of work involved in the measurements of cell parameters using ocular micrometers, screens, or linear micrometers. Modern computer technology and microscopic image analysis provide the prerequisites for more efficient measurements of cell structures across sequences of tree rings, i.e. the evaluation of the inevitably large quantities of data (e.g. Lee and Rosen 1985, Yanosky and Robinove 1986, Schnell and Sell 1989, Lewark and Klosa 1992). High quality preparation of samples is required in order to realise the complete potential of software-supported analysis (Sell 1978, Sachsse 1984, Lewark and Klosa 1992). Using such an extensive sample preparation procedure plus a high-resolution method of analysis, which is finely tuned to the preparation method, this investigation examined samples from different sites along the Rhine valley. In this, the established approach of investigating radial increment is combined with an analysis of vast sets of cell parameters to identify the invisible links between cell parameters on one hand and environmental occurrences on the other.

MATERIALS

This investigation considers two phenomena: first, the impact of insect defoliation on the increment of oaks, and – as the second focus – growth as observed in dying oaks. For this purpose, a total of 21 sample trees were selected from two areas of the upper Rhine valley.

The first area covered by this investigation is the *Bienwald*, the area in the Rhineland-Palatinate most affected by the gypsy moth calamities observed between 1992 and 1994. The *Bienwald* area is located close to the German-French border and in the south-west of Karlsruhe. In stands of *Quercus robur* affected by gypsy moth defoliation, the forest community witnessed an increased number of specimens of all age categories which were in the process of dying. In some cases this resulted in the destruction of entire stands.

The second area of interest in this investigation is the *Hardtwald*, which is located in the upper Rhine valley between Freiburg and Basle and mainly belongs to the south-eastern part of Alsace. In this area, comprising a forest of 18,000 hectares dominated by oak-hornbeam forests, dying oaks have been observed since 1963. Starting in the 90s, a dramatic increase in the number of affected trees became the motive for intensified research efforts.

Table 1 provides some core data describing the two sites selected for this investigation.

Table 1. Core data for the sites examined.

	Bienwald	Hardtwald
Region	Northern part of the upper Rhine valley (Rhineland-Palatinate)	South-western part of the upper Rhine valley (Alsace)
Statistics of climate (long-term mean [1947-1996] of the weather stations Karlsruhe and Basle)		
Mean air temperature / year	10.4 °C	9.7 °C
Mean air temperature / Grow. season (May-September)	17.2 °C	16.2 °C
Precipitation sum / year	765 mm	785 mm
Precipitation sum / Grow. season (May-September)	354 mm	406 mm
Slope	0 %	0 %
Rock stratum	Alluvial detritus and sands deposited by the Rhine ("*Bienwald* gravel")	Rhine alluvium

In the area of *Bienwald* two stands, which showed different growth reactions to the environmental conditions in the years before felling in 1997, were chosen for the investigation of defoliation on the growth of oak. On the first stand (Section 21), about 45% of the oaks died in the aftermath of partial gypsy moth defoliation in 1993 and complete defoliation in 1994. A large number of the remaining specimens of this stand showed a marked reduction in crown foliage. After complete defoliation in 1994, the second stand (Section 26) shows a much smaller mortality of approximately 5%. In addition, the vitality of the surviving specimens has not been reduced as much as in Section 21. The two stands are located at a distance of six kilometres. Thus, with the exception of soil-related stand properties, possible differences in overall environmental factors should be of no importance.

In the late summer of 1997, a total of eleven specimens were selected on these investigational stands and felled during the following winter season. Trunk discs were cut at 1.3 metres. For both sites, representative specimens were chosen, i.e. a crown evaluation was conducted to find trees whose degree of vitality corresponded to the overall condition of the stand. On Section 21, whose oak collective was in the process of dying, the investigator selected specimens of a deteriorated or fatal condition. These trees had suffered defoliation of 70 to 90 percent. In general, the oak collective on Section 26 was healthy and included only individual trees which were in the process of dying. Hence, the specimens felled here were either healthy or showed only minor signs of a deteriorated condition. The degree of defoliation on Section 26 was 35 to 45 percent. For all specimens collected, the investigator ensured that the intra-site growth conditions were identical. In addition, the crown projection areas of the specimens were evaluated with regard to their respective moisture condition. The crown projection areas for the sample trees collected on Section 21 showed a marked impact of water since the vegetation found was typical for wet sites (e.g. *Molinea caerulea, Deschampsia cespitosa*) and the fallen leaves had blackened. In contrast to these observations, the intra-stand growth conditions for the oaks of Section 26 did not include any signs of an obvious impact of surface water, such as colouring of leaves or vegetation with a preference for wet areas.

Table 2 summarises the main statistics for the two *Bienwald* stands affected by gypsy moth defoliation.

Table 2. Main statistics for the two investigational stands in the *Bienwald* area.

	Section 21	Section 26
Gypsy moth defoliation (year, mean defoliation)	in 1993: 40 % in 1994: 100 %	in 1994: 100 %
Mortality (1994 - 1997)	45 %	5 %
Age (years) in breast height at felling date	95.6 (92 - 103)	95.0 (92 - 99)
Radial increment: mean (1906 – 1996)**	2.27 mm	1.90 mm
Description of site		
Hydrology	(moderately) wet	(moderately) wet
Type of site	Layers of loam covered by sands	Sands
Soil classification	Pronounced Gley	(Podzol)-Gley
Microsite in the crown area	ground surface wet, fallen leaves of black colour*	ground surface without any visible influence of water
Rooting space	approx. 80 cm	approx. 90 cm
Altitude	128 m a.s.l.	120 m a.s.l.

* = corresponding vegetation: *Molinia caerulea, Deschampsia cespitosa* (L.) P.B., *Agrostis canina* L., *Carex acutiformis* Ehrh., *Carex elongata* L., *Carex remota* L.
** = maximum common overlap

In 1994 ten predominant and dominant trees were selected and felled in the northern part of the *Hardtwald*. As for the *Bienwald* specimens, the trunk discs used in this investigation were cut at 1.3 metres. At felling, crown evaluation for five of the sample trees found that these trees were either in the process of dying or were dead, while the remaining five showed a normal level of vitality.

Table 3 summarises the main statistics for the vital versus the dead / dying trees felled at the *Hardtwald* stand:

Table 3. Main statistics for the two sub-collectives (alive vs. dying / dead) at the *Hardtwald* stand.

	Alive at felling	Dying / dead at felling
Age (years) in breast height at felling date	123.1 (122 - 124)	122.6 (122 - 124)
Radial increment: mean (1873 - 1994)**	1.45 mm	1.53 mm
Description of site		
Hydrology Ground water level Rooting space Altitude	Fresh 20 m below surface > 100 cm 248 m a.s.l.	

METHODS

Using a band saw, a notch with a length of about one third of the radius was cut into each disc in order to minimise radial cracking. After the discs had been air-dried for several months, examination of radial increment was conducted along eight azimuthally-orientated radii on the basis of these complete trunk discs.

The analysis of vessels was done by means of reflected light microscopy and image analysis (Spiecker et al. 2000). To prepare adequate samples for cell structure analysis, complete cross sections were cut out of the discs and treated with a white wax to emphasise the contrast between the vessel lumina and the vessel walls. In order to produce very smooth surfaces necessary for cell structure analysis, the samples were prepared by an ultra-precise diamond flycutter. First, the sample surfaces processed by the ultra-precise diamond flycutter were recorded by a black-and-white video camera and stored in digitised form. Thus, the digitised images are available for subsequent computer evaluation, independent of the microscopic apparatus. In order to make the analysis of such samples prepared by the ultra-precise diamond flycutter more efficient, a semiautomatic image analysis system for oak was employed in this investigation. This system is adapted to the use of reflected-light microscopy and includes software modules for image taking and the detection of image components. The fundamental and therefore most important software module consists of the computer-supported selection and exact re-positioning of individual digitised images to re-assemble seamless image arrays of complete radii. This module allows the continuous determination of cell structure parameters over the entire life span of a tree and avoids the error-prone patching of sub-sectioned samples. In a second software module, the image components to be analysed are marked automatically on the basis of differences in grey values and identified by pattern recognition.

In this investigation, the earlywood vessel system of oak is of primary interest due to its physiological importance. After the completion of an interactive review, which was implemented to eliminate artefacts, the following distinctive cell parameters of oak were available for further statistical evaluation.

Beside the year of vessel formation and vessel area for each vessel, these parameters include the distance of the vessel from the tree ring border plus the exact location of the centre of gravity for each vessel. Along the radial tracks cut from the sample discs, i.e. from the bark to the core, this complete set of data was determined for each vessel with a diameter of at least 70 micrometers. On the basis of vessel area values and using the mathematical formula for the calculation of circles, a theoretical diameter was calculated for each vessel.

For each year, these parameters need to be combined in a useful fashion, if year-to-year changes within vessel properties are to be detected. The tree-ring area where the earlywood vessels are located constitutes only a section of the tree ring. This area was again divided into three sub-sections in order to reflect the various time-points of formation across the cambium. A system of three vessel rows, which is based on the allocation of vessels on the tree ring, was used as the basis for the division into sub-sections:

- vessel row 1 = distance from the tree ring border equal to or smaller than 70 micrometers
- vessel row 2 = vessels outside the first vessel row with a distance smaller than the average diameter of the vessels within row 1
- vessel row 3 = all vessels outside rows 1 and 2

Consequently, we now have four groups of vessel parameters (for each of the rows plus for the entire earlywood area) which summarise environmental factors of varying time periods. Vessel parameters of high summarising capacity, such as total vessel area or total number of earlywood vessels, describe growth development across longer time spans within the growth period than the remaining, high-resolution parameters, such as the vessel diameter in the last row of earlywood vessels, i.e. in row 3.

RESULTS AND DISCUSSION

Although the ring-porous structure of oaks enables this species to conduct water through a total of up to twenty tree rings, the youngest tree ring plays such a decisive role in the transportation of water that the conductive capacity of each tree ring deserves special attention (Ladefoged 1952, Fleischer 1989, Cermak et al. 1992, Granier et al. 1994). In older tree rings, water transport is almost exclusively implemented by the latewood vessels, since the functioning of the earlywood vessels has been destroyed by occlusion. In contrast to this situation, the earlywood structures of the youngest tree ring stand out within the water system of oak, as they have the highest speed – and thus the largest volume - of water flow.

Using the vessel areas calculated for all vessels on one tree ring in combination with the equation by Hagen-Poseuille, being

$$I = [[r^4 \cdot \pi / (8\ \eta \cdot 1)] \cdot (P_1 - P_2)$$

I = flow rate (μm^3 / s)
r = pipe radius (μm)
P_1 = pressure pipe entrance (Pa)
P_2 = pressure pipe exit (Pa)
l = length of pipe (μm)
η = dynamic viscosity of liquid (Pa · s), for water at 20°C approx. 10^{-3} Pa · s,

approximate values for the hydraulic conductivity of each sample tree were generated. Hydraulic conductivity constitutes a measure for fluid volume which can be transported through a vessel in a given time. In accordance with the Law by Hagen-Poseuille, a tube's water conductivity increases with the 4th power of its radius. This implies that doubling the vessel diameter results in a sixteen-fold increase in transportable water volume. Hence, this physical law underlines the fact that large vessels play a vital part in the water transportation of oak (Zimmermann 1983, Krejzar and Kravka 1998).

Since absolute height is of no interest in this regard - especially annual changes in hydraulic conductivity need to be considered - and due to the fact that values concerning the real pressure conditions (P_1 and P_2) inside the vessels were not determined, the investigator concentrated on the first term in the equation. Doing this, the difference in pressure present between the two ends of a vessel and the length of the vessel were assumed to be one Pascal and one micrometer respectively. The dynamic viscosity of the transported fluid, in this case xylem water, shows only slight variation which follows the minor changes occurring in the concentration of soluble contents and with temperature. Consequently, viscosity is assumed to be constant. The value typical for water and a temperature of 20 degrees Celsius is used. In view of this theoretical approach, one has to bear in mind that hydraulic conductivity as calculated in the context of the present investigation needs to be taken as a measure for the amount of water transportable through the earlywood vessels if a difference in pressure of one Pascal is assumed. With the constrictions just illustrated, this measure does not provide information on the real volume of xylem water transported by these vessels.

BIENWALD

The time series for hydraulic conductivity of the *Bienwald* sample trees (Figure 1) shows a *Gleichläufigkeit* of eighty-one percent. It is especially interesting that already in 1992, i.e. before the defoliation brought about by the gypsy moth, the two graphs show a marked downward trend. In 1993, average hydraulic conductivity for both collectives recovered slightly but from 1994 onwards they start to slump again. In 1995 the value for Section 26 reached the lowest level experienced over a period of 15 years while the corresponding result for Section 21 was even the lowest value determined within forty years. The reduction in average hydraulic

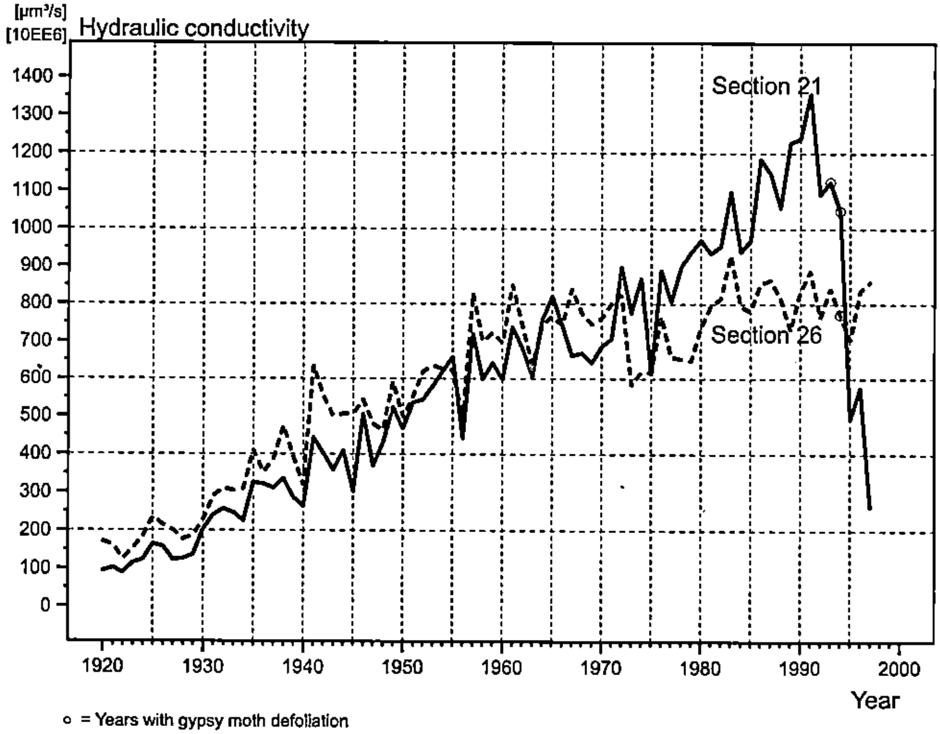

Figure 1. Comparison of annual means of hydraulic conductivity (in accordance with Hagen-Poiseuille) for the two oak stands examined at the *Bienwald.*

conductivity observed between the 1994 and 1995 values of Section 21 was unparalleled within the entire time series. In 1996, hydraulic conductivity showed a slight recovery in both stands, but in 1997 this trend was only continued within Section 26.

Considering the allocation to vessel rows in accordance with the distance of the vessel from the tree-ring border, Figures 2 and 3 show the average vessel diameters for the three rows and various years.

The graphs show that in 1991 and 1989 respectively, the average diameter of vessels in rows one and two started to decrease. After the gypsy moth defoliation in 1993 and 1994, the average vessel diameters of all rows dropped to the lowest levels since the 1920s. In contrast to hydraulic conductivity, this parameter did not recover in 1996 or 1997.

Unlike the results for the oaks on Section 21, the findings for the specimens from Section 26 did not show a decreasing trend. In 1995, there was merely a low result with regard to the vessel diameter in all rows. In the history of the vessel rows 1 and 2, which returned to much higher values in 1996 and 1997, the result of 1995 constitutes the lowest result since the mid-1970s. When compared to the

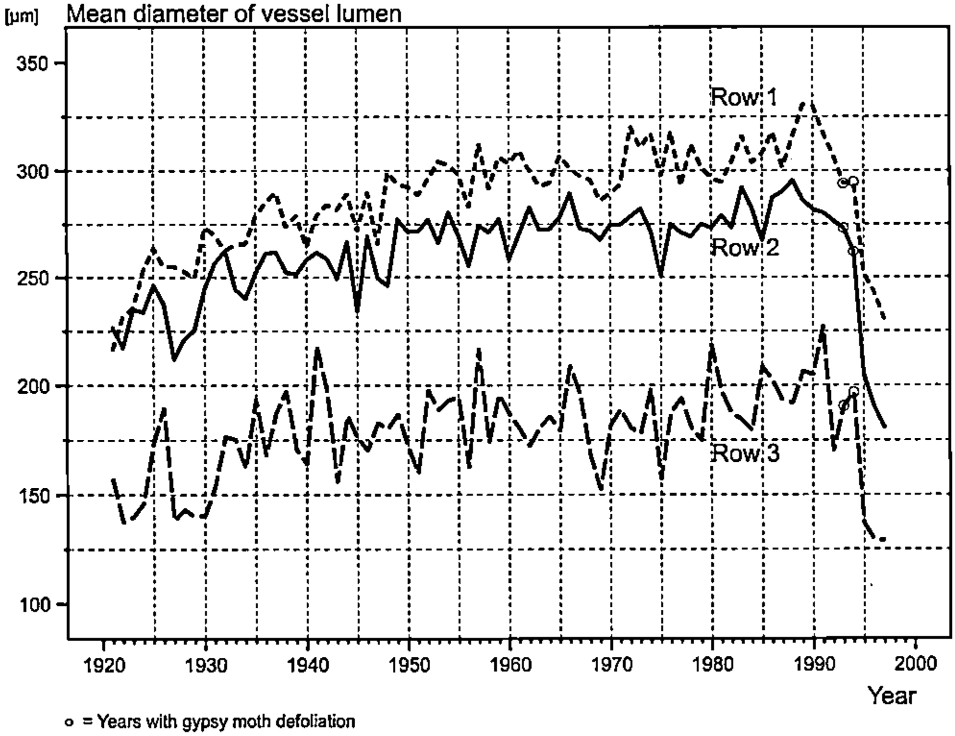

Figure 2. Annual mean vessel diameter for the three vessel rows, calculated for the oaks of Section 21.

corresponding values of the first two rows, the diameter results for the latest vessels (third vessel row) recovered with a delay of one year. As a consequence, the average vessel diameter of the third vessel row did not reach the level of the early 90s before 1997.

The results produced by the analysis of the earlywood structures of the sample oaks show that - regardless of maximum stress factors - all trees formed new earlywood vessels. In 1995, i.e. after defoliation by *Lymantria dyspar*, all earlywood vessel parameters determined for the sample trees show marked deviations from previous patterns.

Since the large majority of earlywood vessels in oak is formed before the budding of leaves, their formation is implemented on the basis of stored reserves from the previous year (Ladefoged 1952, Breda and Granier 1996). If the assimilation and storage of reserves are inhibited, for example in years of defoliation by phytophageous insects, this results in a reduction of the latewood area in the year of occurrence and a reduced formation of earlywood vessels in the subsequent year (Blank 1997). For this reason, the sample trees showed the most marked deviations in earlywood vessel parameters in 1994 and 1995. While the trees from Sec-

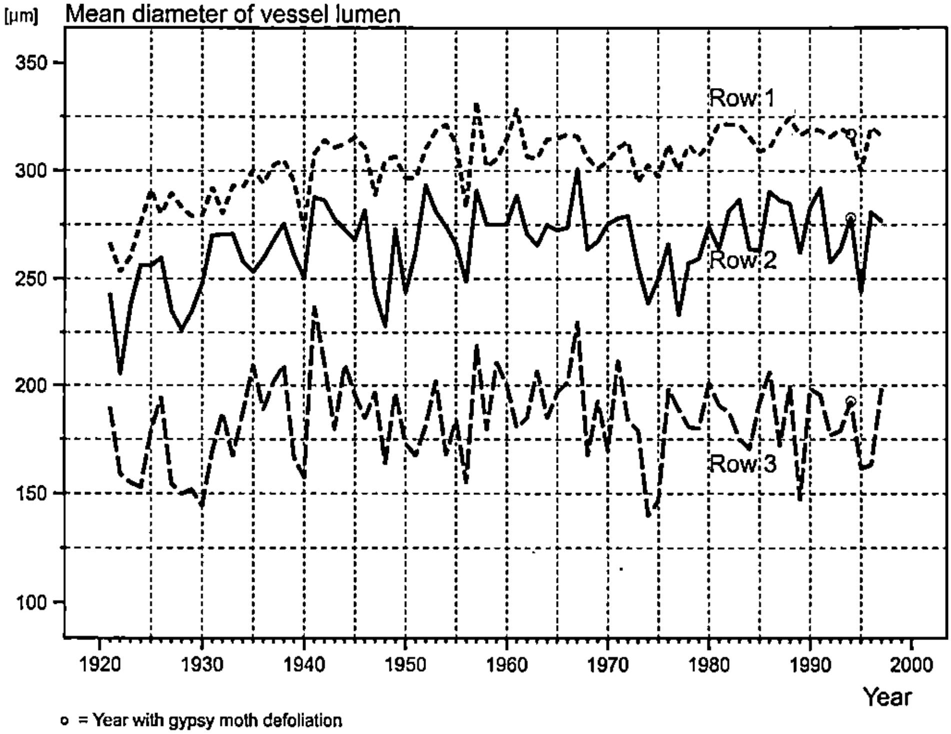

Figure 3. Annual mean vessel diameter for the three vessel rows, calculated for the oaks of Section 26.

tion 26 recovered in the subsequent years, i.e. their vessel parameters reached pre-defoliation levels in 1996 and 1997, the process of dying became manifest in the specimens from Section 21. In 1996, these sample trees enjoyed a short recovery with regard to hydraulic conductivity which did not continue in 1997. The stress factor defoliation hit the oaks on Section 21 in a period when the parameters for earlywood vessels were already in decline, i.e. they already reflected negative influences affecting their vitality. Hydraulic conductivity had declined markedly in 1992 and the vessel diameters of the first and second row of vessels for these trees decreased from 1989 and 1991 onwards. It is remarkable that this development coincided with the aftermath of the low-precipitation period from 1989 to 1991 and 1992, respectively. The annual deviation in moisture index from its long-term mean – as shown in Figure 4 - conveys some insight into this situation.

The moisture index equals precipitation in the growth period divided by the average temperature over the growth period plus 10.

Whether and to what extent such weather conditions may be the cause of the growth reactions illustrated above cannot be determined unless further investigations are conducted. To summarise the results of this investigation, one needs to

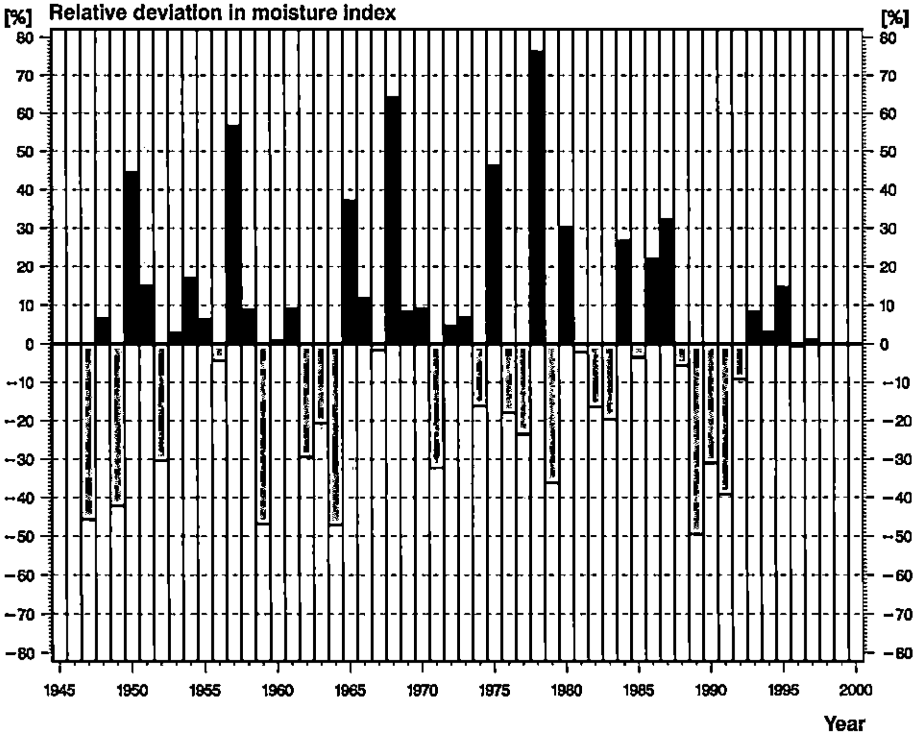

Figure 4. Annual deviation in moisture index for *Bienwald* stands compared to long-term mean.

state that no single factor can be identified that is responsible for the widespread oak calamities erasing even entire collectives. Therefore, it must be concluded that a combination of various stress factors, which - most probably - were present before the gypsy moth defoliation, are the cause of the devastating damage in the *Bienwald* oak stands.

HARDTWALD

The detailed examination of the cross sections by reflected-light microscopy – as done for cell structure analysis – confirmed the findings by the analysis of radial increment: for some of the oaks categorised as dying or dead, the process of dying had taken longer than one year. Showing strong impairment of their vitality, these trees were able to survive for one more year. While the cambium on one radius of the tree is already dead, radial increment is observed on another. Such surviving sections on the circumference of the tree are in some instances limited to a length of several millimetres to a few centimetres. Usually, they do not exceed the border presented by neighbouring wood rays.

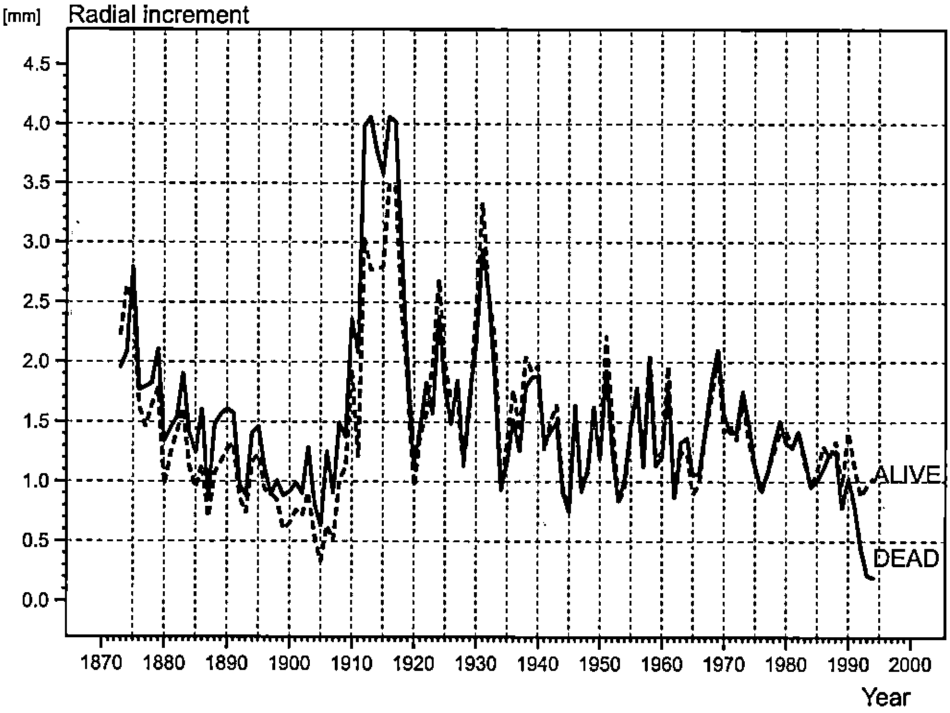

Figure 5. Comparison of mean annual radial increment for *Hardtwald* sub-collectives

Figure 5 shows a comparison of the two *Hardtwald* sub-collectives concerning their means for annual radial increment.

The specimens found dying or dead at felling show only slight growth deviation when compared to the vital sample trees. Especially for the period between 1920 and 1989, the two curves show remarkably close correlation (r = 0.93). Statistically significant differences later than 1925 can only be found for the years 1993 and 1994 (probability of error = 5%). The most striking observation consists of the decline in radial increment of the years 1991 and 1992, which was only reversed by the trees categorised as alive at felling.

Figure 6 provides an illustration of mean hydraulic conductivity of the alive as compared to the dead / dying specimens.

As for the analysis of radial increment for the two sub-collectives, the time series show close correlation (r = 0.93). However, when looking at the years 1986 and 1987, the time series for hydraulic conductivity document that the trees dying / dead at felling had a continued decline while the vital trees showed an upward trend. Due to the large variation in the individual values, the differences calculated fail to be of statistical significance. The only exception is marked by the year 1993.

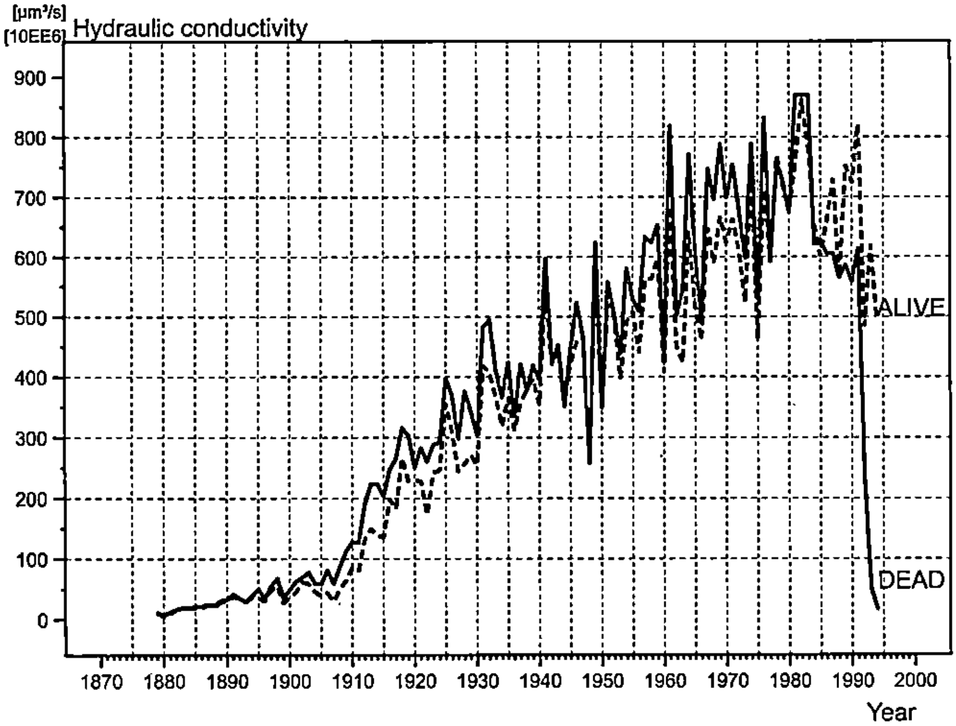

Figure 6. Mean hydraulic conductivity for alive versus dying / dead specimens from *Hardtwald*

It is especially interesting that the curves for both sub-collectives show a marked decline in 1992 which follows a peak in 1991. Only the oaks found alive at felling were able to compensate for this decline. For the other sub-collective, the year 1992 marks the beginning of the dying process.

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DENDROEKOLOŠKA ANALIZA ŽILA NA PRESJECIMA EUROPSKOGA HRASTA

Zbog promjenjivih okolišnih prilika koje utječu na rast, kao što su klima i vrijeme, konkurencija, golobrst zbog napada kukaca itd., stvara se različita stanična struktura u godovima. Na osnovi svojstava stanica i lokacije stanica na godu ta se strukturna varijacija može pretvoriti u kvantitativne podatke. Nova metoda pripreme uzoraka za svjetlosnu mikroskopiju visoke rezolucije u kombinaciji s fino ugođenim sustavom za analizu stanične strukture stvara preduvjete za kontinuiranu mikroskopsku analizu bez gruboga ili finoga usitnjavanja. Provedena je serija mjerenja parametara žila za nekoliko hrastovih skupina posječenih u jugozapadnoj Njemačkoj. Opisom višegodišnje i jednogodišnje distribucije žila ranoga drva preko cijeloga promjera diska ili dijametra diska autor ispituje anatomske uzorke u odnosu na vremenske prilike. Usto je ispitivanje uzelo u obzir pojavu sušenja hrasta i učinak napada gubara u sezoni 1993/94. Rezultati dobiveni tijekom ovih ispitivanja bit će predstavljeni i procijenjeni radi dugoročnoga cilja opisivanja i predviđanja promjena rasta hrastova s obzirom na različite okolišne pojave.

Ključne riječi: žile ranoga drva, promjena rasta, propadanje hrasta, gubar, golobrst

S. Govorčin, T. Sinković: Influence of double sapwood on the quality of slavonian oak
Glas. šum. pokuse 37: 189–200, Zagreb, 2000.

UDK 630*811+812 (Quercus robur L.)

INFLUENCE OF DOUBLE SAPWOOD ON THE QUALITY OF SLAVONIAN OAK

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The phenomenon which can be viewed macroscopically on the cross section of a tree trunk in the form of two rings lighter in colour than the darker heart in heartwood species is called double sapwood. The outer, larger ring which is located peripherally is the outer or true sapwood, while the smaller ring located in the heart itself constitutes double sapwood.

The practical implications of double sapwood result in properties that are as poor as those in true sapwood. This defect is especially significant because of its occurrence in oak trees. This significantly reduces the value of wood, primarily its aesthetic value, and bears heavy consequences in the exploitation of the most valuable assortments because of the development of rot which in turn reduces quality during processing.

In order to assess the influrnce of double sapwood, i.e. the changes in the properties of wood in these areas, a sample was taken from 10 trees of Slavonian Oak (*Quercus robur* L.) in which double sapwood was discovered immediately upon felling.

By monitoring the position of certain physical and mechanical properties of Slavonian Oak wood in a transversal direction, the achieved results enable us to establish the influence of double sapwood on the quality and use values of wood.

Key words: Slavonian Oak, double sapwood, physical properties, mechanical properties, quality

INTRODUCTION

In defect qualifications, double sapwood is sometimes qualified as a defect in colour (Ugrenović, A., 1932), sometimes as a natural defect (Brown, H.P., Panshin, A.J. and Forsaith, C.C., 1949) and sometimes as a wood defect and anomaly, i.e. it is placed in the category of natural defects and defects that appear in the production process (Côté, W.A. 1968), and sometimes it is categorised as a colour change defect (Horvat I., 1973).

Double sapwood is a defect which is visible in the cross section of heartwood species and is manifested in two sapwood rings which differ in colour from the darker heartwood. The outer sapwood ring is larger in diameter and represents common sapwood, while the inner ring (integrated sapwood) is of a lesser diameter and is situated in the heart itself. A ring of heartwood is located in between these two sapwood rings. Double sapwood can be found only in heartwood species and even here it is very rare. Double sapwood is especially present in oaks, but can also be found in larch and arborvitae. The border line of double sapwood is more or less pronounced and overlaps almost exactly with the border lines of growth rings. Buffon and Duhamel du Monceau (1737) established the occurrence of double sapwood in oaks in trees which grew on thin and dry soil and associated this with very low temperatures. Later research confirmed this theory and established that double sapwood appears as a result of the lack of the normal process of duramination due to low temperatures during the time when the inner sapwood ring forms the outerlayer of the tree (Mer E., 1896, Henry E. 1896). Because of the low temperatures, the starch cannot be transformed into duramination substances and because of this the normal duramination process does not occur. Temporary insufficient nutrition due to unfavorable weather conditions can also be a cause of double sapwood (several years of drought).

Although double sapwood in Slavonian Oaks is primarily treated as a colour defect, i.e. of an aesthetic value, in practice the wood has properties that are as poor as wood with outer sapwood. This means that this ring of wood shows significantly reduced durability and, because of this property, the wood is treated as reject wood.

RESEARCH MATERIAL AND METHODS

The material necessary for researching the properties of double sapwood in Slavonian Oak was taken from test trunk samples of 10 trees in Eastern Slavonia. Of the 10 trees, 3 were from the Lipovac Forest Administration, forest area of Topolovac, department 6a, and 7 trees were from the Vrbanja Forest Administration, forest area of Boljkovo, department 130b. The trees were chosen so as to best represent the stand in age, size, habitus, dendrometric elements and outer trunk properties. The trees were healthy, normal, with regular crowns, straight stems, average flawlessness and fulness of bole as well as grain texture. The only defect was the macroscopically evident double sapwood rings whose width indicated the posibility of extracting test samples necessary for establishing the physical and mechanical properties of Slavonian Oak in exactly these areas (Fig.1). The test trunk samples used for establishing the physical and mechanical properties were taken from mid-way between the ground and the first live branch in all 10 trees.

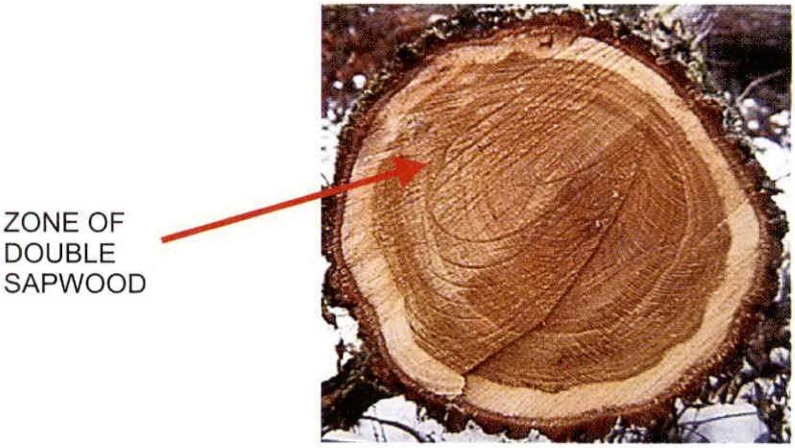

Figure 1. Cross section of oak with double sapwood zone

The trunk samples were taken immediately upon felling and were transported to the sawmill storage where, after approximately 30 days, they were made into heart boards oriented North-South and East-West. The heart boards were stacked and naturally dried until the water content was about 20%.

A maximum number of test samples was made from the heart boards, starting from the outer sapwood (last annual ring) towards the anatomical centre.

To test the physical properties, samples were made for testing the density in an absolutely dry condition, and samples were prepared for testing volumetric shrinkage in accordance with ISO 3131:1975 and ISO 4858:1982. To test the mechanical properties, we made samples for testing compression strength parallel to the grain and samples for testing bending strength in accoradnce with ISO 3787:1976 and ISO 3133:1975.

RESULTS

The results achieved through testing have been classified into areas (zones) which can be macroscopically seen on the cross section of the Slavionian Oaks with double sapwood. The first zone represents the area of true sapwood (outer sapwood), the second is the zone of heartwood and is located between the outer sapwood and double sapwood, the third is the zone of double sapwood and the fourth consitutes the zone of heartwood from the double sapwood to the anatomical centre of the stem.

The test results of the physical and mechanical propreties are given in Table 1 where they are classified according to the property for each individual tree with the respective values and statistical parameters, starting from the outer edge of the sapwood towards the anatomical centre, i.e. in a radial direction.

Table 1. Review of statistical data for density in absolutely dry condition, volumetric shrinkage, bending strength and compression strength parallel to the grain for trees and tree zones

PROPERTY		DENSITY IN ABSOLUTELY DRY CONDITION			VOLUMETRIC SHRINKAGE			BENDING STRENGTH			COMPRESSION STRENGTH PARALLEL TO THE GRAIN		
TREE	TREE ZONE	n	ave	var	n	ave	var	n	ave	var	n	ave	var
1	S	4	0.496	0.0004	4	11	1.65	4	75	33.69	4	44	0.46
	H	7	0.591	0.001	7	13.4	1.79	7	73	78.16	7	43	19.39
	DS	4	0.624	0.002	4	14	0.36	4	89	17.68	4	51	12.32
	H	10	0.647	0.0012	10	16.1	1.87	10	88	73.52	10	54	27.26
2	S	4	0.526	0.0004	4	11	1.12	4	77	40.87	4	44	7.52
	H	10	0.613	0.0003	10	13.8	0.32	10	81	61.27	10	47	10.32
	DS	4	0.568	0.001	4	13.79	0.58	4	86	143	4	47	36.45
	H	8	0.677	0.0014	8	15.8	0.16	8	104	57.92	8	58	7.31
3	S	4	0.489	0.001	4	10.6	3.54	4	72	52.42	4	42	4.5
	H	10	0.650	0.0021	10	14.3	0.72	10	92	208.38	10	50	29.93
	DS	4	0.651	0.0066	4	14.6	2.22	4	97	147.66	4	55	51.75
	H	18	0.725	0.0013	18	16.8	1.6	18	104	107.21	18	57	15.44
4	S	4	0.517	0.0003	4	10.7	0.26	4	91	5.77	4	47	4.54
	H	19	0.589	0.0011	19	13.1	1.57	19	95	56.24	19	53	22.65
	DS	4	0.552	0.0009	4	13.5	1.33	4	75	7.07	4	46	12.73
	H	7	0.622	0.0005	7	14.9	0.64	7	83	46.38	7	55	9.79
5	S	4	0.585	0.0023	4	12.5	0.57	4	111	146.82	4	56	29.83
	H	5	0.594	0.0022	5	13.3	2	5	103	206.25	5	53	20.62
	DS	4	0.657	0.0024	4	14.6	2.25	4	109	145.19	4	63	41.35
	H	17	0.633	0.0016	17	15.2	0.85	17	103	377.42	17	59	18.55
6	S	4	0.564	0.002	4	11.8	0.78	4	92	385.02	4	52	24.48
	H	0	0	0	0	0	0	0	0	0	0	0	0
	DS	4	0.580	0.0023	4	12.6	1.08	4	83	266.68	4	51	43.22
	H	25	0.648	0.0019	25	14.8	1.63	25	99	148.53	25	57	29.94
7	S	4	0.504	0.0005	4	11.4	0.47	4	76	37.53	4	43	4.62
	H	19	0.557	0.0007	19	13.6	1.1	19	84	95.83	19	48	15.14
	DS	4	0.562	0.0012	4	15	0.03	4	87	181.82	4	49	23.27
	H	3	0.632	0.0019	3	15.6	0.33	3	94	47.13	3	50	67.92
8	S	4	0.325	0.0068	4	7.6	4.88	4	39	440.47	4	24	79.89
	H	8	0.545	0.0007	8	12.4	1.49	8	84	82.5	8	51	8.7
	DS	4	0.555	0.0005	4	12.8	0.53	4	85	2.86	4	51	19.46
	H	10	0.618	0.0022	10	14.5	1.05	10	92	118.46	10	56	44.7
9	S	4	0.515	0.0003	4	10.8	1.37	4	85	48.95	4	51	2.1
	H	11	0.562	0.0019	11	12.1	1.65	11	94	97.39	11	55	58.19
	DS	4	0.612	0.0005	4	14	0.93	4	84	143.09	4	62	11.75
	H	9	0.581	0.0011	9	12.9	0.57	9	87	135.62	9	57	25.8
10	S	4	0.547	0.0001	4	10.5	0.81	4	101	18.8	4	57	2.06
	H	9	0.625	0.0009	9	12.8	3.88	9	111	94.6	9	65	13.59
	DS	4	0.635	0.0001	4	11.4	0.6	4	122	21.79	4	70	1.57
	H	15	0.668	0.0011	15	14.1	1.02	15	120	151.6	15	70	27.83

Legend: S-sapwood, H- heartwood, DS- double sapwood, n- number of samples, ave-average value, var- variance (N-1).

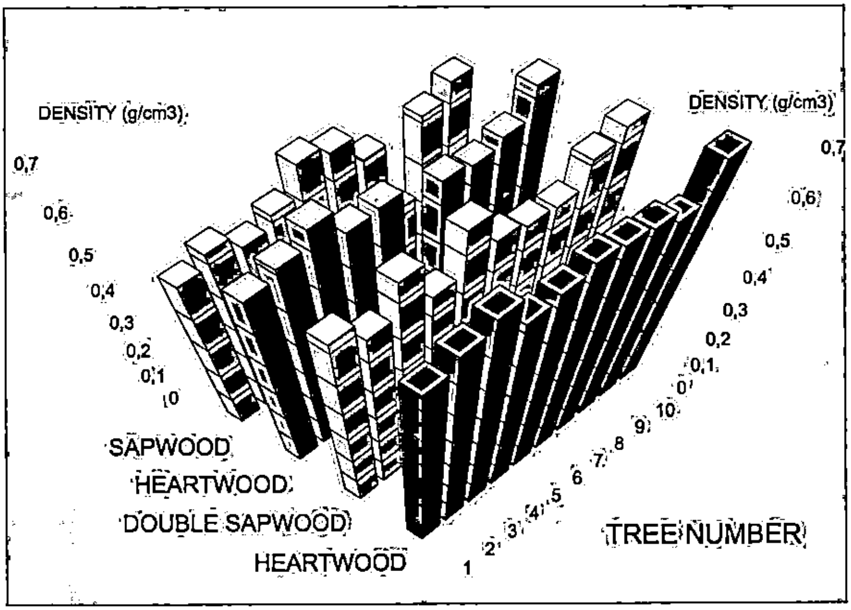

Figure 2. Distribution of density in absolutely dry condition through tree zones (sapwood, heartwood,double sapwood and heartwood) for 10 trees

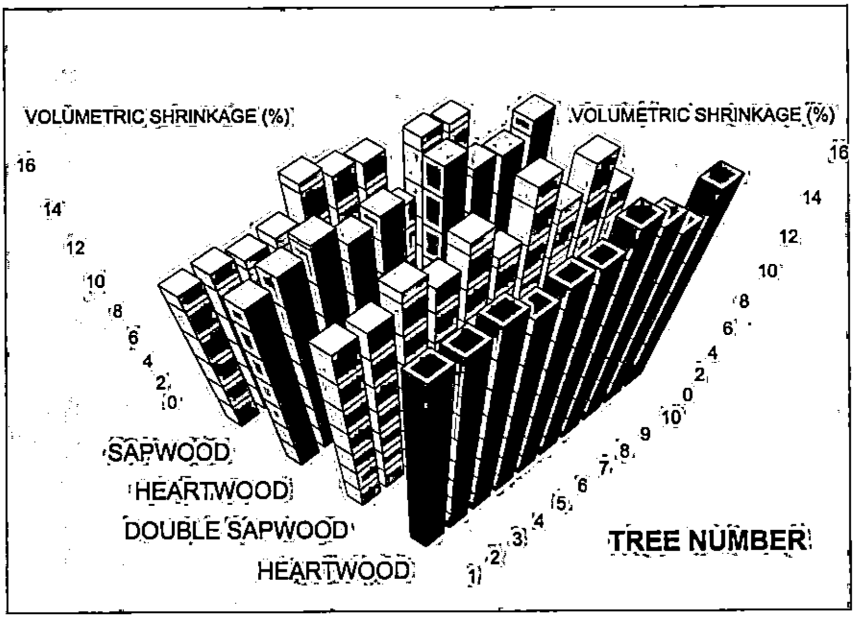

Figure 3. Distribution of volumetric shrinkage through tree zones (sapwood, heartwood, double sapwood and heartwood) for 10 trees

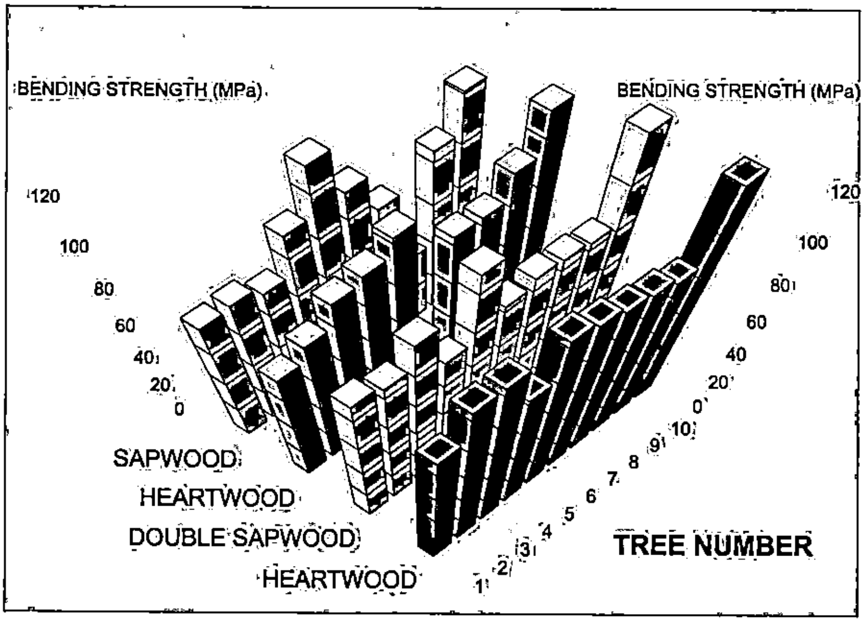

Figure 4. Distribution of bending strength through tree zones (sapwood, heartwood, double sapwood and heartwood) for 10 trees

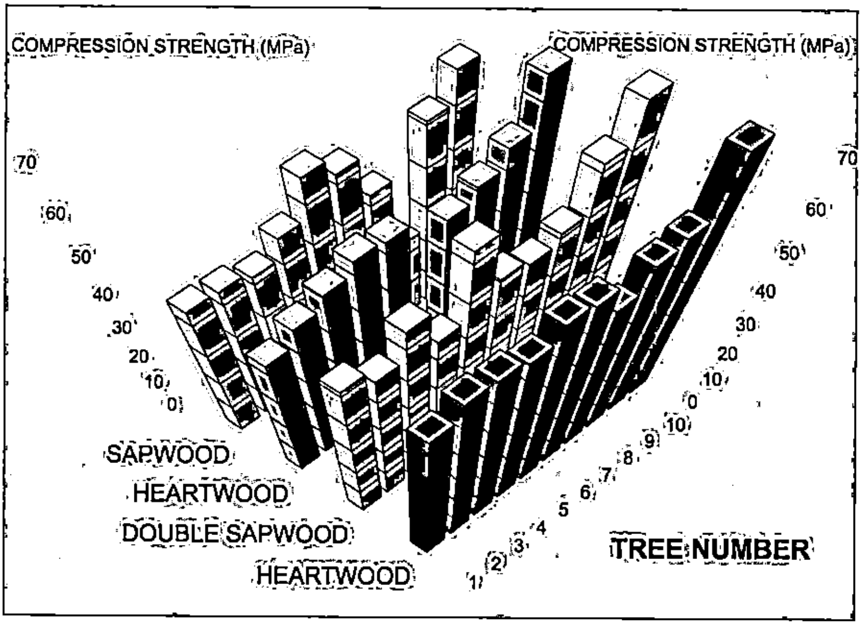

Figure 5. Distribution of compression strength parallel to the grain through tree zones (sapwood, heartwood, double sapwood and heartwood) for 10 trees.

Figure 2 gives a graphical illustration of the density in an absolutely dry condition through all 4 zones for each of the 10 trees.

Results for the density from the bark towards the heart show a trend of growth. The only exception being tree no.2 where the value of ρ_0 =0.5677 g/cm^3 for the double sapwood zone is lower than the value in the zone between the sapwood and the double sapwood which equals ρ_0 =0.6132 g/cm^3.

In tree no.4, the density value for the double sapwood zone of ρ_0 =0.5524 g/cm^3 is lower than the value for the heartwood zone between the sapwood and double sapwood which equals ρ_0 =0.5892 g/cm^3.

Figure 3 gives a graphical illustration of the volumetric shrinkage through all 4 zones for each of the 10 trees.

Results for the volumetric shrinkage from the bark towards the heart show a trend of growth. The only exception being tree no.10 where the value of βv =11.45% for the double sapwood zone is lower than the value in the zone between the sapwood and the double sapwood which equals β_0 =12.78%.

Figure 4 gives a graphical illustration of the bending strength through all 4 zones for each of the 10 trees.

Results for the bending strength through all 4 zones also show a trend of growth. The only exceptions being tree no.4 where the value of σs =75.14 MPa for the double sapwood zone is lower than the value in the zone between the sapwood and the double sapwood which equals σ_0 =94.75 MPa, and tree no. 9 where the value of σs =83.70 MPa for the double sapwood zone is lower than the value in the zone between the sapwood and the double sapwood which equals σ_0 =94.30 MPa. The results for tree no.5 have to be highlighted since they show an opposite trend for the values of bending strength where the highest value of σ_0 =111 MPa applies to the outer sapwood zone and the value for the heartwood equals σ_0 = 103 MPa.

Figure 5 gives a graphical illustration of the compression strength parallel to the grain through all 4 zones for each of the 10 trees.

Results for the compression strength parallel to the grain through all 4 zones also show a trend of growth. Tree no. 4 has the value of σ_t =45.56 MPa for the double sapwood zone which is lower than the value in the zone between the sapwood and the double sapwood which equals σ_t =53.45 MPa. In tree no. 1, the value for the zone between the sapwood and the double sapwood of σ_t =42.87 MPa is lower than the value for the double sapwood zone which equals σ_t =44.07 Mpa. The results for tree no. 5 show a lower value for the zone between the sapwood and double sapwood of σ_t =52.72 MPa in comparison to the value for the outer sapwood zone of σ_t =56.22 MPa.

Table 2 gives a review of mean values for the tested physical and mechanical properties through all 4 zones of the 10 Slavonian Oak trees.

Figure 6 illustrates the mean values of density in an absolutely dry condition through all 4 zones for all 10 trees. The values have an increasing trend from ρ_0 =

Table 2. Review of statistical data for density in absolutely dry condition, volumetric shrinkage, bending strength and compression strength parallel to the grain for all trees together and tree zones

PROPERTY		DENSITY IN ABSOLUTELY DRY CONDITION			VOLUMETRIC SHRINKAGE			BENDING STRENGTH			COMPRESSION STRENGTH PARALLEL TO THE GRAIN		
TREE	TREE ZONE	n	ave	var	n	ave	var	n	ave	var	n	ave	var
	S	40	0.507	0.0057	40	10.8	2.69	40	82	444.3	40	46	96.4
A	H	98	0.589	0.002	98	13.2	1.79	98	90	184.6	98	52	50.2
L	DS	40	0.600	0.0029	40	13.6	1.89	40	92	264	40	54	76.6
AL	H	122	0.652	0.0028	122	15.1	2.15	122	100	243	122	58	46.1

Legend: S-sapwood, H- heartwood, DS- double sapwood, n- number of samples, ave- average value, var- variance (N-1).

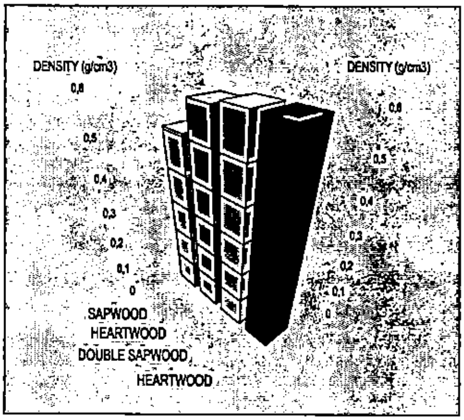

Figure 6. Distribution of density in absolutely dry condition through zones for all trees.

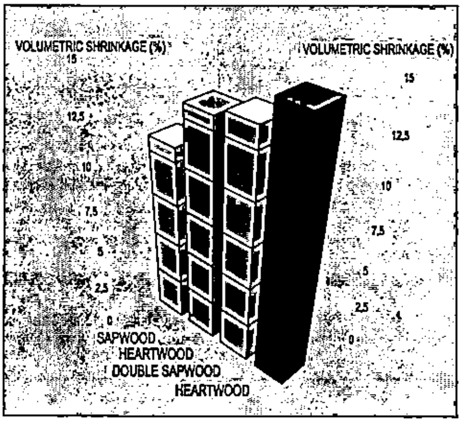

Figure 7. Distribution of volumetric shrinkage through zones for all trees.

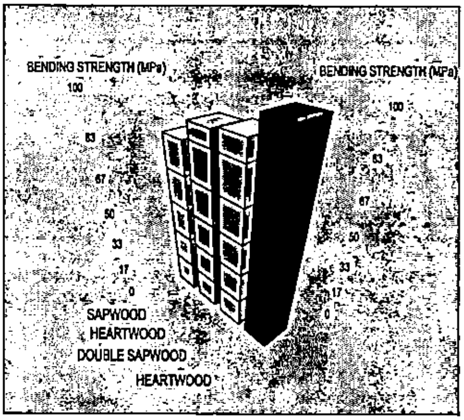

Figure 8. Distribution of bending strength through zones for all trees.

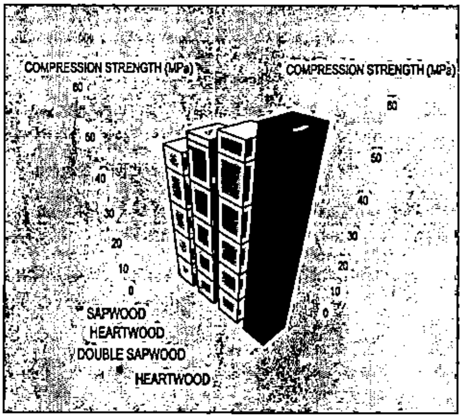

Figure 9. Distribution of compression strength parallel to the grain through zones for all trees.

0.507 g/cm^3 in the outer sapwood zone to ρ_0 = 0.652 g/cm ^{3} in the heartwood zone.

Figure 7 gives the mean values of volumetric shrinkage through all 4 zones for all 10 trees. The values have an increasing trend from β_v = 10.8% in the outer sapwood zone to β_v = 15.1% in the heartwood zone.

Figure 8 gives the mean values of bending strength through all 4 zones for all 10 trees. The values have an increasing trend from σ_s = 82 MPa in the outer sapwood zone to σ_s = 100 MPa in the heartwood zone.

Figure 9 gives the mean values of compression strength parallel to the grain through all 4 zones for all 10 trees. The values have an increasing trend from σ_t = 46 MPa in the outer sapwood zone to σ_t = 58 MPa in the heartwood zone.

DISCUSSION AND CONCLUSION

The test samples for this research were taken from trees in which double sapwood was noticed after felling. Immediately upon felling samples were taken from the trunks, leaving no time for the development of rot in the areas of the outer and double sapwood since the test material, properly stacked, was dried naturally until the water content was adequate for testing.

The test samples in all trees except for tree no. 8 were healthy with no signs of rot. Tree no. 8 had traces of peripheral decay in the outer sapwood area caused by drying ("dead standing" oak) which is evidenced by the research results and the values for all properties.

The distribution of wood density in an absolutely dry condition in each tree through all 4 zones shows an increase in density from bark to core. Values for tree nos. 2 and 4 show lower density values in the double sapwood zones in comparison to the values for the heartwood zones between the sapwood and double sapwood. However, only for tree no. 2 are the density values in the double sapwood zone significantly lower than the density values for the heartwood between the sapwood and double sapwood.

The distribution of wood density in an absolutely dry condition in each tree through all 4 zones shows a constant increase in density from bark to core. With regard to the research on the radial variation of wood density and especially research on the radial variation of oak wood density – oak being in the fourth group of tree species whose density is reduced from heart to bark (Panshin, A. and De Zeeuw, C. 1970), we can generally conclude that the results for density distribution through the 4 zones is normal. This means that in the double sapwood zone there has been no reduction of density values in an absolutely dry condition.

The volumetric shrinkage distribution viewed by tree through all 4 zones shows an increase in the value of volumetric shrinkage from bark to core. In tree no. 9 the results point to a lower value of volumetric shrinkage in the double sapwood zone in comparison to the volumetric shrinkage in the heartwood zone between the sapwood and double sapwood. However, the difference is insignificant.

The volumetric shrinkage distribution viewed by tree through all 4 zones shows an increase in the value of volumetric shrinkage from bark to core. Therefore, there is no reason to believe that double sapwood influenced the values for volumetric shrinkage.

The distribution of compression strength parallel to the grain by tree through all 4 zones shows a general increase in value from bark to core. The only exception is tree no. 4 where the compression strength value for the double sapwood zone is significantly lower than the value in the zone between the sapwood and the double sapwood.

Tree nos. 1 and 5 also deviate from the rule since the values for the heartwood zone between the sapwood and double sapwood are lower. However, in neither case is the difference in the value of compression strength significant.

The distribution of compression strength parallel to the grain by tree through all 4 zones shows a constant increase in value from bark to core. We can conclude that the achieved values are in accordance with the values for density which signifies that in general there has been no change in compression strength values in the double sapwood zone.

The bending strength distribution for each of the 10 trees through all 4 zones shows a general increase in the value of bending strength from bark to core. Tree no. 4 is an exception since the bending strength value for the double sapwood zone is significantly lower than the value in the zone between the sapwood and the double sapwood.

The decrease in bending strength value for tree no. 5 in the heartwood between the sapwood and double sapwood in comparison with the value for the outer sapwood is not significant.

The bending strength distribution for each of the 10 trees through all 4 zones shows a constant increase in value of bending strength from bark to core. This distribution of values is in accord with the values of density, volumetric shrinkage and compression strength, therefore we can conclude that double sapwood did not influence the bending strength properties.

The results of the research of these properties give reason to conclude that Slavonian Oak with double sapwood does not undergo physical or mechanical changes that would negatively affect its quality and user value. In this case, the double sapwood remains only an aesthetic defect.

The results of this research indicate that timely and adequate log processing of double sapwood Slavonian oak can help to avoid enormous damage incurred through slow transport from the stands and the lack of necessary primary processing of this valuable roundwood.

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UTJECAJ DVOSTRUKE BJELJIKE NA KAKVOĆU SLAVONSKOGA HRASTA

Pojava koja se može makroskopski vidjeti na presjeku stabla u obliku dvaju godova čija je boja svjetlija od tamnije srži u osrženim vrstama naziva se dvostruka bjeljika. Vanjski, svjetliji god koji je smješten periferno jest vanjska ili prava bjeljika, dok je manji god smješten u samoj srži i tvori dvostruku bjeljiku.

Praktične implikacije dvostruke bjeljike jednako su nepovoljne kao i implikacije prave bjeljike. Ta je mana osobito važna jer se pojavljuje u hrastovim stablima. Time se vrijednost drva, ponajprije njegova estetska vrijednost, znatno smanjuje, a u eksploataciji najvrednijih sortimenata nastaju teške posljedice zbog stvaranja truleži koja smanjuje kakvoću drva pri obradi.

Za procjenu utjecaja dvostruke bjeljike, to jest promjena u svojstvima stabala u ovim područjima, uzet je uzorak od 10 stabala slavonskoga hrasta (*Quercus robur* L.) u kojima je otkrivena dvostruka bjeljika odmah nakon sječe.

Praćenjem položaja određenih fizičkih i mehaničkih svojstava slavonskoga hrasta u transverzalnom smjeru dobiveni rezultati omogućuju da se ustanovi utjecaj dvostruke bjeljike na kakvoću i uporabnu vrijednost drva.

Ključne riječi: slavonski hrast, dvostruka bjeljika, fizička svojstva, mehanička svojstva, kakvoća

M. Čater, F, Batič: Ecophysiological parameters as a possibile tool for the assessment of natural and artificial regeneration in pedunculate oak ... Glas. šum. pokuse 37: 201–213, Zagreb, 2000.

UDK 630*181+181.3+(497.1) (Quercus robur L.)

ECOPHYSIOLOGICAL PARAMETERS AS A POSSIBILE TOOL FOR THE ASSESSMENT OF NATURAL AND ARTIFICIAL REGENERATION IN PEDUNCULATE OAK IN LOWLAND PARTS OF SLOVENIA

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In the last decade there has been a noticeable decline and physiologically weakening of the pedunculate oak (*Quercus robur* L.) in lowland parts of Slovenia due to a drier climate, unfavourable precipitation patterns, and human influence through changes in watercourses and the water table. Regeneration and future management of this tree species is therefore under question.

In order to define a critical groundwater table and light conditions which would permit successful regeneration, an experiment was carried out in two bigger pedunculate oak forest complexes (Murska Šuma and Krakovo Forest), differing by the degree of the level of decline and the physiological weakness of the adult trees.

Within each forest complex two locations with permanent high and low groundwater tables were chosen. On each location pedunculate oak seedlings (2+2) were planted in three different light regimes (without canopy cover, under minimal, medium and maximal tree canopy).

In every aspect (spring, summer, autumn), measurements of pre-dawn and midday water potential and photosynthetic activity on natural and planted seedlings were performed daily. Groundwater table measurements and qualitative analysis were carried out through the whole measuring period.

The experiment confirmed significant differences between physiological indicators within each forest complex as well as between both Murska Šuma and Krakovo Forest. The critical groundwater level in connection with the light conditions for efficient regeneration in those forest complexes was also defined.

Key words: pedunculate oak (*Quercus robur* L.), groundwater conditions, water potential, light, photosynthetic activity

INTRODUCTION

Slovenian lowland forests have been under severe pressure since the times of first settlement. Since these were the most easily accessible forests over the past centuries, they were frequently cleared by the settled communities and represent today a mere 2% of the total forest area in Slovenia, where 54% of the total area is forests.

They are composed largely of Pedunculate oak (*Quercus robur* L.), common hornbeam (*Carpinus betulus* L.), and common alder (*Alnus glutinosa* Mill.) and are restricted only to smaller areas, when larger areas of these forests are found only in moist sites less suited for agriculture. The most distinct floodplain forests are situated in the north-east of Slovenia and represent the north-western remnants of the famous Slavonian oak forests. Other important oak lowland forests are located in the south-east, situated between the highway Ljubljana-Zagreb and the Krka River.

Over the last hundred years these forests have been severely affected by human activities. Heavy cutting of pedunculate oak at the beginning of the century, extensive regulation of watercourses subjected to flooding, and unsuitable management of agricultural land have had an adverse effect on biotopes. The situation is worsened by conflicts of interest in terms of land use. Over the century, the evident weakening and mortality of oaks in Slovenia have especially affected pedunculate oak (*Quercus robur* L.), which is a key tree species in the lowlands (Hager, Smolej 1995). The decline is most evident in the north-east of Slovenia, most likely because of the drier climate, unfavourable precipitation distribution, severe hydromelioration causing changes in the groundwater table (Levanić 1993, Čater 1998) and eutrofication. Especially older and mature trees are affected. A decline in health is confirmed by an annual crown defoliation inventory on permanent research plots all over Slovenia.

Most probably there is not a single factor which causes the decline of oaks. The complex of interactions among factors is specific to the environment. Not only the changed water regime, but also emissions, management errors and the consequences of a changed water table also play an important role. Physiologically weakened trees become susceptible to many secondary, biotic factors, which would not be fatal in other circumstances. In contrast to the recovery of some other tree species, oaks have not improved in health and their decline is even increasing (Mavsar 1999). The regeneration and future management perspective of pedunculate oak in particular is therefore under a big question.

The main research objectives in our experiment were to characterise the ecophysiological conditions for the successful regeneration of pedunculate oak and to define the differences between natural and planted oak seedlings.

MATERIAL AND METHODS

To define the importance of the groundwater table, a pilot experiment was carried out in north-east Slovenia within a forest complex with different degrees of declining trees on deep eutric fluvisols. Every plot was represented by ten adult pedunculate oaks, with breast height trunk diameter over 35 cm, where measurement of the xylem leaf pre-dawn water potential (Plant Moisture Vessel SKPM 1400, Skye, UK) and el. resistance of cambial zone (Bolmann Systeme, Rielasingen, Germany) were performed every month from March to September. At the time of full crown development, crown defoliation estimates were also made (June-September). The groundwater table (weekly) and qualitative analysis (pH, NO_3^-N, NH_4^-N, Pb, Zn, Cd) as well as foliar analysis (N, P, K, Ca and Mg) were performed, too (Čater et al. 1999).

After the first experiment which confirmed differences in the groundwater table and the strong connection between stress and the groundwater table, a second experiment was carried out on a larger scale, including the same and more damaged parts of the Murska Šuma forest complex in the north-east of the country and Krakovski Gozd, a new site, which is better supplied with water and shows less damage, in the south-east of Slovenia.

On both forest complexes, new locations were determined with low and high levels of groundwater and within each location different light conditions according to the canopy of the stand (open, minimum shelter, medium shelter, maximal shelter), where seedlings (2+2) of the site provenance were uniformly planted and fenced one year before measurements. In each category there were at least 15 seedlings. After planting, the seedlings were not treated with any chemical. Because of strong deer grazing, it was impossible to find the same categories of natural oak seedlings on all sites, so naturally regenerated seedlings were observed only in two categories, light and maximal shelter. Parameters were observed and measured in spring, summer and autumn aspect, always starting at the Murska Šuma forest complex because of its earlier phenological activation and followed by Krakovski Gozd. Every aspect lasted 8-10 days.

The main observed and measured parameters were:

- water relations (pre-dawn and midday xylem water potential on adult trees and seedlings; groundwater table and quality analysis and meteorological data for comparison);
- light conditions (relative light exposure/average per aspect, direct photosynthetic active radiation - PAR);
- photosynthetic activity (net CO_2 assimilation, stomatal conductivity) measured on seedlings;
- soil characteristics (Urbančič et al. 2000) and
- other (crown defoliation estimate).

In parallel to the field measurements, a pot experiment was designed in a controlled environment with six year-old pedunculate oaks, where water relations (PWP, MWP) and photosynthetic activities were measured in three groups of different watering regimes: watering 2x weekly, 1x weekly and without watering. In parallel, 15 oaks were included in order to define water stress in controlled conditions. Differences between parameters were tested with AVAR and regressions for the relations between measured parameters (Excel 7, Statistica 5).

RESULTS

WATER RELATIONS

A comparison of precipitation arrangements showed differences in sites well supplied with water and also a deficit in summer according to 30 years' average precipitation (Fig. 1).

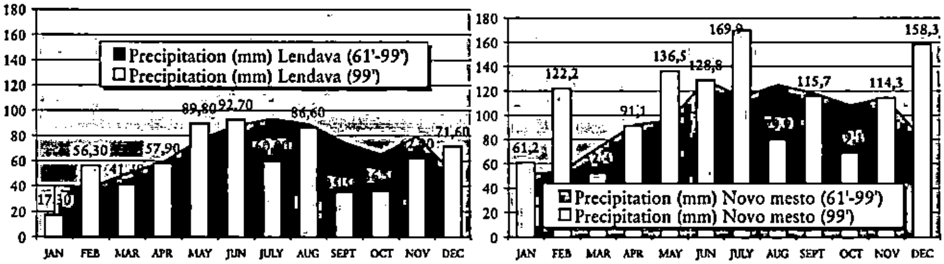

Fig. 1. Precipitation in 1999: Lendava (near Murska Šuma) and N. mesto (near Krakovski Gozd)

Total precipitation in 1999 for Murska Šuma was 707.6 mm, which is 100 mm lower than the 30 years' average value, and for Krakovski Gozd 1299.4 mm - 140 mm above the same average period.

Groundwater tables (GW) on both sites rose after the summer rains on plot P1 (Murska Šuma), while also on plot P2 the influence of the Mura River table was present. GW dynamics in both forests showed a decline over the whole vegetation period and reached a minimum in the autumn aspect.

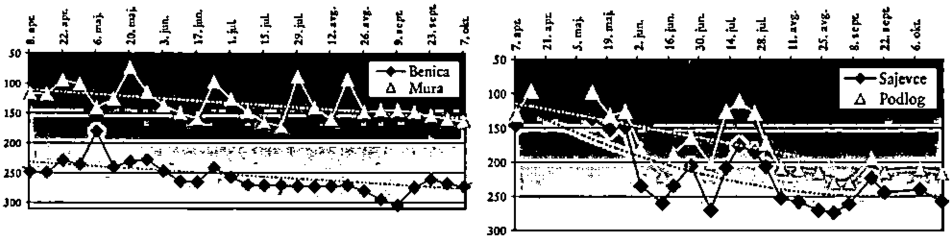

Fig. 2. Annual groundwater dynamics in both forest complexes

Measurements of pre-dawn water potential (PWP) were performed every day from 4.00 AM to 5.30 AM and the midday xylem water potential (MWP) from

11.30 AM to 1.00 PM. Differences between plots increased towards the autumn aspect. Dependence on the GW table was significant (p=0.05), especially on the site with lower GW (plot P1, Murska Šuma). Precipitation within a measuring aspect had a stronger effect on the momentary/daily PWP of the seedlings than the GW dynamics, which could be evident in the autumn aspect in both forests, when stress was strongest. Relatively low MWP in summer (Krakovski Gozd) was connected to a higher vapour saturation deficit (VSD) in that period (Dp=11.4 hPa/kg) compared to that in Murska Šuma (Dp=7.57 hPa/kg).

WATER POTENTIAL /Murska šuma forest complex

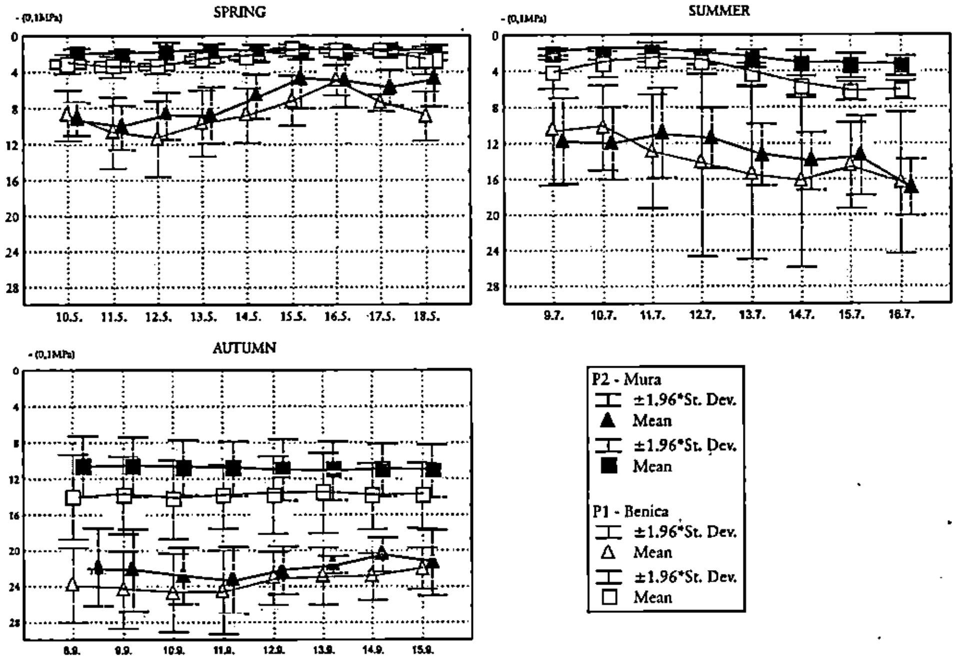

Fig. 3. Pre-dawn and mid-day xylem water potential, Murska Šuma

According to PWP, no water stress was measured in springtime, while in summer slight stress was detected on P1 in Murska Šuma. The variation and dynamics of PWP and MWP within the aspect was noticed on all plots and was the highest in summer. This could most probably be explained by the variation of precipitation at that time.

In autumn, moderate stress on plot P2 (-1.2 MPa) and strong water stress on plot P1 (-1.7 MPa) were present in Murska Šuma, with GW reaching its minimum (Fig. 5). At the same time both plots in Krakovski Gozd were unaffected (-0.6 MPa, -0.7MPa). A comparison of precipitation for that period indicated differen-

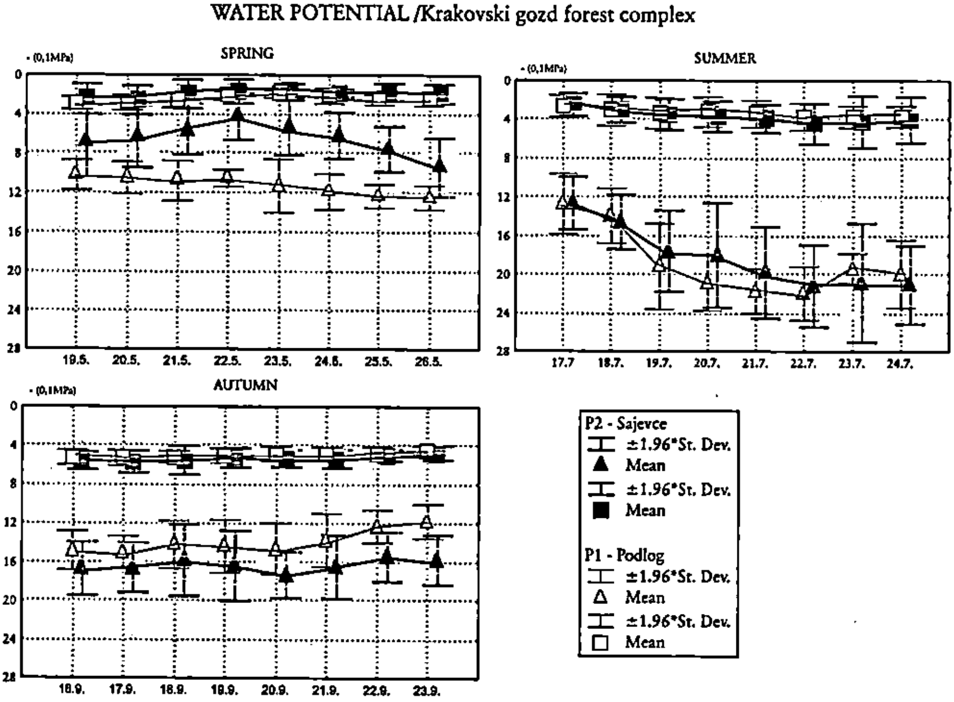

Fig. 4. Pre-dawn and midday xylem water potential, Krakovski Gozd

ces between both forests - depletion of precipitation in Murska Šuma and no difference compared to average values in Krakovski Gozd. Differences in PWP within plots (different light regime) with the same GW table (not significant, yet constant) showed lower negative values in the open and less negative values under shelter (data not shown) in all aspects.

The correlation between PWP and GW was always significantly higher [$R^2 = 0.55 - 0.93$, $p \leq 0.05$] than the correlation between PWP and precipitation $R^2 = [-0.05 - -0.38$, $p \leq 0.05]$. Precipitation influenced PWP on all plots, the most in summer.

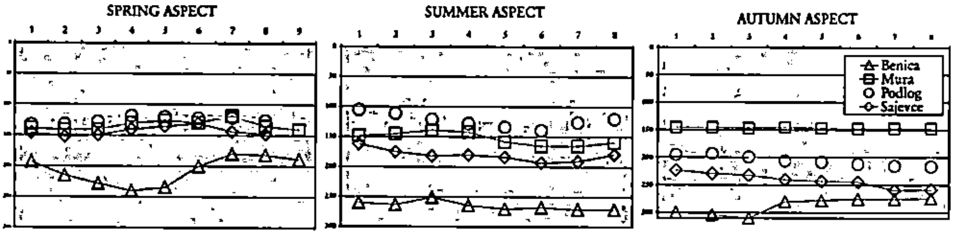

Fig. 5. Groundwater table in measured aspects

LIGHT CONDITIONS

Every location with the same GW table had one open plot and the other at the forest edge. Within the second plot three categories were defined according to the light conditions. The orientation of the forest edge was the same on all plots: NE-SW with the opening of the canopy towards E direction. Light intensity was measured relatively to the open plot, which was considered 100%. The springtime average photosynthetic active photon flux density on the open plot (PPFD) was 1207.71 ± 61.08 ìmol $m^{-2}s^{-1}$, in summer 1317.93 ± 94.48 ìmol $m^{-2}s^{-1}$ and in autumn 1274.31 ± 79.60 ìmol $m^{-2}s^{-1}$.

The average light intensity on the open plots was constant and did not change significantly during the vegetation period, except for a slight change from the spring to summer aspect. On plots under tree canopy, the highest decrease of direct PAR was noticed from spring to summer: 2.73% average decrease in minimum shelter, 7.71% in medium shelter and 13.84% in maximal shelter, connected with crown development. From the summer to autumn aspect, the light conditions "improved": +2.15% in minimum, +3.48% in medium and +2.97% in maximal shelter.

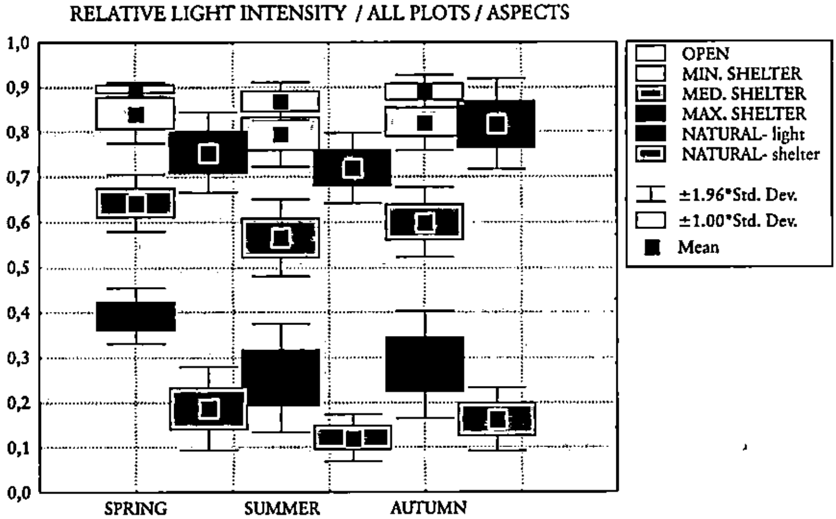

Fig. 6. Average light conditions on plots / aspects

Natural seedlings were more evenly distributed in shelter, while on the light plot it was located in light conditions which were similar to the PFD values of the planted seedlings between minimal and medium shelter. On all plots, no natural seedlings were found in open light with 100 % PAR.

The photosynthetic activity of seedlings was measured in three optimal days within each aspect on every plot starting at 11.00AM. Net CO_2 assimilation rate (A) on all plots in optimal light

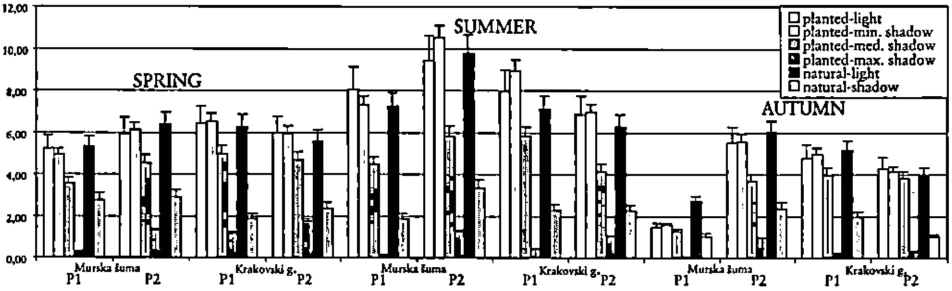

Fig. 7. Net CO_2 assimilation rate (A= ìmol $m^{-2}s^{-1}$) / plots / aspects

(Fig. 7) is significantly different between plots P1 and P2 in both natural and planted seedlings (Murska Šuma; $p \leq 0.001$) in the summer and autumn aspect ($p \leq 0.000$). In most cases, A in planted seedlings was higher than in the open plot with higher PPFD values. It was also interesting that the A of natural seedlings in shelter was always much higher than the A of planted seedlings under maximal shelter ($p \leq 0.000$). Differences between spring and summer might indicate that leaves in spring were still developing (also Fig. 8), while summer-autumn differences originated from drought and the gradual ending of the vegetation period.

A comparison between photosynthetic light efficiency (Φ = net photosynthesis / PPFD * 100) and PWP on all plots and among all aspects showed a decrease with increasing negative PWP (drought), especially on plot P1, Benica, in autumn. According to the measured net photosynthesis, the most efficient category of seedlings was at minimum shelter and not in open light with highest PAR. Stomatal conductance values were parallel to the values of net photosynthesis and showed changes when PWP values were below –0.8MPa to -1MPa in summer and autumn. More evident and almost complete stomatal closure appeared below –1.55 MPa ~ –1.72 MPa PWP in autumn at Murska Šuma, which was comparable with the data from the pot experiment. The threshold for the beginning of stomatal closure was below – 0.86 MPa and the second (wilting point) below PWP –1.68 MPa ~ –1.83 MPa in planted seedlings ($p \leq 0.05$). Natural oaks were more adapted to drought and showed the first threshold below – 0.94 MPa, the second below

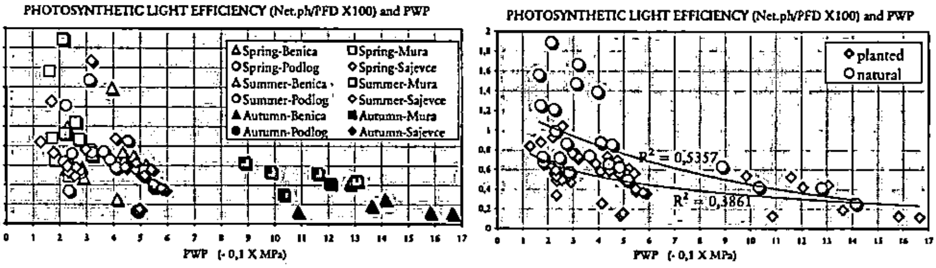

Fig. 8. Average Φ values for plots / aspects and comparison: natural - planted seedlings

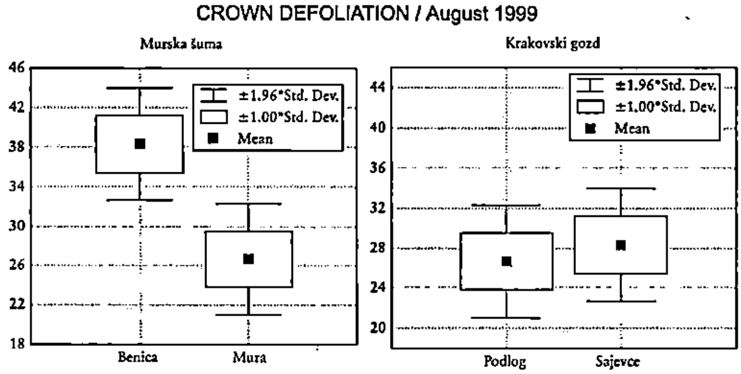

Fig. 9. Crown defoliation

–1.89MPa ($p \leq 0.05$) and also a higher Φ than the planted seedlings. The lowest values of Φ were in autumn at P1 Murska Šuma, while values from Krakovski Gozd were similar to the summer values (Fig. 8).

The assessment of crown defoliation was performed in August and indicated a significant difference between plots in Murska Šuma and nonsignificant differences in Krakovski Gozd. This was similar to the GW table conditions - the lowest on plot P1, Benica, with also the highest crown defoliation. In the estimate were included ten adult trees, the closest to each plot in governing social position.

Nitrogen values of the qualitative groundwater analysis were higher than normal in both forest complexes, especially at Murska Šuma, indicating the high influence of the agricultural use of the neighbouring fields.

spring	pH	EP	NH3	NO3	SO4	CL
			mg/l	mg/l	mg/l	mg/l
Murska šuma	6.63	423.66	1.72	9.27	106.18	10.61
Krakovski gozd	7.71	502.60	4.13	3.05	17.12	3.65
summer						
Murska šuma	6.86	461.78	3.75	10.93	88.24	11.00
Krakovski gozd	7.98	466.00	0.85	7.35	16.20	2.71
autumn						
Murska šuma	/	/	0.54	0.00	6.36	5.70
Krakovski gozd	/	/	1.23	3.31	14.51	4.55

Fig. 10. Qualitative groundwater analysis

DISCUSSION

Precipitation on both plots in 1999 was close to average values, with the exception of Murska Šuma in the summer-autumn period, when evident drought conditions were present. In the experiment we defined differences between plots in Murska Šuma and Krakovski Gozd (low and high GW table) and confirmed the connection between PWP and GW. The decline of PWP values caused stomata closure and consequently reduced the net CO_2 assimilation ratio, also mentioned in ecophysiological studies (Dickson and Tomlinson 1996, Tyree and Cochard 1996, Tribulout et al. 1996, Vivin et al.1996). The decline of GW in the summer to 280 cm induced stress, while the autumn values below 300 cm and the absence of precipitation caused a critical descent of PWP values to the point of severe stomata closure. Natural seedlings showed fewer reactions in the same GW regime as the planted seedlings, but were also affected at lower values of PWP (below –1.89MPa ($p=0.05$) than the planted seedlings (PWP –1.68 MPa č-1.83 MPa).

Tolerance to water stress is connected with osmoregulation, according to environmental changes (Dreyer et al. 1991, Vivin et al 1996). In spite of the fact that no osmotic component of water potential was measured, the connection between PWP and stomata closure indicated differences between natural and planted seedlings. Unfavourable conditions affected the reduction of net CO_2 assimilation more than the reduction of light (van Hees 1997); in stress, fine roots are affected (Gemmel et al. 1996), assimilation ability is lowered (Epron and Dreyer 1993), and the transformation of light energy into biomass is reduced (Gemmel et al. 1996). Too much water on the other hand also reduces photosynthetic activity (flooding, root hipoxia), induces necrosis, wilting (Dreyer et al. 1991, Wagner and Dreyer 1997) and increases mortality, especially if the water is poor in oxygen.

Significant differences between plots of the same forest complex therefore confirmed the importance of the GW table for the survival of oak seedlings.

Stomata closure and photosynthetic light efficiency in connection with PWP also showed accordance with other parameters measured in old trees and with the results from the first part of the experiment (Čater et al. 1999). Ground vegetation was present, but not in such abundance to compete with oak seedlings for light. However, it reduced the available amount of water, as mentioned in Welander and Ottoson (1997).

We believe that reduced vitality and crown defoliation in Murska Šuma was also caused by high amounts of nitrogen and sulphate ions in the groundwater (Fig. 10).

Photosynthetically the most effective in all three aspects was the plot under minimal tree shelter with an average PAR of 84 % in spring, 80% in summer and up to 82 % in autumn, and not the open plot with 100% PAR (Gemmel et al. 1996). Planted seedlings were active (net CO_2 assimilation) at PAR above 10 %, but were less effective than natural seedlings at lower PAR (Fig. 6), in spite of adequate provenance. Welander and Ottoson (1997) report that one-year oaks survive at 1-2% PAR, but their growth is slow and mortality increases with age, because of increasing light demands. 10% of PAR is a limiting value, where dry mass of leaves increases (Welander, Ottoson 1997), when 18% of PAR is sufficient to enable height growth (Gemmel et al. 1996). The drop in photosynthetic efficiency in connection with the decrease in PWP between natural and planted seedlings was significantly different in all three measured aspects.

CONCLUSIONS

The most favourable light conditions for planted seedlings in Murska Šuma and Krakovski Gozd forests would be in minimal shelter conditions (80% PAR) and GW depth not lower than 280-300cm below the surface, especially in times lacking precipitation. The survival of planted seedlings was possible if PAR was higher than 10 % of open PAR (considered 100%). Minimal shelter also offers protection against possible frosts and gives the possibility to influence ground vegetation competition with light intensity. Natural seedlings are more resistant to water stress and tolerate more shadow than planted seedlings. Photosynthetic yield was in all aspects higher, the drop in yield was, with increasing water stress, lower and the survival strategy better in natural seedlings. The experiment confirmed the importance of light and water conditions for the regeneration of pedunculate oak, especially in an environment with water supply as the key-minimum factor.

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EKOFIZIOLOŠKI PARAMETRI KAO MOGUĆE SREDSTVO U PROCJENI PRIRODNE I UMJETNE OBNOVE HRASTA LUŽNJAKA U NIZINSKIM DIJELOVIMA SLOVENIJE

U posljednjem je desetljeću hrast lužnjak (*Quercus robur* L.) u nizinskim dijelovima Slovenije znatno propao i fiziološki oslabio zbog suše klime, nepovoljnih oborinskih prilika i ljudskoga utjecaja na promjenu vodnih tokova i razine podzemne vode. Obnova i buduće gospodarenje ovom je vrstom prema tomu pod velikim znakom pitanja.

Kako bi se odredila kritična razina podzemne vode i svjetlosni uvjeti koji bi omogućili uspješnu obnovu, proveden je pokus u dva veća kompleksa hrastovih šuma (Murska šuma i šuma Krakovo), koje se razlikuju po stupnju razine propadanja i fiziološke slabosti odraslih stabala.

U svakom su šumskom kompleksu izabrane dvije lokacije s trajnom visokom i niskom razinom podzemne vode. Na svakoj su lokaciji posađene sadnice hrasta lužnjaka (2 + 2) na tri različita režima svjetlosti (bez sklopnoga pokrova, pod minimalnim, srednjim i maksimalnim sklopom drveća).

U svakom aspektu (proljeće, ljeto, jesen) svaki su dan prije zore i u podne mjereni vodni potencijal i aktivnosti fotosinteze na prirodnim i posađenim sadnicama. Tijekom cijeloga mjernoga razdoblja mjerena je razina podzemne vode i provodile su se kvalitativne analize.

Pokus je potvrdio značajne razlike među fiziološkim indikatorima u svakom šumskom kompleksu kao i između Murske šume i šume Krakovo. Također je određena kritična razina podzemne vode u vezi sa svjetlosnim uvjetima za učinkovitu obnovu u ovim šumskim kompleksima.

Ključne riječi: hrast lužnjak (*Quercus robur* L.), uvjeti podzemne vode, vodni potencijal, svjetlost, fotosinteza

M. Urbančić, et al.: Pedunculate oak stands in the lowland regions of Slovenia – soil water conditions.
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UDK 630*181.3+116+48+(497.1) (Quercus robur L.)

PEDUNCULATE OAK STANDS IN THE LOWLAND REGIONS OF SLOVENIA – SOIL WATER CONDITIONS

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In 1999 soil-water conditions in the two largest pedunculate oak-forest complexes in Slovenia were studied. Soil characteristics were determined and soil water storage up to a depth of 90 cm was measured on 6 research objects. The quality of groundwater was analysed and the health status of trees was also assessed. As a rule, in the more moist oak stands on gleysols and planosols, the tree crowns were less defoliated than in the oak stands on fluvisols with an average groundwater table deeper than 2.5 m.

Key words: *Quercus robur*, hydromorphic forest soils, soil moisture observations, defoliation, Slovenia

INTRODUCTION

In 1992 an intensive increase of oak decline was observed in Slovenia which triggered complex research on the vitality and decline of lowland pedunculate oak stands. Several permanent research plots up to 1 ha in size were set up in 4 areas of eastern and north-eastern Slovenia (Krakovski gozd, Cigonca, Hraščica, Murska šuma) in 1993 and 1998. The studied oak stands mostly grow on hydromorphic soils (gleysols, planosols, fluvisols) with additional moisture inflow from groundwater or flood water. Alternatively, moisture is retained in upper soil layers due to poorly permeable lower layers. Nevertheless, pedunculate oak stands can also be found on eutric and dystric cambisols which are well permeable, have no contact with groundwater and where the only source of moisture is precipitations. The assumption that oak has been declining because of the simultaneous and synergistic effects of several stress factors (increment, phytocoenology, hydrology, soils, physiology, entomology and other) has resulted in extensive research work (Smolej and Hager 1995).

One of the most important hypothetical causes for the decline in lowland oak forests is the change of water regime. To begin with, the study of the soil-water regime in lowland oak stands in Slovenia was limited to the indirect determination of its characteristics by means of the morphologic phenomena of the oxidation-reduction processes (appearance of mottles caused by seasonal waterlogging and strong reduction processes due to continuous saturation with stagnant water) which were observed on soil cores and soil profiles and by the data of groundwater levels in piezometers. To obtain a better insight into the soil-water regime of 6 research objects where intensive ecophysiological studies have been continuing (Čater 1998, Čater and Batič 2000), a detailed investigation of soil-water and other (physical, chemical) soil properties was made. In addition, momentary soil-water content during the vegetation period has been determined to obtain the available water content (AWC) and to make it possible to compare this with the tree vitality and crown defoliation of the pedunculate oak on the research objects.

METHODS AND MATERIALS

Research objects were set in the two largest forest complexes of pedunculate oak in Slovenia. Two objects (Sajevce and Podlog) are found in the vast forest complex of Krakovski Gozd near Kostanjevica (over 2000 ha large) in the north-eastern part of Slovenia; the other four objects (Benv, Led8, Mur10 and Murn) are set in the forest complex of Murska Šuma (474 ha large) in the eastern part of Slovenia.

Table 1. Annual rainfall and mean temperature of forest regions, locations and altitudes of research objects, representative soil profile identification codes

Forest region	Annual rainfall; temperature	Location of research object	Altitude (m)	Soil profile codes
Krakovski gozd	1100 mm; 10 °C	Near the hamlet Sajevce	151	Sajevce 1, 2
Krakovski gozd	"	In the district Podlog	153	Podlog 1, 2
Murska šuma	770 mm; 10 °C	Near the hamlet Benica	155	Benv
Murška šuma	"	At the river Ledava	153	Led8/1, Led8/2
Murska šuma	"	At the river Mura	152	Murn
Murska šuma	"	Near the river Mura	155	Mur10

PEDOLOGICAL METHODS

The soil conditions and morphologic properties of the soil on the research plots were examined with a semicircular sound, which reaches down to a depth of 110 cm. According to the soil homogeneity of the plot, one or two places for a representative soil profile were chosen. From the soil profiles, soil samples were taken and sent to the lab. Samples were taken from organic horizons and from soil layers with fixed depths (0 - 5 cm, 5 - 15 cm, 15 - 30 cm, 30 - 50 cm, 50 - 70 cm, 70 - 90 cm).

For each soil sample, the pH in de-ionised water and in 0.01 M calcium chloride, the content of carbonates, organic carbon, humus, total nitrogen, C/N ratio, texture class, apparent bulk density (by Kopecky's cylinders) and soil moisture characteristics were determined in the lab. The moisture characteristics of the soil samples (field capacity (FC), the permanent wilting point (PWP), the pF curve, etc., were determined by standard press plates.

From three spots at each profile, soil samples at approximately 3 m distance were taken (twice in the spring and twice in the summer) from soil depths 0 - 5 cm, 10 cm, 20 cm, 40 cm, 60 cm and 80 cm. For each sample, momentary soil-water content was determined by thermogravimetry. The average momentary humidity (MH) of three samples from the same depth was considered as the momentary humidity of the adequate profile soil layer (for example: the moisture of samples from a depth of 60 cm represents the moisture of the profile soil layer from a depth of 50 - 70 cm).

GROUNDWATER QUALITY

Samples of groundwater were taken from piezometers in all six research plots on 20th May, July 16th and September 1st 1999. The pH (potentiometry), NO_3 and SO_4 by ion chromatography and NH_4 by spectrophotometry (Nessler reag.) in water samples were determined. In September 1999, foliar samples of oak leaves were taken on the objects Benv, Murn, Sajevce and Podlog. After grinding and air drying, N was determined by the micro Kjeldahl method.

HEALTH STATUS - DEFOLIATION

The defoliation of oak trees was assessed and classified according to the EU methods and criteria (Commission Regulation ..... 1987, Manual on Methods and Criteria ..... 1998). The assessment of the forest health status in 1997 and 1999 was carried out on the 100 x 250 m grid (Mavsar 1999). The nearest transections of the grid were used for our studies. Some were close to the plot and others were up to 150 m away. Additionally, on some studied plots (soil profiles), the 10 closest oaks were assessed as well (Čater 1999). Only dominant and codominant trees were taken into consideration.

RESULTS

SOIL CHARACTERISTICS

With these 6 research objects, a considerable span of soil conditions characteristic of pedunculate oak sites is represented. According to the international classification (FAO-Unesco, 1989), three major soil groupings were found: Planosols (on marl), Gleysols (on pleistocene and alluvial sediments), and Fluvisols (on alluvial sediments).

Table 2. Profile identification codes, soil units (FAO-Unesco, 1989), soil types (Škorić 1986), parent material

Profile	Soil unit	Soil type	Parent material
Sajevce 1, Sajevce 2	Eutric Planosols	Pseudogley	Marl
Podlog 1, Podlog 2	Eutric Gleysols	Hypogley	Pleistocene sediments
Led8/1, Led8/2	Eutric Gleysols	Hypogley	Alluvial sediments
Benv	Eutric Fluvisols	Semigley	Alluvial sediments
Mur10	Eutric Fluvisols	Semigley	Alluvial sediments
Murn	Eutric Gleysols	Hypogley	Alluvial sediments

For soil layers of representative profiles, symbols of dominant horizons (FAO 1990), key chemical parameters, textural classes, field capacities (FC - determined at 0.033 MPa), permanent wilting points (PWP FC - determined at 1.5 MPa), available water capacities (AWC = FC - PWP), bulk density (BD) and momentary soil humidity, measured in the early spring (MH_1) and at dry end of the summer (MH_2) are shown in Table 3.

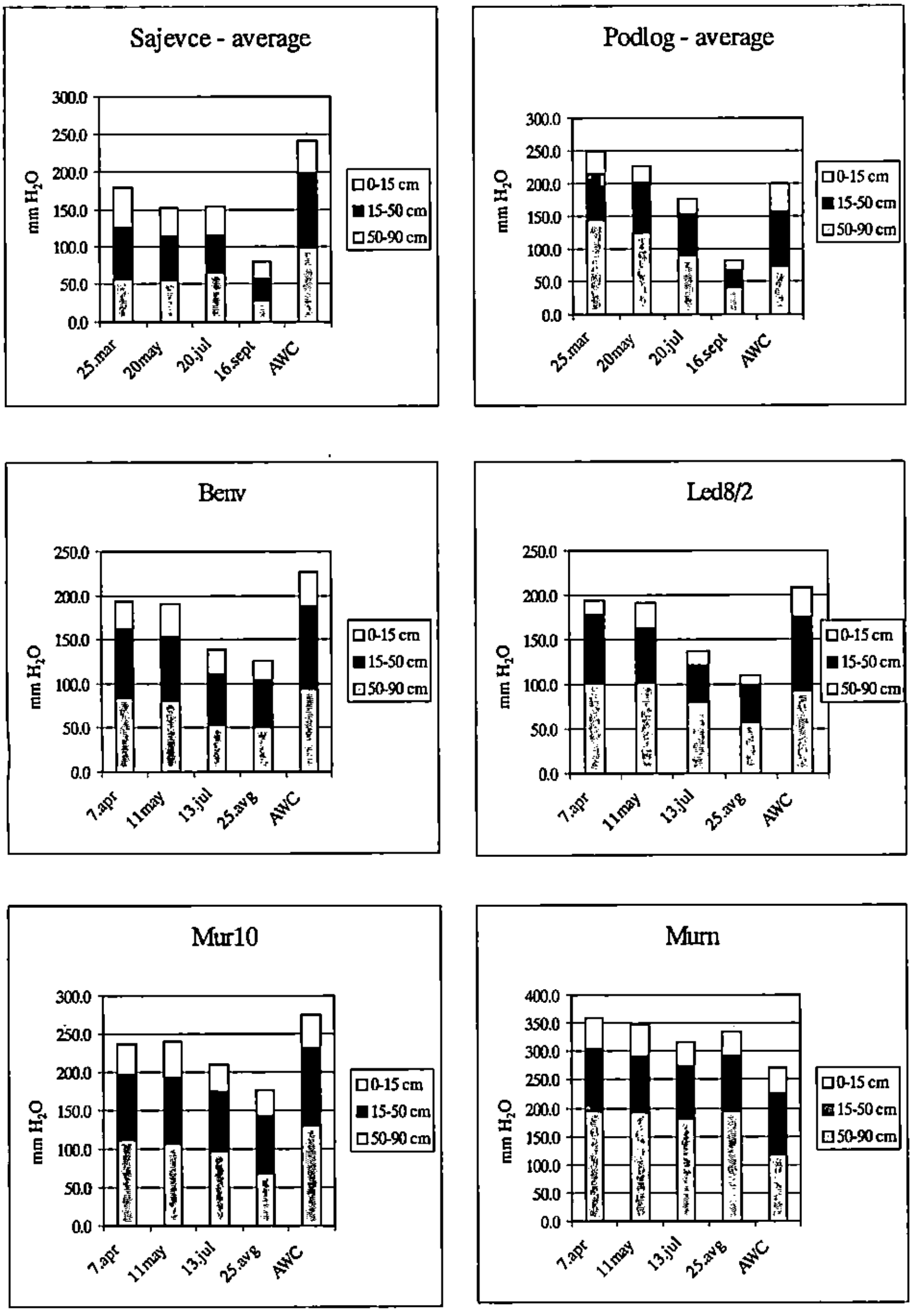
On the object Sajevce, planosols on the marl appear. This consists of about 4 to 6 cm thick A horizon of humus accumulation under organic O horizon. Under it, elluvial E horizon with a silty loam (SiL) texture reaches a depth of 35 cm to 45 cm. It is followed by a silty clay loamy (SiCL) to silty clayey (SiC) B horizon with an illuvial accumulation of clay (for this characteristic the symbol $_t$ is used according to FAO 1990) and a concentration of carbonates (symbol $_k$). This is slowly permeable and causes the seasonal waterlogging and gleying (symbol $_g$) of upper soil layers (E_g, B_g) by surface water. On 25th March 1999, the momentary humidity in the upper parts of the soil was approximately equal to or higher than the field capacity of these layers (Table 3) and the average content of water in the upper soil layer was greater than the plant-available water capacity (AWC)(graph 1). On the 20th May and 20th July, the soils of object Sajevce up to 90 cm in depth were well supplied with available water (represented in mm of water (H_2O) which reached about 63 % of AWC) but on the dry 16th September the available water supply was noticeably smaller (only 67 mm to 93 mm H_2O or about 33 % of AWC).

Gleysols of object Podlog have developed on rather carbonated sediments of gravel, sand, silt and clay. In late autumn, winter and spring, the groundwater table can rise to a depth of 25 cm and in late summer and early autumn can sink lower than 2 m in depth. On March 25th and May 20th, the soil layers 50 to 90 cm were wet to saturated because of the groundwater table at 55 to 60 cm. In the layer 0 to

Table 3. Symbols of dominant horizons (FAO 1990), pH values, contents of calcium carbonate, organic matter and total nitrogen, the ratio of organic carbon to total nitrogen, textural classes (C=clay, L=loam, Si=silt, S=sand, SiCL=silty clay loam etc.), field capacities (FC), permanent wilting points (PWP), available water capacities (AWC = FC - PWP), bulk density (BD) and momentary soil humidity, measured in the early spring (MH_1) and at the end of the summer (MH_2) for soil layers of representative profiles

Horizon	Depth (cm)	pH ($CaCl_2$)	$CaCO_3$ %	Humus %	N_{total} %	C/N	Textural class	FC mass %	PWP mass %	AWC mm H_2O	BD g/cm3	MH_1 mass %	MH_1 mm H_2O	MH_2 mass %	MH_2 mm H_2O
Profile:	Sajevce 1										Date:	25. 3. 99	25. 3. 99	16. 9. 99	16. 9. 99
Ol,f	6/2-0	5.05		63.95	1.36	27									
AhE	0 -15	4.04 - 4.86	0	14.83	0.52	16	SiL	42.4	18.0	40.8	1.115	42.6	39.9	30.8	21.4
EBtg	15 - 50	4.88 - 6.48	1.28	1.22	0.09	8	SiCL	36.6	17.1	99.9	1.466	30.1	66.1	21.9	24.8
Bgk	50 - 90	7.45 - 7.62	44.82		0.04		SiCL	27.2	12.1	89.8	1.482	27.6	87.7	20.6	46.9
BgkC	90 + 220	7.62 – 7.51	42.57 - 24.35		0.04		SiCL								
Profile:	Sajevce 2										Date:	25. 3. 99	25. 3. 99	16. 9. 99	16. 9. 99
Ol,f	6/2-0	4.58	0.00	65.51	1.40	27									
AhE	0 -15	3.78 - 4.14	0.00	7.87	0.23	12	SiL	41.6	15.9	45.9	1.190	57.5	65.8	30.4	25.2
EBtg	15 - 50	4.39 - 6.23	0 - 0.21	1.52	0.08	11	SiL - SiCL	36.0	16.3	99.7	1.445	30.3	71.1	22.3	30.9
Bgk	50 - 90	7.56 - 7.61	34.69		0.05		SiC	37.2	19.1	107.1	1.485	23.5	26.7	20.7	10.4
BgkC	90 + 200	7.58 - 7.67	20.03 - 70.65		0.40		SiCL - L								
Profile:	Podlog 1										Date:	25. 3. 99	25. 3. 99	16. 9. 99	16. 9. 99
Ol,f	6/2-0	4.47	0.00	76.63	1.65	27									
AhBw	0 -15	3.75 - 4.08	0.00	16.75	0.72	14	L	68.9	26.4	41.9	0.703	65.9	38.5	46.1	23.0
Bg	15 - 50	4.17 - 5.03	0.00	1.83	0.09	10	L -CL	33.0	10.7	89.9	1.253	31.5	84.8	20.9	41.5
BCg,r	50 + 90	6.91 - 7.17	0.43 - 24:32	0.53	0.06	5	CL - SL	20.2	8.8	75.6	1.664	31.5	148.3	14.1	34.7
Profile:	Podlog 2										Date:	25. 3. 99	25. 3. 99	16. 9. 99	16 .9. 99
Ol,f	6/2-0	4.89	0.00	74.13	1.65	26									
AhBw	0 -15	4.52 - 3.97	0	14.88	0.62	15	SiL	72.7	26.4	42.7	0.718	63.7	31.1	36.5	8.8
Bg	15 - 50	4.23 - 5.78	0 - 0.88	3.06	0.14	12	L - CL	31.2	12.2	79.6	1.305	26.3	59.2	15.1	13.2
BCg,r	50 + 90	6.98 - 7.63	16.34 - 52.86	1.36	0.06	13	L -SL	17.4	7.4	71.0	1.786	26.8	138.4	13.7	44.7
Profile:	Benv										Date:	7. 4. 99	7. 4. 99	25. 8. 99	25. 8. 99
Ol,f	0/3-0	5.84		36.50	1.39	26									
Ah	0 -15	5.41 - 5.13	0.40	3.22	0.29	11	SiL	43.2	21.4	38.4	1.215	39.9	32.4	34.5	22.8
AhC	15 - 50	5.26 - 5.48	0.41	0.95	0.10	9	SiL - L	32.0	13.5	94.4	1.464	28.7	77.6	23.8	52.4
Cg	50 - 90	5.52 - 5.73	0.43 - 0.85	0.40	0.05	8	L - SL	22.2	6.9	93.8	1.537	20.6	84.3	15.2	51.0
Cg	90 + 180	5.83 - 6.15	0.42 - 0.21	0.16	0.03	7	SL								

Horizon	Depth	pH	$CaCO_3$	Humus	N_{total}	C/N	Textural	FC	PWP	AWC	BD	MH_1	MH_1	MH_2	MH_2
	(cm)	($CaCl_2$)	%	%	%		class	mass %	mass %	mm H_2O	g/cm3	mass %	mm H_2O	mass %	mm H_2O
Profile:	Led8/1										Date:	7. 4. 99	7. 4. 99	25. 8. 99	25. 8. 99
Ol,f	1/3-0	5.35		70.68	2.58	16									
Ag	0 -15	4.87 - 4.65	1.14	12.59	0.87	11	SiC	74.7	32.6	49.0	0.826	91.7	71.5	67.2	42.0
Cg	15 - 50	4.97 - 5.40	0.14	3.87	0.30	8	SiC	54.5	30.0	86.5	1.016	64.9	124.4	48.3	64.7
Cg,r	50 + 90	5.55	0.20	3.02	0.27	7	SiC	44.0	21.3	115.1	1.258	59.5	196.8	34.4	64.5
Profile:	Led8/2										Date:	7. 4. 99	7. 4. 99	25. 8. 99	25. 8. 99
Ol,f	2/5-0	4.30	0.00	77.58	1.20	38									
Ah	0 -15	5.25 - 4.75	0.4 - 0	6.29	0.33	11	SiCL	51.5	27.8	32.5	0.963	39.0	15.6	35.1	10.0
AhCg	15 - 50	4.86 - 5.12	0 - 0.43	2.20	0.14	9	CL - L	33.5	16.7	83.1	1.413	32.0	77.0	25.0	42.4
Cg	50 - 90	5.23 - 5.61	0.43 - 0.84	0.50	0.06	6	SCL - L	21.8	7.1	93.0	1.581	23.0	101.0	16.2	57.6
Cg	90 - 120	5.83	0.41	0.43	0.02	13	L								
Cg,r	120-200	6.37	0.40	0.35	0.03	7	SiL								
Cr	200+230	6.26	0.62	0.48	0.01	28	SL								
Profile:	Murn										Date:	7. 4. 99	7. 4. 99	25. 8. 99	25. 8. 99
Ol,f	4/0-0	5.59	0.00	56.89	0.89	37									
Ah	0 -15	4.92 - 4.67	0.00	7.18	0.38	11	SiCL	64.6	29.2	45.8	0.887	70.1	53.9	62.3	42.5
AhCg	15 - 50	4.97 - 4.92	0 - 0.21	2.50	0.14	10	SiCL - SiL	45.9	18.6	108.0	1.138	46.4	110.9	42.5	96.8
Cg,r	50 + 90	4.95 - 5.58	0 - 0.2	0.96	0.04	18	SiL - S	26.0	5.1	118.3	1.444	38.6	195.2	38.4	194.6
Profile:	Mur10										Date:	7. 4. 99	7. 4. 99	25. 8. 99	25. 8. 99
Ol,f	1/3-0	5.35	0.00	37.93	0.92	24	.								
Ah	0 -15	4.83 - 4.7	0.00	5.09	0.26	11	SiL	44.5	17.5	42.3	1.060	43.1	40.5	38.7	33.5
AhC	15 - 50	4.6 - 4.88	0.00	2.38	0.13	11	SiL	36.5	12.6	101.6	1.218	32.3	84.2	30.5	75.7
Cg	50 - 90	5.04 - 5.18	3.02 - 0.41	1.07	0.07	9	SiL	33.8	10.4	130.4	1.393	30.5	112.0	22.6	68.2
Cg	90 - 150	5.27 - 5.73	0.4 - 0.43	0.66	0.04	9	SiL								
Cg,r	150+210	5.52	1.24	0.52	0.05	6	SiL								



Graphs 1. Momentary contents of accessible and drainage water (=MH - PWP) up to 90 cm of soil depth and available water capacities (AWC) for research objects

15 cm, the soil moisture almost reached field capacity. In addition, on July 20th, the soils were well supplied with available water, even though the groundwater table had decreased to a depth of about 1 m. On September 16th, the groundwater table was at 195 cm and the upper half metre thick soil layer was rather dry. The available soil water content to a depth of 90 cm was on average 83 mm, almost the same as on the object Sajevce.

The soils of the objects in Murska Šuma have developed on recent alluvial sediments. The objects Benv and Led8 are located at the river Ledava; considering the groundwater table, they differ a great deal, as do the objects Mur10 and Murn at the river Mura. In the soil profiles of the objects Benv and Mur10, signs of oxidation and reduction can be found under a depth of 50 cm. However, the groundwater in the vegetation period was mostly too deep to affect the moisture of the upper soil layers (Table 6).

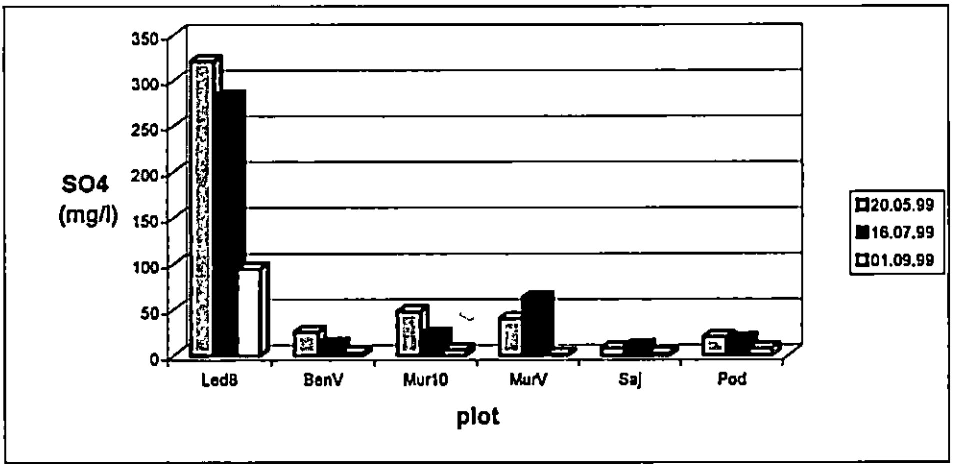
The soil conditions on object Len8 are presented by two soil profiles. Profile Len8/1 was dug on the border between a pedunculate oak site and a more moist site of black alder (*Alnus glutinosa*) and ash (*Fraxinus angustifolia*). There, the soil has a silty clay texture, it is inundated until late spring and is wet to moist all the year; the groundwater table is usually not lower than 1 meter deep. Profile Len8/2 represents the typical soil conditions of the object. The surface is about half a metre higher than on profile Len8/1, the soil is mostly loamy, and signs of oxidation and reduction appear under a depth of 55 cm. On August 25th the soil water content in the upper half-metre layer was less than the same layer on the otherwise drier object Benv.

The soil of object Murn was humid to wet over the year. Even on the dry 25th of August, the water content of the lower layers exceeded field capacity. In the soil of object Mur10, signs of oxidation and reduction appear under a depth of 50 cm. Over the vegetation period groundwater was too low to affect the upper soil layers (Table 6). On August 25th, the soil of object Mur10 held 177 mm, while the soil of the object Murn held 334 mm of available water in the upper 90 cm layer.

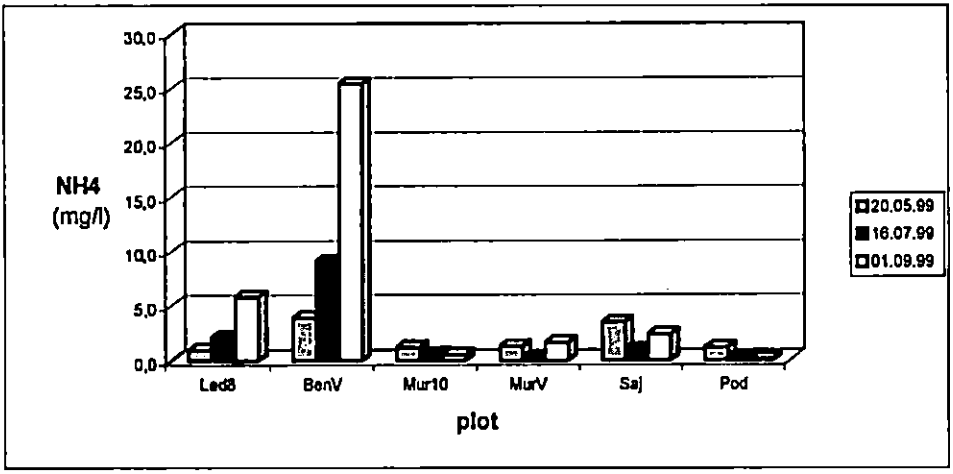
Table 3: Symbols of dominant horizons (FAO 1990), pH values, contents of calcium carbonate, organic matter and total nitrogen, the ratio of organic carbon to total nitrogen, textural classes (C=clay, L=loam, Si=silt, S=sand, SiCL=silty clay loam etc.), field capacities (FC), permanent wilting points (PWP), available water capacities (AWC = FC - PWP), bulk density (BD) and momentary soil humidity, measured in the early spring (MH_1) and at the end of the summer (MH_2) for soil layers of representative profiles

GROUNDWATER QUALITY

Groundwater sulphate concentrations (Graph 2) were diminished in 1999 for most of the plots in the period May until September 1999. The highest sulphate concentrations in comparison with other plots were at plot Benv; in May and July 1999 they exceeded critical concentrations for drinking water (200 mg/l; Pravilnik

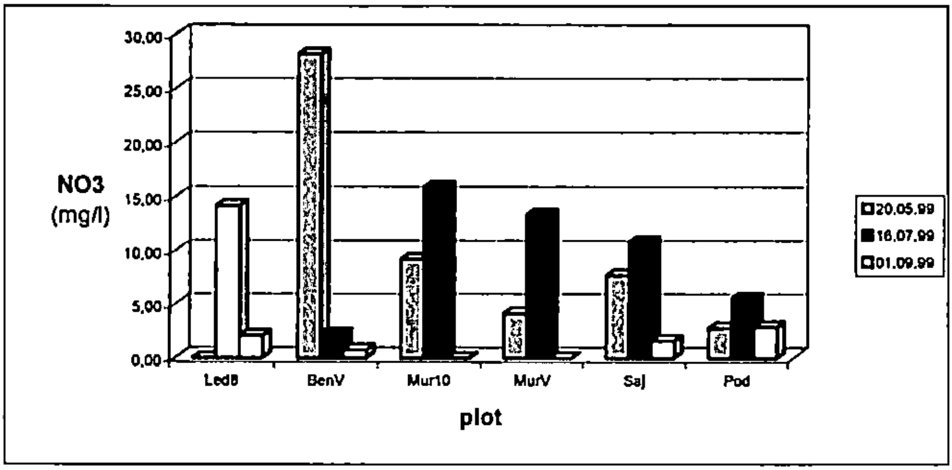


Graph 2. Sulphate concentrations (mg/l) in groundwater for research plots for three time-periods in 1999



Graph 3. Ammonia concentrations (mg/l) in groundwater for research plots for three time-periods in 1999

o higienski ....1987). In the period May until September, ammonia concentrations increased only on plots Led8 and Benv where we determined the highest values which exceeded critical concentrations for drinking water (0.5 mg/l N-NH_4; Pravilnik o higienski ....1987) (Graph 3). Total nitrogen groundwater concentrations are the highest for research plots Benv near the River Ledava and the intensive agriculture region Benica (Table 4) and the lowest for plot Podlog at Krakovski Gozd.



Graph 4. Nitrate concentrations (mg/l) in groundwater for research plots for three time-periods in 1999

Table 4. Average concentrations of N ($N\_NO_3 + N\_NH_4$; mg/l) in groundwater for period May till September 1999 on oak research plots

Area	Plot	$N\_NO_3 + N\_NH_4$ (mg/l)
Murska šuma		4.16
	Benv	12.28
	Led8	2.84
	Mur10	1.99
	Murn	2.24
Krakovski gozd		2.33
	Sajevce	3.37
	Podlog	1.16

Table 5. Nitrogen content in oak leaves from oak research plot (mg/g; September 1999)

Plot	N (mg/g)
Benv	20.2
Murn	22.3
Sajevce	22.1
Podlog	22.9

Results of foliar nitrogen content from different oak research plots (Benica, Mura, Sajevce and Podlog) are presented in Table 5. Average nitrogen concentrations of oak-tree foliage (composite sample from 10 trees per plot) are in the optimal range regarding levels of nutrition, which have been presented by different authors (Simončič cit. in Smolej and Hager, 1995, ICP FOREST 1997).

HEALTH STATUS OF FOREST IN MURSKA ŠUMA AND KRAKOVSKI GOZD

In 1999 defoliation of trees in the complex of Murska Šuma was on average 28.38 % (altogether 1100 dominant and codominant trees). Defoliation of pedunculate oak (*Quercus robur* L.) reached 36.20 %, of black alder (*Alnus glutinosa* L.) 23.75 % and of hornbeam (*Carpinus betulus* L.) 19.77 %. According to the defoliation classes of the EU, pedunculate oak is classified as moderately defoliated and the others as slightly defoliated tree species (Mavsar 1999).

On the plots, the defoliation rates of oak (Čater and Batič 1999) were similar and probably related to the level of groundwater. Statistical analysis shows only one significant difference in 1999 – Mur10 : Murn. The difference in the defoliation rates of other tree species are not significant.

Table 6. Health status of pedunculate oak and groundwater level

Plot	Defoliation 1999 (%)	Defoliation 1997 (%)	Average (min. and max.) depth of groundwater table 1999 (apr.-oct.) (cm)
Led8	37.5	27.0	184 (97 – 223)
Benv	32.9		256 (180 – 304)
Mur10	47.3	38.5	347 (234 – 419)
Murn	26.7		137 (74 – 173)
Sajevce	28.3		215 (104 – 274)
Podlog	26.7		174 (96 – 230)

DISCUSSION

The ecophysiological investigation undertaken in 1997 shows differences in crown defoliation between two research objects in Murska Šuma (Čater 1998). On the plot Ledava (Led8) with a groundwater table 80 - 140 cm under the surface, there was average crown defoliation of 27.0 %. On the plot nearer the Mura river (Mur10) with a higher average crown defoliation (38.5 %), the groundwater table was deeper (220 - 300 cm). In the case of water potential and electrical resistance of the cambial zone, the differences between the two comparable plots were significant (Čater et al., 1999) as a possible consequence of different soil moisture conditions.

In 1999 an experiment was set up in two pedunculate oak forest complexes (Murska Šuma and Krakovo forest) with four research objects (Čater and Batič 2000). On four new (Benv, Murn, Sajevce, Podlog) and two older objects (Led8 and Mur10), the soil-water characteristics were studied. On two objects with gleysols (Murn, Podlog), the average defoliation for 1999 was cca 27 %, on the object Sajevce with planosols it was 28.3 %, near the River Ledava (Led8) it was 37.5 % (higher than in 1997 when the groundwater table was higher). On the objects Benica (Benv) and Mura (Mur10), where the groundwater table was the lowest (average 256 cm and 347 cm) and where the soils are only under the influence of precipitation, average crown defoliation was estimated at 32.9 and 47.3 %.

Nitrogen nutritional levels for oaks at the research plots in Murska Šuma and Krakovski Gozd are relatively good and within the optimal ranges (Simončič cit. in Smolej and Hager, 1994). Groundwater concentrations of nitrogen ($NH_4 + NO_3$) are highest on the plot Benica (Benv) in the Murska Šuma region. Foliar nitrogen contents did not follow these trends, which indicates only moderate nitrogen emissions from the nearest intensively cultivated fields and farms. More evident was groundwater pollution, especially on the plot Benica. It is near the River Ledava which is closely linked up with the drainage system of the fields. No relations between groundwater quality and crown defoliation of pedunculate oak on the research plots were stated in 1999.

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SASTOJINE HRASTA LUŽNJAKA U NIZINSKIM PODRUČJIMA SLOVENIJE – STANJE VODE U TLU

U 1999. godini proučavani su uvjeti tla i vode u dvama najvećim šumskim kompleksima hrasta lužnjaka. Utvrđena su svojstva tla i izmjerene zalihe vode u tlu do dubine od 90 cm na 6 istraživanih objekata. Analizirana je kakvoća podzemne vode i procijenjen je zdravstveni status stabala. Krošnje stabala u vlažnijim hrastovim sastojinama na glejsolu i planosolu u načelu su manje osipane od hrastovih sastojina na fluvisolu, gdje je prosječna razina podzemne vode dublja od 2,5 m.

Ključne riječi: *Quercus robur*, hidromorfna šumska tla, praćenje vlage tla, osipanost, Slovenija

B. Prpić: The role of climate and hydraulic operations in the stability of the pedunculate oak (*Quercus robur* L.) stands in Croatia. Glas. šum. pokuse 37: 229–239, Zagreb, 2000.

UDK 630*181+181.3+111+908 (Quercus robur L.)

THE ROLE OF CLIMATE AND HYDRAULIC OPERATIONS IN THE STABILITY OF THE PEDUNCULATE OAK (*QUERCUS ROBUR* L.) STANDS IN CROATIA

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In around 200,000 ha of lowland forests in the river valleys of Croatia, in variously moist habitats, the peduncled oak, in bigger or smaller proportions, composes forest ecosystems with other plant and animal species. Differing as to the component plant species, mainly hygrophytes, these ecosystems have in common a considerable proportion of peduncled oak.

Water is a direct ecological factor in the growth of peduncled oak. Either below the minimum, or above the maximum, it will cause the physiological weakening of the tree, frequently even its dieback. Among the lowland forest trees, the peduncled oak belongs to a very susceptible species. Today in Croatia, about 30% of all peduncled oak trees are endangered, and will die before reaching their commercial maturity.

While it successfully survives climatic excesses including drought and very humid seasons, hydraulic operations that disturb the forest areas cause its dieback in all forest ecosystems.

Key words: lowland forests of the peduncled oak, climatic excesses, hydraulic operations, changes in water regime, peduncled oak, dieback.

INTRODUCTION

The peduncled oak belongs today to the most endangered tree species in Croatia. According to the IPC Forests method, in 1988 there were 28.5% damaged trees of the species (over 25% crown damage). Since 1980, over 600,000 m^3 of peduncled oak trees have died in the lowland forests of Pokuplje, Posavina and Podravina.

This paper will offer evidence proving that anthropogenic impacts originating from the changes in the water regimes due to hydraulic or other operations in the areas of lowland forest habitats have been the major reasons for the dieback of the peduncled oak. This primarily refers to the water steps at the hydroelectric plants on the River Drava; exhaust canal dams and barriers in former natural retentions for high water protection; forest roads without drainage; deep trenches along drained agricultural areas, etc.

All these impacts change the water regimes of the forest habitats, causing either their swamping or drying, depending on the character of the operation. Deep trenches decrease the groundwater level, while hydroelectric plant accumulations turn forests into swamps. The impact of hydraulic operations depends on the microrelief, geological and pedological circumstances, and the network of natural and artificial streams in the area.

Frequent changes in the water regime caused by the infrastructure, particularly in the second half of the century, endangered the peduncled oak and other tree species through the change of the "chemical climate", while the lowland ecosystems have been under the impact of polluted waters.

At least 4 million cubic metres of trees have died since the first records of oak dieback were made in Croatia in 1909.

Climatic changes and excesses, natural changes in the river levels, phenomena causing considerable, though temporary, falls or rises in groundwater levels, together with forest tree pests and diseases, belong to the adverse factors that can be controlled. These adverse factors did not prevent the peduncled oak forests from developing normally and retaining their stability for centuries.

Man's interference in these areas in the twentieth century with the change in the "chemical climate", i.e. the activities that can be controlled, have caused higher or lesser degrees of dieback of peduncled oak and almost all other tree species. However, knowing how resistant the peduncled oak is toward the input of harmful gases, we conclude that the change of the water regime in its habitats is a major cause of its dieback.

THE EFFECTS OF FIELD ELM DIEBACK UPON THE MICROCLIMATE

The dieback of field elm in the area of Croatian lowland forests from 1930 until 1960 ended with its near extinction. The largest proportion of lowland elm was in the Slavonian peduncled oak forest (*Genisto elatae-Quercetum roboris*) where it composed the lower tree layer with such types as the hornbeam in the forest of peduncled oak and common hornbeam (*Carpino betuli-Quercetum roboris)*. The two had similar microclimates. The loss of the field elm caused the warming up of the Slavonian peduncled oak forests.

The mean maximum summer air temperature in the Slavonian forest before the elm dieback was 4 degrees C lower than in the field. With elm dieback, the difference decreased by 2 degrees (Prpić, 1975). The gradual development of the brush layer following the extinction of the elm with the formation of the canopy helped the habitat to recover, a process which lasted between 10 and 15 years, depending on the number and distribution of the dead elms in the stand. If other adverse ecological factors appear, e.g. diseases and pests, climatic excesses, or hydraulic groundwater-lowering and habitat-swamping operations, the result might be the dieback of peduncled oak.

By entirely retaining the natural relations in forest tree proportions with the hornbeam as the lower tree layer controlling the specific forest climate, peduncled oak with common hornbeam has proved to be a much more resistant ecosystem.

MICROCLIMATE CHANGES

According to Vajda 1983, in the early 20th century the climate changed in terms of frequent dry springs and summers with high air temperatures and more than average humid, cold periods. However, climate cannot be the main reason for the dieback of peduncled oak, since this species has been in these regions for thousands of years and has been well adapted to natural climatic changes.

Climatic deviations from the average, mainly in the series of dry seasons in the second half of the 20th century, have had an adverse impact on the peduncled oak, in particular when accompanied by another unfavorable ecological factor, e.g. pests or hydraulic operations changing the water regimes in the habitat, in most cases ending up with dieback of the oak at a higher or lesser intensity. If there is no additional adversity, one humid season that follows is sufficient for its recovery.

HYDRAULIC OPERATIONS IN THE LOWLAND FOREST AREA AND THEIR IMPACT ON THE PEDUNCLED OAK

The first hydraulic operation in Posavina took place in the 1930s when dams along the Sava banks were built for the protection of villages against flood, changing the rhythm of floods in the lowland forest of Spačva. The consequence was considerable dieback of peduncled oak in Spačva.

Further large-scale dieback occurred in Posavina, Pokuplje and Podravina in the following chronological order:

1. Following the disastrous flood in the city of Zagreb in 1964, water was directed to the cassette-shaped peduncled oak forests (drainless roads were built through the cuts in the square-formed sections), resulting in massive oak dieback due to the swamping of all forest ecosystems (anaerobiosis).
2. The enclosing of the Bosnian Dubica valley by dams along the rivers Sunja and Dubica in Ribasko Polje resulted in the dieback of the field ash and peduncled oak in 1966.

3. The building of the Zagreb-Karlovac road in 1972 and the Kupa-Kupa canal were reasons for swamping and a fall in the groundwater level, both resulting in considerable oak dieback in the region.
4. The disastrous oak dieback in the Kalje forest in 1984 and 1985 was caused by the flooding of the River Odra during the vegetation season, and by the fall of the groundwater level, both due to cassette-shaping operations in the area.
5. Considerable oak dieback started in 1986 in the forest of Turopoljski Lug due to the building of the outlet channel Sava-Odra, which resulted in a fall in the groundwater level. The process has continued until today.
6. Three power plants are being built on the River Drava - Varaždin, Čakovec, and Dubrava - causing the dieback of oak and other lowland forest trees due to the swamping of the areas along the accumulations and also as a result of a fall in the groundwater levels along the outlet canals. This has lasted from 1968 until today.
7. The peduncled oak was dying from 1987 until 1995 in the Repaš forest, caused by drought and a general fall in the Drava level and, consequently, by a fall in groundwater levels.

SOME OF THE RESEARCH ON THE CAUSES OF PEDUNCLED OAK DIEBACK IN CROATIA

In 1984 Klepac conducted research on the peduncled oak increment in the Lipovljani forests between 1950 and 1981. He considered the increment measured in the period 1950-1955 as normal and compared it with that of the following periods. For the period 1962-1967, he calculated a fall by 45%; 1968-1971 by 27%; 1972-1977 by 25%; 1978-1981 by 40%. Klepac points out that the oak did not show any loss of vitality in spite of the considerable fall in increment which he associated with the dry periods and absence of the regular annual floods of the River Sava.

In her dendrochronological research in 1996, Pranjić suggests that the diameter increment is the major indicator of habitat changes, hinting that all habitat factors are cumulatively registered in diameter increments. She illustrates this with research on the diameter increment in the Slavonian forest of pedunculate oak and great greenweed (*Genisto elatae-Quercetum roboris* Ht. 1938), where a powerful and short adverse impact was connected with the extremely dry season of 1983. Team research on the disastrous oak dieback in the Kalje forest (Prpić et al. 1994) revealed that the cause was an extremely dry season, a summer flood in the cassette-shaped forest area with polluted water and a fall in the groundwater level (see diagram 1).

Big hydraulic operations in the region of Kupčinske Šume connected with the building of the Zagreb-Karlovac road and the outlet canal Kupa-Kupa caused, ac-

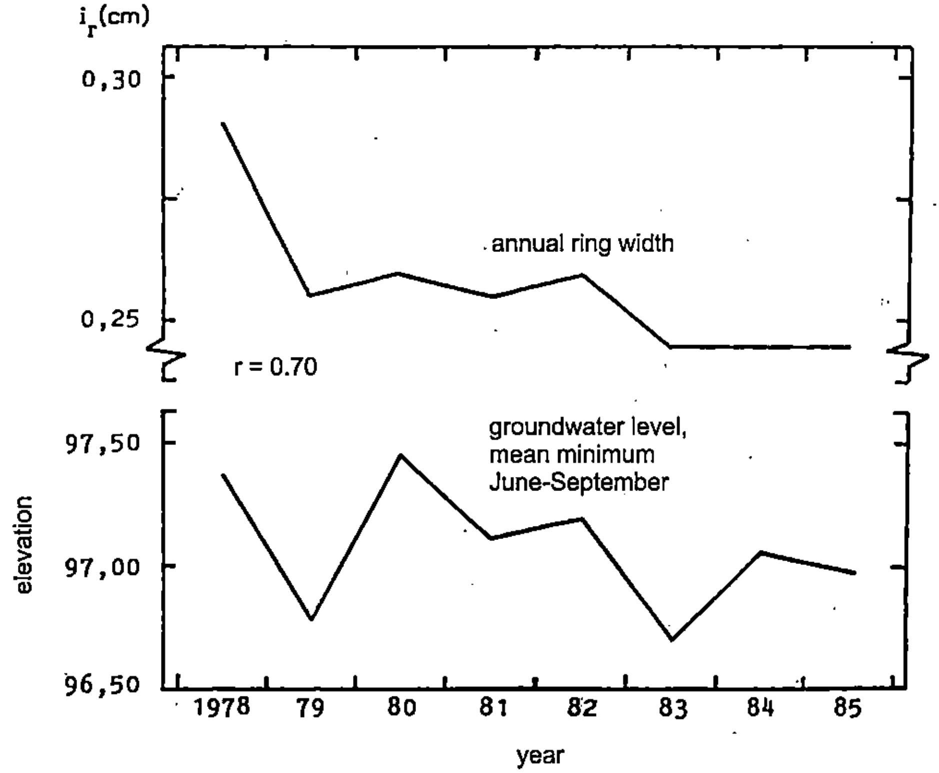

Diagram 1. The dependence of the radial increment of the peduncled oak upon the minimum groundwater level in the Kalje forest

cording to Mayer 1996, an expansion of oak dieback and the conquest of drier forest associations. The author established that the high groundwater levels advanced the increment of the peduncled oak forests.

According to Mayer 1998, following the construction of the hydroelectric power plant Varaždin on the River Drava in the area of the outlet canals, there was a fall of 1.5 to 2m in the groundwater levels in the pebbled water tank, together with flood reduction. Over large areas, groundwater became inaccessible for the roots of the flood plain forests. The trees dried, and later afforestation of these areas had no success.

Based on extensive research, Mayer concluded that in the drained forests of northwest Croatia the peduncled oak on pseudogley and eugley soils directly depended on the quantity and distribution of rainfall, since the groundwater became unreachable for the roots of the middle-aged and old stands of the lowland peduncled oak forests.

The research of Prpić 1984 and 1994 referring to the swamping of the peduncled oak habitats in the forests of Kupčine and in the Kalje forest suggests that young oak dieback took place after the artificially provoked flood during the vegetation period; the diameter increment of the peduncled oak trees also decreased in the artificially flooded stand. The content of carbon dioxide in the accumulation horizon of the soil was measured, as it becomes toxic when its values go above 50 mg/l.

Ivkov 1994 established a considerable connection between the diameter increment of the peduncled oak and the physiologically active soil moisture in the Repaš forest (diagram 2).

Prpić 1986 proved that the groundwater in the Repaš forest and the water levels of the river Drava are closely connected, and that the changes in the water regimes following the construction of the hydroelectric power plant Đurđevac were disastrous for the forest (diagram 3).

The team research on the Repaš forest (Prpić et al. 1987) revealed that the middle-aged, old and very old peduncled oak trees prolong their roots geotropically positively to the groundwater which, due to the riverbed erosion, drops yearly by 2-3 cm. This fact points to the possibility of the adaptation of the grown oaks to small falls in groundwater levels, which they need during dry summer months for transpiration and photosynthesis (Fig. 1).

According to Matić et al. 1998, the middle-aged, old and very old peduncled oak stands with decreased levels of groundwater are submitted to a less intensive dieback process. The stands with an increased level and duration of retention surface waters, i.e. in the case of swamping, die quickly.

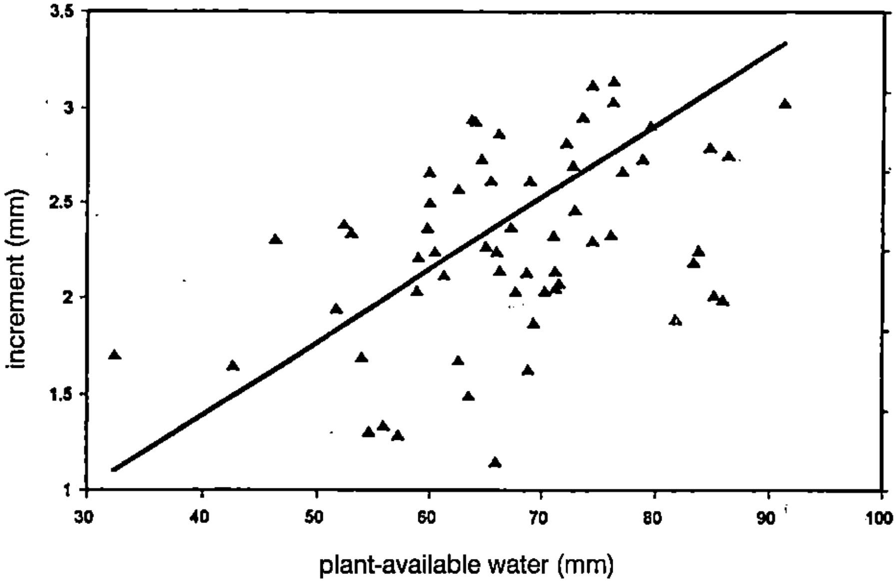

Diagram 2. Relationship between plant-available water in soil and peduncled oak radial increment in the Repaš forest (Ivkov 1994)

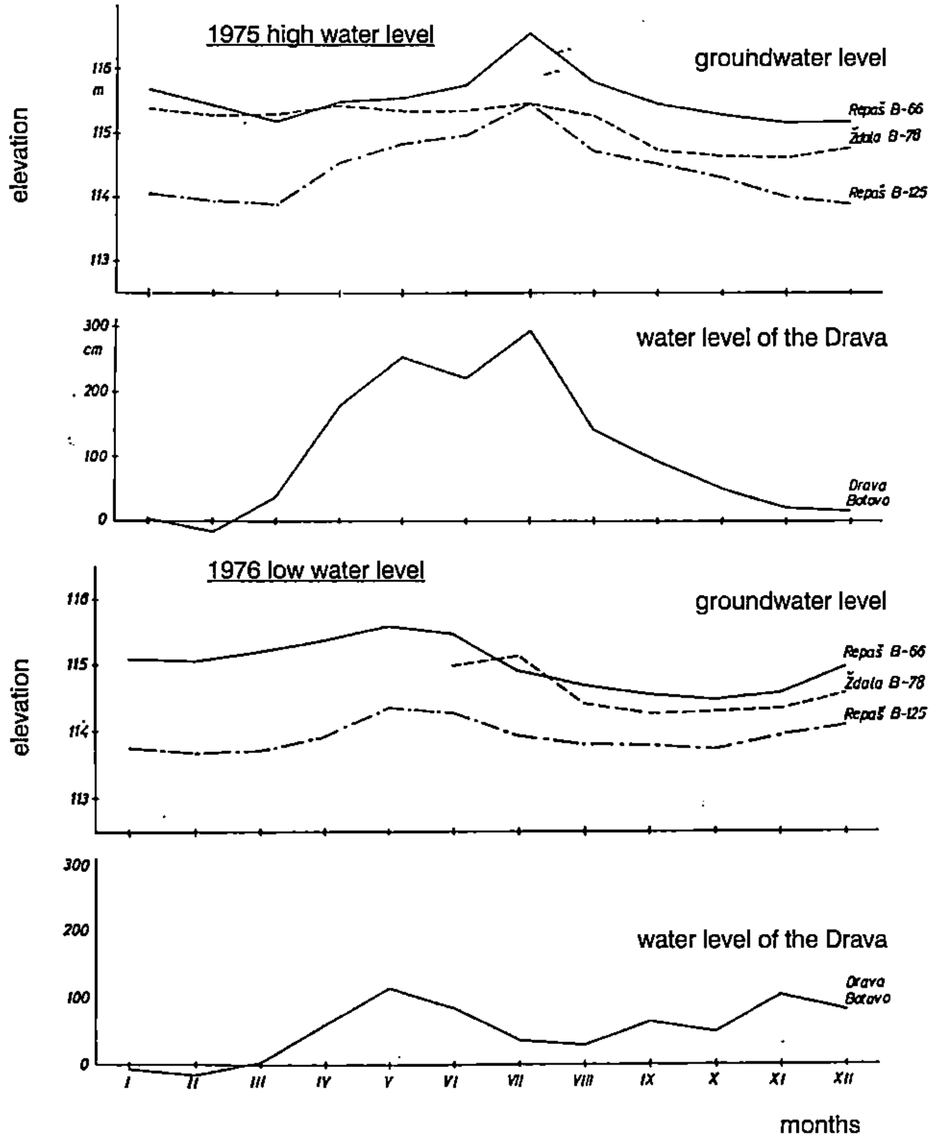

Diagram 3. Groundwater level in the Repaš forest and the water level of the river Drava at Botovo

Vukelić and Baričević 1998 completed their research on forest association successions in the areas of peduncled oak dieback in Croatia, showing the long duration of the positive succession and massive dieback of peduncled oak in the forest of Žutica.

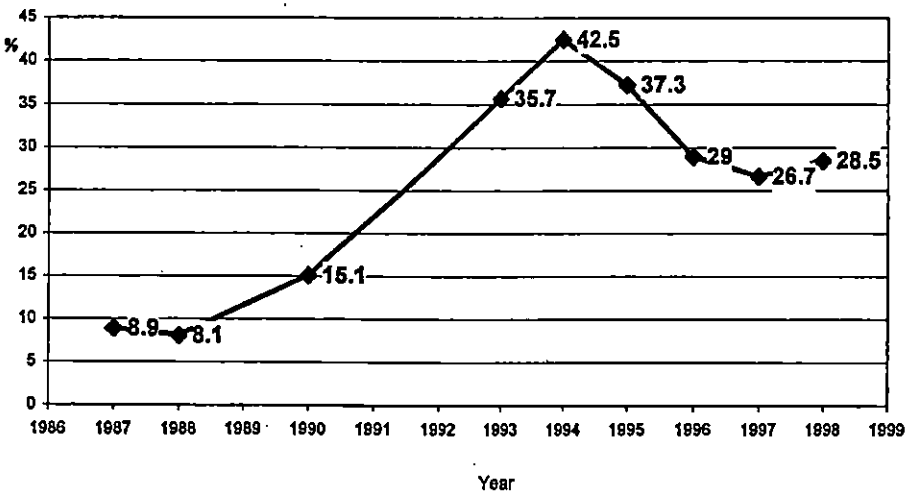

Diagram 4. The percentage of moderately to severly damaged peduncled oak trees in Croatia (Potočić-Seletković 2000)

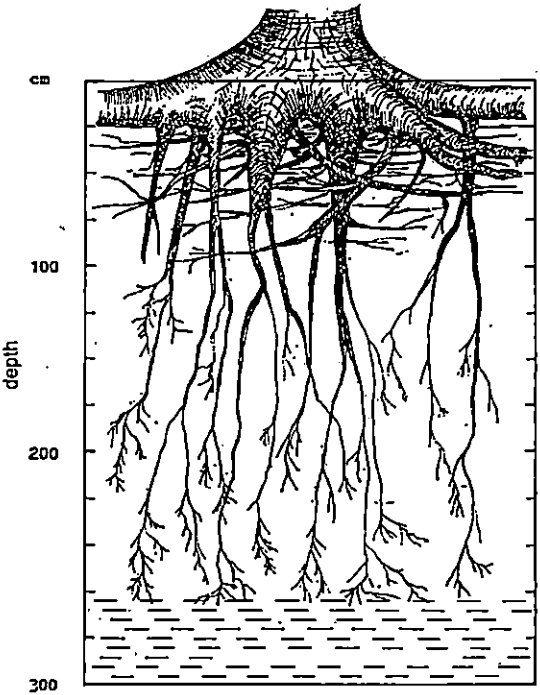

Figure 1. Root system of the peduncled oak in semigley in the peduncled oak and common hornbeam forest in the Repaš forest. The depth of rooting compared to the summer groundwater level.

Finally, there is a graphical presentation of the peduncled oak dieback situation according to Potočić and Seletković 2000, showing a relatively high percentage of considerably endangered trees after the IPC Forests method, as well as the response of the peduncled oak to the favorable climatic conditions of 1994.

CONCLUSIONS

Hydraulic operations causing habitat changes in the lowland forests of the peduncled oak lead to the physiological weakening of the species and various degrees of its dieback.

Natural climatic changes do not cause peduncled oak dieback, as the tree is adaptable to climatic excesses. If, however, these climatic excesses are linked with adverse natural biological impacts (pests and diseases), or with anthropogenic adversities (hydraulic operations; air/water/soil pollution), the peduncled oak and other lowland forest trees will die.

Any hydraulic engineering interference in the forest areas of the river valleys should be carried out so that it does not cause any changes in the water regimes within the lowland forest habitats.

A lowland forest should be considered in view of its general benefits, environmental protection, and its biological diversity - the values that must be considered in an analysis of the costs and benefits of investments and forests.

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UTJECAJ KLIME I HIDROTEHNIČKIH ZAHVATA NA STABILNOST HRASTA LUŽNJAKA (*Quercus robur* L.) U HRVATSKOJ

Hrast lužnjak, zajedno s ostalim biljnim i životinjskim vrstama, u manjem ili većem obujmu tvori šumske ekosustave na oko 200 000 ha nizinskih šuma u riječnim dolinama Hrvatske na staništima različite vlažnosti. Ti se ekosustavi razlikuju po sastavnim biljnim vrstama, uglavnom higrofitima, ali ono što im je zajedničko jest značajan udio hrasta lužnjaka.

Voda je izravan ekološki čimbenik koji utječe na rast hrasta lužnjaka. Ako je voda ispod minimuma ili iznad maksimuma, hrast lužnjak fiziološki slabi, a često se i suši. Među nizinskim šumskim vrstama hrast lužnjak pripada u vrlo osjetljive vrste. Danas je u Hrvatskoj oko 30 % svih hrastova lužnjaka ugroženo i oni će se osušiti prije nego što dosegnu svoju komercijalnu zrelost.

Premda ova vrsta uspješno podnosi klimatske ekscese, na primjer sušne i mokre godine, hidrotehnički zahvati koji ometaju šumske površine uzrokuju sušenje hrasta u svim šumskim ekosustavima.

Ključne riječi: nizinske šume hrasta lužnjaka, klimatski ekscesi, hidrotehnički zahvati, promjene u vodnom režimu, hrast lužnjak, sušenje

UDK 630*585+561+469 (Quercus robur L.)

RELATIONSHIP BETWEEN DIAMETER INCREMENT AND DAMAGE STATUS OF PEDUNCULATE OAK (*Quercus robur* L.)

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The research of the relationship of diameter increment and the damage status of Slavonian oak (pedunculate oak - *Quercus robur* L.) was carried out on colour infrared (CIR) aerial photographs (APs) in the famous lowland forests in the Sava Valley. For the assessment of the relationship between the increment and damage status of pedunculate oak, the increment cores were taken on the ground, using colour infrared (CIR) aerial photographs (APs) for the identification of a particular tree. 247 cores were taken. The width of the annual rings in the year of obtaining the colour infrared (CIR) aerial photographs (APs) were measured on the cores and compared with the damage status of particular oak trees. The relationship between 5-years current annual diameter increment (i_{d5}) and the damage status at the end of the period was also investigated.

The increased damage of pedunculate oak trees reduces their growth. The diameter increment is a very good indicator of damage status since, even in the case of minor vitality decrease, it is reduced considerably. This was proved by the correlation analysis.

The correlation between the damage stage in percentages assessed on color infrared aerial photographs and the width of annual rings in the year in which the aerial photographing was made is very strong ($r = -0.9430$).

The correlation between 5-years current annual diameter increment and the damage stage in percentages at the end of the 5-year period is also strong ($r = -0.8475$).

The damage status was determined along natural and man-made communication lines in the forest. The analysis of stand damage status was performed within 100 and 200 metre zones along linear infrastructures. Along meliorated marshes, public roads and channels the damage is high; along natural streams and simple forest roads it is much smaller. These results showed that the stability and health of oak stands are highly dependent on the disturbance of the natural water regime.

Key words: pedunculate oak, colour infrared (CIR) aerial photographs (APs), diameter increment, damage status, natural and man-made linear infrastructure

INTRODUCTION

Pedunculate oak is the most important species in the lowland forests of Croatia in terms of its economic value. For a number of years forests of pedunculate oak have suffered changes affecting their stability, which is directly linked to their productivity. These changes are most frequently reflected in a physiological weakening of individual oak trees and stands and in a reduced increment. The increment of damaged trees and stands has been studied by a number of authors (Athari and Kramer 1983, Kenneweg and Nagel 1983, Kenk et al. 1984, Kalafadžić 1987, Hočevar and Hladnik 1988, Kalafadžić and Kušan 1989, Pranjić and Lukić 1989, Pernar 1994, and others). They all observed a reduction in the tree diameter increment resulting from an increased damage status. Diameter increment is a good indicator of damage status, as it decreases considerably even when the vitality is only slightly weakened. Individual or joint action of all positive and negative factors in a site affects the width of annual rings, or diameter increment. The result of their action is always cumulatively expressed in the width of an annual ring. This is a measurable, stable function that does not change after formation (Pranjić and Lukić 1989). The paper examines the rate of pedunculate oak (*Quercus robur* L) increment at various extents of damage.

AIM OF RESEARCH

The main aim of this work is to find out the extent to which the increment of pedunculate oak decreases if the damage status increases. In order to achieve the set goal, several concrete tasks had to be accomplished, including:

- establishing the damage status of pedunculate oak with colour infrared (CIR) aerial photographs according to the existing photointerpretative key (Pernar 1994)
- determining the increment of pedunculate oak according to the degree of damage
- comparing the obtained results.

RESEARCH AREA

The relationship between the increment and the damage status of pedunculate oak was studied using the CIR aerial photographs of lowland pedunculate oak forests in Slavonian Posavina. Samples of aerial photographs were taken in the form of strips in the forest basin "Spačva" in 1989. Two strips of 49.08 km in total were recorded in a north-south direction and one in an east-west direction (Figure 1). The 157 compartments were recorded partially or completely in 99 aerial photographs on a scale of 1: 6123.

Figure 1. Map of area covered by aerial photographs in strips

METHODS OF WORK

The cores used for the increment analyses were taken in the field with the help of aerial photographs. Oak trees with dbh ranging from 40 to 50 cm (which was the range of the mean diameter at breast height of these stands) were found with aerial photographs in stands of about 100 years of age (95 - 110 years). The cores, used for the ring width analysis, were taken from the selected trees with Pressler's drill. The damage status of every tree was assessed in the CIR aerial photographs applying the valid photointerpretation key for pedunculate oak (Pernar 1994). A total of 247 cores were taken, and the widths of annual rings were measured on the cores. The measurement was done with special measuring instruments, where cores were observed with a binocular microscope with 3x, 8x and 10x magnification. The widths of rings were measured with a vernier scale of m = 0.05 mm.

As the studied area is abundantly intersected with natural streams, channels and man-made communication lines, the CIR photographs also determined the damage status along these facilities. The extent of individual damage status was determined within 100 and 200 m along these facilities. Forest areas along the so-called forest highways (asphalt road with deep side ditches), forest roads, natural streams, meliorated marches, man-made canals, and the Zagreb - Lipovac motorway were analysed.

RESULTS OF RESEARCH

The ring width from 1989 was compared with the damage status of pedunculate oak determined by the CIR photographs (Table 1, Figure 2).

Table1. Annual ring width and damage status

Percentage of damage (%)	Number of trees	Annual ring width (mm)
10	1	2.00
15	3	1.63
20	60	1.66
25	82	1.57
30	35	1.20
35	30	1.16
40	20	1.05
45	8	1.09
55	3	0.83
60	2	0.80
65	1	0.35
70	2	0.40

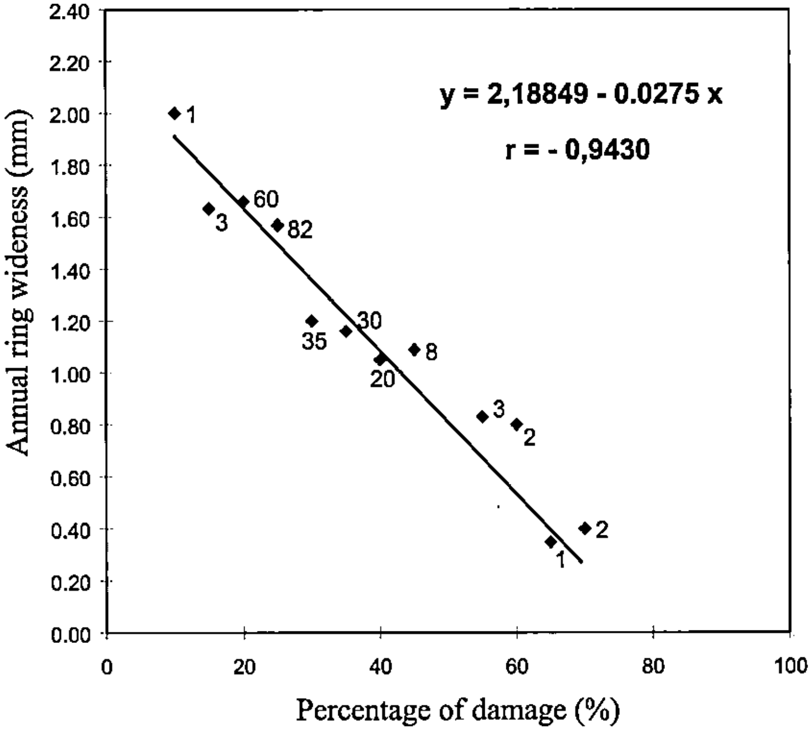

Figure 2. Relationship between annual ring width and damage status

The relationship between the current annual diameter increment for the period 1985. - 1989 and the damage status of trees at the end of this period was also analysed (Table 2, Figure 3).

Table 2. Diameter increment (i_{d5}) and damage status

Percentage of damage (%)	Number of trees	Diameter increment (i_{d5}) (mm)
10	1	4.28
15	3	3.68
20	60	3.54
25	82	3.45
30	35	3.16
35	30	2.99
40	20	2.92
45	8	3.07
55	3	2.03
60	2	3.87
65	1	1.14
70	2	1.50

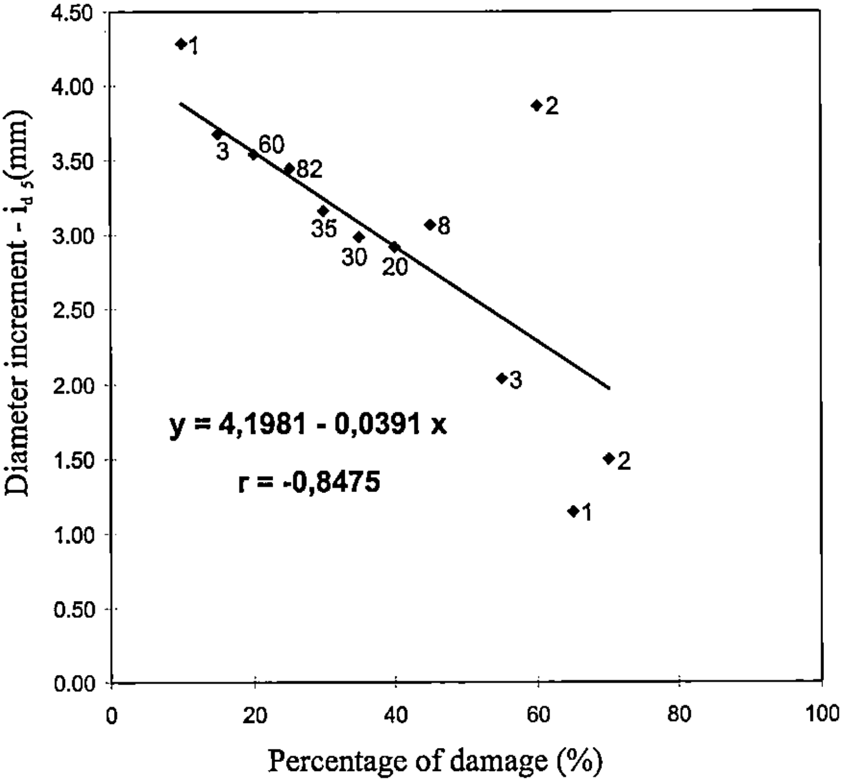

Figure 3. Relationship between diameter increment (i_{d5}) and damage status

The cores taken with Pressler's drill were analysed and the following was established: there is a strong negative correlation (r = - 0.9430) between the damage rate of pedunculate oak selected in aerial photographs and the annual width at breast height in the year of recording.

This relationship is linear, and can be expressed with a regression equation:

$$Y = 2.18849 - 0.0275X \text{ where}$$

X = percentage of damage determined by aerial photographs, and
Y = ring width in the year of recording (1989).

There is also a very strong negative correlation (r = - 0.8475) between the damage percentages of pedunculate oak determined in the aerial photographs and the current annual diameter increment for the period 1985 – 1989:

$$Y = 4.1981 - 0.0319X \text{ where}$$

X = percentage of damage determined by aerial photographs, and
Y = current annual diameter increment for the period 1985 - 1989.

The measured data can follow the fitted line up to 45% of the damage status, which is shown in Figure 3. This means that these trees have not displayed any significant oscillations in increment in the last five years, which is decreasing linearly.

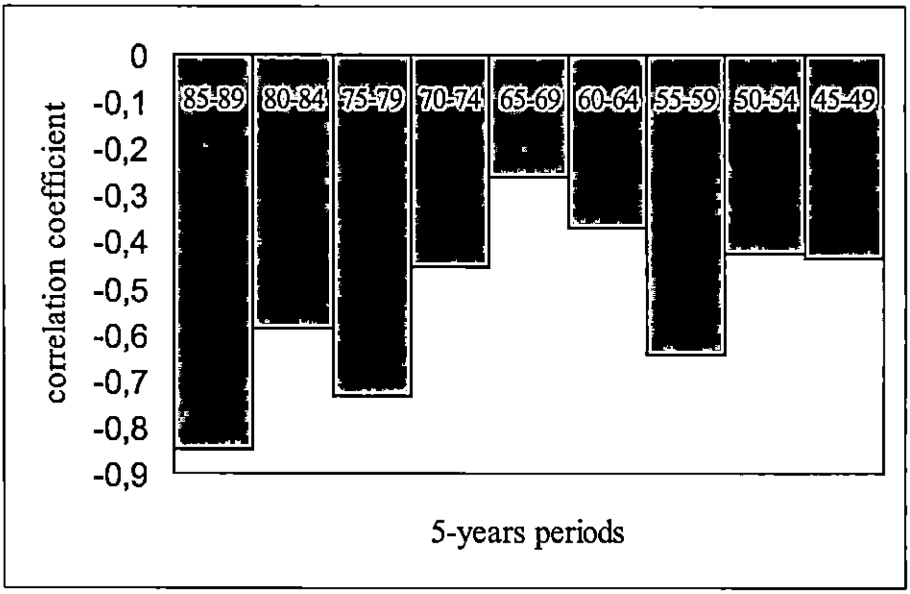

Figure 4. The changes in correlation coefficients between 5-year diameter increment and damage statuses in the period from 1945 to 1990

Significant deviations from the fitted line for more severely damaged trees are an indication of cases of acute dieback, because these deviations were not present in the ring widths in the year of aerial recording.

The analysis of the changes in correlation coefficients between 5-year increments and the damage status of pedunculate oak in the period from 1945 to 1990 shows that there has been a continuous increase (Figure 4). This growing trend of correlation coefficients points to changes in the site occurring in the past 45 years.

A link between the degree of stand damage and the kinds of natural or man-made infrastructure was also established (Table 3, Figure 5). The extent of damage was the highest along meliorated marches, asphalt roads with deep side ditches, and man-made canals. The areas along forest roads and natural streams, as well as along the motorway, are less damaged.

Table 3. The area share of damage statuses along the linear communication

Linear communications	Interpreted		Stand damage class	
			1	2.1
			11-25%	26-40%
	km	ha	area percentage	
1. Ameliorated marshes	1.9	38	9.0	91.0
2. Public roads	9.2	92	28.3	71.7
3. Channels	12.2	244	32.3	67.7
4. Motorway	16.5	330	54.5	45.5
5. Natural streams	29.5	590	62.1	37.9
6. Forest roads	26.6	532	64.1	35.9

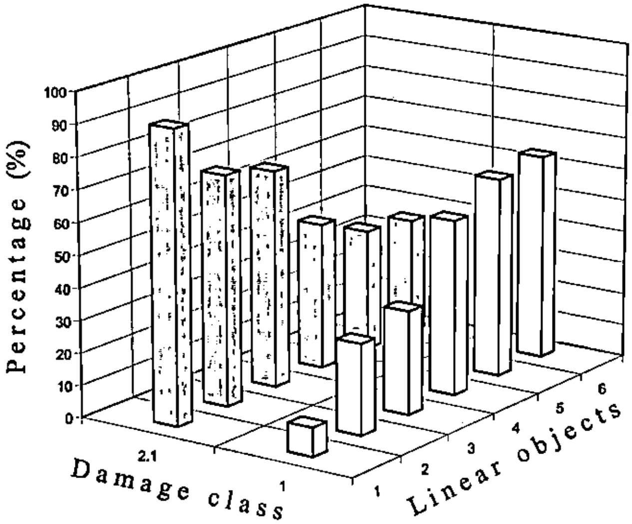

Figure 5. Stand damage near natural and built linear communication in the forest basin "Spačva"

INTERPRETATION OF RESULTS

The analysis shows that an increase in the damage status of pedunculate oak has resulted in a lowered increment. Diameter increment is a good indicator of damage, as it decreases even at a slight weakening of vitality, which was confirmed with the correlation analysis. A negative correlation (r = - 0.9430) was established when the ring width in the year of the recording was compared with the damage observed in the aerial photographs. A current annual diameter increment in the 5-year period (1985-1989) also shows a negative correlation (r = - 0.8475) with the damage percentage determined in the aerial photographs.

The correlation coefficient trend points to significant changes taking place around 1970. According to some earlier research, important changes adversely affecting pedunculate oak occurred in 1977/78, resulting in a constant decreasing of ring widths. The strong impact of highly adverse short-lasting factors induced stress in the pedunculate oak in 1982/83, the result of which was a more pronounced dieback of its trees (Pranjić and Lukić 1989).

The dependence of forest damage on the conditions in the field is exemplified with a link between the damage status and natural and man-made linear communications in the forests. Damage depends on the intensity of interventions in natural hydrological conditions. Damage is more extensive along meliorated marshes, asphalt roads with deep side ditches and man-made canals than along natural streams, simple forest roads and the motorway. Low-scale damage along the Zagreb - Lipovac motorway can be explained either by the fact that a better-quality design and execution of the work did not unduly disrupt natural conditions or by the fact that 50-year-old stands of that time have adapted to the new conditions. This assertion is confirmed by earlier research in the area (Kalafadžić et al. 1993).

CONCLUSION

The relationship between the diameter increment and damage status of pedunculate oak (*Quercus robur* L.) assessed in colour infrared (CIR) aerial photographs was studied in the lowland forests of pedunculate oak in Slavonska Posavina.

The research and the obtained results point to the conclusion that an increase in the damage status of pedunculate oaks has resulted in a decrease in the increment. Accordingly, diameter increment is a good indicator, as it decreases considerably even when the vitality is only slightly weakened. Severely damaged trees react poorly to changes in their surrounding, which in turn leads to a decrease in the diameter increment variability at a higher damage status. According to research results, pedunculate oaks with a degree of damage over 45% have not displayed any major oscillations in increment in the last 5 years, but have a long-term decrease instead. A continuous growth was observed in the correlation coefficients between 5-year increments and the extent of damage of pedunculate oak in the period 1945

- 1990. Dendrochronological research should also be included into the problem of increment in those trees suffering from varying degrees of damage.

The relationship between the damage status of pedunculate oak and the kinds of natural or artificial communications in the forests was also established. The size of damage depends on the intensity of interventions in natural hydrological conditions. Expert teams from various scientific fields should join forces to study these phenomena further.

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ODNOS IZMEĐU DEBLJINSKOGA PRIRASTA I STUPNJA OŠTEĆENOSTI HRASTA LUŽNJAKA (*Quercus robur* L.)

Istraživanje odnosa prirasta i oštećenosti hrasta lužnjaka provedeno je na infracrvenim kolornim aerosnimkama (ICK) u nizinskim šumama hrasta lužnjaka u slavonskoj Posavini. Radi utvrđivanja odnosa prirasta i stupnjeva oštećenosti hrasta lužnjaka na terenu su uzimani izvrci. Uz pomoć aerosnimaka pronađeno je 247 hrastovih stabala različitih stupnjeva oštećenosti. Na izvrcima su izmjerene širine godova.

Uspoređena je širina goda u godini aerosnimanja i stupnja oštećenosti stabala hrasta lužnjaka određenoga na infracrvenim kolornim aerosnimkama. Usto je analiziran i odnos tečajnoga godišnjega debljinskoga prirasta za petogodišnje razdoblje (i_{d5}) i stupnja oštećenosti stabala na kraju toga razdoblja (godina aerosnimanja).

Analizom izvrtaka izbušenih Presslerovim svrdlom ustanovljeno je da se s povećanjem oštećenosti stabala hrasta lužnjaka smanjuje njihov prirast. Pri tome je debljinski prirast dobar indikator oštećenosti, jer se i pri manjem slabljenju vitalnosti on znatno smanjuje. To je potvrđeno korelacijskom analizom. Usporedbom između postotaka oštećenosti stabala hrasta lužnjaka određenih na aerosnimkama i širine goda u prsnoj visini u godini aerosnimanja postoji jaka negativna korelacijska veza (r = – 0,9430). Postoji također i jaka negativna korelacijska veza (r = – 0,8475) između tečajnoga godišnjega debljinskoga prirasta u posljednjih 5 godina i postotka oštećenosti stabala hrasta lužnjaka u godini aerosnimanja.

Također je uočena povezanost stupnja oštećenosti šume i vrste prirodnih ili ljudskom rodu načinjenih linijskih objekata uz koje se te šume nalaze. Određen je površinski udio pojedinih stupnjeva oštećenosti na širini od 100 i 200 m s obje strane tih objekata. Na taj se način nastojao ustanoviti utjecaj tih objekata na stupanj oštećenosti i pad prirasta okolnih šumskih sastojina.

Analizirane šumske površine uz isušene bare, asfaltirane ceste s dubokim postranim kanalima, te uz prokopane kanale pokazuju vrlo velika oštećenja. Uz šumske ceste i prirodne vodotoke oštećenost je manja, iz čega se može zaključiti da stupanj oštećenosti ovisi o intenzitetu zahvata u prirodne hidrološke uvjete.

Ključne riječi: hrast lužnjak, infracrvene kolorne aerosnimke, debljinski prirast, stupanj oštećenosti, prirodni i izgrađeni linijski objekti, slavonska Posavina

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UDK 630*114+111+221 (Quercus robur L.)

PEDOLOGICAL AND MICROCLIMATIC PROPERTIES OF SOME EXPERIMENTAL PLOTS OF PEDUNCULATE OAK (*QUERCUS ROBUR* L.) PLANTATIONS IN CROATIA

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Research was conducted on 12-year-old experimental plots representing artificially raised stands of pedunculate oak. One experimental plot is located in Central Croatia, where pedunculate oak was planted at different spacings on a site of pedunculate oak and common hornbeam on planosol. The pre-treatment vegetation consisted of a pure stand of common hornbeam. A similar experiment was also carried out in eastern Croatia (Slavonia), where pedunculate oak was planted identically to the former experiment on calci-mollic gleysol with meadow vegetation. In terms of synecology, this site corresponds to the association of pedunculate oak and great greenweed with remote sedge.

Pedological research in the experiments mentioned above showed that the planting arrangement did not have any significant effects on the properties of the topsoil. This is in line with the fact that the evolution of soil and its properties is very slow. Distinct spatial variability of pedological parameters of the topsoil of the pedosphere is another key factor in annulling the importance of potential differences in the soil arising from different planting spacing.

This variability, as well as micro-climatic characteristics, reflects the natural diversity of this forest ecosystem.

Micro-climatic properties of the sites in combination with water regimes in both localities point to pedogenetic processes, which will probably increase the differences among pedological parameters in experimental plots in the future.

Key words: pedunculate oak, soil, humisation, microclimate

INTRODUCTION

Regeneration of pedunculate oak stands and afforestation with pedunculate oak, thanks to its biological properties and ecological and economic characteristics, are intended for large and bare (formerly cleared and possibly prepared) areas. The forestry profession is well acquainted with the stress occurring in the ecosystem during the regeneration of pedunculate oak stands. This stress, related to drastic changes in the cycle of matter and energy, is manifested in the release of energy reserves. Energetic changes of particular proportions occur in the surface part of the pedosphere - in the humus - accumulative horizon (Korotaev 1988, Raulund-Rasmussen and Vejre 1993, Van Breemen 1995). Oxidation processes are intensified, and the humisation trend is mainly determined by micro-climatic and hydrological properties of the site, the young stand (young growth) and the quality and quantity of leaf litter constantly accumulating on the soil surface (Arrouays et al. 1995, Pastor & Post 1988, Schoenau & Bettany 1987). Micro-climatic changes taking place in the course of stand development (Seletković 1981, 1984, 1996), as well as the qualitative and quantitative stabilisation of organic matter production lead to a decrease in energy flow levels and to an equilibrium in the top part of the soil. These changes are in the function of crown closure of the young growth, or the number of plants per surface unit, provided the effects of silvicultural treatments, such as tending and cleaning, are excluded.

If non-forest soil and pastureland is left unploughed or untreated prior to afforestation, the ecosystem does not suffer any significant stresses. Changes in the topsoil are relatively slow, and humisation processes assume positive trends and become a direct function of the microclimate and the quality and quantity of dead organic matter (leaf litter and roots of grass vegetation). Micro-climatic changes, litter production and the retreat of grassy vegetation under similar other conditions (ecological conditions, silvicultural treatments) also depend exclusively on the number of plants per surface unit.

With regard to the changes occurring in the ecosystem during regeneration or the establishment of pedunculate oak stands, it should be borne in mind that soil is a biologically active system and represents the best buffer mechanism for the ecosystem. Biologically and energetically, the most active niche of the forest ecosystem is the surface part of the soil - the organic and humus-accumulative horizon. It is hard to decide on the extent to which changes in the matter and energy cycle are reflected in the soil in pedunculate oak stands. Research presented in this paper is based on the assumption that there is correspondence between changes (development) in the topsoil and those in the microclimate accompanying the growth of a pedunculate oak stand. The aim was to quantify pedological and micro-climatic properties dictated by the thickness of the crown canopy of the young growth and thicket, that is, by the number of planted pedunculate oaks per surface unit in the contrasting hydro-pedological and climatic conditions of pedunculate oak area in Croatia.

RESEARCH METHODS AND AREA

Research was carried out in experimental plots established 12 years ago in the Forestry Office of Vrbovec and Forestry Office of Strošinci (Fig. 1). Two-year-old

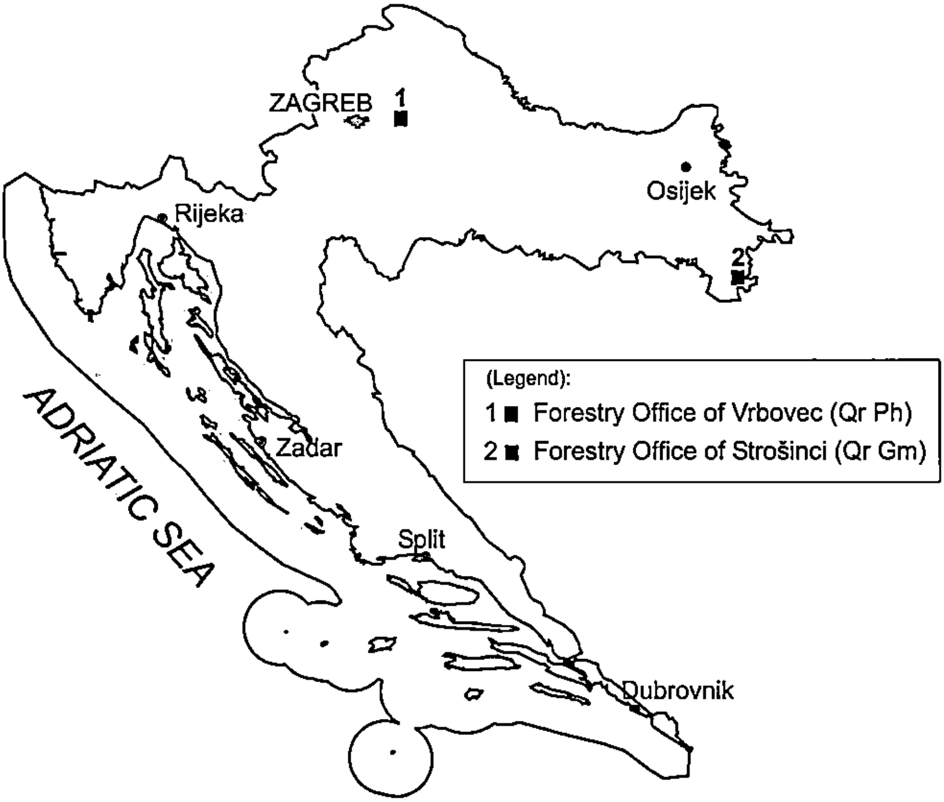

Figure 1. Experimental plot locations

seedlings of pedunculate oak were planted at different distances, and the experiment was established according to a random block system (Fig. 2).

Pedological and microclimatic research was done in the field in the summer of 1999. In both experiments, a pedological profile was opened in the middle of the plot with the largest spacing. Soil samples from each horizon were taken in order to obtain general pedological characteristics. The soil samples, forming the pedological base of this paper, are composed of seven individual samples taken at the depths of 0 - 10 cm below the O-horizon. In the Forestry Office of Vrbovec, control soil samples were taken from the stands of common hornbeam in the vicinity of the experimental plots (two composite samples). Sampling was done with a probe, and two composite samples were assembled in each plot (Fig. 2). The humus content was determined with the bichromatic method of total nitrogen according to Kjerdahl, and the pH was determined electrometrically in the soil suspension in water and in the 0.01 M $CaCl_2$. The extractability of organic matter (group humus content) was determined using Kononova's and Bjelchikova's method. Statistic analysis was based on the random block system of experimental plots.

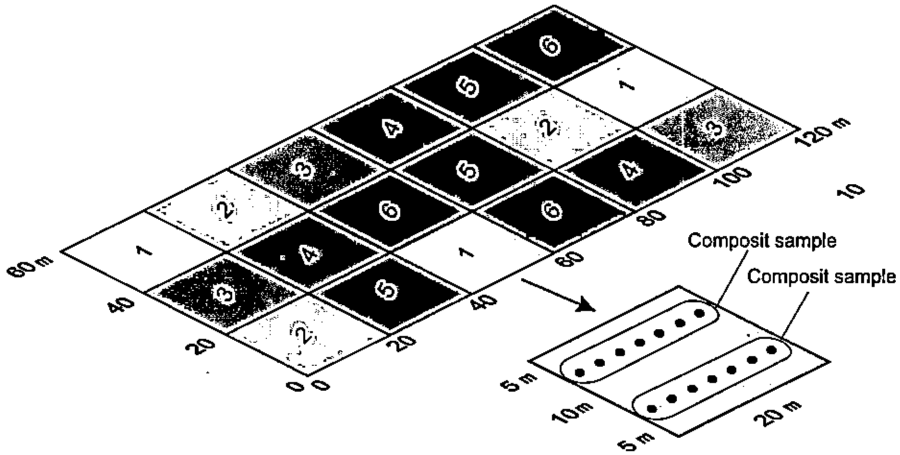

Figure 2. Schematic preview of experiment structure. Planting spacing: 1) 1.8 x 1.8 m (3000 ha^{-1}); 2) 1.4 x 1.4 m (5000 ha^{-1}); 3) 1.2 x 1.2 m (7000 ha^{-1}); 4) 1 x 1 m (10000 ha^{-1}); 5) 0.8 x 0.8 m (15000 ha^{-1}); 6) 0.7 x 0.7 m (20000 ha^{-1}).

Microclimatic research involved the measurement of air and soil temperature and the relative light intensity. Air temperature was taken with automatic thermographs Rotronic placed 2 m above the ground on pedunculate oak trees in medium stand conditions of the 1st, 3rd and 6th treatment. Soil temperature was measured with a geo-thermometer and the relative light intensity with digital light meters over the whole experimental plot. In the Forestry Office Vrbovec (QrPh), the measurements relate to the period from 14 September - 1 October 1999 and in that of Strošinci (QrGm) to the period from 6 July - 4 August 1999.

The experiment in the Forestry Office Vrbovec was established on the site of pedunculate oak and common hornbeam on haplic planosol at the NNW exposition, with an inclination of 5°. This was a pure hornbeam stand, which was felled prior to the experiment.

The experiment in the Forest Office Strošinci (QrGm) was done on the site of pedunculate oak and great greenweed with remote sedge on calci-mollic gleysol. The vegetation was of a grassland type.

In terms of climate, the studied area belongs to the temperate rainy climate characterised by a mean annual air temperature of about 10.5 °C and annual precipitation between 700 - 900 mm. Generally, the area of Strošinci (QrGm) is somewhat warmer and has less precipitation than that of Vrbovec (QrPh).

RESEARCH RESULTS

According to research, the soil in the QrPh experiment is haplic planosol, with a typical profile structure and properties characteristic for the soils of pedunculate stands in Central Croatia (Table 1). The soil in the QrGm experiment is mollic gleysol. This soil has a distinct clayey texture with a high humus and total nitrogen content per surface unit.

Table 1. Soil properties in experiment QrPh i QrGm.

No.	Horizont	Depth	2,0 - 0,2 mm	0,2 - 0,02 mm	0,02 - 0,002 mm	<0,002 mm	Texture	pH H_20	pH $CaCl_2$	Humus	Nitrogen	C:N
			(%)							(g kg-1)		
QrPh												
1	A	0-12	2.0	57.5	31.2	9.3	loam	4.90	4.19	73.90	3.20	13.4
2	Eg	12-40	1.2	50.1	30.9	17.8	clay loam Ilovača	5.50	4.28	11.30	2.00	3.3
3	BgI	40-80	1.4	47.9	33.5	17.2	clay loam	6.12	5.20	5.10	1.70	1.7
4	BgII	80-105	1.1	46.6	31.3	21.0	clay loam	6.43	5.44	2.00	1.13	-
5	III	105-150	0.5	49.7	23.5	26.3	light clay	6.75	5.67	1.00	1.13	-
QrGm												
1	Amo,a,vt	0-45	1.31	30.09	37.30	31.30	light clay	6.91	6.46	48.00	2.90	9.6
2	Gso	45-85	1.69	19.51	37.50	41.30	light clay	8.05	7.37	10.30	0.90	6.6
3	Gso,ca	85-120	1.82	30.38	38.70	29.10	light clay	8.08	7.48	6.80	0.70	5.6
4	GsoGr,ca	120-150	1.14	38.56	32.20	28.10	light clay	8.30	7.69	7.70	0.80	5.6
5	Gr	>150	0.14	29.56	34.30	36.00	light clay	8.19	7.50	9.80	0.80	7.1

The variance analysis of humus and nitrogen, the pH values and the extractability of organic matter (group humus content) showed that the QrPh experiment (Fig. 3) was homogenous in total, which means that planting spacing did not affect the properties of the topsoil significantly. A high correlation between the humus and nitrogen content, as well as the pH values and humus and nitrogen content, was also noted.

The variance analysis in the QrGm experiment did not prove homogenous. In other words, statistically significant differences were observed in the properties of the surface part of the soil. The differences among individual treatments are explained by the differences in the nitrogen content (Fig. 4) with 97.3% probability. Treatment No. 3 stands out by having much higher nitrogen content than that in treatments 4, 5 and 6. Treatment No. 6 has considerably less nitrogen than plots 1 and 2. On the other hand, significant differences in the extractability of organic matter were noted in the blocks. Block C displayed much lower extractability of organic matter than that in blocks A and B. Significant differences among treatments concerning the nitrogen content can be explained with the effect of planting distances on a low nitrogen cycle. As the highest nitrogen content was observed in treatment 3 and the lowest in treatments 1 and 2, it is evident that the planting spa-

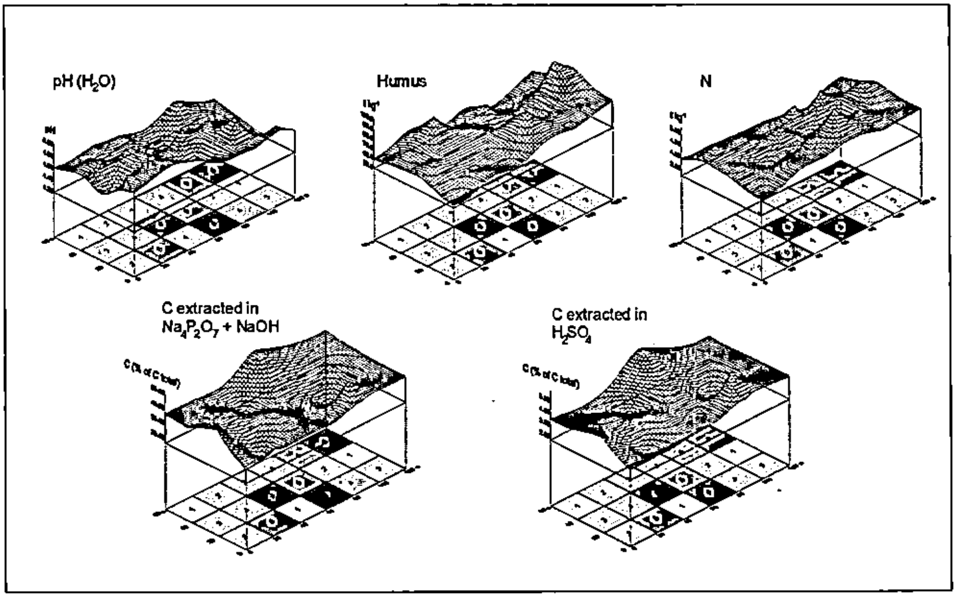

Figure 3. Experiment QrPh – soil parameters

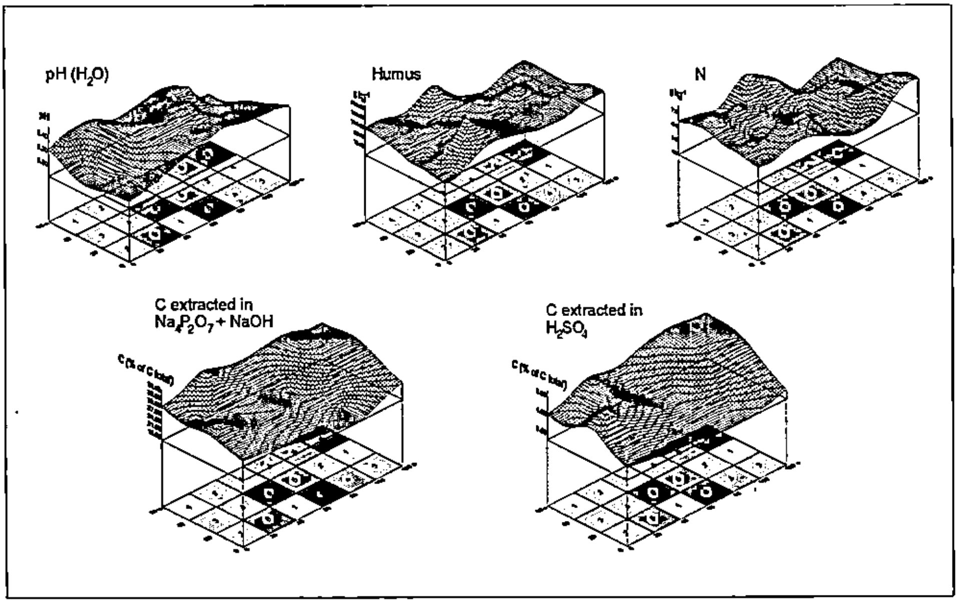

Figure 4. Experiment QrGm – soil parameters

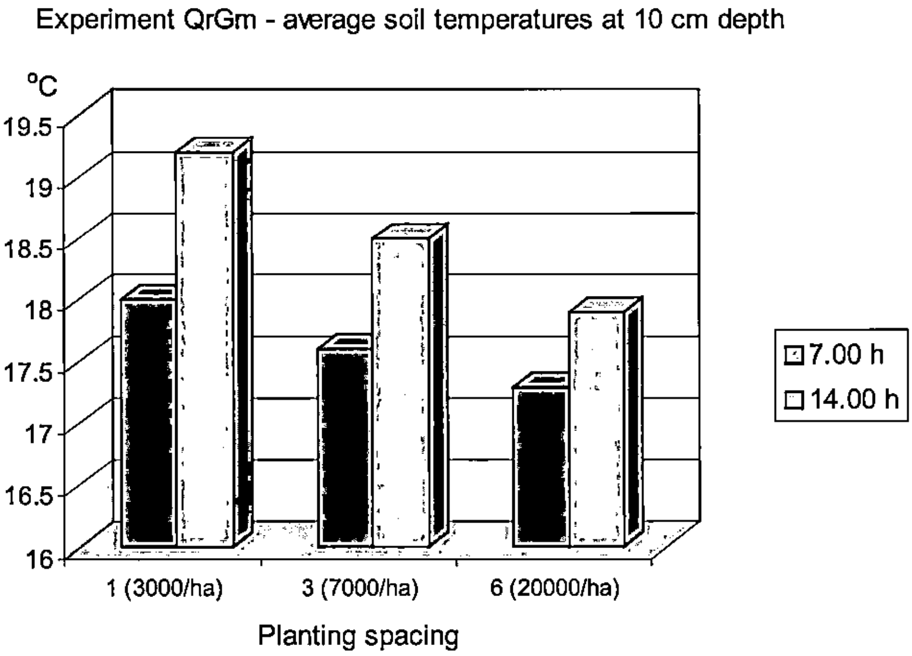

Figure 5. Experiment QrPh – average soil temperatures at 10 cm depth

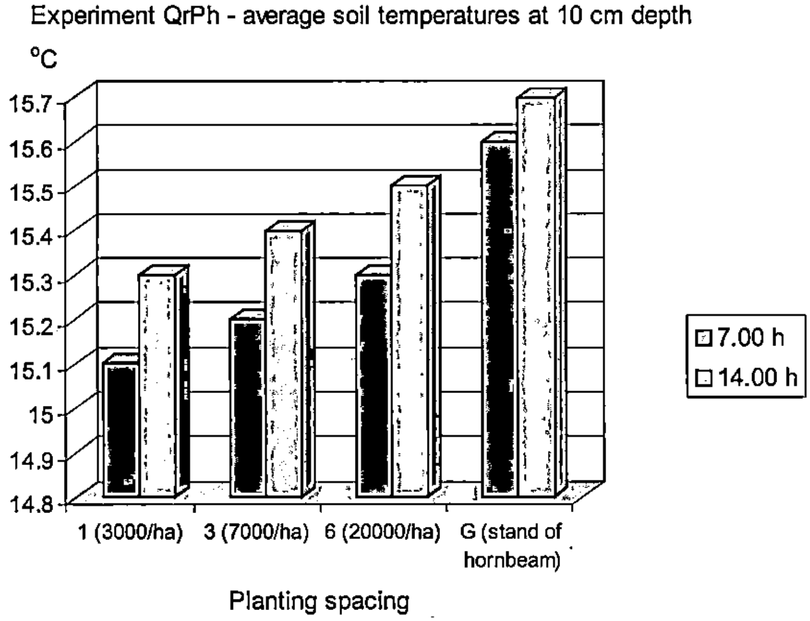

Figure 6. Experiment QrGm – average soil temperatures at 10 cm depth

cing - nitrogen content ratio is not of a linear character, and is therefore difficult to interpret. Differences among the blocks relating to the extractability of organic matter indicate uncontrolled impacts that could be linked to the accumulation regime and organic matter transformation (litter) on the soil surface and the role of tannin in the soil organic complex.

In the QrPh plot experiment (treatment 1), 12 years after planting there were 24,275 trees ha^{-1} (a very high content of common hornbeam, so young hornbeams prevail). The relative light intensity was only 1.58% on this plot. In experimental plot No. 3, there are 10,425 trees ha^{-1}, and the relative light intensity is 10.53%, while on plot No. 6 there are 10,725 trees ha^{-1}, with a relative light intensity of 8.58%.

There is an old stand of common hornbeam next to the experimental plots in which the value of light intensity was found to be 6.9%.

Air temperatures on these experimental plots differ to some extent from those in the experiment QrGm, but the difference is still small. A somewhat thicker canopy affected the values of both air and soil temperatures.

Soil temperatures at a depth of 10 cm, shown in Fig. 5, range from 15.1 - 15.5 °C in young stands, which corresponds to the mentioned uniform stand conditions in terms of the number of trees.

In the QrGm experiment, experimental plot No. 1 contained 2,575 trees of pedunculate oak ha^{-1} 12 years after planting, experimental plot No. 3 had 5,950 trees, and experimental plot No. 6 18,475 trees ha^{-1}. These are the only trees that formed the young stand.

Different values of relative light intensity were also measured in these stand conditions. In experimental plot No. 1 characterised with the rarest canopy, the relative light intensity was 77%. Experimental plot No. 3 with 5,950 trees showed a value of relative light intensity of 21%, and in experimental plot No.6 with the largest number of trees (18,475), the relative light intensity was only 2%.

Air temperatures have a characteristic daily pattern, but the differences among experimental plots are not particularly distinct. On the contrary, the differences are so minimal that they are almost uniform.

A higher correlation in terms of the number of trees was found when soil temperatures were measured at depths of 10cm (Fig. 6). Experimental plots with the smallest number of trees had the highest temperature. Thus, the mean morning temperature in experimental plot 1 was 18.0 °C, in plot No 3 it was 17.6 °C, and in plot 6 it was 17.3°C. Afternoon temperatures followed the 19.2 °C - 18.5 °C - 17.9 °C pattern.

DISCUSSION

One of the most important factors in ecosystem stability is the buffer soil potential. This research has shown that the buffer potential, the natural mechanism that protects the soil from rapid changes, proved decisive in comprehending the almost insignificant effects of the differences in stand characteristics on the properties of the soil, although two distinctly different sites were involved. Stands of pedunculate oak in Croatia are characterised by different hydro-morphous soils. In the central semi-humid and humid area, these are various gleyic soils and planosols, and in the eastern, semi-arid area gleyic soils prevail. Undoubtedly, the temperature and water regime of the sites has a profound influence on soil evolution (Amelung et al. 1997). In view of this, the importance of stable soil properties and the "coexistence" of soil and vegetation can be appreciated.

Very slight differences in the properties of the soil in only one of the experiments, and some microclimatic differences on the other hand, point to a chain that firmly links all the niches of the ecosystem and mitigates the sharp borders. This chain is microbiological activity. Products of organic matter transformation depend directly on microbiological activity. Differences in the nitrogen content, displayed in the treatments in the QrGm experiment, can be explained by this factor.

The degree of structural unit condensation of the humus matter and condensate polymerisation is manifested in the extractability of organic matter. The differences in the extractability of organic matter in experiment QrGm could be attributed to the influence of oak litter (tannin) on the quality of the humus. Although these differences can seemingly be explained by the influence of the blocks, we believe that the impact of wind on litter distribution should be taken into account in cases when a stand is located in an open area (grassland).

The aim of this paper was not to study the impacts of vegetation type on the soil and microclimate. However, this issue normally arises within the framework of a discussion on a general law. In this sense, the results of the research lead to a complex conclusion based on the fact that vegetation is a pedogenetic and microclimatic factor. The effect of vegetation on microclimate can be measured even when there are very small differences in the crown canopy (floor coverage). The influence of vegetation on the soil is far more complex because it is determined by a number of factors (quality and quantity of organic matter, microclimate, soil properties, etc.). In relation to a hypothetical zero state, the extent of this influence depends on the closeness of the vegetation and soil properties in a pedogenetic sense. The worse the physiographic properties of the soil, the more degraded the soil, and the weaker the pedogenetic link between the soil and the vegetation under analysis are, the higher the influence on the soil can be. Although both experiments dealt with in this paper were established in the natural distribution area of pedunculate oak in Croatia in very different ecological conditions, the soils have all the properties that correspond to the pedogenetic characteristics of pedunculate oak. In such conditions, in the stand established on haplic planosol after the removal of forest vegetation, the planting distance of pedunculate oak seedings did not affect the soil properties 12 years after planting. Certain effects on the soil (nitrogen in the soil) in the stand erected on calci-mollic gleysol with grassy vegetation can directly be attributed to microbiological activity, that is, to recorded microclimatic differences (particularly soil temperatures and relative light intensity).

CONCLUSIONS

The following conclusions can be drawn from the study of pedological and microclimatic characteristics in the two experiments involving the pedunculate oak in Croatia:

1. After the establishment of pedunculate oak stands, in the stages of pole and young growth, a considerable influence of planting spacing can be expected on the soil properties and microclimatic characteristics of the site. In other words, planting spacing influences the evolution of the forest ecosystem. During artificial regeneration of pedunculate oak stands, the effect of the planting arrangement on the balanced development of the forest ecosystem is not always important, with the exception of regeneration on sites with degraded soils.
2. Predictable effects are manifested particularly through the air and soil temperature regimes and through the nitrogen cycle in the ecosystem.
3. The extent of the effect of stand parameters on the soil during stand regeneration depends on the closeness of vegetation and soil properties in the pedogenetic sense and on the degree of soil degradation.

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PEDOLOŠKE I MIKROKLIMATSKA OBILJEŽJA HRASTA LUŽNJAKA (*Quercus robur* L.) NA NEKIM POKUSNIM PLOHAMA U HRVATSKOJ

Istraživanja su provedena u 12-godišnjim pokusnim plohama na kojima su umjetno podignute sastojine hrasta lužnjaka. Jedan se pokus nalazi se u središnjoj Hrvatskoj gdje je na staništu hrasta lužnjaka i običnoga graba na pseudogleju posađen hrast lužnjak s različitim razmacima. Prethodnu vegetaciju činila je čista sastojina običnoga graba. Sličan pokus postavljen je i u istočnoj Hrvatskoj (Slavonija). Tu je na ritskoj crnici s livadnom vegetacijom posađen hrast lužnjak po planu kao u prijašnjem pokusu. Ovo stanište sinekološki odgovara zajednici hrasta lužnjaka i velike žutilovke s rastavljenim šašem.

Pedološka istraživanja u navedenim pokusima pokazala su da razmaci sadnje nisu značajno utjecali na značajke površinskoga dijela tla. Ovo se slaže s činjenicom da je evolucija tla i njegovih svojstava vrlo spora. Izrazito visoka prostorna varijabilnost pedoloških parametara površinskoga dijela pedosfere također je bitan čimbenik anuliranja značaja potencijalnih razlika u tlu ovisno o razmaku sadnje.

Ova varijabilnost, kao i mikroklimatska obilježja odraz su prirodne raznolikosti takva šumskoga ekosustava.

Mikroklimatska obilježja staništa u konstelaciji s vodnim režimom jednoga i drugoga lokaliteta usmjeravajući su čimbenici pedogenetskih procesa koji će se u budućnosti vjerojatno odraziti na povećanje razlika između pedoloških parametara na pokusnim plohama.

Ključne riječi: hrast lužnjak, tlo, humizacija, mikroklima

G. Struck, et al.: Effects of initial density, fertilisation and logging slash removal in young sessile oak stands. Glas. šum. pokuse 37: 263–276, Zagreb, 2000.

UDK 630*232.4+(430) (Quercus petraea Liebl.)

EFFECTS OF INITIAL DENSITY, FERTILISATION AND LOGGING SLASH REMOVAL IN YOUNG SESSILE OAK STANDS

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The objective of this investigation was to analyse the effects of different spacing (dense / moderate / wide) in combination with fertilisation variants (fertilised / non-fertilised). In addition, the effects of radical site preparation by removing the logging slash were investigated. The basis for the data collection was 24 sessile *oak (Quercus petraea)* experimental plots which were established in 1975 with three different initial densities (9000, 14000 & 23000 plants/ha). Half of the 24 experimental plots were fertilised in 1976 and 1977. The aim of the investigation was to quantify the long-term effects on yield, stem quality and the ecology of the different establishment treatments for unthinned stands. 2520 individuals were registered by yield measurements and quality estimations. In addition, stem analysis was done for trees from the fertilised and unfertilised plots for all different densities. The ecological investigations included the nutrition situation of the soil, the humus layer and the leaves. On the basis of the stem analysis data, models were calculated in order to determine the over-ground dry matter. For the estimation of quality, a branch-index (Asix) was developed.

The radical logging slash removal had negative effects both on yield and on the quality of the oak trees. With increasing distance to the slash ramparts, the diameter and the height of the trees decreased. The results of stem analyses showed that the rampart effect began 2 - 3 years after plantation and had a duration of about 16 years. Trees at a further distance from the ramparts where characterised by a smaller bole length and comparably bigger branches. Compared with crowded- and mean-space plantation, the wide-space areas were affected less. Obviously, the wider space between the young trees compensated for the bad nutrition conditions. The increased competition, however, had no effects on the quality features. Stem analyses showed a strange decrement of yield 6 - 8 years after fertilisation. The decrease of yield on the fertilised plots is the result of higher competition compared to the unfertilised plots. Higher competition was impelled by a reduced mortality on the fertilised plots. Mortality was dependant on the amount of fertiliser. The wide-space plantation showed no fertilisation effects.

Key words: sessile oak, competition, stand quality, nutrients, logging slash removal

INTRODUCTION

An important aim of European silviculture is to establish new forest stands. Concerning the regeneration of existing forests, in many countries the objective is to increase the portion of hard woods. Besides beech (*Fagus sylvatica*), the areas of both oak-species (*Quercus petraea* and *Q. robur*) should be essentially increased. So it is useful to optimise the methods of stand establishment and to support the possibilities of high-quality development.

The present investigation is based on an extensive afforestation trial from 1975. Compared with the arrangement of plants today, the establishment was very dense. In addition, every second plot was supported by initial fertilisation. The most spectacular phenomenon of these experimental plots was the creation of very different site potentials, caused by the typical soil preparation at this period: logging slash was concentrated on large ramparts.

Even before the beginning of the described investigation, the effects of this soil preparation became visible by a strong decrease in tree height depending on the distance of the trees to the humus-ramparts. The combination of these three variants of spacing, nutrient supply and fertilisation created an experimental design to obtain detailed information on the interaction between nutrient supply, intraspecific competition, growth and quality development.

MATERIALS

INVESTIGATION PLOTS

The plots were established in north-western Germany in the nature park "Steinhuder Meer", about 30 km north-west of Hanover (forest district Fuhrberg, comp. 1618 and 1624).

The climate is characterised by an average precipitation of 670 mm / year, and 315 mm were measured during the forest vegetation period (May - September). The average annual temperature amounts to 8.6 °C and 14.7 °C during the forest vegetation period. The average annual temperature has increased by about 0.6 °C during the last decade (Otto 1989).

The site conditions were mostly influenced by the glacial periods. A soil test as part of the site mapping found for the most part more or less huge layers of glacial sands on large sandy formations with low nutrient supply. The water regime ranges from moderate dry to moderate moist.

ESTABLISHMENT OF THE EXPERIMENT

In spring 1975 the logging-slash of the harvested old pine stand was concentrated on ramparts. This was done with large bulldozers, which also led to a concentration of almost the total humus layer on these ramparts. This was the usual method to get the damaged forests into production again after the storm catastrophe in North Germany in 1972.

In autumn 1975, 24 experimental plots of 0.1 hectares each were afforestated with two-year-old oak-seedlings (*Quercus petraea*, provenance Westfranken, 2+0). Three planting patterns were established, repeating each one eight times (within row 0.3, 0.5, 0.8 m and 1.4 m distance between rows). In 1976 the trees of every second plot were fertilised with 20 g magnesium-fertiliser for each plant (15 % P_2O_5, 5% K_2O, 10% MgO, 22% CaO). In 1977 a further 15 g of N-fertiliser were applied. Hence, there were twenty-four plots consisting of three planting patterns with two fertilisation variants (fertilisation, control) and four repetitions. The whole area was fenced against browsing risk.

During the first four years after stand establishment the tending of the young stand mainly consisted of the chemical removal of competing vegetation. In 1977 treatment with insecticides and fungicides was necessary. Since 1981 no further forest treatments were made.

METHODS

For the selection of the measurement trees, the effects of the removal of the logging slash were taken into account. Every plot bordered a humus and logging slash rampart. Starting at these ramparts, from every second planting row fifteen neighbouring trees were chosen to gain the data. Hence, there were 105 measured trees on each plot, that is, a total number of 2520 trees for this examination.

For each single tree a number of yield and quality parameters were taken:

- DBH – diameter at breast height (cm)
- Height in total (m)
- Social class (according to Kraft)
- Height of the crown base (m)
- Height of the lowest living branch (m)
- Height of the lowest dead branch (m)
- Crown width (m)
- Diameter of the thickest branch (cm)
- Inclination of the stem
- Form of the stem (code with three different classes)
- Branching architecture (code with three different classes)

The concentration of nutrients in the leaves is frequently used to evaluate the common nutrition situation of the tree (Berki 1991, Büttner 1994, 1997a, 1997b, Fiedler & Czerny 1970, Fischer 1998, Thomas & Büttner 1992). By analysing the leaves, it should be verified whether or not the intensive soil preparation methods were reflected in the nutrition situation of the trees. From 40 trees, about 1000 leaves were collected and the leaf areas measured. The leaves were taken from the light and shade influenced parts of the crown, with 50% being taken from the fertilised trees 50% from the non-fertilised trees.

Stem analysis: From the 40 trees mentioned above, at 1 to 2 m distances of each tree, stem disks were cut out to reconstruct the growth development of the trees by analysing the annual rings. In this way, the dependence between dimension development, density of stand, fertilisation and the distance to the ramparts was examined.

Estimation of biomass: From these 40 trees, the biomass of leaves, bark, branches and stems were also determined. Therefore, branches were partially measured by a representative selection-system in order to obtain comprehensive information on the biomass of all tree-compartments (without roots) by a regression-analysis.

RESULTS

THE EFFECTS OF THE RADICAL REMOVAL OF LOGGING SLASH

The most striking phenomenon in the plots was the extreme differentiation in increment. The growth of the 23-year-old oaks decreased considerably with the increasing distance from the ramparts. This was mainly visible in the height-growth of the trees (Fig. 1). While the individuals close to the rampart reached an average height of 6 m, the other trees had an average height between 3 and 4 m.

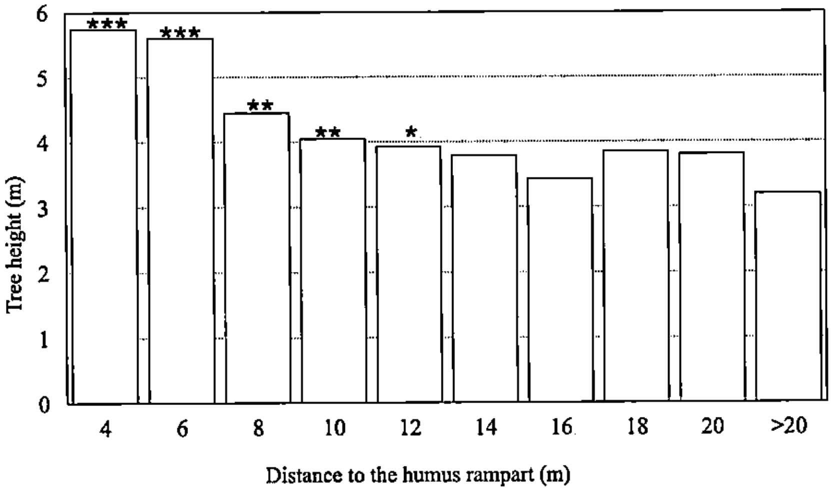

Fig. 1. Influence of the distance to the humus ramparts on the average height growth

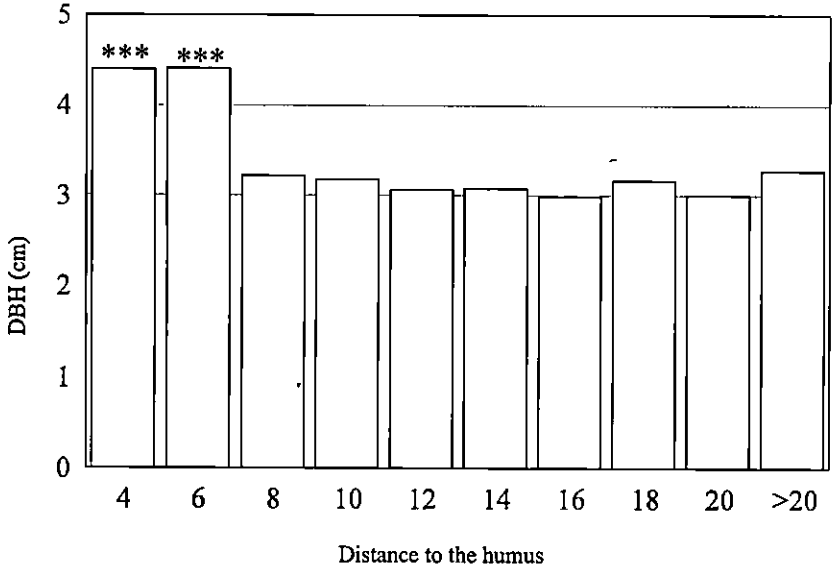

Fig. 2. Influence of the distance to the humus ramparts on the average diameter growth (DBH)

The effects of the ramparts on the secondary diameter-increment were less distinct compared to the height-growth (Fig. 2). Only at a 6m distance from the ramparts was the average diameter of the trees significantly bigger than that of the other trees. Considering the distribution of the 20% biggest individuals of the plots (Fig. 3), the effect of the rampart can be seen very clearly. The 20 m wide plots were divided into 5 zones of the same size, arranged in parallel to the ramparts. The closest zone to the rampart contained 40% of the biggest trees. In the following zone only a portion of 27% of these individuals was remarked. The next contained 19% and the fourth and fifth area only possessed 10% each. The stem analysis of representative trees taken from each zone showed differences in growth after three years for the first time. After ten years these trees divided distinctly from the other individuals.

The different effects of the ramparts on height- and diameter-increment necessarily led to a change in slenderness (height / DBH-ratio). At the same DBH (for example 10 cm), the trees in a position far from the ramparts, which means in lower intraspecific competition, were significantly smaller (6 m) than the individuals closer to it (10 m). Accordingly, the height / DBH-ratio changed from 100 to 60.

As expected, the rampart-depending decrease of the tree-heights was combined with a decrease in the average height of the crown base. The crown base was defined by the first living branch which was no water sprout or crotch. As shown in Figure 4, this relationship between tree-height and crown base was not constant: in direct proximity to the rampart the crown-portion counted less than 40% and increased with growing distance to the rampart to 45% (Fig. 4). At the same time,

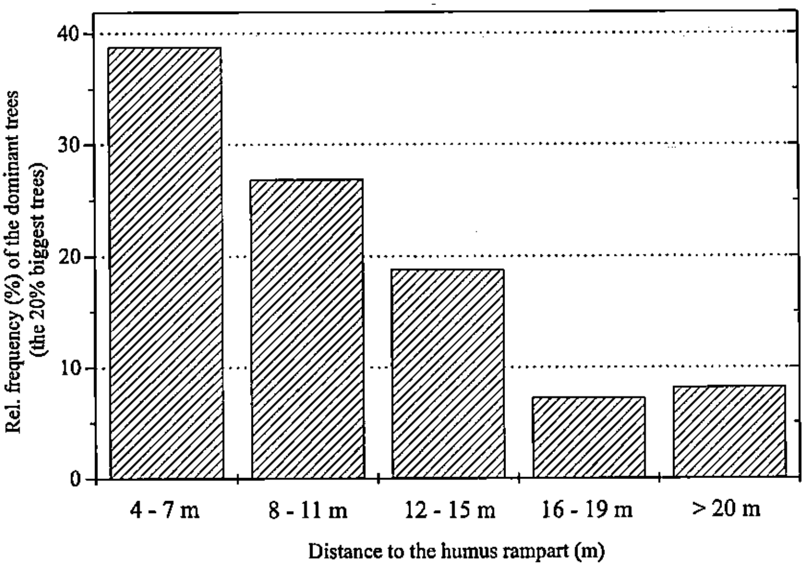

Fig. 3. Distribution of the 20% biggest trees depending on the distance to the humus ramparts

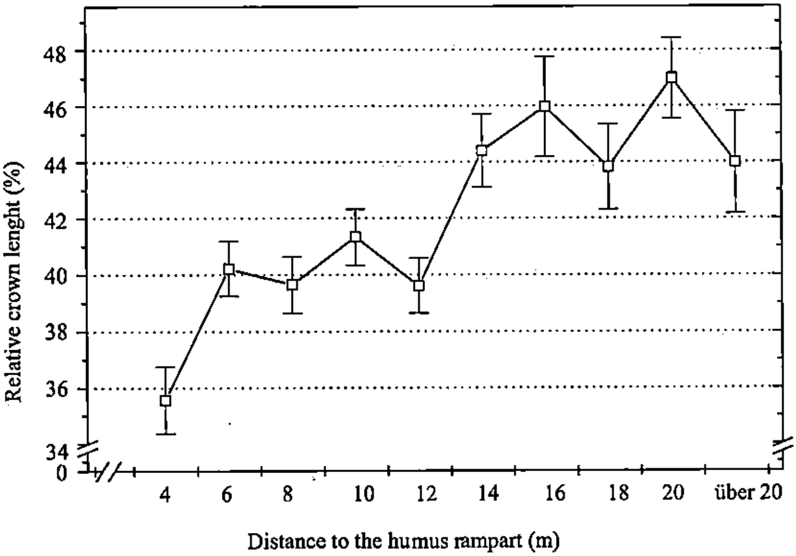

Fig. 4. Change of the relative crown length (%) depending on the distance to the humus ramparts

the relative length of the stems decreased from 55% to 45%. It is remarkable that there was no trend in the average crown width depending on the ramparts. Here the spacing had a more distinct effect on the extension of the crown.

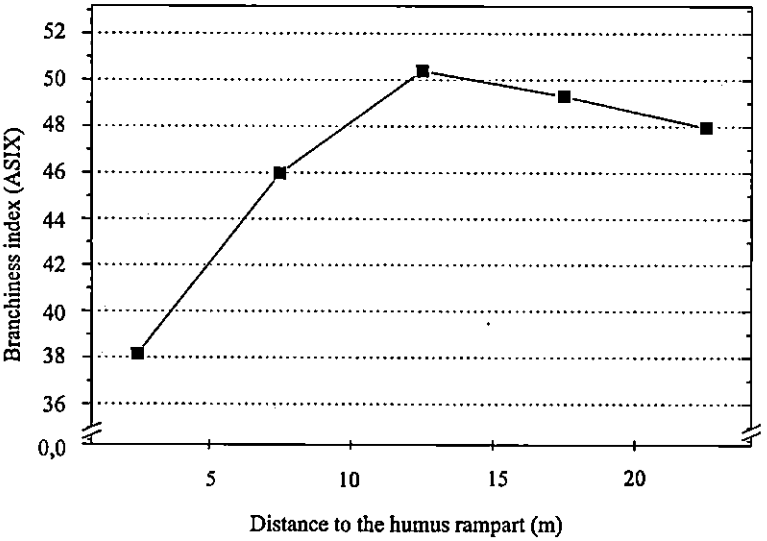

Fig. 5. Change of the brachiness-index (ASIX) depending on the rampart distance (n=2157)

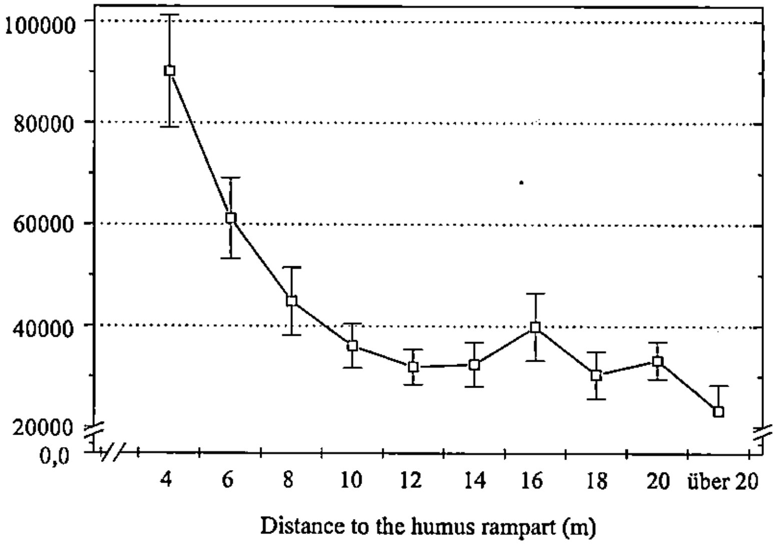

Fig. 6. Effect of the humus ramparts on the accumulation of tree biomass

There was no correlation between the absolute branch-diameters and the distance from the ramparts, either. Smaller and thinner trees also had strong branches like the tall trees close to the rampart where the nutrient supply was better, but the intraspecific competition, however, was stronger. For a quality evaluation, it is useful not to limit the measurements to the absolute branch-diameters, but to take the whole qualitative impression into consideration, too. So it is also sensible to look at the relation of branch-to-stem diameter (DBH).The branchiness-index can be calculated as a quotient of maximum diameter of the branch bases and DBH. In the present investigation, the branchiness-index increased distinctly with the increasing distance from the rampart. Close to the rampart the trees had branch-indexes of 0.38, which means that the biggest branches of these trees had a diameter of 38% of the DBH. Farther from the ramparts, where the site conditions were more unfavourable, but less competitive, indexes of 0.5 were measured (Fig. 5).

With increasing distance between the trees and the rampart, the average biomass of each tree decreased distinctly. Within the first 5 metres the average biomass decreased from 6 to 7 kg to less than 4 kg. A number of correlation analyses were done to calculate the biomass of the 40 collected trees of the whole diameter-range. With this method, the dry mass of leaves and branches and the volume of stem and bark were estimated as a function of the DBH (coefficient of determination between 0.82 and 0.98). In terms of biomass per area-unit (each single tree row was transformed into metric tons per hectare), the productivity decreased with the growing distance to the ramparts. The tree rows close to the ramparts had a three-times higher total production (90 t / ha) than the plots at a further distance with a range of above-ground biomass between 25 and 35 t / ha (fig. 6). So the competition between the individuals considerably decreased with the growing distance to the ramparts. Two decades after the removal of the logging-slash and stand establishment, only a few humus- and soil-parameters were still affected.

This rampart effect combined with the different initial stand densities showed an interesting interaction: the denser the establishment of the stands, the more the trees were affected by the ramparts. In the dense-spacing plots with almost 24,000 planted trees / hectare which were close to the ramparts, the biomass of the tree rows was three times higher compared to the rows farther away. In stands with an average density (about 14,000 trees / ha), the biomass right next to the rapmarts was 2.6 times higher and in the so-called broad-spacing plots (about 9,000 trees / ha) it was only 2 times higher than the trees farther away.

In terms of the element-concentrations of the leaves, an effect of the rampart was only found concerning nitrogen. There were no significant correlations between other nutrients in the leaves and the distance of the trees from the rampart. However, the C/N-ratio slightly increased with the distance from the rampart from 23 to 27. More than 20 years after the removal of the logging-slash, the good C/N-ratio in the oak leaves led to better site conditions in the proximity of the ramparts. More than 20 years after the site preparation, there were only small effects of the slash-removal on humus- and soil-chemistry. The base cation saturation was 3% lower next to the ramparts than at a distance of 18 m farther away. Otherwise the soil was not influenced by the rampart.

SPACING

In general, a decrease in increment was caused by very high initial planting densities. Stem analysis showed an increase of competition in extremely dense stands 8 years after the establishment. Consequently, a distinct reduction of incre-

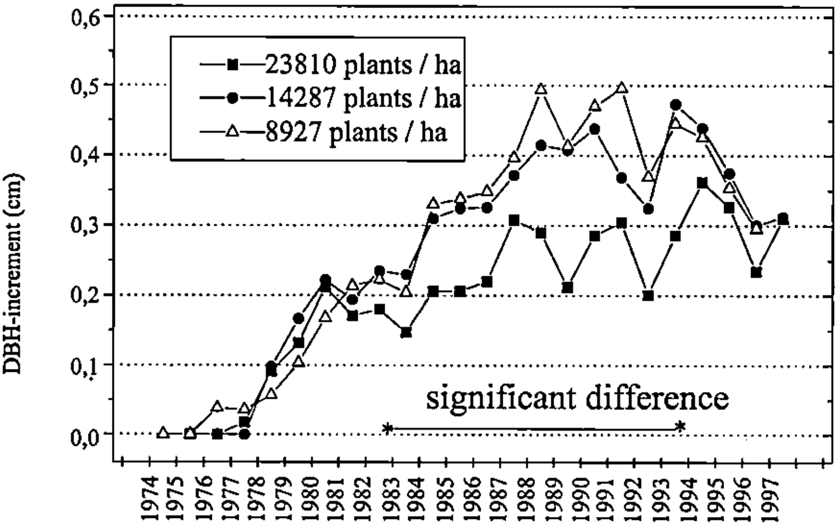

Fig. 7. DBH-increment of the three different spacings (n = 40)

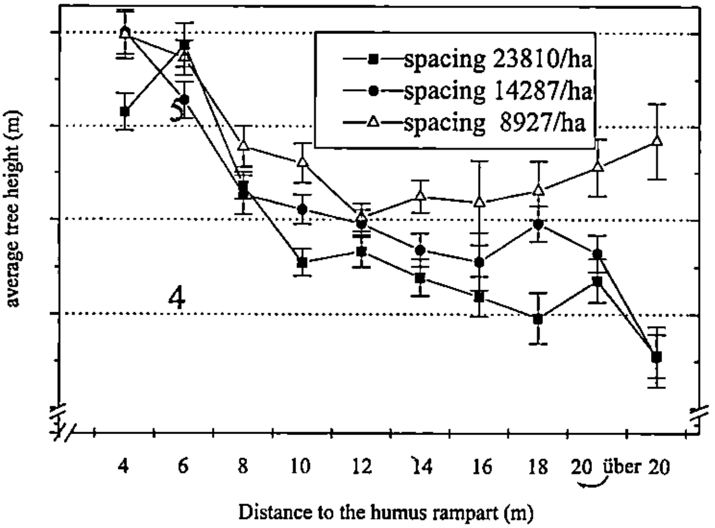

Fig. 8. Influence of the humus ramparts on the average tree height, broken down by different spacings (n= 2491)

ment, compared to the wider spacings, could be shown (fig. 7). As expected, the secondary diameter-increment was more affected by increasing competition than the height-increment. The quality of future elite trees did not differ between the three spacing variants. In the understorey, however, the portion of badly-shaped stems was higher in the very dense spacing.

The ecological conditions of soil, humus and leaves did not depend on the spacing. Only by comparing the fertilised to the non-fertilised plots in the more dense plots was there found to be a higher accumulation of biomass. Considering both rampart and spacing, they affected the trees up to a distance of 10 m: in the dense and average-spaced stands, the trees within this reach were significantly higher than the others. In wider spacing, the effect was not as distinct as in the denser stands (Fig. 8). This means that it is possible to compensate for bad site conditions with wider plant spacing.

FERTILISATION

The main effect of fertilising the plots was a highly significant decrease of mortality of the trees. Especially the understorey profited from the fertilisation, while the overstorey was not affected. After two decades, the mortality on the non-fertilised plots was 62% higher than on the fertilised plots (Table 1). Hence, competition was considerably aggravated in these plots. The denser the initial spacing was, the more the differences in mortality differed. While in very dense stands the fertilisation led to half of the mortality, there were no differences bet-

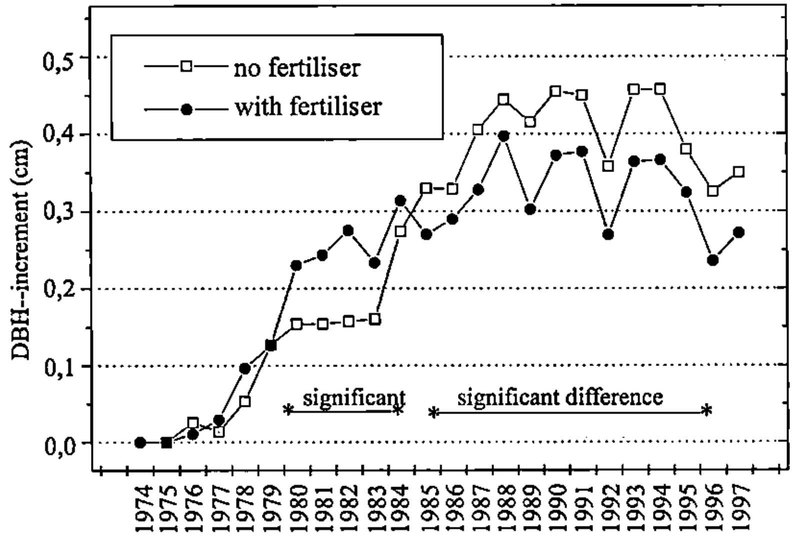

Fig. 9. Development of the DBH-increment for fertilised and control trees (n = 40)

ween fertilised and non-fertilised plots in the widely-established stands (9000 trees / ha).

Table 1. Effects of fertilisation on mortality

mortality (N = 468)	expected number of dead trees per variant	observed number of dead trees (fertilised plots)	observed number of dead trees (non-fertilised trees)	X²-Test fertilised / non-fertilised
all spacing	234	178	290	< 0.001 ***
narrow spacing (23,810 trees/ ha)	88.5	56	121	< 0.001 ***
medium spacing (14,287 trees/ ha)	62	44	80	0.0012 **
wide spacing (8,927 trees/ ha)	83.5	78	89	0.39

These distinct differences in mortality had effects on the increment, because of the changed situation of competition. The fertilisation of each single tree with 20 g magnesium led to a significantly better diameter-increment after six years (Fig. 9). Four years later, the growth-lead of these diameters was exhausted. From this time on, the annual increment of the ten-year-old fertilised trees was lower than the increment of the control-trees. This was a surprising phenomenon at first, which could be explained by the competition mentioned above.

A long-term effect of fertilisation on the humus conditions could not be found. The concentration of phosphorus and ferric components in the soil and in the leaves was higher on the fertilised plots compared to the controlled plots (Table 2). Nearly two decades later there were no differences in the soil parameters (base cation saturation, pH, ion-ratio). Analysing the leaves, it was remarked that the leaves of the non-fertilised plots were to a highly significant extent larger than the leaves of the fertilised trees. This applies to sun- and shade-leaves.

Table 2. Effects of fertilisation on the element-concentration in the leaves (20 years after application)

Elements	non-fertilised trees concentration in mg/ g dry mass	fertilised trees concentration in mg/ g dry mass	t-Test fertilised / non-fertilised
N	19.47 ± 0.61	19.78 ± 0.62	0.48
P	2.15 ± 0.09	2.42 ± 0.09	1.7×10^{-4} (***)
K	9.13 ± 0.46	8.97 ± 0.55	0.31
Mg	1.43 ± 0.13	1.43 ± 0.13	0.98
Ca	6.39 ± 0.50	6.4 ± 0.49	0.98
Fe	0.10 ± 0.01	0.15 ± 0.01	4.6×10^{-8} (***)
Mn	3.49 ± 0.35	3.35 ± 0.28	0.53
Zn	2.4 ± 0.001	2.61 ± 0.002	0.063

DISCUSSION AND CONCLUSION

The described experimental design offered the possibility of examining the different conditions of competition on growth and quality development. The different conditions of competition were given by the 3 tree-spacing variants and the graded site conditions. Therefore, it must be mentioned that the commonly-used plant numbers of the 70s were much higher than the spacings in forestry today. So, the results of this examination are useful to show the basic connections between the competition and reaction of plants and their interaction with silvicultural treatments.

The branchiness and the stand quality can be controlled by higher intraspecific competition created by dense spacing. An expected side effect is an increasing height-increment (Leibundgut 1965, Schaper 1978, Spellmann and Baderschneider 1988). Consequently, the limited diameter-increment caused by the competition is acceptable. The present examination verified the negative effect on the secondary diameter-increment, but did not attest the positive effect on the height-increment. This corresponds to the results of Manderscheid (1984) and Guericke (1996). In very dense stands on soils with a low nutrient supply, a decreasing height-increment was observed.

Quality development must be considered in more detail: it could be shown that the more dense the spacing, the more the branchless part of the stem increased (Gaul and Stüber 1996). The total branchless stem length, however, is distinctly shorter due to the worse growth. Concerning these aspects, it is not advisable to establish dense stands on soils with a low nutrient supply. Furthermore, it is expected that dense stands have a positive effect on the diameter of branches (Kenk 1981, Melzer et al. 1992). This can be verified by this examination. Especially the differences in competition caused by the ramparts showed the useful employment of quotients to describe quality parameters like branchiness *(ASIX)* instead of using absolute values.

One of the most remarkable results was the fertilisation effect on a dense culture on sites with a low nutrient supply, where the understorey was encouraged and kept alive. Hence, competition was aggravated at the same time, so this method should be used carefully. Fertilisation does not always have the positive effects that are expected. Radical site preparation and the concentration of logging-slash and nutrients on a few ramparts have long-term negative effects on stand development. Even if these methods were not used any more, the presented results should remind us to handle soil- and humus-systems carefully.

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UČINCI POČETNE GUSTOĆE, GNOJIDBE I ODSTRANJIVANJA OTPADAKA SJEČE U MLADIM SASTOJINAMA HRASTA KITNJAKA

Predmet je ovoga istraživanja analiza učinaka različitoga razmaka (gusti / srednji / veliki) u kombinaciji s varijantama gnojidbe (gnojeno / negnojeno). Usto su istraživani učinci radikalne pripreme staništa odstranjivanjem otpadaka sječe. Osnova za prikupljanje podataka su 24 pokusne plohe hrasta kitnjaka (*Quercus petraea*) koje su postavljene 1975. s tri početne gustoće (9000, 14 000 i 23 000 biljaka / ha). Polovica su pokusnih ploha gnojene godine 1976. i 1977.

Svrha je ovoga istraživanja kvantificiranje dugoročnih učinaka na prinos, kakvoću stabla i ekologiju različitih postupaka u neprorjeđivanim sastojinama. Mjerenjem prinosa i procjenom kakvoće zabilježeno je 2520 stabala. Usto su analizirana debla iz gnojenih i negnojenih ploha za sve različite gustoće. Ekološka istraživanja obuhvatila su hranidbeno stanje tla, sloj humusa i lišća. Na osnovi podataka analize debla izračunati su modeli kako bi se odredila suha tvar na površini tla. Za procjenu kakvoće napravljen je indeks granatosti (ASIX).

Radikalno odstranjivanje otpadaka sječe imalo je negativan učinak i na prinos i na kakvoću hrastovih stabala. Povećavanjem udaljenosti prema hrpama otpadaka nakon sječe promjer i visina stabala se smanjuju. Rezultati analize debla pokazuju da učinci hrpa počinju 2 – 3 godine nakon sadnje i traju oko 16 godina. Stabla koja su udaljenija od hrpa karakterizira manja visina debla i relativno veće grane. U usporedbi s gusto i srednje napučenim kulturama, područja sa širokim razmacima su manje izložena. Očigledno je da širi razmak između mladih stabala nadoknađuje loše hranidbene uvjete. Povećana konkurencija, međutim, nije imala nikakva utjecaja na kakvoću. Analiza je debla pokazala neobično opadanje prinosa 6 – 8 godina nakon fertilizacije. Smanjenje prihoda na gnojenim plohama je rezultat veće konkurencije u usporedbi s negnojenim plohama. Ta je veća konkurencija posljedica smanjene smrtnosti na gnojenim plohama. Smrtnost je ovisna o količini hraniva. Kulture sa širokim razmacima nisu pokazale nikakve učinke gnojidbe.

Ključne riječi: hrast kitnjak, konkurencija, kakvoća sastojine, hraniva, odstranjivanje otpadaka sječe

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UDK 630*188+48 (Quercus robur L.)

DEVELOPMENT OF VEGETATION IN LOCALITES OF PEDUNCULATE OAK DIEBACK IN CROATIA

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Dieback of pedunculate oak forests in lowland Croatia is one of the most important forestry problems today. A synergistic action of various adverse impacts has resulted in the forced felling of some 600,000 m³ of stemwood on 20,000 ha of the most acutely affected areas in the north-west of Croatia over the last thirty years. Dieback has had the most severe impact on the forest association of pedunculate oak and *Genisto elata (Genisto elatae-Quercetum roboris)*. In the majority of localities this association was in a progressive developmental stage towards the forest of pedunculate oak and common hornbeam (*Carpino betuli-Quercetum roboris*). Changes in the vegetation in the localities of forest dieback have led to the disappearance of both pedunculate oak and numerous members of a well-structured phytocoenosis on the one hand, and the expansion of some pioneering floral elements on the other. Among the latter, those growing on more humid, waterlogged and open sites are particularly prominent.

Key words: pedunculate oak, floral composition, vegetation development, indicative values, lowland Croatia

INTRODUCTION

Forests of pedunculate oak (*Quercus robur* L.) extend over about 200,000 ha in the valleys along the rivers Sava, Drava, and Danube and their tributaries, which is 10% of the total area under forests in Croatia. Their overall growing stock amounts to 55million m³ and the current annual increment reaches 1.4million m³. These forests are mixed in terms of their natural and structural characteristics. Apart from the pedunculate oak, there is also common hornbeam (*Carpinus betulus)*, narrow-leaved ash (*Fraxinus angustifolia*), black alder (*Alnus glutinosa*), elms (*Ulmus carpinofolia* and *U. laevis*), poplars (*Populus* sp.), willows (*Salix* sp.) and other species of lowland regions. Water is the principal ecological factor that influences the development of forest associations of pedunculate oak.

In the last hundred and fifty years the lowland region has been affected by various factors, primarily those of anthropogenic origin. The result has been considerable deviations from a normal natural succession. As some of these effects have followed natural processes or have not caused any stresses, the succession can be regarded as natural. This relates, first of all, to the lowland regions of Croatia in general, where the areas under the associations of drier sites have increased in comparison to those of more humid ones. However, man's interference with nature has brought about shocking changes, to which ecological-biological properties of species have not been able to find a satisfactory answer (tolerance threshold). As a result, large forest complexes have suffered dieback. Therefore, plant communities have not progressed; on the contrary, their entire development has been stopped and has often returned to the beginning. In Croatia, the best known localities in this sense are those along the River Drava near Varaždin, the lowland forests in the Pokupsko basin, the forests in the area of Turopolje-Lekenik, Žutica near Ivanič Grad, and partly the forests of Spačva.

The following factors, often combined into synergistic action, are cited as the most common causes of the disturbed natural stability and appearance of associations of pedunculate oak, as well as a cause of the overall destabilisation of the forest ecosystem:

- epidemic mortality of lowland elms (change in the microclimate)
- badly executed regulations of water courses and melioration (lowered levels of groundwater and changes in the natural flood rhythm)
- an increasing frequency of dry periods during the growing season
- intersecting the terrain with a network of hard roads with poor drainage (waterlogging)
- poisoned and polluted water of the River Sava and its tributaries
- excess of polluted air (SO_2, NOx, heavy metals, etc)
- biotic factors (weakened tree resistance opens a path to attacks by harmful entomofauna, primarily of gypsy moths, and plant diseases, first of all mildew)
- large-scale felling, pedunculate oak monocultures, and inadequate forest management in the past (change in the microclimate)

Water is of decisive importance for the growth of pedunculate oak and its associations in Croatia, while differences in the micro-relief condition the occurrence of various associations. Thus, micro-elevations represent fresh sites but with no excess of water, and micro-depressions abound in water in some parts of the year (spring, autumn). The former are suited to the growth of forests of pedunculate oak and common hornbeam (*Carpino betuli-Quercetum roboris*), while the latter are conducive to forests of pedunculate oak and greenweed *(Genisto elatae-Quercetum roboris)*, which is the subject of our discussion. The results and models obtained or confirmed by Barićevič (1998 and 1999), Matič *et al.* (1994), Rauš and Vukelič (1989), Rauš *et al.* (1996), Vukelič and Rauš (1993), Vukelič *et al.* (1997) have been party used for this work.

FOREST OF PEDUNCULATE OAK AND GREENWEED (*GENISTO ELATAE-QUERCETUM ROBORIS* HT. 1938)

This association (*Genisto elatae-Quercetum roboris*) is characterised by some of the best known forest stands in Croatia, the sources of the world-renowned Slavonian oakwood. It is distributed in the valleys of large rivers and their tributaries, such as the Sava, Drava, Kupa, Danube, and others. These areas abound in vast forest complexes; for example those in the area of Spaćva, Pokuplje and Česma, the forests of Lipovljani, the forests of ÿutica and Repaš, those growing in the region of Našice and Donji Miholjac, and the forests of Slatina.

The terrain of these associations is several meters above the normal water table. It is periodically flooded, but floods are either of short duration or the sites are out of reach of floods, but still abundantly fresh.

In the vegetative succession of lowland forests, this association is a step below the forest of pedunculate oak and common hornbeam. As humidity decreases, it gradually passes into this terminal association within natural progression. However, it is above the forest of narrow-leaved ash and black alder, which grows on a lower terrain and in more humid conditions, in which pedunculate oaks cannot survive.

This highly diverse association has an interesting appearance, composition and value thanks to a mixture of numerous dry and humid vegetative elements. The transition of a micro-elevation into a micro-depression causes the disappearance of common hornbeam and a majority of mesophyllous species of the order *Fagetalia*, and the appearance of hygrophyllous species of the order *Populetalia albae*, which are adapted to floods and raised levels of groundwater.

Pedunculate oak is the dominant species of the very rich tree layer, followed by a considerable proportion of narrow-leaved ash, black alder, lowland elm and spreading elm. The shrub layer is also rich and diverse and is composed, apart from the species from the tree layer, of *Genista elata, Crataegus oxyacantha, Crataegus monogyna, Prunus spinosa, Pyrus pyraster, Viburnum opulus, Frangula alnus,* and other species.

The ground layer is particularly diverse in springtime after floods. It consists of the following species: *Carex remota, Carex strigosa, Rumex saguineus, Cerastium sylvaticum, Valeriana dioica, Lycopus europaeus, Solanum dulcamara, Glechoma hederacea, Galium palustre, Ranunculus repens, Lysimachia numularia, Lysimachia vulgaris, Stachys palustris, Succisa pratensis, Polygonum hydropiper, Mentha aquatica, Aegopodium podagraria, Euphorbia palustris*, and others.

The well-known and described association in Central Europe, that of *Querco-Ulmetum* Oberd. 1953, is very similar to the Croatian association *Genista elatae-Quercetum roboris*, but the differences in their floral composition are evident (*Fraxinus angustifolia, Genista tinctoria ssp.elata*).

The forest of pedunculate oak and greenweed is subdivided into several sub-associations, but decline is present in the following two:

Genisto elatae-Quercetum roboris caricetosum remotae Ht. 1938
Genisto elatae-Quercetum roboris caricetosum brizoides Ht. 1938.

The forest of pedunculate oak and greenweed with quaking sedge (*Genisto elatae-Quercetum roboris caricetosum brizoides* Ht. 1938) thrives on pseudogley and mineral-swampy, slightly acid, non-flooded soils. The sites are usually humid micro-elevations and dry micro-depressions. In the spring and late autumn, the level of groundwater is very high. The differentiating species of the sub-association are *Carex brizoides, Deschampsia caespitosa, Polytrichum attenuatum, Melampyrum silvaticum, Potentilla erecta, Veratrum album*, and others. A typically developed floral composition of this association in undisturbed systems is shown in Table 1, recordings 1 - 3 (Rauš 1993).

The sub-association with remote sedge (*Genisto elatae-Quercetum roboris caricetosum remotae* Ht 1938) grows in flat areas sporadically covered with both flood and stagnant surface water. In the vertical sense, it takes up a position slightly below the previous sub-association, from which it differs by the following genera: *Carex remota, Iris pseudacorus, Cerastium silvaticum, Carex strigosa, Carex elata, Caltha palustris* and other species of more humid sites. The typically developed floral composition of this association in undisturbed ecosystems is shown in Table 2, recordings 1-3 (Rauš 1973).

RESEARCH RESULTS AND DISCUSSION

The succession of lowland forests follows the pattern from the willow "malat" – young germ on sandbanks, through willow forests, poplars, mixed stands of pedunculate oak, elms, black alder and ash, to pedunculate oak-hornbeam forests. The succession or the changes are the result of external ecological factors, but also of an internal development of the association itself. When the development is normal and natural, the succession takes a long time, but the intensive changes of some factors, provided their abruptness and strength do not cause stress, accelerate the process. If the factors that limit the development act continuously, the final association will not develop but will remain in its permanent stage.

FOREST OF PEDUNCULATE OAK AND GREENWEED WITH QUAKING SEDGE (*GENISTO ELATAE-QUERCETUM ROBORIS CARICETOSUM BRIZOIDES* HT. 1938)

Research in the localities of pedunculate oak dieback in the forest of pedunculate oak and greenweed with quaking sedge in Turopoljski Lug have shown that both the floral composition of stands and their physiognomy and structure have completely lost the character of a typically developed sub-association *caricetosum brizoides.* Plants such as *Salix cinerea, Juncus effusus, Cirsium palustre* and *Peucedanum palustre* that are atypical for this association (Table 1, recordings 4, 5 and

6), are permanently present. Corkscrew rush (*Juncus effusus*), normally a regular occurrence in the lowland forests of Croatia, covers up to 100% of dried sites. The eco-indicative properties of the present species point to a waterlogged biotop, which was not the case before. This is testified by the presence of a stunted common hornbeam occurring here some ten to twenty years previously, and whose development was abruptly ended. It has been replaced with *Salix cinerea, Frangula alnus* and *Alnus glutinosa.*

As seen from the above, the stressful changes of ecological factors and their impact on stands and sites in a normal succession have had very serious consequences. In place of standard representatives, plants that indicate changes in the biotop, namely waterlogging, dominate the floral composition. Excess moisture is primarily the result of badly executed hydrotechnical and infrastructural interventions in the stands. This was additionally increased many times over by the degradation of pedunculate oaks, which had utilised humidity from the soil.

This is confirmed by the presence of species that indicate humid sites in the localities of dieback in the Pokupsko basin (Table 1, recordings 7 and 8), the forests of Posavina around Sunja and Dubica (Table 1, recordings 9 and 10), and in the forest of ÿutica (Barićevič 1998). Apart from the mentioned differentiating species, a large proportion of the following was noted: *Frangula alnus, Polygonum hydropiper, Myosotis scorpioides, Galium palustre, Lysimachia vulgaris, Carex elongata, Stachys palustris, Ranunculus repens, Lytrum salicaria* and others. More mesophyllous elements from typically structured associations were absent.

A drastic example of changes of this kind is the forest of ÿutica. The site of the sub-association with quaking sedge established some thirty years ago (Medvedovič 1975) is today taken up by a forest of black alder on 50 ha, a forest of narrow-leaved ash on 30 ha, and a more humid sub-association with quaking sedge on 120 ha. On the other hand, the normal progression of the association is found on 40 ha where ecological changes were not so drastic. About 20 ha of the site are covered by the more arid sub-association with common hornbeam, and a further 20 ha by the association of pedunculate oak and common hornbeam.

FOREST OF PEDUNCULATE OAK AND GREENWEED WITH REMOTE SEDGE (*GENISTO ELATAE-QUERCETUM ROBORIS CARICETOSUM REMOTAE* HT. 1938)

Phytocoenological recordings and analyses of floral compositions in the localities of dieback in the forest region of Kalje and the Forest Office Sunja also show changes. These changes have taken two directions (Table 2, recordings 4-9):

I. There is a vast presence of species that are not present in this sub-association under normal and healthy conditions, such as *Amorpha fruticosa, Carex riparia, Carex elata, Filipendula ulmaria* and *Lytrum salicaria.* The analysis of auto-ecological properties of these species according to Ellenberg (1979), Oberdorfer (1983), Zolyomi *et al.* (1967) shows that all these species are linked exclusively to wet, regularly flooded sites, and some are moreover cited as indicators of floodplain regions. The floral composition of this sub-association also contains a higher than normal proportion and coverage of the following species: *Bidens tripartita, Polygonum hydropiper, Alisma plantago-aquatica* and *Juncus effusus*. The auto-ecological properties of these species also indicate that these are the plants of very wet and flooded sites and that they do not occur in drier sites. In terms of their relation to light, these species show that they favour semi-light and light conditions.

II. Species that are otherwise permanently present in normally structured stands are either absent or occur in an incomparably smaller coverage and proportion. These are *Carex strigosa, Solanum dulcamara, Ranunculus repens, Geum urbanum, Circaea lutetiana, Glechomoma hederacea, Aegopodium podagraria, Carex remota* and *Lysimachia nummularia*. These are plants of mostly humid sites and none is an indicator of flooded sites. The analysis of the relationship of these plants to light shows completely different relations than is the case with newly present plants in these sites. They are mostly plants of semi-shade, while *Carex remota, Carex strigosa* and *Lysimachia nummularia* are plants of the shade.

The very aggressive *Amorpha fruticosa* in the shrub layer has taken over completely, while the genera of the order *Crataegus*, and even *Genista elata*, the carriers of this layer's structure in normal stands, are missing.

The research carried out in the forest ÿutica in 1998 showed similar conditions and changes in this association.

According to Prpić (1989, 1996) and Prpić *et al.* (1994), these changes are the result of a drop in minimal levels of groundwater. The same is true for many other sites of the lowland region, where deep man-made drainage canals have had adverse effects on forests. If the level of groundwater in an oak site decreases significantly in the summer season, trees of pedunculate oak physiologically weaken and then die, which is especially dangerous for middle-aged and old stands. As in the previous association, the surface has become waterlogged due to the inability of forest trees and other members of the biocoenosis to utilise water.

The second type of pedunculate oak dieback and changes in the development of the association were found in the stands established artificially on pastureland or on the site of narrow-leaved ash with autumn snowflake. These stands were established by building mounds, that is, by elevating the terrain for the purpose of avoiding surface and floodwater. The association was developing progressively until 30 years ago, when large-scale disturbances in the ecosystem took place (regulation of the River Sava, building of canals, dams and forest roads, polluted water flooding the forest and other events). This has led to the physiological weakening of the existing phytocoenosis and the beginning of the regression of the entire association. The unstable ecosystem of the pedunculate oak (artificially-raised forest) caved in under the constant pressure of unfavourable synecological factors, and abrupt dieback of pedunculate oak took place some fifteen years ago, culminating in 1985 and 1986, when almost the entire oak community died.

After cutting standing deadwood, the site was prepared and seedlings of black alder and narrow-leaved ash, as well as some pedunculate oaks, were artificially planted, resulting in the present mixed young stand of satisfactory structure and stability.

In the Spaćva basin in the eastern part of Croatia, ecological changes that would have led to large-scale dieback similar to that in the north-west did not take place. However, in the last twenty years this sub-association has undergone succession and has transformed into drier associations of *Genisto elatae-Quercetum roboris aceretosum tatarici* and *Carpino betuli-Quercetum roboris* over 21% of the area (Rauš 1990).

CONCLUSIONS

Research into the development of vegetation in the localities of pedunculate oak dieback in Croatia has revealed fundamental deviations from natural succession. They are the result of the adverse synergistic action of a combination of ecological factors that have led to a change in the water regime.

Interventions of a hydro-technical and other infrastructural nature in the forests and adjacent areas have caused a drop in groundwater levels in one part of the stands and site waterlogging in the other. Stands of pedunculate oak of 80 years or more have degraded, and narrow-leaved ash and black alder as pioneering species have, either naturally or artificially, replaced pedunculate oak in the sites that are too moist for the latter. In many places the physiognomy and structure of the stands' floral composition have lost the character of typically-developed associations. A large number of species indicating increased humidity or degraded sites have abundantly covered the site. These *are Amorpha fruticosa, Bidens tripartita, Filipendula ulmaria, Carex riparia, Myosotis scorpioides, Galium palustre, Peucedanum palustre, Juncus effusus, Polyganum hydropiper,Lytrum salicaria, Alisma plantago aquiatica, Carex elata* and others.

As a declining trend continues (but to a lesser extent), areas under more humid associations are expected to increase in the future. For this reason, it is necessary to manage the water regime (drain waterlogged areas, prevent a drop in groundwater levels, minimise water pollution) in order to maintain the stability of lowland ecosystems.

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Table 1.

Association:					*Genisto elatae - Quercetum roboris*					
Subassociation:					*caricetosum brizoides* Ht. 1938					
Number of recording:	1	2	3	4	5	6	7	8	9	10
Area:	Bedenik	Žablji lug	Lubardenik		Turopoljski lug		Pokupski bazen		Sunja	Dubica
Plot size (m2):	400	400	400	400	400	400	400	400	400	400
Cover (%):										
Tree layer	90	80	90	20	30	50	100	100	60	70
Shrub layer	30	10	10	20	30	30	10	2	30	20
Ground vegetation layer	100	100	100	100	100	100	100	100	100	100
FLORAL COMPOSITION										
Characteristic species of the association, alliance (*Alno-Quercion*) and order (*Alnetalia glutinosae*):										
Quercus robur L. A	5	5	3	2	2	3	4	5	3	4
Alnus glutinosa (L.) Gartn.	.	.	+	1	+	+	1	.	+	1
Frangula alnus Mill. B	+	1	.	1	1	1	1	+	.	+
Genista tinctoria subs. *elata* L.	+	.	+	.	1	+	+		1	.
Alnus glutinosa (L.) Gartn.	.	.	.	+	.	+	1	.	.	1
Fraxinus angustifolia Vahl.	.	.	.	.	.	.	.	.	1	1
Ulmus carpinifolia Gled.	R	.	.	.	+	.	.	.	R	+
Quercus robur L.	.	.	.	.	1	+	.	.	.	3
Viburnum opulus L.	.	.	.	+	.	+	.	.	.	.
Acer tataricum L.	+	.	.	.	.	.	.	.	.	.
Ulmus laevis Pall.	.	.	.	.	.	.	.	.	.	+
Carex brizoides L. C	4	5	3	.	1	+	3	2	2	+
Quercus robur L.	+	.	+	.	1	+	1	+	.	.
Rumex sanguineus L.	.	.	.	.	+	.	+	+	+	+
Cerastium silvaticum W.K.	.	.	+	.	.	.	.	+	+	+
Lycopus europaeus L.	.	.	.	+	+	+	.	1	1	+
Impatiens noli tangere L.	.	.	+	.	.	.	.	.	.	.
Lysimachia nummularia L.	+	.	+	.	.	.	+	1	.	.
Angelica silvestris L.	+	.	+	.	.	.	.	.	.	+
Dryopteris carthusiana	.	.	.	+	1	1	.	.	.	+
Nephrodium spinulosum Strem.	1	+	.	.	.	.	+	1	+	.
Solanum dulcamara L.	.	.	.	.	+	+	+	+	+	.
Glechoma hederacea L.	R	+	.	+		+	.	.	+	.

Rubus ceasius L.	R	.	.	.	+	.	1	.	+	.
Carex strigosa Huds.	.	.	.	.	.	.	.	.	+	+
Valeriana dioica L.	.	.	.	.	.	.	.	1	+	.
Viburnum opulus L.	.	.	.	+	.	.	.	.	.	
Carex remota L.	.	.	.	.	.	.	.	.	+	
Frangula alnus L.	.	.	.	.	.	.	+	.	.	.
Characteristic species of the order (*Fagetalia*) and class (*Querco-Fagetea*):										
Carpinus betulus L. A	+	.	2	.	+	.	.	.	+	+
Fagus silvatica L.	.	.	R	.	.	.	.	.	.	.
Carpinus betulus L. B	3	2	2	.	2	1	.	.	R	.
Acer campestre L.	+	.	.	.	.	.	.	.	R	.
Crataegus monogyna Jacq.	+	1	.	.	.	.	+	.	+	1
Euonimus europaea L.	.	.	.	.	.	.	1	.	.	.
Crataegus oxyacantha L.	1	+	.	.	.	.	.	+	.	.
Pirus pyraster (L.) Borkh.	+	.	.	.	.	.	+	1	.	R
Corylus avellana L.	.	.	.	.	.	.	3	+	.	.
Fagus silvatica L.	.	.	+	.	.	.	.	.	.	.
Aegopodium podagraria L. C	+	+	+	.	.	.	+		R	.
Urtica dioica L.	.	.	+	.	.	.	.	.	+	+
Dryopteris filix mas (L.) Sch.	.	.	+	.	.	.	+	.	.	.
Circaea lutetiana L.	+	.	+	+	.	.	+	+	.	.
Viola reichenbachiana Jor.	.	.	.	.	.	.	.	+	.	.
Ajuga reptans L.	.	.	.	.	.	.	+	+	.	.
Veronica montana L.	.	.	+	.	.	.	.	+	+	.
Lamiastrum galeobdolon L.	.	.	+	.	.	.	.	+	.	.
Brachypodium silvaticum R.S.	.	.	+	.	.	.	.	.	.	.
Stellaria holostea L.	.	.	+	.	.	.	+	.	.	.
Scrophularia nodosa L.	.	.	.	.	+	.	1	+	+	+
Geranium robertianum L.	.	.	.	.	.	.	.	+	.	.
Corylus avellana L.	.	.	.	.	.	.	+	.	.	.
Species - indicators of changes:										
Salix cinerea L. B	.	.	.	1	+	+	.	+	.	.
Peucedanum palustre Monch. C	.	.	.	1	+	2	1	1	+	+
Juncus effusus L.	.	.	.	5	3	4	1	1	1	+
Polygonum hydropiper L.	+	.	.	1	+	+	1	2	+	+

Myosotis scorpioides L.		.	.	.	.	.	.	+	1	1	
Galium palustre L.		.	.	.	.	.	.	1	1	+	+
Ranunculus repens L.		.	.	.	+	+	+	.	1	+	.
Lysimachia vulgaris L.		.	.	.	.	.	+	1	+	+	+
Lytrum salicaria L.		.	R	.	+	+	+	+		+	+
Poa palustris L.		.	.	.	.	.	.	+	+	1	+
Stachys palustris L.		.	.	.	+	.	.	1	1	+	+
Cirsium palustre (L.) Scop.		.	.	.	+	1	1	.	.	.	.
Other species of wet and flooded sites:											
Deshampsia caespitosa Beau.	C	1	+	1	.	1	+	1	1	1	1
Iris pseudacorus L.		.	.	.	.	.	+	.	.	+	+
Festuca gigantea (L.) Vill.		R	.	.	.	+	.	.	.	+	+
Carex elongata L.		.	.	.	.	.	.	.	.	+	.
Euphorbia palustris L.		R	.	.	.	.	.	.	.	.	.
Alisma plantago aquiatica L.		.	.	.	.	.	.	.	.	+	.
Lychnis flos cuculi L.		.	.	.	1	+	1	.	.	.	.
Mentha aquiatica L.		.	.	.	.	.	.	.	+	+	+
Other species:											
Rubus fruticosus L.	B	.	.	.	+	2	1	+	1	.	+
Rhamnus cathartica L.		.	.	.	.	.	.	.	.	R	.
Amorpha fruticosa L.		.	.	.	.	.	.	.	.	3	.
Rosa canina L.		.	.	.	.	.	.	.	.	+	.
Galeopsis tetrahit L.	C	+	.	+	.	2	+	+	.	+	+
Geum urbanum L.		.	.	.	.	1	+	.	.	+	+
Hypericum quandragulum L.		.	.	.	.	.	.	.	.	1	+
Agrostis alba L.		.	.	.	.	.	.	.	.	1	1
Athyrium filix femina (L.) Roth.		.	+	+	.	.	.	+	.	.	.
Eupatorium canabinum L.		.	.	.	.	.	.	.	+	.	.
Rubus hirtus W.K.		.	.	1	.	.	.	.	.	.	.
Pulmonaria officinalis L.		R	.	.	.	.	.	.	.	+	.
Euphorbia amygdaloides L.		+	.	.	.	.	.	.	.		.
Galium vernum L.		.	.	+	.	.	.	.	.	.	.
Fragaria vesca L.		.	.	.	.	2	+	.	.	.	.
Carex hirta L.		.	.	.	.	2	+	.	.	.	.
Melampyrum nemorosum L.		.	.	.	.	.	+	+	.	.	.

Potentilla erecta (L.) Hampe.	.	.	.	.	.	.	+	.	.	.
Cynanchum vincetoxicum (L.) Pers.	.	.	.	.	.	.	+	.	.	.
Verbatum album L.	.	.	.	.	.	.	+	.	.	.
Bidens tripartita L.	.	.	.	.	.	.		.	+	+
Stenactis annua (L.) Ness.	.	.	.	.	.	.	.	.	1	+
Prunella vulgaris L.	.	.	.	.	.	.	.	+	+	+
Oxallis stricta L.	.	.	.	.	.	.	.	.	+	+

Explanation of abbreviations:
A - Tree layer
B - Shrub layer
C - Ground vegetation layer
"+, 1, 2, 3, 4, 5 - Combined assessment of abundance and cover (Braun-Blanquet 1964)

Table 2.

Association:		*Genisto elatae- Quercetum roboris*											
Subassociation:		*caricetosum remotae* Ht. 1938											
Number of recording:		1	2	3	4	5	6	7	8	9	10	11	12
Area:		Opeke	Žutica	Pokupski		Kalje			Sunja			Turopoljski lug	
Plot size (m2):		400	400	400	400	400	400	400	400	400	400	400	400
Cover (%):													
Tree layer		90	80	90	30	25	20	20	25	20	90	75	70
Shrub layer		30	40	20	30	20	30	60	50	60	60	15	60
Ground vegetation layer		100	100	100	100	100	100	100	90	95	80	100	100
FLORAL COMPOSITION													
Characteristic species of the association, alliance (*Alno-Quercion*) and order (*Alnetalia glutinosae*):													
Quercus robur L.	A	5	5	4	2	1	1	1	1	1	4	4	4
Fraxinus angustifolia Vahl.		1	.	.	.	+	+	.	.	.	+	+	+
Alnus glutinosa (L.) Gartn.		.	.	1	+	1	1	.	+	.	1	+	.
Ulmus carpinifolia Gled.		1	.	.	.	.	.	.	R	.	.	.	.
Ulmus laevis Pall.		.	.	.	1	.	.	.	.	.	.	3	3
Fraxinus angustifolia Vahl.	B	2	+		1	1	2	.	+	.	2	.	.
Ulmus carpinifolia Gled.		.	1	1	.	.	.	.	.	.	.	1	1
Alnus glutinosa (L.) Gartn.		+	.	.	1	1	3	.	.	.	1	.	+
Viburnum opulus L.		.	.	+	+	.	.	.	.	.	+	+	+
Genista tinctoria subs. elata L.		2	3	.	R	.	.	.	.	+	+	.	+
Quercus robur L.		.	.	.	.	.	.	.	+	.	+	+	.
Frangula alnus Mill.		.	.	+	+	1	1	.	.	.	2	+	.
Ulmus laevis Pall.		.	.	.	2	.	.	.	.	.	.	.	.
Carex remota L.	C	5	1	2	.	.	.	1	.	.	.	+	.
Quercus robur L.		2	1	+	.	.	.	.	.	.	.	.	.
Rumex sanguineus L.		1	.	.	+	R	.	.	.	.	.	+	1
Lycopus europaeus L.		+	1	1	+	+	+	1	.	1	1	.	.
Lysimachia nummularia L.		2	.	+	+	.	.	+	.	.	+	.	.
Leucoium aestivum L.		+	. .	.	1	1	.	.	.	.	+	.	+

Nephrodium spinulosum Strem.		.	.	+	.	+	.	.	.	.	.	.	+
Carex strigosa Huds.		1	.	1	.	.	.	.	.	.	.	.	.
Solanum dulcamara L.		.	.	.	.	R	+	.	.	.	+	+	.
Valeriana dioica L.		3	2	.	+	+	.	.	.	.	.	.	.
Glechoma hederacea L.		2	2	1	+	.	.	.	.	.	.	.	+
Rubus ceasius L.		.	+	2	+	.	.	.	.	.	.		
Fraxinus angustifolia Vahl.		3	.	.	.	.	.	.	.	.	+		
Ulmus carpinifolia Gled.		+	.	.	.	.	.	.	.	.	.	.	.
Viburnum opulus L.		.	.	.	.	.	.	.	.	.	+	+	+
Characteristic species of the order (*Fagetalia*) and class (*Querco-Fagetea*):									.			+	.
Carpinus betulus L.	A	.	.	+	.	.	.	.	.	.	.	+	.
Pirus pyraster (L.) Borkh.		.	.		.	.	.	.	R	.	.		
Acer campestre L.	B	.	.	+	.	.	.	.	.	.	.		
Crataegus monogyna Jacq.		.	.	1	.	.	.	.	.	.	.	.	.
Crataegus oxyacantha L.		+	.	1	+	.	.	.	.	.	.	.	.
Carpinus betulus L.		.	.	1	.	.	.	.	.	.	.	.	.
Pirus pyraster (L.) Borkh.		.	.	+	.	+	.	.	.	.	.	.	.
Corylus avellana L.		.	.	1	.		.	.	.	.	.	.	.
Urtica dioica L.	C	+	+	+	+	+	.	.	.	+	.	.	.
Circaea lutetiana L.		.	+	+	.	R	.	.	.	.	.	.	.
Ajuga reptans L.		.	.	+	.	.	.	.	.	.	.	.	.
Aegopodium podagraria L.		+	.	+	+	+	+	.	.	.	.	.	.
Scrophularia nodosa L.		.	.	2	.	.	.	.	.	.	.	.	.
Carex maxima		.	.	+	.	.	.	.	.	.	.	+	
Species - indicators of changes:												.	.
Amorpha fruticosa L.	B	.	.	.	3	.	.	3	2	3	.	.	.
Carex riparia Curt.	C	.	.	.	2	3	3	.	2	1	3		
Juncus effusus L.		1	+	.	+	1	+	2	+	1	1		
Polygonum hydropiper L.		+	+	+	+	+	1	2	2	3	1	.	+
Bidens tripartita L.		.	+	.	+	2	1	1	1	+	1	+	.
Lytrum salicaria L.		.	1	.	.	.	+	+	+	+	1	1	+
Alisma plantago aquiatica L.		+	.	.	1	1	1	+	+	+	+		+

Filipendula ulmaria (L.) Max.		.	.	.	2	1	1	.	.	.	2	+	.
Myosotis scorpioides L.		.	.	.	+	+	+	.	.	.	.	.	+
Carex elata All.		.	1	.	+	+	1	+	.	+	+	.	1
Other species of wet and flooded sites:												+	1
Salix cinerea L.	B	.	.	1	+	+	.	.	R	.	+	+	.
Deshampsia caespitosa Beau.	C	.	.	.	.	.	.	.	.	.	.	+	+
Galium palustre L.		3	+	1	1	+	+	.	.	.	+	1	+
Peucedanum palustre Monch.		.	+	+	+	+	+	.	.	.	+	.	.
Iris pseudacorus L.		.	+	+	.	.	.	R	+	+	+	+	+
Ranunculus repens L.		+	2	+	1	+	+	.	.	+	1	.	.
Lysimachia vulgaris L.		2	.	1	+	+	+	+	.	.	+	.	.
Poa palustris L.		.	.	.	R	+	.	+	.	.	.	.	+
Stachys palustris L.		.	1	+	1	+	.	.	.	.	+	.	.
Carex elongata L.		1	.	.	+	1	+	.	+	.	.	+	.
Symphytum officinale L.		+	+	.	+	1	.	+	.	.	.	1	.
Caltha palustris L.		.	.	+	.	.	.	.	.	.	.	1	+
Euphorbia palustris L.		1	.	.	+	.	.	.	.	.	.	4	4
Succisa pratensis Mch.		2	1	1	+	+	.	.	.	.	+	.	.
Cirsium palustre (L.) Scop.		.	.	.	.	.	+	.	.	.	.	.	+
Lychnis flos cuculi L.		.	.	.	.	.	.	.	.	.	+	.	.
Mentha aquatica L.		+	+		+	.	.	.	+	+	.	.	.
Glyceria fluitans (L.) R. Br.		.	.	+	.	.	.	.	.	.	.	2	+
Veronica longifolia L.		.	.	.	1	+	+	.	.	.	.	.	.
Carex vesicaria L.		.	.	.	+	1	.	.	.	.	.	.	.
Carex vulpina L.		.	.	.	R	+	.	.	.	.	.	.	+
Senecio palustris D.C.		.	.	.	+	.	+	.	.	.	.	.	.
Other species:													
Rhamnus cathartica L.	B	.	.	.	R	.	.	.	.	.	.	.	.
Cornus sanquinea		.	.	+	.	.	.	.	.	.	.	.	.
Geum urbanum L.	C	+	.	+	.	.	+	.	.	.	+	.	.
Hypericum acutum L.		.	.	.	.	R	.	+	.	.	.	.	.
Agrostis alba L.		.	.	.	.	R	.	+	+	+	.	.	.

Solidago sp.	.	1	.	.	.	.	.	.	.	.	.	.
Acer tataricum L.	+	.	.	.	.	.	.	.	.	.	.	.
Scutellaria galericulata L.	.	.	.	.	.	.	+	+	+	.	.	.
Stenactis annua (L.) Ness.	.	.	.	.	.	.	+	.	+	.	+	.
Ranunculus ficaria L.	1	.	.	.	.	.	.	.	.	.	.	.
Erigeron annuus (L.) Pers.	.	.	.	.	.	.	.	.	.	1	.	.
											+	+

Explanation of abbreviations:

A - Tree layer
B - Shrub layer
C - Ground vegetation layer
"+, 1, 2, 3, 4, 5 - Combined assessment of abundance and cover (Braun-Blanquet 1964)

J. Vukelić, D. Baričević: Development of vegetation in localites of pedunculate oak dieback in Croatia. Glas. šum. pokuse 37: 277–293, Zagreb, 2000.

RAZVOJ VEGETACIJE U LOKALITETIMA SUŠENJA HRASTA LUŽNJAKA U HRVATSKOJ

Sušenje je šuma hrasta lužnjaka u nizinskoj Hrvatskoj jedan od najznačajnijih šumarskih problema našega doba. U posljednih je trideset godina sinergističko djelovanje različitih nepovoljnih čimbenika dovelo do prisilne sječe oko 600 000 m^3 drva na 20 000 ha u sjeverozapadnoj Hrvatskoj, području koje je najteže pogođeno. Sušenje je osobito pogodilo šumsku zajednicu hrasta lužnjaka i velike žutilovke (*Genisto elatae-Quercetum roboris*). Na većini lokaliteta ta je asocijacija bila u progresivnoj razvojnoj fazi prema šumi hrasta lužnjaka i običnoga graba (*Carpino betuli-Quercetum roboris*). Zbog promjena u vegetaciji na lokalitetima na kojima se šuma suši nestao je hrast lužnjak, ali i brojni članovi dobro strukturirane fitocenoze, a proširile su se neke pionirske vrste, među kojima se posebno ističu one koje rastu na vlažnijim, zamočvarenim i otvorenim staništima.

Ključne riječi: hrast lužnjak, florni sastav, razvoj vegetacije, indikativne vrijednosti, nizinska Hrvatska

M. Bobinac: Stand structure and natural regeneration of common oak in the nature reserves "Vratična" and "Smogva" near Morović. Glas. šum. pokuse 37: 295–309, Zagreb, 2000.

UDK 630*228+231+(497.1) (Quercus robur L.)

STAND STRUCTURE AND NATURAL REGENERATION OF COMMON OAK IN THE NATURE RESERVES "VRATIČNA" AND "SMOGVA" NEAR MOROVIĆ

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The basic stand structure elements and natural regeneration of common oak were studied in the nature reserves "Vratična" and "Smogva" near Morović - the last remains of ancient common-oak forests in the Bosut basin. In the nature reserve "Smogva" – a terminal community of common oak - narrow-leaved ash forest in a former flooded area, common oak is represented by 220 trees per *ha*, diameter 4-171 *cm*. In the nature reserve "Vratična" – a more moist variant of common oak - narrow-leaved ash - hornbeam forest in the flooded area, common oak is represented by 29 trees per *ha* on average, diameter 24-224 *cm*. In the total number of trees, common oak is represented by 3.2 - 4.4%, while the number of old trees in the more preserved parts is 27-32 trees per *ha*. The maintaining of adult phases of common oak is more favoured in common oak - narrow-leaved ash forests. The last regeneration cycle took place 20-25 years ago. In the common oak-narrow-leaved ash-hornbeam forest, it is an accidental phenomenon, and the last regeneration cycle occurred 45-50 years ago. In conditions of low illumination in the ground layer, oak mildew (*Microspaera alphitoides* Grif. et Maubl.) causes common oak ontogenesis to be interrupted in the phase of seedlings or in the initial phase of forming young growth. The forming of young growth is conditioned by the synchronisation of canopy disintegration and the acorn seed year. The optimally synchronised disintegration of the canopy occurs immediately before the formation of seedlings.

Key words: Common oak (*Quercus robur* L.), nature reserves, Morović, stand structure, natural regeneration.

INTRODUCTION

In the region of Slavonia (Republic of Croatia) and south-west Srem (SR Yugoslavia), which, in the geographical sense, make an entity, there are only fragments of ancient common oak forests, which were, after Prpić (1987), virgin forests on more than 700,000 *ha* at the beginning of the 17th century. Over centuries, at the border of two empires, Austria and Turkey, this region was under military authorities and was the Military Border zone - Vojna krajina. By anthropogenic influences, the area covered by common oak forests was reduced by 1868 to 210,045 *ha* (Vyskot 1958, after Austrian statistics). In 1870 there were 74,744 *ha* of old common-oak forests (Metlaš 1926).

The only surviving stands in this area are: the strict nature reserve "Prašnik", area 53.35 *ha* (Matić et al. 1979, Rauš 1995, Vukelić and Španjol 1996), the strict nature reserve "Vratična", area 10.3 *ha* and the nature monument "Smogva", area 4.3 *ha* (Mišić and Broz 1962, Erdeši 1983, Kolarović 1985, Bobinac 1998), as well as some groups of old common-oak trees in the Bosut basin (Bobinac 1999). By the characteristics of their structure, dimensions and age of trees, these are the last remains of common-oak virgin forests.

According to data of the management plan from 1865, in the region which belonged to the 9th Petrovaradin Regiment there were 3,931.40 *ha* of common-oak forests more than 140 years old (Plavšić 1975). The last remains of ancient common-oak forests survived up to the middle of the 20th century in the region of the Bosut basin in the forest complexes "Vratična" and "Smogva" (Panić and Kravcev 1954). With the aim of preserving its fragments, the Ministry of Forests and Mines of the Kingdom of Yugoslavia in 1929 protected 3 trees of remarkable dimensions as rarities of nature. During the period 1951-1954, the Institute for Nature Protection of the PR of Serbia designated "Vratična" over an area of 10.30 *ha* and "Smogva" over an area of 4.30 *ha*, near Morović, as nature reserves. According to Erdeši (1983), the age of trees in the nature reserves was estimated to be 350-450 years. Their beginnings can be linked to the historical period in which Srem, after the occupation of Belgrade by the Turks (1521) and their victory at Mohač (1526), was a part of the Ottoman Empire in a relatively peaceful period, being one of the provinces left in the background until the end of the 17th century. In that period common-oak forests were virgin forests. Until the end of the 18th century, only individual trees were felled for the use of the local population. Their development over wide areas was caused by specific, ecologically and historically continuously favorable factors in lowland virgin forests which had a different mixture scale at that time (Kozarac, 1897).

In order to preserve the diversity of common oak (site-conditioned and the most valuable edificator in nature reserves) and the system of regeneration of economic stands, which, after Korpel (1997), is most rational if based upon forestry close to nature, the principal regularities can be estimated in the conditions of the less disturbed sites. The aim of this paper is to describe the stand structure and natural regeneration of common oak in the oldest nature reserves in the region of south-west Srem, under the conditions of the specific utilisation and protection of different forest ecosystems.

METHODS

Forest phytocoenoses and soils in these nature reserves are presented based on the results of ecological and typological investigations of common-oak forests in the broader region of Srem (Jovanović et al. 1983, Jović et al. 1989/1990). Forest phytocoenose classification to higher taxonomic categories is according to Jovanović (1997).

Study results are based on the diameter measurements of all common oak trees, the assessment of their health condition and on the analysis of the regeneration characteristics in the total area of the nature reserve, as well as on permanent sample plots, size 1 *ha*, in structurally more preserved parts. The establishment of sample plots and tree measurement were performed in 1997-1998. The data were collected as follows:

- Tree girth was measured at dbh by steel tape, with an accuracy of 1 *cm*;
- The health condition of common oak trees was assessed visually by the percentage of living and dying parts of the crown (branch tips and central axis) in the total length. The following classifications were used:
  A_o= crown with individual dead branches,
  A_1=crown affected by dying up to 1/3 of total length,
  A_2= crown affected by dying 1/3 to 1/2 of total length,
  A_3= crown affected by dying more than 1/2 of total length,
  A_4= completely dead trees;
- The characteristics of the previous regeneration process of common oak were analyzed on the basis of the presence and spatial position of young common-oak trees in relation to the zone of the present or assumed horizontal crown projection of old standing trees. The age of young common-oak trees was determined by Pressler's increment cores extracted at a height of 50 *cm*, on 3 average trees in the lowest diameter class;
- The actual regeneration process of common oak was analysed only in the nature reserve "Vratična" in the seed year (1996). Seedling formation was monitored in conditions of the very low presence of livestock and wildlife as significant factors in the natural regeneration of common oak in the study area. Within the horizontal crown projection of each common oak, 2 sample plots of an area of 1 m^2, were set and all seedlings of common oak were counted at the beginning of the growing season;
- On permanent plots (100×100 *m*), all present trees with diameters more than 1 *cm* were measured at dbh. The stand structure is presented on the basis of tree distribution (*N*) and basal area (*G*) per diameter class, 10 *cm*.

CHARACTERISTICS OF STUDY AREAS

The nature reserves "Vratična" and "Smogva" are located in south-west Srem, in the part between the left bank of the Sava River and the catchment area of the lower course of the Bosut and Studva rivers at an altitude of 79-81 *m*. Based on the data from the meteorological station Sremska Mitrovica for the period 1900-1995, this area is characterised by a temperate continental climate with a mean annual air temperature of 11.0°C (min. 9.1°C, and max. 12.9°C) and mean annual precipitation of 620 *mm* (min. 395 *mm*, max. 1005 *mm*). On the basis of hydric balance after Thornthweite, the climate is subhumid - more humid, type C_2.

The nature reserve "Smogva" contains a terminal community of common oak - ash forest in a former flooded area, and the nature reserve "Vratična" contains the most humid variant of common oak - narrow-leaved ash - hornbeam forest in a flooded area. Forest phytocoenoses in the investigated nature reserves, in a systematic sense, belong to the following syntaxonomic categories:

Class: *Querco-Fagetea* Br.-Bl. et Vlieg. 1937.
Order: *Quercetalia pubescentis* Br.-Bl. (1931) 1932.
Alliance: *Alno-Quercion roboris* Ht. (1937) 1938.
- Group: Forest of common oak and narrow-leaved ash: *Fraxino- Quercetum roboris* Rud. (1941) 1949 s. l.
Subass.: *Fraxino- Quercetum roboris subass. aceretosum* Jov. and Tom. 1980.
- Group: Forest of common oak - narrow-leaved ash - hornbeam:*Carpino-Fraxino-Quercetum roboris* Mish. and Broz (1962) 1974 s. l.
Subass.: *Carpino-Fraxino-Quercetum roboris subass. inundatum* Jov. and Tom. 1978.

Forests of common oak and narrow-leaved ash are the most humid variants of common-oak forests in the region of Srem. In an ecological sense, these forests are between the humid monodominant communities of narrow-leaved ash (alliance: *Alnion glutinosae* Malc. 1929, Drees 1936) and the monodominant communities of common oak (alliance: *Alno-Quercion roboris* Ht. 1937, 1938). Depending on the width of the flooded terrain and the available space for forming these forests in transitional habitats, here a series of subassociations can occur, from the most humid ones, with the dominance of narrow-leaved ash on humogley, to the driest ones, with the dominance of common oak, field maple and Tatarian maple on semigley soils. The community *Fraxino angustifoliae-Quercetum roboris subass. aceretosum* Jov. and Tom. 1980 is less influenced by underground water and occurs on humosemigley to semigley soils with signs of lessivage. This is the terminal community of common oak and narrow-leaved ash forest and, until 1934, it was exposed to frequent floods. In the tree and shrub layer there are about 20 species. The shrub layer is very rich in species, and along with *Crataegus monogyna* V^{+-3} and *Crataegus oxyacantha* IV^{+-3}, the species of *Acer tataricum* III^{+-1}, *Acer campestre* II^{+-1}, *Pyrus piraster* II^{+-1} and *Carpinus betulus* II^{r-1} are present to a high degree. In an ecological sense, this community is the previous, more humid member occurring before the polydominant community of common oak, narrow-leaved ash and hornbeam, in places where the insufficiently differentiated habitats change mosaically.

Forests of common oak, narrow-leaved ash and hornbeam (*Carpino-Fraxino-Quercetum roboris* Miš. and Broz (1962), 1974 s. l. in an ecological sense (primarily regarding soil moisture) are between forests of common oak with narrow-leaved ash and common oak with hornbeam. The community *Carpino-Fraxino-Quercetum roboris subass. inundatum* Jov. and Tom. 1978. occurs in flooded areas on semigleys. The flooding, to which hornbeam is very susceptible, lasts for a short period, and during the dry season the rhizosphere is supplied by the capillary rising of underground water. The influence of floodwater and a greater hornbeam shade in the tree layer make this community floristically poorer in other layers. Along with narrow-leaved ash and hornbeam, *Acer campestre, Ulmus minor, Crataegus monogyna* and *Crataegus oxyacantha* have a higher degree of presence in the understorey.

After the suspension of the military organisation in 1871, the stands belonged to the Petrovaradin Estate County, with a specific way of utilisation which influenced the present structure. Until 1930, the stands had a preserved canopy with a great number of trees reaching more than 100 cm in diameter and heights above 35 *m*. Today, in the phase of the physical destruction of old trees and the frequent breaking of the branches and the central axis, only the secondary crown is viable in most cases. During the past period, the processes of unsuccessful regradation of common oak have been recorded (Mišić and Broz 1962, Bobinac 1998).

RESULTS

STAND STRUCTURE

The total number of common oaks in the nature reserve "Smogva" is 945, or 220 trees per *ha*, on average (Table 1). The representation of trees per diameter class shows two groups of common-oak trees. In the first group (90% of trees), diameters are from 4 to 50 *cm* with an average diameter of $D_g=15.4$ *cm*; the second group of old tree diameters are 83 to 171 *cm* with an average diameter of $D_g=121$ *cm*. The total number of old common-oak trees is 96 or 22 trees per *ha* on average. In the group of old trees, there is an old narrow-leaved ash with a diameter of 147 *cm*. From the total number of standing oaks, in the nature reserve category A_0 there are only trees from the group of younger trees (Table 2). The group of younger trees has 7.2% dead trees with a mean diameter of 7.5 *cm* due to the natural differentiation of trees. A small number of old trees (5.2%) belongs to category A_1, while dead trees (A_4) and trees in the final phase of dieback (A_3) amount to 45.8%.

Table 1. Diameter structure of standing common oaks in nature reserves

d [*cm*]	"Smogva" (4.30 *ha*)		"Vratična" (10.30 *ha*)	
	N	%	N	%
1-10	303	32.1		
11-20	420	44.4		
21-30	110	11.6	6	2.0
31-40	14	1.5	6	2.0
41-50	2	0.2	8	2.7
51-60			6	2.0
61-70			8	2.7
71-80			11	3.7
81-90	3	0.3	21	7.0
91-100	16	1.7	38	12.7
101-110	10	1.1	42	14.0
111-120	19	2.0	49	16.4
121-130	21	2.2	39	13.0
131-140	16	1.7	32	10.7
141-150	6	0.6	11	3.7
151-160	3	0.3	11	3.7
161-170	1	0.1	5	1.7
171-180	1	0.1	5	1.7
181-190				
191-200				
201-210				
211-220				
221-230			1	0.3
Total	945	100	299	100
Per *ha*	220		29	

Table 2. Health condition of common oak in nature reserves

Health condition	"Smogva"- 4.30 *ha*		"Vratična"-10.30 *ha*	
	N	%	N	%
A_0	788	83.4	4	1.3
A_1	5	0.5	84	28.1
A_2	47	5.0	72	24.1
A_3	36	3.8	69	23.1
A_4	69	7.3	70	23.4
Total	945	100	299	100

Permanent sample plot (Table 3) contains 3168 living trees, basal area 51.07 m^2ha^{-1}. The most frequent species are *Crataegus monogyna* and *Crataegus oxyacantha* 60.6%, *Fraxinus angustifolia* 15.2% and *Umus minor* 10.9%. Common oak is represented by 140 trees or 4.4%, basal area 35.60 m^2ha^{-1} or 69.7%. Number of old common-oak trees is 32 trees per *ha*, health condition categories A_2 and A_3. Trees with diameters of 8 to 26 *cm* belong to the group of younger common-oak trees. The sample plot contains 1148 standing dead trees of all tree species which in the recent past were 4316 trees per *ha*, with about 53 $m^{2}?ha^{-1}$. In the total structure of standing dead trees, *Crataegus monogyna* and *Crataegus oxyacantha* are the most numerous 87.1%. Dead trees are most frequent in the diameter class 1-10 *cm*.

Table 3. Basic data on stand structure in the nature reserve "Smogva"

Species	Distribution of living trees and basal area per diameter class (in *cm*) on sample plot 100×100 *m*											
	1-10		11-20		21-30		31-40		41-50		91-100	
	N	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	*G*
Q. robur	16	0.07	80	1.45	12	0.56					8	6.20
F. angustifolia	272	0.89	136	2.19	56	2.70	12	1.0	4	0.57		
C. betulus	56	0.12	44	0.78	8	0.40						
A. campestre	56	0.12										
C. monogyna	1792	2.73	128	1.85								
U. minor	336	0.90	8	0.10								
A. tataricum	0		4	0.05								
Other deciduous species	64	0.11	52	0.97								
Total	2592	4.95	452	7.38	76	3.65	12	1.0	4	0.57	8	6.20
%	81.8	9.7	14.3	14.46	2.4	7.2	0.4	1.9	0.1	1.1	0.3	12.0
Species	101-110		111-120		121-130		131-140		Total			
	N	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	%	G	%
Q. robur	8	7.16	4	4.32	8	9.96	4	5.88	140	4.4	35.60	69.7
F. angustifolia									480	15.2	7.35	14.4
C. betulus									108	3.4	1.30	2.5
A. campestre									56	1.8	0.12	0.2
C. monogyna									1920	60.6	4.59	9.0
U. minor									336	10.9	1.00	2.0
A. tataricum									4	0.1	0.05	0.1
Other deciduous species									116	3.7	1.08	2.1
Total	8	7.16	4	4.32	8	9.96	4	5.88	3168	100	51.07	100
%	0.3	14.0	0.1	8.5	0.3	19.5	0.1	11.5	100		100	

Mean diameter (Dg): *Fraxinus angustifolia* 14.0 *cm*, *Carpinus betulus* 12.4 *cm*, *Acer campestre* 5.2 *cm*, *Crataegus* sp. 5.5 *cm*, *Ulmus minor* 6.2 *cm*, *Acer tataricum* 12.6 *cm*, *other deciduous species* 10.9 *cm*.

The total number of standing common oaks in the nature reserve "Vratična" is 299 or 29 trees per *ha*, on average (Table 1). Another 18 lying trees were in the phase of decaying, so that the total number of trees in the recent past was 30.8 trees per *ha*. Common oak diameters are from 24 to 224 *cm*. Of the total number of standing trees, category A_0 consists of the group of younger trees. Dead trees (A_4) and trees in the final phase of dying (A_3) are 46.5% of the total number of trees (Table 2).

The sample plot (Table 4) contains 931 living trees, basal area 38.40 $m^2?ha^{-1}$. Common oak is represented by 30 trees or 3.2% and a basal area of 27.09 $m^2?ha^{-1}$ or 70.5%. The number of living common oaks (diameter more than 80 *cm*) is 26 trees per *ha,* and there were 7 standing dead trees. The total number of old common-oak trees on the plot in the recent period was 33 trees per *ha*. The group of the youngest common oaks consists of 3 trees with diameters of 30-40 *cm*. A total of 168 dead standing trees of all species were recorded on the sample plot, meaning that in the past there were 1099 trees per *ha* and a basal area of *ca* 44 $m^2?ha^{-1}$. The most represented species of living trees are: *Carpinus betulus* 50.4%, *Acer campestre* 36.6%, *Crataegus monogyna and Crataegus oxyacantha* 4.6%. Dead trees are the most frequent in the diameter class up to 10 *cm: Acer campestre* 33.5%, *Crataegus monogyna* and *Crataegus oxyacantha* 32.3%, *Carpinus betulus* 19.2% and *Ulmus minor* 8.4%.

Table 4. Basic data on stand structure in nature reserve "Vratična"

Species	Distribution of living trees and basal area per diameter classes (in cm) on sample plot 100×100 m													
	1-10		11-20		21-30		31-40		71-80		81-90		91-100	
	N	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	*G*
Q. robur					1	0.06	2	0.22	1	0.47	2	1.20	2	1.49
F. angustifolia	1	0,00	5	0.11	4	0.20	12	1.13						
C. betulus	224	0.54	210	3.48	35	1.47								
A. campestre	141	0.52	198	3.06	2	0.10								
C. monogyna	41	0.06	2	0.02										
U. minor	19	0.06	16	0.28										
A. tataricum	4	0.01	2	0.05										
Other deciduous species	3	0.01	6	0.12	2	0.08								
Total	433	1.2	439	7.1	44	1.9	14	1.3	1	0.4	2	1.2	2	1.4
%	46.5	3.1	47.1	18.5	4,7	4.9	1.5	3.5	0.1	1.2	0.2	3.1	0.2	3.8
Species	101-110		111-120		121-130		131-140		141-150		Total			
	N	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	*G*	*N*	%	*G*	%
Q. robur	5	3.89	9	9.31	5	6.09	2	2.76	1	1.59	30	3.2	27.1	70.6
F. angustifolia											22	2.4	1.4	3.8
C. betulus											469	50.4	5.5	14.3
A. campestre											341	36.6	3.7	9.6
C. monogyna											43	4.6	0.1	0.2
U. minor											35	3.8	0.3	0.9
A. tataricum											6	0.6	0.1	0.2
Other deciduous species											11	1.2	0.2	0.6
Total	5	3.8	9	9.3	5	6	2	2.7	1	1.5	931	100	38.40	100
%	0.5	10.1	0.9	24.2	0.5	15.8	0.2	7.1	0.1	4.1	100		100	

Mean diameter (Dg): *Fraxinus angustifolia* 28.9 *cm*, *Carpinus betulus* 12.2 *cm*, *Acer campestre* 11.7 *cm*, *Crataegus* sp. 5.1 *cm*, *Ulmus minor* 11.1 *cm*, *Acer tataricum* 11.3 *cm*, *other deciduous species* 15.5 *cm*.

NATURAL REGENERATION OF COMMON OAK

The presence of groups of younger common oak trees in the nature reserves is the result of regeneration processes taking place in cycles during the recent multidecennial period. On the basis of the age of their representatives and the total absence of common oak regeneration, it may be concluded that common oak regeneration was absent in the nature reserve "Smogva" for 20-25 years, and in the nature reserve "Vratična" for 45-50 years.

In the nature reserve "Smogva", 849 younger common-oak trees are concentrated in larger openings in the canopy in the whole area (Fig. 1). In the border zone of the nature reserve, 10 *m* wide (18.4% of the area), 36.6% younger trees are concentrated. In the immediate border zone of the present or supposed horizontal crown projections of old trees, there are 16.8% trees, and 82.6% of trees are closer to the centre of the canopy opening. Out of 96 standing old trees of common oak, 0.6% younger common oak trees (diameter 8 to 13 *cm*) were registered only near 2 border trees, located in the zone of horizontal crown projection.

In the nature reserve "Vratična", young common-oak trees (up to 80 *cm* in diameter) are found, predominantly on areas which, during the recent period, have been under anthropogenic influence, along the border parts and former roads, in the part of the nature reserve where the Slavic necropolis was, originating from the 10-11th century (Bobinac 1998), and in the more homogenous parts of the nature reserve, only in 3 larger openings in the canopy.

The characteristics of the actual regeneration of common oak were analysed only in the nature reserve "Vratična" during the seed year, which was for the wider region of the investigated locality characterised as the year of average crop (Bobinac 1999). Of the total number of living common oaks in the nature reserve, the seedlings were registered under 87.8% trees (Table 5). The average number of seedlings, under old trees belonging to categories A$_1$ and A$_2$, was 21.2 - 24.7 seedlings per m^2. Under 61 trees (30%), the number of seedlings was more than 20 per m^2. Only under 15 trees (7.5%) were there 50-100 seedlings per m^2, and under 2 trees (1.0%) 100-150 seedlings per m^2. The maximal number of seedlings was found under one tree, 400 seedling per m^2.

Table 5. Characteristics of the common oak seed crop in the nature reserve "Vratična"

Health cond.	Acorn crop 1996[1]							
	Trees							
	Total number	without seedlings	With seedlings					
	N	%	N	%	N	%	Seedlings per m^2	
							Average	Min-max
A$_0$	4	1.3	-	-	4	100.0	24.0	9-51
A$_1$	84	28.1	4	4.8	80	95.2	21.2	1-122
A$_2$	72	24.1	8	11.1	64	88.9	24.7	1-400
A$_3$	69	23.1	16	23.2	53	76.8	9.9	1-91
A$_4$	70	23.4	70	100.0	-	-	-	-
Total	299	100	98	32.8	201	67.2	19.9	

[1] Crop is determined after number of seedlings in 1997.

Fig. 1. Nature reserve "Smogva"- recruitment of young common-oak trees is, as a rule, outside the zone of the horizontal projection of the crowns of old trees

The conditions of an undisturbed surface soil layer, with a deep litter layer in the forest of common oak, narrow-leaved ash and hornbeam, were suitable for the conservation of the acorn during the winter period and its germination during the next spring. The seedlings were formed normally, having the characteristics of shade growth (Grime 1981). At the beginning of June, the symptoms of oak mildew (*Microsphaera alphitoides* Griff. and Maubl.) appeared on the seedlings. At the end of June, leaves started to fall, and on denuded seedling shafts embryonal buds were activated (mostly terminal ones) and summer shoots occurred. The development of one-year-old common oaks, from April to September continued in the form of maximally 3 (and 4) growth phases (Gruber 1992, Bobinac 1994). In the typically developed regeneration areas in the nature reserve, common oak seedlings at the end of August showed symptoms of devitalisation (Fig. 2). At the beginning of the next growing season, more than 50% of individuals did not form a new shoot. The remaining individuals did not form their shoot from the terminal bud. At the end of the second growth season, the regeneration originating from the 1996 seed year was completely dead.

DISCUSSION

The Morović reserves of "Vratična" and "Smogva" are the last remains of the oldest common-oak forests in the Bosut basin. Compared to other protected oldest common-oak forests (Matić et al. 1979, Vyskot 1959, Vyskot et al. 1981, Stanek and Bartak 1989, Korpel 1989), the structure and natural regeneration of common oak in the nature reserves "Vratična" and "Smogva" show specific characteristics. The distribution of trees per diameter and the dimensions of the largest-diameter trees undoubtedly confirm that they are unique specimens of common-oak trees.

The interior structure of the stands in the study reserves is the result of historical development, in which, along with ecological factors, anthropogenic and zoo-

Fig. 2. Nature reserve "Vratièna" - number of common oak seedlings (100-150 plants per m^2) and its appearance due to attack of oak mildew (*Microsphaera alphitoides* Griff. et Maubl.) at the end of August 1997.

genic factors have had a significant role. The traditional way of utilisation of old common-oak stands, for grazing and oak masts, caused the specific structure of the understorey. In such conditions, their regeneration developed in cycles in the period of the disintegration of the canopy and the prohibition of grazing. This is confirmed by the recent common-oak regenerations in the nature reserves coinciding with the period of special protection in 1951-1954, and the general treatment of the prohibition of grazing in the regeneration period on areas in the immediate surroundings.

On the basis of a higher percentage of younger common-oak trees in the nature reserve "Smogva", we can conclude that common oak regeneration and the maintenance of adult developmental phases are more favoured in the common oak - narrow-leaved ash forest, whereas in the common oak - narrow-leaved ash - hornbeam forest this is an accidental phenomenon. By the coenological structure of the understorey, we can conclude that in the nature reserve "Smogva" natural regeneration has not taken place over the last 20-25 years, and in the nature reserve "Vratična" over the last 45-50 years. Along with the periodic factors which reduce the acorn crop, oak mildew (*Microsphaera alphitoides* Grif. et Maubl.), in conditions of low illumination in the herb layer, cause an interruption to the cyclic regeneration of common oak in the development phase of seedlings or in the initial phase of forming the young growth (Bobinac and Karadžić 1994, Bobinac 1999).

Today, in the nature reserves, more than 45% of old common oaks are dead (A_4) or in the final phase of dying (A_3). After Korpel (1989), the development cycle of old stands can be characterised as at the stage of degradation. Due to the presence of a greater number of tree species in the understorey, at shorter or longer time intervals, depending on the coenological structure, low values of illumination in the herb layer affect the regeneration of common oak. Due to reduced moistening and succession in the protected area (against floods), these processes have similar effects on the terminal community of the common oak - narrow-leaved ash forest in the nature reserve "Smogva" and in the common oak - narrow-leaved ash - hornbeam forest in the nature reserve "Vratična". Forming the young growth of common oak is conditioned by the synchronisation of canopy disintegration and acorn crop, and optimal synchronised disintegration of the canopy occurs immediately before seedling formation.

The survival of the adult phases of common oak occurs, as a rule, only in greater openings in the canopy and their long-term absence in the zone of the horizontal crown projections of old trees (where acorn concentration is the highest) indicates the competitive impact of parent trees. In the stage of the degradation of old stands, the essence of the strategy of natural regeneration and the survival of common oak in the studied ecosystems is reduced to the synchronised disintegration of the stand canopy (understorey) and abundant corn crop before the total dying of the old trees.

CONCLUSIONS

The nature reserves "Vratična" and "Smogva" are the last remains of ancient common-oak forests in the Bosut basin. Their state and internal structure are the result of historical development in which, besides ecological factors, anthropogenic and zoogenic factors have also had a significant role.

In the nature reserve "Vratična", common oak is represented by 29 trees per *ha* on average, with a diameter of 24 to 224 *cm*. A total of 931 living trees with a basal area of 44.09 m^2 were registered on 1 *ha*. The percentage of the common oak is 3.2% in the number of trees and 70.5% by basal area.

In the nature reserve "Smogva", common oak is represented by 220 trees per *ha* on average, with a diameter of 4 to 171 *cm*. A total of 3168 living trees with a basal area of 51.07 m^2 were registered on 1 *ha*. The percentage of common oak is 4.4% in the number of trees and 69.7% by basal area.

The number of old trees in more reserved parts is 27-32 trees per *ha*. In the total number of old trees, dead trees (A_4) and trees in the final phase of dying (A_3) make up more than 45%.

The survival of the adult phases of common oak is more favoured in the common oak - narrow-leaved ash forest, where the last regeneration cycle was 20-25 years ago, whereas in the common oak - narrow-leaved ash - hornbeam forest, regeneration is an accidental phenomenon, with the last regeneration cycle 45-50 years ago.

After the seed year in the nature reserve "Vratična", seedlings were found under 201 trees (87.8%). Under 61 trees (30%), the number of seedlings was more than 20 per m^2, under 15 trees (7.5%) 50-100 seedlings per m^2, and under 2 trees (1.0%) 100-150 per m^2. The maximal number of seedlings was found under one tree, with 400 trees per m^2.

In conditions of low values of illumination in the herb layer, oak mildew (*Microsphaera alphitoides* Grif. and Maubl.) caused the interruption of the cyclic regeneration of common oak in the phase of seedlings or in the initial phase of young growth.

The forming of young growth is conditioned by the synchronisation of canopy disintegration and abundant acorn crop, and optimal synchronised canopy disintegration occurs immediately before seedling formation.

The presence of adult phases of common oak in the nature reserves, as a rule, occurs only in greater openings in the canopy. This indicates that in the zone of concentration of the greatest amount of acorns, the competitive impact of parent trees is the decisive factor in oak regeneration survival.

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STRUKTURA SASTOJINE I PRIRODNA OBNOVA HRASTA LUŽNJAKA U PRIRODNIM REZERVATIMA "VRATIČNA" I "SMOGVA" BLIZU MOROVIĆA

Prikazani su osnovni elementi sastojinske strukture i prirodne obnove hrasta lužnjaka u prirodnim rezervatima "Vratična" i "Smogva" blizu Morovića – posljednji ostaci vrlo starih šuma hrasta lužnjaka u bosutskom bazenu. U prirodnom rezervatu "Smogva" – terminalnoj zajednici šume hrasta lužnjaka i poljskoga jasena na bivšem poplavnom području – nalazi se 220 stabala običnoga jasena po hektaru, prsnoga promjera 4 – 171 cm. Međutim, u prirodnom rezervatu "Vratična" – vlažnijoj varijanti šume hrasta lužnjaka, poljskoga jasena i običnoga graba na poplavnom području – u prosjeku se po hektaru nalazi 29 jasenovih stabala, a raspon se prsnoga promjera kreće 24 – 224 cm. U ukupnom je broju stabala hrast lužnjak predstavljen s 3,2 – 4,4 %, dok broj starijih stabala s bolje očuvanim dijelovima iznosi 27 – 32 stabla po hektaru. Održavanje je razvojnih faza lužnjaka jednostavnije u šumama hrasta lužnjaka i poljskoga jasena, ali se posljednji regenerativni ciklus zbio prije 20–25 godina, dok se razvojne faze u šumama hrasta lužnjaka, poljskoga jasena i običnoga graba događaju slučajno, a posljednji se regenerativni ciklus zbio prije 45–50 godina. U uvjetima slabe osvijetljenosti pepelnica (*Microsphaera alphitoides* Grif. et Maubl.) uzrokuje prekid u ontogenezi hrasta lužnjaka u razvojnom stadiju ponika ili početnom stadiju mladika, ali mladik se stvara zbog sinkronizacije dezintegracije sklopa i uroda žira. Optimalna sinkronizirana dezintegracija sklopa javlja se neposredno prije stvaranja ponika.

Ključne riječi: hrast lužnjak (*Quercus robur* L.), prirodni rezervati, Morović, struktura sastojine, prirodna obnova

D. Hatić, et al.: Growth of old oak trees in Croatia: The preliminary results of the TGECC programme
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UDK 630*560+181 (Quercus robur L., Q. petraea Liebl., Q. pubescens Willd., Q. ilex L.)

GROWTH OF OLD OAK TREES IN CROATIA: THE PRELIMINARY RESULTS OF THE *TGECC* PROGRAMME

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This paper presents part of the long-term research programme žTree Growth and Environmental Change in Croatia' (TGECC). This programme includes the development of the dendrochronological database for all dominant tree species and the use of the analytical methods for the correlation of tree growth with environmental change. The methods used in this programme, from sampling in the field to data analysis, are presented. The method for detecting environmental change using tree growth is introduced and tested on 135 pedunculate oak trees from the Repaš forest, where groundwater level change was recognised in previous research. The growth of old individuals of four oak species (*Quercus robur* L., *Quercus petraea* Liebl., *Quercus pubescens* Willd. and *Quercus ilex* L.) is presented and interpreted in the paper. Some of these are among the oldest individuals within these species in Croatia (e.g. holm oak from the island Rab with an estimated age of 436 years, a pubescent oak from the island Krk with an estimated age of 318 years and several pedunculate oaks from the forest Repaš, Prekodravlje, with estimated ages between 240 and 300 years).

Keywords: environmental change, growth function, tree age, tree core

INTRODUCTION

In 1999, OIKON Ltd. established a long-term research programme entitled 'Tree Growth and Environmental Change in Croatia' (TGECC). This is a self-financed research programme (OIKON Ltd. is a commercial consultancy company), from which the company expects to gain knowledge and expertise required for Environment Impact Assessments (EIA projects) and forest silviculture and management tasks in Croatia. The programme encompasses: 1) the development of a dendrochronological database covering all dominant tree species in the forests of Croatia, 2) modelling of the relation between tree growth and environmental variables (e.g. Chang and Aguilar, 1985, Friend and Hafley, 1989 or Devall et al., 1991, Antonić et al., in press, see also Antonić et al., poster abstract in the same volume) and 3) detecting *apriori* unknown environmental changes using tree growth as a retroactive monitoring variable.

Within the programme, special attention is given to old trees. Old trees have a large number of rings representing long-term records that correspond to the past states of the environment and they usually contain undisturbed (by human-induced environmental change) growth data in their young years. A dendrochronological database is filled with records which are: 1) collected especially for the TGECC programme (targeting old individuals) or 2) collected for applied dendroecological research (see, for example, Antonić et al., 1999a, 1999b and Antonić et al., in press). By the end of January 2000, the database had 366 processed tree cores with 26,485 rings.

Outside the general presentation of the TGECC programme, the special aims of this paper are: 1) the introduction of the method for detecting environmental change by growth analysis of differently aged trees growing in the same environment and 2) the presentation of growth of some old individuals belonging to four major oak species present in Croatia: pedunculate oak (*Quercus robur* L.), sessile oak (*Quercus petraea* Liebl.), pubescent oak (*Quercus pubescens* Willd.) and holm oak (*Quercus ilex* L.).

MATERIAL AND METHODS

The data used in this work were separated into two datasets. The first dataset comprises growth data from 135 pedunculate oak individuals from the Repaš forest (Fig. 1), with a known site age from 84 to 104 years (obtained from forest management documentation). These data were collected for the purpose of modelling a groundwater regime acceptable for the survival of the forest after the building of the žNovo Virje' hydro-electric power plant (Antonić et al., 1999a and Antonić et al., in press). This dataset was used in this work for the testing of the method for detecting environmental change. Selected trees belong to the same forest type (even-aged forest of pedunculate oak and common hornbeam, *Carpino betuli – Quercetum roboris* Rauš 1971). The second dataset comprises growth data from old oak individuals (see Fig. 1, Fig. 2 and Table 1), including four pedunculate oaks sampled in the Repaš forest, four sessile oaks sampled at Mt. Medvednica near the city of Zagreb, one pubescent oak from Krk island (near the city of Baška) and two from Rab island (on the Kalifrant peninsula), and finally three holm oaks from Rab island (on the Kalifrant peninsula).

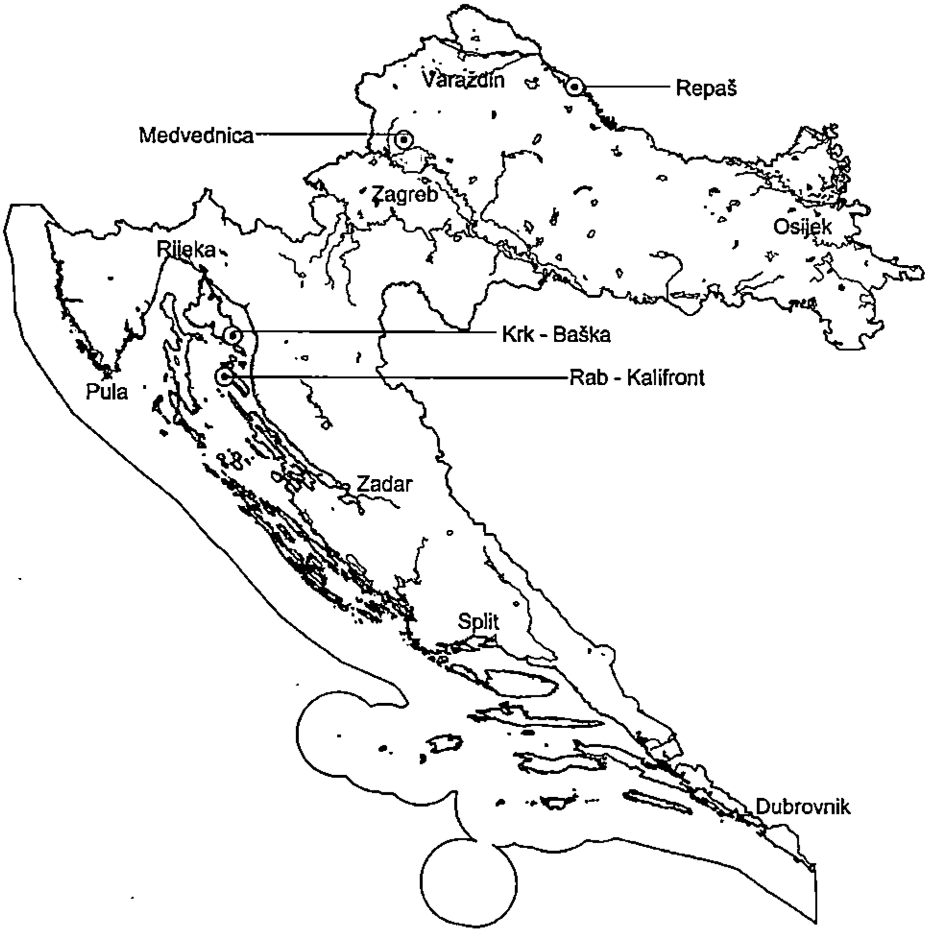

Fig. 1. Locations of the dendrochronological samples examined in this paper in the Republic of Croatia

Dendrochronological data acquisition for the TGECC programme could be separated into three phases: field sampling, sample preparation and measurement and data transformation. Dendrochronological samples are sampled with a motorised Pressler drill capable of taking long tree cores (up to 50 cm). The cores of such length enable the centre of all trees up to 1 m in diameter to be reached, covering very long tree ring time series without tree felling. The holes left in the trees are filled with self-expanding foam with fungicide and insecticide additives. Following sampling, tree cores are transported and stored in a refrigerated environment to prevent drying and changes in dimensions. Prior to measurement, the cores are glued to special holders and polished. Prepared samples are then digitised by high resolution scanning (600 to 800 dpi, 24 bit colour) on a scanner calibrated espe-

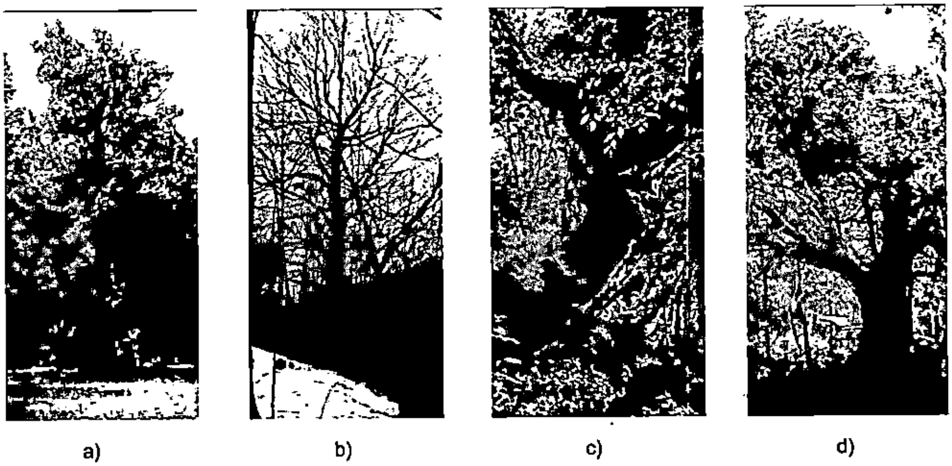

Fig. 2. Examples of the old oak trees examined in this paper: a) *Quercus robur* (T331), b) *Quercus petraea* (T369), c) *Quercus pubescens* (T339) and d) *Quercus ilex* (T358). Tree codes correspond to Table 1.

cially for this purpose. These scans (see Fig. 3) are used for permanent storage of source data, which enables repeatable measurements. Tree ring measurement is undertaken with special dendrochronological software which can magnify samples up to 64 times and record data on ring width and ring angle (for ring width correction). These measurements are then transformed and corrected for eccentricity. For the purpose of this paper, tree ring widths were recalculated on the diameters

Table 1. Description data about old oak trees presented in this paper. DBHOB is diameter at breast height over bark. Forest types are as follows: A-pedunculate oak and common hornbeam forest, B-sessile oak and European beech forest, C-pubescent oak and hop hornbeam forest and D-holm oak and flowering ash forest.

code	species	DBHOB (cm)	height (m)	age (years)	source of age estimation	locality	altitude (m)	aspect	forest type
T331	*Quercus robur*	148.1	39.9	300	growth function	Repaš	116	flat	A
T332	*Quercus robur*	115.3	34.7	238	growth function	Repaš	116	flat	A
T333	*Quercus robur*	161.4	32.3	189	growth function	Repaš	116	flat	A
T335	*Quercus robur*	147.6	36.0	240	growth function	Repaš	116	flat	A
T366	*Quercus petrea*	64.8	16.5	109	ring count	Medvednica	590	W	B
T367	*Quercus petrea*	52.6	13.2	132	ring count	Medvednica	520	W	B
T368	*Quercus petrea*	65.4	14.5	128	ring count	Medvednica	530	flat	B
T369	*Quercus petrea*	76.8	17.1	126	growth function	Medvednica	540	flat	B
T339	*Quercus pubescens*	125.7	_	318	growth function	Krk	175	E	C
T361	*Quercus pubescens*	50.0	14.0	115	ring count	Rab	36	N	D
T364	*Quercus pubescens*	71.5	13.0	100	ring count	Rab	30	S	D
T358	*Quercus ilex*	95.8	8.0	436	growth function	Rab	50	NW	D
T360	*Quercus ilex*	50.0	9.5	110	growth function	Rab	38	SE	D
T365	*Quercus ilex*	67.5	13.0	102	growth function	Rab	26	S	D

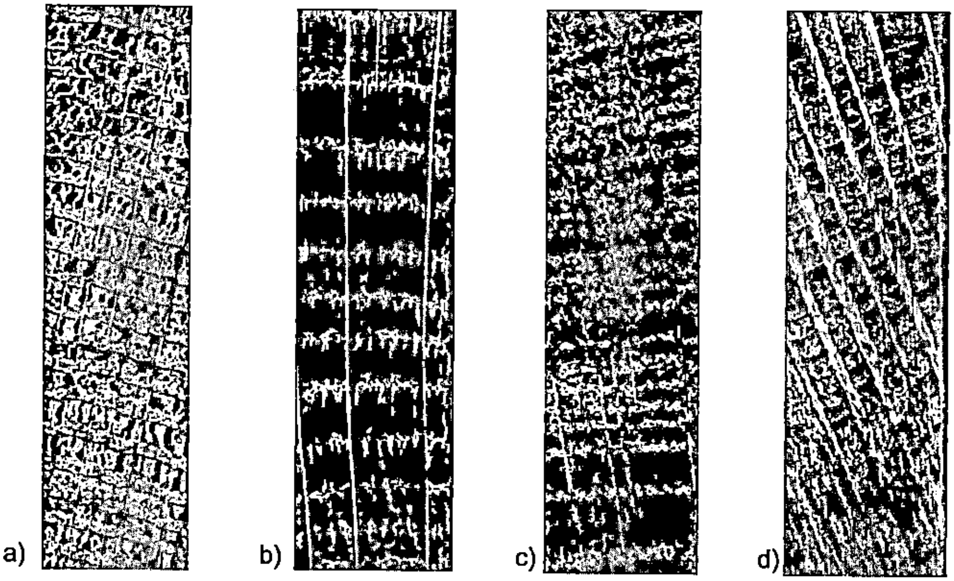

Fig. 3. Examples of the polished and scanned cores of old oak trees examined in this paper: a) *Quercus robur* (T331), b) *Quercus petraea* (T366), c) *Quercus pubescens* (T361) and d) *Quercus ilex* (T360). Tree codes correspond to Table 1.

over breast height under bark (DBHUB) for respective year, which was chosen as a growth variable.

The method of detecting environmental change is based on the testing of the hypothesis that the parameters of the growth function should change over time. The following expression was used to describe changes in the DBHUB over time:

$$\mathrm{DBHUB} = a\, e^{-b/T} \qquad 1)$$

where T is respective age and a and b are empirical parameters. The expression 1) is called Terezaki's function (Pranjić and Lukić, 1997). This function is linearised by logarithmic transformation into the form:

$$\ln \mathrm{DBHUB} = \ln a - b(1/T) \qquad 2)$$

and parameters are expressed as a function of calendar year (t):

$$\ln a = k_0 + k_1 t \qquad 3)$$

$$b = k_2 + k_3 t \qquad 4)$$

This transformation enables the use of a general linear modelling procedure (Ott, 1993) to test the significance of the contribution of the particular linear terms (regressors) using t-test (Ott, 1993). The hypothesis is that in a stable environment, parameters of regressors that contain the calendar year (k_1 and k_3) cannot be significantly different from zero, which means that parameters of the growth function (a and b) are constant over time. In contrast, the significance of the parameter k_1 indicates the significant change in growth magnitude over time and the significance of parameter k_3 indicates the significant change in the growth function shape. It is important to emphasise that the method is meaningful only if differently aged individuals are included in the analysis, otherwise age (T) and calendar year (t) are linearly dependent. The other conditions for using the method are: 1) ages of selected trees have to be known, 2) relatively old trees should be included, and 3) included trees should reside on the same forest type.

In order to compare growth of the old oak trees, their age was estimated directly (by ring counting) for the individuals drilled to the tree centre and indirectly, by fitting and extrapolation of the growth function for other individuals. In both cases, the age of the breast height was neglected. In the second case the following function was used:

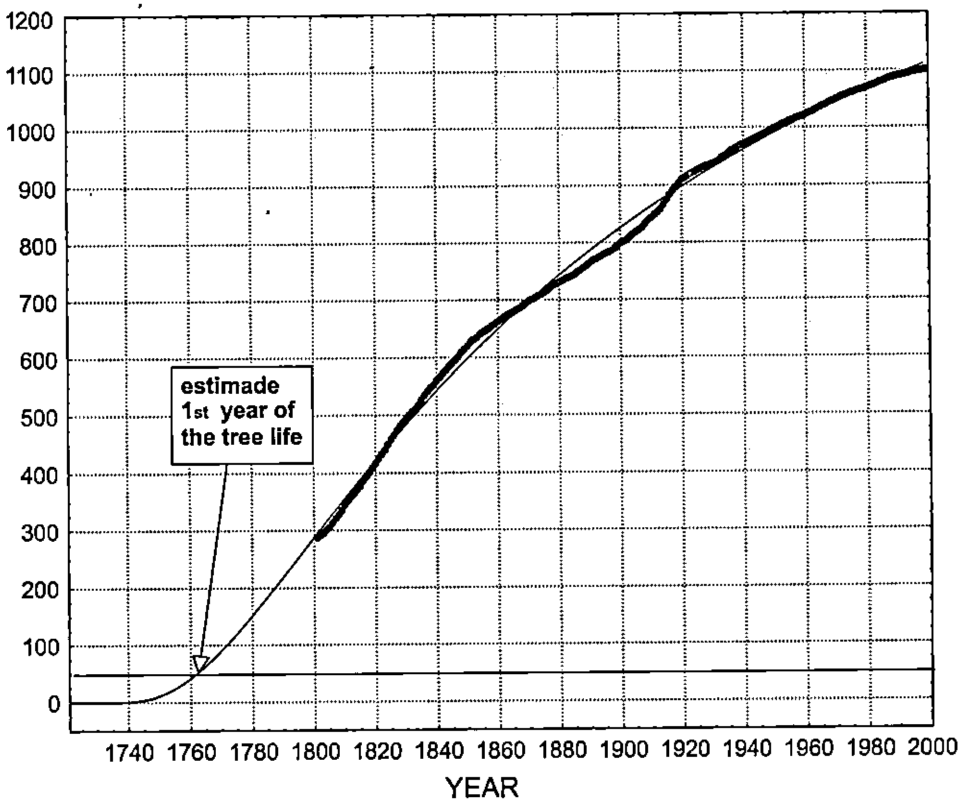

Fig. 4. Example of estimation of the tree age using extrapolation of the growth function. DBHUB is diameter over breast height under bark. Bold line represents real growth of the pedunculate oak T332 (see Table 1) and thin line represents fit by growth function. Further explanation is in the text.

$$DBHUB = a\ e^{-b/(t-c)} \qquad 5)$$

where t is calendar year and a, b and c are empirical parameters. The expression 5) is basically the same as expression 1), only the age (T) is expressed as the difference between the calendar year (t) and the empirical parameter (c) which represents the estimate of the first year of the tree's life. However, it was found that the use of the parameter c yields unrealistic results and the year in which DBHUB was equal to 5 cm was used instead (see Fig. 4).

RESULTS AND DISCUSSION

Results of the general linear model application on the above-mentioned 135 pedunculate oaks from the Repaš forest are shown in Table 2. The yielded growth model is site-specific and cannot be used generally. All regressors have a significant contribution to the regression. This suggests that the parameters of the growth function change over time, which indicates the change in the environment. Fig. 5 (upper left) shows two hypothetical growth lines with the calendar year set to constant (an assumption of two different but stable environments), arising from expressions 1) to 5) and the parameters from Table 2. These hypothetical growth lines have different shapes; the growth line for the later calendar year being steeper and with the inflexion point happening later. The hypothetical growth line which relates to the year 1995 mostly corresponds to the standard diameter growth function for pedunculate oak on first site quality described by Špiranec (1975). All these results could be interpreted as an increase in site productivity for the trees included in the analysis.

The yielded results were expected, because the Repaš forest has been exposed to the lowering of the mean groundwater table, due to the changes in the riverbed morphology of the nearby River Drava during the last century (Biondić & Vidaković-Šutić, 1998, Antonić et al., 1999, Antonić et al., in press). Pedunculate oak is a typical flood-plain species which is very sensitive to changes in groundwater levels (see, for example, Prpić et al., 1994). When the mean groundwater levels are high, this species grows more slowly than under lower mean groundwater levels, as long

Table 2. Regression model for estimating logarithm of DBHUB for pedunculate oak (*Quercus robur*) in Repaš. General linear model follows expressions 2) to 4). Regression coefficient is R=0.8405. Ratio between regression mean square and residual mean square is F=7954.7, with respective probability of p(F)=0.000. The t-value and respective p-value were used to test the hypothesis that respective empirical parameter (k_i) is equal to zero.

parameter	value	st. error	t	p(t)
k_0	-28.08179	0.44312	-63.37	0.000
k_1	0.017525	0.00022	77.98	0.000
k_2	-1108.608	33.2150	-33.38	0.000
k_3	0.588142	0.01744	33.72	0.000

as deep roots are permanently submerged in the groundwater (Prpić et al., 1987). If this condition is not met, pedunculate oak suffers dieback, which has been evident in the Repaš forest during the last decade (according to forest management documentation).

The presented method yields interpretable results; i.e. tree growth could be used as an indicator of environmental changes. The question for future research is how these results could influence forest management, regarding the use of standard yield functions constructed under the assumption of an unchanging environment (e.g. Špiranec, 1975). To answer this question, the application of the method to other tree species and to other environments is required, e.g. on the European silver fir (*Abies alba* Mill.) in the Gorski Kotar region, where forests are endangered by aeropollution and acid rains (see, for example, Prpić, 1987).

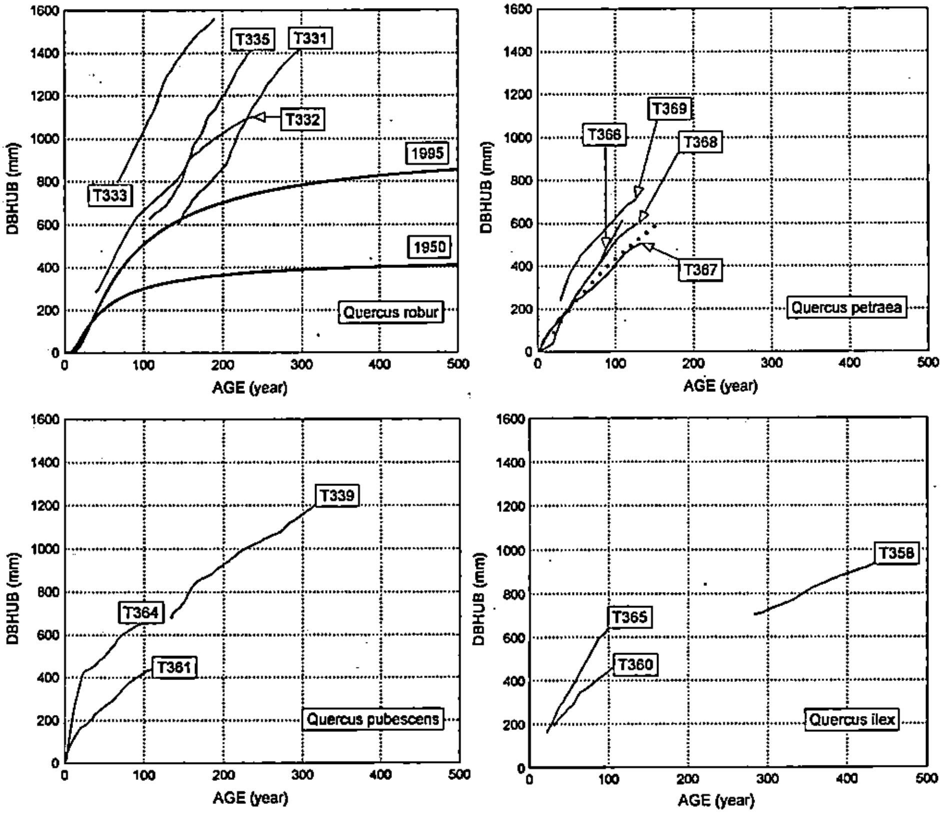

Fig. 5. Obtained growth lines for fourteen old oak individuals from four species. Tree codes correspond to Table 1. Tree ages were estimated by ring counting for the individuals drilled to the tree centre and by fitting and extrapolation of the growth function for other individuals. Bold lines on upper left graph represent hypothetical growth lines with assumption of two different but stable environments (see further explanation in the text). Bold dots on the upper right graph represent standard diameter growth function for sessile oak on the first site quality (Špiranec, 1975).

Comparing the growth of the old pedunculate oaks and the hypothetical pedunculate oak growth described above (Fig. 5, upper left), it is noticeable that the growth of old oaks has a significantly larger magnitude. It is the consequence of the dominant position of these trees in relation to the neighbours, probably for at least one century, because these individuals are the remaining elements of the natural, undisturbed flood-plain forests, which are very rare in Croatia and Europe.

The growth of four individuals of sessile oak mostly corresponds (see Fig. 5, upper right) to the standard diameter growth function for this species on first site quality (Špiranec, 1975). From the view of the presented results for pedunculate oak in the Repaš forest, constant environmental conditions could be assumed. To prove this hypothesis, the use of a larger sample is required.

Interpretation of the growth of the sampled pubescent and holm oaks from the view of theoretical growth is not possible due to the lack of standard diameter growth functions for these species. Nevertheless, despite the negligible sample size, a possible theoretical growth for these two species could be recognised (Fig. 5, lower left and right).

Some of the sampled oaks are among the oldest individuals within the respective species in Croatia, with an age of several centuries (compare Table 1). The *TGECC* programme started recently, and it is reasonable to expect that more old individuals will be identified and processed in the future, filling the *TGECC* database and enabling a wider analysis of the relation between tree growth and the environment in Croatia.

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RAST STARIH HRASTOVIH STABALA U HRVATSKOJ: PRELIMINARNI REZULTATI PROGRAMA *TGECC*

U radu se predstavlja dio dugoročnoga istraživačkog programa "Rast drveća i okolišne promjene u Hrvatskoj (TGECC)". Program obuhvaća razvoj dendrokronološke baze podataka za sve dominantne vrste drveća, te povezivanje rasta drveća i promjena u okolišu analitičkim metodama. Predstavljene su metode koje se u programu primjenjuju, od uzorkovanja na terenu do obrade podataka. Prikazana je metoda otkrivanja okolišnih promjena pomoću podataka o rastu stabala, koja je testirana na 135 stabala hrasta lužnjaka iz šume Repaš, gdje su iz prijašnjih istraživanja poznate promjene razine podzemne vode. Rast starih primjeraka četiriju vrsta hrasta (*Quercus robur* L., *Quercus petraea* Liebl., *Quercus pubescens* Willd. and *Quercus ilex* L.) prikazan je i interpretiran u radu. Neki su hrastovi među najstarijim jedinkama unutar tih vrsta u Hrvatskoj (npr. crnika s Raba s procijenjenom starošću od 436 godina, medunac s Krka procijenjen na 318 godina, te lužnjaci iz Repaša između 240 i 300 godina).

Ključne riječi: funkcija rasta, izvrtak stabla, okolišne promjene, starost stabla

IUFRO UNIT 2.08.05
GENETICS OF QUERCUS

Leader: Kim Steiner
Deputy: Peter S. Savill

INTRODUCTORY REMARKS

KIM C. STEINER

There may be no genus of trees as important to humans as *Quercus*. The only other serious contender for this position is *Pinus*, but the role of oak in our cultures and our economies has been so great that pines must surely rate a second-place standing. Consider, for example, how different the course of history would have been if the native forests of England had been pine instead of oak. Without the oak resource and its implications for agriculture, industry, commerce, and defense, England would likely have been a weak and relatively impoverished country in the 17th and 18th centuries, the political development of the New World colonies would have been radically different, and the global emergence and spread of democracy might well have started and ended with the French Revolution and Napoleon. Such "what if" exercises are essentially trivial (no one can really know how a different event would have influenced the full course of history), but the role of oak in this example is not trivial. It has been, and is, a tree of preeminent economic value. Oak timber is an abundant and versatile resource, and veneer-quality oak logs are some of the most valuable in the world for their age and size.

All of that said, the process of *domesticating* the oaks is not as seriously underway as one might expect from their value as a resource. Indeed, we are much farther along in domesticating other groups of forest trees, and the domestication of oaks may perhaps never become a realistic goal. By domestication, of course, I mean the process of bending a species to human purposes through the breeding, selection, and cultivation of useful varieties. It is ironic that the forests in which the science and art of silviculture was first developed, the European oak forests, should still be managed as essentially wild populations, while other forest trees are now bred and cultivated in the manner of agricultural crops. But oaks are rather intractable as candidates for domestication: they are relatively slow to reach reproductive maturity, inefficient to control pollinate, unproductive of seed per unit area of orchard, difficult to vegetatively propagate, and expensive to plant and tend in plantations. Finally, as "crops" the oaks are among the very slowest to yield a return on investment because harvest rotations are typically 100 to 240 years in length.

These facts mitigate hard against large investments in oak breeding and selection. That is not to say that there is no place for genetic improvement programs in the oaks, and progeny testing and studies of heritability will continue to contribute usefully to our store of knowledge about oaks. However, on the whole, practical improvements in the quality and yield of oak timber can be achieved much more readily through refinements in the knowledge and application of silviculture than through breeding and genetic selection.

Because oaks are managed primarily as wild populations, it is altogether reasonable that research in oak genetics should seek first of all to characterize and understand genetic diversity in wild populations. Indeed, most research in oak genetics seems to have this focus, an emphasis that is clearly reflected in the topics of papers to be presented in the days ahead: oak systematics, population genetic structure and geographic patterns of genetic diversity, distinguishing and identifying populations, detecting genetic contamination from non-local sources, identifying colonization routes and seed sources, conservation of intraspecific genetic variation, and genetic restoration of degraded populations. These subjects are all pertinent to the improvement and silviculture of oak stands, the principal interest of our "sister" working group in this joint conference. Directly or indirectly, most of the genetics papers to be delivered over the next three days will address the following key questions:

What is the ecological significance of genetic diversity in oak populations, including diversity that arises through introgressive hybridization?

How is the long-term health of oak forests affected by a loss of genetic diversity or by introductions of non-native germplasm?

How can genetic diversity and stand genetic quality be maintained or enhanced through silvicultural practices?

These questions will probably never be answered to our fullest satisfaction, but they are critically important to the sound management of oak forests, and even tentative answers will be better than none. Furthermore, it is important that oak geneticists have a full understanding of the problems faced by those who study and practice oak silviculture. That is why it is appropriate that our two IUFRO Working Groups, P1.06.00 and S2.08.05, should hold this joint meeting. If the meeting is successful, then both groups will be enriched by the exchange of information.

UVODNE NAPOMENE

Za ljude vjerojatno ne postoje važnije vrste drveća od roda *Quercus*. Jedini drugi ozbiljni takmac za ovo mjesto je *Pinus*, ali je hrast u našim kulturama i našem gospodarstvu oduvijek imao tako veliku ulogu da se borovi svakako s pravom nalaze na drugom mjestu. Zamislimo, na primjer, kako bi tijek povijesti bio sasvim drugačiji da su prirodne šume u Engleskoj bile borove a ne hrastove. Bez hrastovih resursa i njegovih implikacija za poljoprivredu, industriju, trgovinu i obranu Engleska bi u 17. i 18 stoljeću po svoj prilici bila slaba i relativno siromašna zemlja, politički razvoj kolonija Novoga svijeta bio bi radikalno drugačiji, a globalna pojava i razvoj demokracije mirno bi mogli i započeti i završiti s Francuskom revolucijom i Napoleonom. Pitanja tipa "što bi bilo da ..." u osnovi su trivijalna (nitko ne zna kako bi neki različiti događaj utjecao na tijek povijesti), ali uloga hrasta u ovom primjeru nije trivijalna. To je oduvijek bilo, i još uvijek jest, drvo neporecive gospodarske važnosti. Hrastovo je drvo obilan i svestran resurs, a furnirski hrastovi trupci po svojoj su starosti i veličini jedni od najvrednijih na svijetu.

Međutim, postupak *udomaćivanja* hrastova ne teče onako glatko kako bi se moglo očekivati s obzirom na njegovu vrijednost kao resurs. Ustvari smo mnogo dalje odmakli u udomaćivanju ostalih grupa šumskoga drveća, a udomaćivanje hrastova možda nikada neće postati ostvaren cilj. Pod udomaćivanjem, naravno, mislim na postupak prilagođavanja vrste ljudskim potrebama kroz oplemenjivanje, selekciju i kultivaciju korisnih varijeteta. Ironično je da se šumama u kojima je znanost i umjetnost uzgajanja započela najranije, to jest, europskim hrastovim šumama, još uvijek gospodari kao s divljim populacijama, dok je ostalo šumsko drveće danas oplemenjeno i kultivirano na isti način kao što su oplemenjene poljoprivredne kulture. Međutim, kao kandidati za udomaćivanje, hrast je prilično neukrotiv: relativno sporo dostiže reproduktivnu zrelost, ne može se kontrolirano oprašivati, ne proizvodi dovoljno sjemena po prostornoj jedinici plantaže, teško se vegetativno razmnožava, i skup je za sadnju i njegu na plantažama. I konačno, kao "kultura" hrastovi najsporije vraćaju uloženu investiciju jer se završne sječe obavljaju u ophodnjama koje obično traju 100 do 240 godina.

Ove činjenice uvelike određuju veličinu ulaganja u oplemenjivanje i selekciju hrastova. To ne znači da nema mjesta za programe genetskoga oplemenjivanja hrastova, a testiranje će potomstva i proučavanje nasljedstva igrati korisnu ulogu u obogaćivanju našega znanja o hrastu. Međutim, sve u svemu, praktična poboljšanja u kvaliteti i prinosu hrastova drva mnogo se bolje postižu detaljnijim znanjem i primjenom uzgojnih postupaka nego oplemenjivanjem i genetskom selekcijom.

Budući da se hrastovim šumama gospodari u prvom redu kao s divljim populacijama, razumno je očekivati da cilj istraživanja genetike hrasta bude karakterizacija i razumijevanje genetske raznolikosti divljih populacija. I zaista, čini se da se najveći broj genetskog istraživanja hrasta bavi ovom temom, što je naglašeno u temama referata koji će se ovih dana predstaviti: sistematika hrasta, genetska struktura populacije i zemljopisni obrasci genetske raznolikosti, razlikovanje i identifikacija populacija, otkrivanje genetskih kontaminacija iz nelokalnih izvora, identifikacija putova kolonizacije i izvora sjemena, konzervacija međuvrsne genetske varijacije i genetska obnova degradiranih populacija. Svi ti čimbenici su važni za oplemenjivanje i uzgajanje hrastovih sastojina, što je glavni interes naše "sestrinske" radne grupe na ovoj zajedničkoj konferenciji. Neposredno ili posredno, većina će se referata o genetici koji će se čuti u ovih nekoliko dana baviti sljedećim ključnim pitanjima:

Kakvo je ekološko značenje genetske raznolikosti u hrastovim populacijama, uključujući raznolikost koja izranja iz introgresivnog oplemenjivanja?

Na koji način gubitak genetske raznolikosti ili uvođenje nenativne germplazne utječe na dugoročno zdravlje hrastovih šuma?

Kako se uzgojnim postupcima može održati ili poboljšati genetska raznolikost i genetska kvaliteta sastojine?

Na ta pitanja vjerojatno nikada nećemo dobiti sasvim zadovoljavajuće odgovore, ali ona su veoma važna za zdravo gospodarenje hrastovim šumama, pa su čak i nepotpuni odgovori bolji od nikakvih. Usto je važno da su genetičari potpuno svjesni problema s kojima se suočavaju oni koji se bave proučavanjem i uzgajanjem hrasta. Zbog toga je i dobro da naše dvije radne grupe IUFRO-a, P1.06.00 i S2.08.05, imaju zajednički sastanak. Ako sastanak bude uspješan, onda će obje grupe biti obogaćene zbog razmjene informacija.

W.D. Maurer et al. : Provenance trials on *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl. in Rhineland-Palatinate (Germany): preliminary results ... Glas. šum. pokuse 37: 329–345, Zagreb, 2000.

UDK 630*166+(430) (Quercus robur L., Quercus petraea Liebl.)

PROVENANCE TRIALS ON *QUERCUS ROBUR* L. AND *QUERCUS PETRAEA* (MATT.) LIEBL. IN RHINELAND-PALATINATE (GERMANY): PRELIMINARY RESULTS OF PHENOTYPIC AND GENETIC SURVEYS

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Both pedunculate oak *(Quercus robur)* and sessile oak *(Quercus petraea)* originating from a variety of different German and European localities are currently being tested in separate provenance trials. These trials were established in 1992. Some results are presented here which refer to phenotypic traits at the early stage of plant development with the inclusion of growth, mortality, frost hardiness, and stem form. Moreover, by genotyping based on 20 and 18 enzyme coding gene loci, respectively, the genetic variation in both species was quantified exemplarily as gametic multilocus diversity. The significance of these trials for Rhineland-Palatinatian forestry is discussed.

Key words: *Quercus robur, Quercus petraea,* provenance trial, phenotypic traits, genetic diversity, isoenzyme genemarker

INTRODUCTION

Provenance research, as the oldest research field in forest genetics and plant breeding, works on the natural variation of different traits of forest woody plants and, by performing provenance experiments, aims in particular to follow the question of the genetic background of obvious variation (König 1986). While earlier general papers on this subject reflect such considerations like, for example, the design, layout, and control of provenance experiments (Edwards 1956), the definition of the objective, method and preparation of provenance trials (Schober 1961), and the historical development, state and future tasks of provenance research in forestry (Kleinschmit 1974), a more recent publication focuses on new applications for provenance trials including, for example, the vitalisation of results from provenance trials (Lindgren and Persson 1997) or the effects of environmental change on the productivity of tree populations (Mátyás 1997).

Provenance trials were initiated in Europe around the turn of the 20th century, predominantly for coniferous tree species like the indigenous Scots pine *(Pinus sylvestris)*, Norway spruce *(Picea abies)*, and silver fir *(Abies alba)*, as well as for the North American Douglas-fir *(Pseudotsuga menziesii)* and later on, for example, the noble fir *(Abies procera)* and giant fir *(Abies grandis)*. The first reported provenance trial on a deciduous tree species was initiated in 1904 in Germany on pedunculate oak *(Quercus robur)* by Cieslar (1923) and included 21 seed sources. For a survey of early provenance testing, *cf.* Kleinschmit (1974). Two more recent oak provenance trials with experimental plots located in Northern Germany are reported by Kleinschmit and Svolba (1995), one trial established by Krahl-Urban in 1950 with 115 German and 2 Austrian seed sources (65 sessile oaks and 52 pedunculate oaks), and the other as a joint Franco-German trial for pedunculate oak in 1983 (11 French and 6 German provenances). The very youngest oak provenance trials, however, were established in 1992 in the German Federal State of Rhineland-Palatinate where pedunculate oak and in particular sessile oak play an important role in forestry due to their economic and ecological significance. The objectives of these trials are to obtain valuation fundamentals for [1] regional ecological adaptability in view of stability towards biotic and abiotic dangers; [2] parameters that are relevant in forestry, like growth, bole and crown form, and quality and mass production; and [3] moreover, these trials are intended to supply supportive information for setting up scientifically sound provenance and cultivation recommendations which can be used in the future to improve the productivity of oak in its function as renewable raw material by selecting appropriate seed sources. This paper reports in this early developmental stage on the first phenotypic assessments of the pedunculate and sessile oak plants concerning growth, mortality, frost hardiness, and stem form. In addition, preliminary results of an isoenzyme study are presented in order to start the genetic characterisation of the provenances.

MATERIAL AND METHODS

QUERCUS ROBUR PROVENANCE TRIALS

Seeds were collected from 26 German and 4 Dutch sources (designated below as provenances). The origins of the selected provenances are distributed over the whole area of Germany. In addition, lowland provenances (altitudinal zonation below 200 m) of Northern Germany and the Netherlands are included, as given in Figure 1 and Table 1. For the whole trial three experimental plots were established in Rhineland-Palatinatian forest districts at three different altitudes: 180 m above sea level (colline altitudinal zonation, Saarburg, Saar River valley), 385 m a.s.l. (submontane altitudinal zonation, Wittlich, lower Eifel Mountains) and 530 m a.s.l. (montane altitudinal zonation, Neupfalz, Hunsrück Mountains), respectively. Two-year-old seedlings were planted in spring 1992 in three randomised complete blocks at a spacing of 2 x 1 m, *i.e.* each provenance per plot in 5 rows of 10 plants

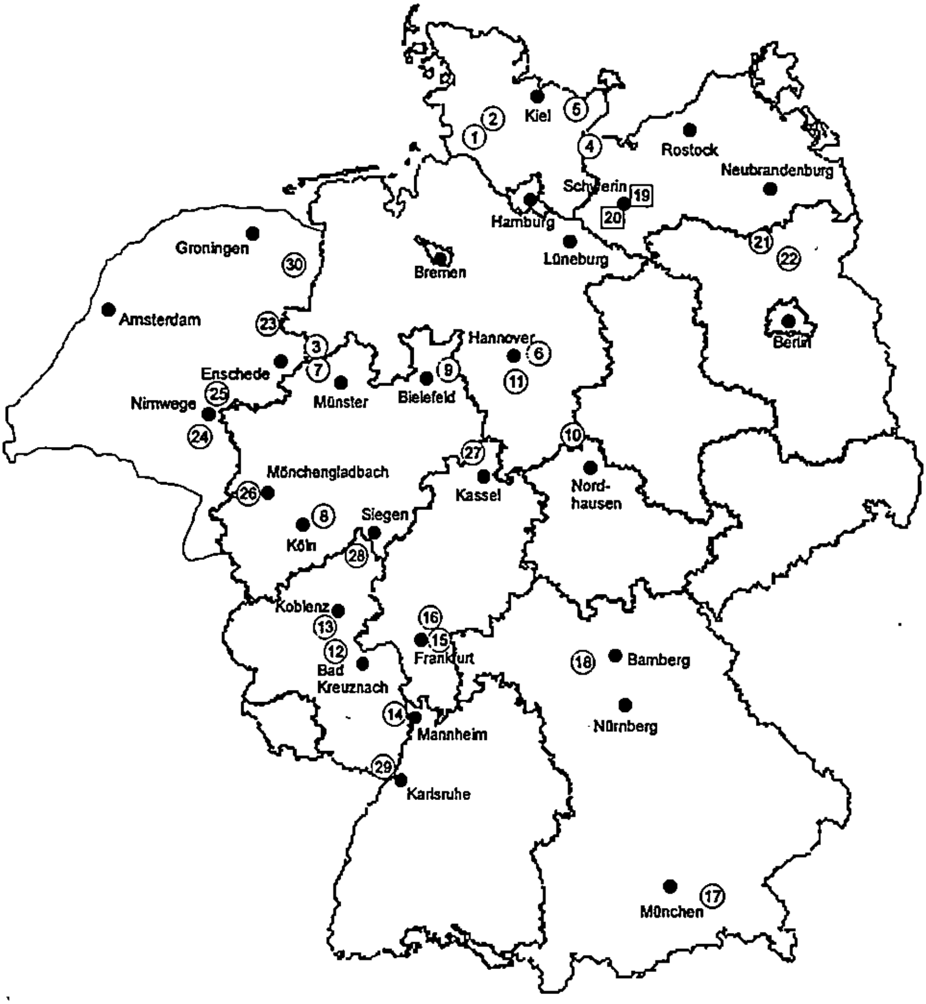

Figure 1. Geographical locations of the provenances included in the pedenculate oak provenance trial (no. 19 and no. 20 in squares: origin of mixtures)

Table 1. Origin of the German and Dutch pedunculate oak (*Quercus robur*) provenances

Provenance no.	Country / German Federal State	Origin of the pedunculate oak provenances	Designation of the region of provenance
1	D / SH	Barlohe, Abt. 247c	Baltic Sea coastal region
2	D / SH	Rendsburg, Abt. 325C+D, 333B, 334A	Baltic Sea coastal region
3	D / NI	Bentheim, Fürstl. Verwaltung in Steinfurt, Abt. 18a, 18c, 19a	Lower Saxony coastal region and Rhenish-Westfalian Bay
4	D / SH	Stadtforst Lübeck, Abt. 136/7	Baltic Sea coastal region
5	D / SH	Eutin (no data available)	Baltic Sea coastal region
6	D / NI	Peine (extremely late flushing oak), Abt. 343a3	(Lüneburg) Heath and Altmark
7	D / NW	Steinfurt (L. Lintel), Abt. 4K	Lower Saxony coastal region and Rhenish-Westfalian Bay
8	D / NW	Eitdorf (Graf Nesselrode), Abt. 80c, 81c	West German Bergland
9	D / NW	Duingerwald, Abt. 54c	West German Bergland
10	D / NI	Walkenried, Abt. 106b1	West German Bergland
11	D / NI	Seed orchard Berkel	(Lüneburg) Heath and Altmark
12	D / RP	Argenthal (Hunsrück Mountains), Abt. 13a	West German Bergland
13	D / RP	Burg Eltz (late flushing oak), Abt. 28c1	West German Bergland
14	D / RP	Mutterstadt, Abt. I 63; 71	Upper Rhine valley
15	D / HE	Nidderau, Stadt Langenselbold, Abt. 15a, 16	West German Bergland
16	D / HE	Wolfgang, Abt. 76A, 77A, 88B, (standard)	West German Bergland
17	D / BY	Wasserburg (Laimbach), Abt. V 3a0	South German Hügel- and Bergland incl. Alps
18	D / BY	Ebrach, Abt. XIII Eichholz (standard)	South German Hügel- and Bergland incl. Alps
19	D / MV	Schwerin (mixture)	Baltic Sea coastal region
20	D / MV	Hagenow (mixture)	Baltic Sea coastal region
21	D / BB	Menz, Abt. 4 417a^1	Eastern German Lowlands
22	D / BB	Zehdenik, Abt. 285c^5 / d^1	Eastern German Lowlands
23	NL	Bremerberg (rare category), 01 NL.ZS.8.2.03-01	The Netherlands
24	NL	Elsendorp (rare category), NL.S.3.3.21-01	The Netherlands
25	NL	The Netherlands, III Wageningen	The Netherlands
26	D / NW	Stadt Viersen, Abt. 36B, 38	Lower Saxony coastal region and Rhenish-Westfalian Bay
27	D / HE	Hofgeismar, Abt. 164B, 165A	West German Bergland
28	D / RP	Mündersbach (Westerwald Mountains), Abt. 5a^2	West German Bergland
29	D / RP	Hagenbach, Abt. VII 112	Upper Rhine valley
30	NL	Stadskanaal (rare category), NL.S.4.01-01	The Netherlands

abbreviations used for the respective German federal state:BB, Brandenburg; BY, Bavaria; HE, Hesse; MV, Mecklenburg-Vorpommern; NI, Lower Saxony; NW, North Rhine-Westfalia; RP, Rhineland-Palatinate; SH, Schleswig-Holstein for the respective European state: D, Germany; NL, The Netherlands

each. Surveys were carried out for the respective mortality and growth in the falls of 1992, 1994 and 1996. Frost damage was assessed in May 1995 and additionally in May 1997 for trial Neupfalz exclusively) by scoring each plant according to a scheme ranging from grade 1 (no visible frost damage present on a plant) through 2 (leaves are damaged in part), 3 (up to 2/3 of the leaves with damage), 4 (more than 2/3 of the leaves with damage) to grade 5 (all leaves and shoots of a plant are damaged by frost).

QUERCUS PETRAEA PROVENANCE TRIAL

The collection was initiated by S. Madsen (Hørsholm, Denmark) in 1989 in the framework of European co-operation to cover the total distribution range of sessile oak. Originally, two provenances per participating country should have been collected. For the German trials, 18 additional provenances were included by A. König and K. Liepe (Grosshansdorf, Germany). A list of the 38 different seed sources is given in Table 2. The following six experimental trials were established: Plön (Northern Germany), Müncheberg (Eastern Germany), Siegburg (Western Germany), Büdingen (Central Germany), Wiesentheid (Southern Germany) and Eppenbrunn (Southwest Germany). The last trial established in the forest district Eppenbrunn (Southern Palatinate Forest) is assumed to be of particular significance because it is the southernmost one, and it is located in the core area of the natural distribution range of sessile oak. In Eppenbrunn only 31 provenances are studied. Two-year-old seedlings pre-cultivated in the nursery of the Federal Research Centre for Forestry and Forest Products in Grosshansdorf (Germany) were planted in spring 1992. The trial was established in four randomised complete blocks at a spacing of 1 x 1.5 m, with 7 x 9 plants per plot. Height was measured at plant age 4, 6 and 8. From these data mortality was estimated. Additionally, at age 8, stem form was assessed in one block only according to the boniture scheme of Kleinschmit and Svolba (1995) scoring from grade 1 (very straight) to grade 5 (very crooked).

GENOTYPING IN THE *QUERCUS ROBUR* AND *QUERCUS PETRAEA* PROVENANCE TRIALS

For isoenzyme analyses (Müller-Starck et al. in preparation), twigs with dormant buds were sampled in the pedunculate oak experimental trials Wittlich and Neupfalz in late fall 1996 and in the sessile oak trial Eppenbrunn in late fall 1998. Sampling was carried out preferentially in plots with lowest losses in order to detect differences in the composition of the genetic constitution of the provenance material unaffected by possible selective effects of the planting site. Each provenance is represented by 100 individuals (deviating sample sizes in a few cases). By means of starch gel electrophoresis based on 13 enzyme systems, each individual was genotyped at 20 and 18 enzyme coding gene loci for pedunculate and sessile oak respectively (*cf.* Table 3). For analytical procedures as well as the genetic control of the enzyme gene markers, see. Müller-Starck et al. (1996) and Zanetto et al.

Table 2. Origin of the sessile oak (*Q. petraea*) provenances of the trial Eppenbrunn (D/RP) (collection in 1989) (*in italics: provenances which are not included in trial Eppenbrunn*)

Provenance no.	Country / German Federal State	Origin of the sessile oak provenances	Geographical longitude	Geographical latitude	Altitude above sea-level in m
1	D / SH	Stadtforst Mölln, Büffelskopf Abt.16	10°45'	53°37'	36
2	D / SH	FA Rantzau, Rfö. Kummerfeld, Esinger Wohld Abt. 83A	09°46'	53°43'	10
3	D / NI	FA Göhrde, Abt. 84a	10°51'	53°06'	80-95
4	D / NI	FA Sprakensehl, Rfö. Hagen Abt. 210b	10°36'	52°48'	115
5	D / NW	FA Recklinghausen, Stadtforst Haltern, Rfö. Frettholz Abt. 202	07°11'	51°46'	75
6	D / NW	FA Recklinghausen, Stadtforst Haltern, Rfö. Frettholz Abt. 204a	07°10'	51°46'	71
7	D / HE	FA Bad Hersfeld, Rfö. Stadtwald, Abt. 571a^1	09°40'	50°53'	240-330
8	D / HE	FA Wolfgang, Rfö. Rodenbach Abt. 43B1, 44A1, 47A1, 48A	09°03'	50°09'	140-200
9	D / BY	FA Riedenburg, Rfö. Essing II, Distr. XIII, 1a^1 and Distr. XVI, 2a^1, 2b^1	11°49'	48°58'	450-465
10	D / BY	FA Ebrach, Rfö. Koppenwind, Distr. II Rambach	10°30'	49°51'	390
11	D / RP	FA Cochem, Rfö. Ediger-Eller Abt.13 a^2, b^2	07°03'	50°05'	400
12	D / RP	FA Elmstein-Nord, Rfö. Speyerbrunn, Distr. XVII, Abt.1b^1	07°56'	49°21'	400-505
13	D / RP	FA Johanniskreuz, Rfö. Burgalb, Distr. XIV, Abt. 2a, b^2, c^2	07°53'	49°24'	460
14	D / SH	FA Farchau, Rfö. Ravenskamp Abt. 55	10°46'	53°40'	35-50
15	D / NI	FA Lappwald, Rfö. Weidensol Abt. 68b	10°54'	52°12'	180
16	D / BY	FA Ebrach, Rfö. Koppenwind, Distr. II Rambach	10°30'	49°51'	400
17	DK / Århus	DDH Silkeborg, Hørbylunde, Jenssen-Buchske plt. 6k, 7f	09°25'	56°08'	65-90
18	DK / Århus	Løndal Næs, Næsset 7a, 7b	09°36'	56°04'	25
19	A /NÖ	Wienerwald, Purkersdorf TrEi 5(III/4/3-6)	16°10'	48°12'	290-370
20	A / Burgenland	Klostermarienberg	16°34'	47°25'	310
21	A /NÖ	Mistelbach, Heidleiten	16°34'	48°38'	280
22	TR	Bolu, Ayikayasi 48	31°40'	40°55'	900-1500
23	GB / Glos.	Dymock SOK 4008	2°27'W	51°57'	70
24	B / O.Flandern	Fagnes, Bois de Chimay, Queue de l´Herse	04°22'	50°05'	220-230
25	B / Hainaut	Gent , Buggenhout Comp. 4, 9, 11	04°12'	50°59'	24
26	D / NI	FA Lüß, Rfö. Kempelhorn Abt. 108c$_1$, 128b$_1$,	10°18'	52°50'	110
27	D / RP	FA Elmstein-Nord, Rfö. Speyerbrunn, Distr. XVII, Abt.1b^1	07°56'	49°21'	400-505
28	PL / Kalisz	Syców, Smardze 97bc, 98c, 99bc, 126c, 127b, 128a	17°56'	51°11'	210
29	F / Sarthe	ONF Le Mans, Berce01 CR 03 (H1 89142)	0°27'	47°47'	120
30	F / Allier	ONF de Moulin, Dreuille 06 CR 02 (H1 89172)	02°53'	46°28'	300
31	F / H. Marne	ONF de Langres, Bussieres 11 CR 04 (H1 89221)	05°50'	47°45'	360
32	F / Vienne	ONF de Poitiers, Vouillé St Hilaire 02 CR 03 (H1 89261)	0°20'	46°37'	143
33	D / BY	FA Ebrach, Rfö. Koppenwind Abt. 7a^1	10°30'	49°51'	380
34	H	no data available			
35	N / V.-Agder	Søgne, Vest-Agder landbruksskole	07°50'	58°06'	25
36	GB / Glos.	Forest of Dean, Blakeney Comp. 402, 403, POK 4001	2°30'W	51°47'	76
37	GB / Glos.	Forest of Dean, Sutton Bottom Comp.446, POK 4007	2°29'W	51°49'	120
38	D / BB	Amt für Forstwirtschaft Müncheberg, Buckow Abt. 3329 a^1	14°05'	52°34'	50

abbreviations used for the respective German federal state : BB, Brandenburg; BY, Bavaria; HE, Hesse; NI, Lower Saxony; NW, North Rhine-Westphalia; RP, Rhineland-Palatinate; SH, Schleswig-Holstein; for the respective European state: A, Austria; B, Belgium; D, Germany; F, France; GB, Great Britain; H, Hungary; N, Norway; PL, Poland; TR, Turkey

Table 3. Enzyme systems and coding enzyme gene loci (note: * for pedunculate oak only)

Enzyme system (abbrev. / E.C. no.)	Quaternary structure	Gene loci
aspartate aminotransferase (AAT / 2.6.1.1)	Dimer	AAT-B, AAT-C*, AAT-D*
aconitase (ACO / 4.2.1.3)	monomer	ACO-A
alcohol dehydrogenase (ADH / 1.1.1.1)	dimer	ADH-A
aminopeptidase (AP / 3.4.11.1)	monomer	AP-A, AP-B
esterase (EST / 3.1.1.1)	monomer	EST-A
glutamate dehydrogenase (GDH / 1.4.1.2)	hexamer	GDH-A
isocitrate dehydrogenase (IDH / 1.1.1.42)	dimer	IDH-A, IDH-B
malate dehydrogenase (MDH / 1.1.1.37)	dimer	MDH-B, MDH-C
menadione reductase (MNR / 1.6.99.2)	tetramer	MNR-A
6-phosphogluconate dehydrogenase (6PGDH / 1.1.1.44)	dimer	6PGDH-A, 6PGDH-B
phosphoglucose isomerase (PGI / 5.3.1.9)	dimer	PGI-A, PGI-B
phosphoglucomutase (PGM / 2.7.5.1)	monomer	PGM-A
shikimate dehydrogenase (SKDH / 1.1.1.25)	monomer	SKDH-A

(1996); for genetic variation measures, see. Gregorius et al. (1986) and Hattemer et al. (1993).

RESULTS

QUERCUS ROBUR PROVENANCE TRIALS

Growth. Table 4 gives an overview of the relative growth rates of the different provenances in the three trials as assessed in fall 1996 after five vegetation periods. Absolute mean heights calculated for each trial are 122 cm for Neupfalz (530 m a.s.l.), 133 cm for Wittlich (385 m a.s.l.) and 133 cm for Saarburg (180 m a.s.l.). Provenance 18 Ebrach ranges lowest in all three trials with only half of the average heights. On the other hand, the Dutch provenance 23 Bremerberg grows highest in all trials by exceeding the average values by a range of 36-50 %. Out of the 30 provenances, 11, 15, and 14 are below the mean height on the trials as arranged above. Provenance 16 Wolfgang is very close to the mean value calculated both for Neupfalz and Wittlich, whereas it is 20 % lower in Saarburg. While the provenance 6 Peine, which is described as extremely late flushing, is about 15 % above average in Neupfalz and Wittlich, but is 15 % below the mean value in Saarburg. Heights range from 60-170 cm in Neupfalz, 66-200 cm in Wittlich, and 66-181 cm in Saarburg.

Mortality. The losses of the pedunculate oak provenances after 5 vegetation periods are presented in Table 5. No, or very few, losses were observed in fall 1992 after planting the seedlings, but after 3 vegetation periods different mortalities became evident. In 1996 losses were estimated to range from 1-49 % in Neupfalz, 1-21 % in Wittlich, and 3-45 % in Saarburg. Among the most affected provenances in all three trials was Hagenow. For the extremely late flushing provenance 6 Peine, 1-2 % losses occurred in Neupfalz and Wittlich; however in Saarburg, the

Table 4. Height growth (as % of experimental mean) assessed for the pedunculate oak (*Quercus robur*) provenance trial in fall 1996 after five vegetation periods (a.s.l., above sea-level)

trial Saarburg (180 m a.s.l.)		trial Wittlich (385 m a.s.l.)		trial Neupfalz (530 m a.s.l.)	
provenance no. / origin of source	% of mean	provenance no. / origin of source	% of mean	provenance no. / origin of source	% of mean
18 Ebrach (Standard)	46	18 Ebrach (Standard)	49	18 Ebrach (Standard)	49
22 Zehdenik	65	22 Zehdenik	62	22 Zehdenik	57
20 Hagenow (mixture)	76	19 Schwerin (mixture)	75	20 Hagenow (mixture)	63
16 Wolfgang (Standard)	80	20 Hagenow (mixture)	76	19 Schwerin (mixture)	77
19 Schwerin (mixture)	80	21 Menz	76	21 Menz	77
12 Argenthal / Hunsrück	84	26 Stadt Viersen	76	12 Argenthal / Hunsrück	82
6 Peine (late flushing oak)	85	15 Nidderau, Stadt Langensebold	78	15 Nidderau, Stadt Langensebold	84
17 Wasserburg	86	12 Argenthal / Hunsrück	80	17 Wasserburg	89
15 Nidderau, Stadt Langensebold	89	3 Bentheim	82	13 Burg Eltz (late flushing oak)	92
3 Bentheim	92	29 Hagenbach	91	3 Bentheim	94
13 Burg Eltz (late flushing oak)	96	16 Wolfgang (Standard)	94	5 Eutin	98
8 Eitdorf (Graf Nesselrode)	97	28 Mündersbach / Westerwald	97	16 Wolfgang (Standard)	101
28 Mündersbach / Westerwald	97	1 Barlohe	98	29 Hagenbach	103
14 Mutterstadt	99	13 Burg Eltz (late flushing oak)	99	7 Steinfurt (L.Lintel)	105
9 Duingerwald	100	27 Hofgeismar	99	1 Barlohe	107
26 Stadt Viersen	101	10 Walkenried	104	14 Mutterstadt	107
5 Eutin	106	17 Wasserburg	104	26 Stadt Viersen	107
21 Menz	107	4 Stadtforst Lübeck	105	27 Hofgeismar	108
7 Steinfurt (L.Lintel)	109	5 Eutin	105	28 Mündersbach / Westerwald	108
1 Barlohe	110	30 Stadskanal (NL)	106	11 Seed orchard Berkel	110
10 Walkenried	110	7 Steinfurt (L.Lintel)	110	9 Duingerwald	112
2 Rendsburg	112	14 Mutterstadt	112	24 Elsendorp (NL)	112
4 Stadtforst Lübeck	113	8 Eitdorf (Graf Nesselrode)	113	6 Peine (late flushing oak)	114
11 Seed orchard Berkel	114	6 Peine (late flushing oak)	116	10 Walkenried	115
27 Hofgeismar	115	2 Rendsburg	127	8 Eitdorf (Graf Nesselrode)	116
25 Hauptgeb. NL III (Wageningen)	119	11 Seed orchard Berkel	129	4 Stadtforst Lübeck	117
24 Elsendorp (NL)	121	25 Hauptgeb. NL III (Wageningen)	131	30 Stadskanal (NL)	117
30 Stadskanal (NL)	124	9 Duingerwald	133	2 Rendsburg	120
29 Hagenbach	129	24 Elsendorp (NL)	133	25 Hauptgeb. NL III (Wageningen)	130
23 Bremerberg (NL)	136	23 Bremerberg (NL)	150	23 Bremerberg (NL)	139
absolute mean height (100%) in cm	133	absolute mean height (100%) in cm	134	absolute mean height (100%) in cm	122
	66		66	min-value in cm	60
	181		200	max-value in cm	170

lowest altitudinal location, 19 % were estimated. In general, lowest losses were observed in Wittlich as compared to the two other trial plots.

Table 5. Mortality (%) in the pedunculate oak *(Quercus robur)* provenance trial after 5 vegetation periods in fall 1996, plants affected by frost damage (%) as observed in May 1995 and mean grade of damage for the surveys in May 1995 and May 1997

Provenance no.	trial Saarburg (180 m a.s.l.)			trial Wittlich (385 m a.s.l.)			trial Neupfalz (530 m a.s.l.)			
	% mortality	frost damage 1995		% mortality	frost damage 1995		% mortality	frost damage 1995		
		% plants damaged	mean grade		% plants damaged	mean grade		% plants damaged	mean grade	
									1995	1997*
1	5	61	1.9	1	96	4.3	3	95	4.6	1.9
2	15	82	2.0	2	88	3.8	4	90	4.1	1.7
3	13	65	1.9	7	98	4.5	19	93	4.6	1.7
4	17	80	2.1	21	83	3.4	19	78	3.3	1.7
5	25	72	1.9	10	85	3.3	39	88	4.3	1.8
6	19	38	1.5	1	40	2.1	2	39	1.7	1.2
7	23	71	1.9	7	87	3.9	11	87	4.0	1.7
8	27	69	1.9	7	96	4.2	30	95	4.3	1.8
9	21	76	1.9	3	92	3.9	49	81	3.9	1.3
10	19	37	1.5	7	96	4.2	23	96	4.0	1.7
11	12	80	1.8	1	85	3.7	33	91	4.3	1.4
12	22	81	1.8	7	89	3.8	36	78	3.7	1.9
13	11	76	2.0	3	83	3.5	5	63	3.2	1.7
14	22	59	1.6	5	96	4.1	7	96	4.5	1.9
15	9	73	1.9	2	97	4.5	6	96	4.6	1.8
16	3	74	2.0	2	99	4.6	1	99	4.7	1.7
17	8	79	2.1	1	94	3.8	3	88	3.9	1.8
18	19	61	2.5	21	96	4.2	24	68	3.5	2.1
19	28	80	2.1	10	90	3.8	16	82	4.1	1.8
20	45	70	2.2	18	94	3.9	47	83	3.2	2.2
21	13	65	1.8	5	82	3.9	22	73	3.8	1.8
22	33	84	2.9	13	86	3.9	18	58	2.9	1.7
23	15	45	1.5	1	59	2.1	12	72	2.9	1.7
24	14	72	2.0	4	44	2.0	20	55	2.5	1.8
25	9	48	1.6	1	93	3.9	12	94	4.0	1.6
26	3	41	1.6	4	98	4.0	1	65	2.7	1.7
27	17	67	1.8	13	93	3.6	17	92	4.5	2.0
28	16	74	2.2	3	97	3.7	3	67	2.9	1.6
29	16	57	1.6	6	100	4.6	7	99	4.8	2.4
30	33	67	1.9	6	82	3.0	24	68	2.9	1.5
mean	18	67	1.9	6	87	3.7	17	81	3.7	1.8
st. dev.	9	13	0.3	6	15	0.7	14	15	0.8	0.2
min	3	37	1.5	1	40	2.0	1	39	1.5	1.2
max	45	84	2.9	21	100	4.6	49	99	4.8	2.4

abbreviations used: st. dev. = standard deviation; min = minimum value; max = maximum value
1997*: survey for trial Neupfalz exclusively

Frost hardiness. A survey on frost damage was carried out in all trials in May 1995 and in May 1997 for trial Neupfalz exclusively (*cf.* Table 5). The relative mean damage reflecting the number of plants concerned was calculated to be 67 % in Saarburg, ranging from 37 to 84 %, but was elevated to 87 % (40-100%) in Wittlich and 81 % (39-99%) in Neupfalz. Least affected by frost effects was provenance 10 Walkenried (D/NI) in Saarburg. Provenance 6 Peine (D/NI) showed both in Wittlich and Neupfalz the least damage; moreover, this provenance ranged second lowest in Saarburg: most severely damaged by frost was provenance 22 Zehdenik (D/BB) in Saarburg, while nearly all plants of provenance 29 Hagenbach (D/RP) both in Wittlich and Neupfalz were harmed. The mean grades reflect the frost damage qualitatively. Thus, in Saarburg, an overall mean grade of 1.9 makes it clear that the leaves of an individual plant are damaged in part, whereas grade 3.7 for both Wittlich and Neupfalz shows severe damage occurring in up to 2/3 of the leaves of an individual plant. The maximum values of 4.6 and 4.8 for provenance 29 Hagenbach in Wittlich and Neupfalz, respectively, reveal that almost every part of an individual plant is affected by frost. Another survey on frost damage performed two years later in Neupfalz exclusively revealed that this trend was followed by the provenances growing there, although the mean grades in general were lower, ranging from 1.2 to 2.4 (mean: 1.8; *i.e.* the leaves of an individual plant were damaged in part). Again, provenance 29 Hagenbach scores highest with 2.4. In general, the provenances under study showed frost damage symptoms which were increased fourfold both in Wittlich and Neupfalz as compared to Saarburg. The damaging of plants by frost was found to occur at a lower level in Neupfalz in May 1997.

QUERCUS PETRAEA PROVENANCE TRIAL

Growth. Table 6 gives an overview of the height development of the sessile oak provenances growing in Eppenbrunn as assessed at the ages of 4, 6 and 8. At age 4, heights range between 41 cm [19 Wienerwald (A)] and 62 cm [37 Dean (GB)]; two years later, at age 6, between 100 cm [15 Lappwald (D/NI)] and 130 cm [12 Elmstein-Nord (D/RP)]; and another 2 years later, 138 cm [15 Lappwald (D/NI)] and 188 cm [12 Elmstein-Nord (D/RP)]. The overall mean reflects an average increase of 62 cm from age 4 to 6, and 45 cm from age 6 to 8. This rate of increase is followed more or less equally by most of the provenances. In particular, provenance 12 Elmstein-Nord which originates from an approved stand located in the Palatinate Forest at about 40 km north of trial Eppenbrunn deviates from these mean values by revealing a more rapid increase in height growth, with 69 cm from the age of 4 to 6, and 58 cm from the age of 6 to 8.

Mortality. Relative losses at the age of 8 are given in the penultimate column of Table 6 and range from 4 % [6 Recklinghausen (D/NW)] to 19 % [15 Lappwald (D/NI)] with a mean value of about 10 %. High losses were also observed for the provenances 38 Müncheberg (D/BB) and 8 Wolfgang (D/HE) at about 18 % each, and for the provenances 24 Fagnes (B) and 20 Burgenland (A) at about 15 %. These high losses coincide with the survey of fall 1993 (data not shown). Affected by comparatively low losses are the provenances 11 Cochem (D/RP) at 5 % and the provenances 3 Göhrde (D/NI), 7 Bad Hersfeld (D/HE), 12 Elmstein-Nord (D/RP), 14 Farchau (D/SH), 18 Århus (DK), and 19 Wienerwald (A) at 6 % each. Similar results were obtained in the survey of fall 1993.

Table 6. Growth, mortality and form assessments as performed in the sessile oak provenance trial Eppenbrunn at different plant ages

Provenance no.	Mean height [cm]			Mortality [%]	Mean value stem form (block 4 only)
	age 4	age 6	age 8	age 8	age 8
1	51	107	147	6,7	4,2
2	54	116	155	9,2	4,2
3	48	110	163	5,9	3,6
4	no data available				
5	no data available				
6	55	113	159	4,1	4,2
7	51	111	146	5,6	4,2
8	46	102	139	17,5	4,1
9	45	106	157	7,9	4,1
10	*not included in Eppenbrunn*				
11	45	106	148	5,3	4,1
12	61	130	188	6,4	3,8
13	49	115	162	9,2	3,8
14	51	113	150	6,4	4,2
15	48	100	138	19,0	4,2
16	48	104	152	10,2	3,7
17	49	111	143	9,2	4,2
18	44	107	151	5,7	4,1
19	41	106	152	6,0	3,9
20	48	114	152	15,3	4,5
21	52	111	160	6,8	4,1
22	*not included in Eppenbrunn*				
23	57	117	163	11,8	3,8
24	46	107	154	14,7	3,8
25	*not included in Eppenbrunn*				
26	43	107	152	12,8	3,8
27	*not included in Eppenbrunn*				
28	46	110	157	7,9	
29	52	113	162	8,7	4,1
30	*no data available*				
31	48	109	179	9,8	
32	49	110	163	10,0	4,0
33	*not included in Eppenbrunn*				
34	*not included in Eppenbrunn*				
35	*not included in Eppenbrunn*				
36	62	128	176	6,8	3,8
37	62	129	182	7,2	3,8
38	47	111	158	18,4	4,0
overall mean	49,9	111,5	157,4	9,5	4,0
standard deviation	5,5	7,4	12,1	4,2	0,2
min-value	41	100	138	4,1	3,6
max-value	62	130	188	19,0	4,5

Form. A good stem form is a significant characteristic trait for the quality of oak. Although the plant material of sessile oak provenances is still in its early stage of growth, the stem form was evaluated at the age of 8. In Table 6 (last column), mean values for the various provenances are given. Scoring ranges from 3.6 in provenance 3 Göhrde (D/NI) to 4.5 in provenance 20 Klostermarienberg (A/Burgenland), thus showing that there is no significant differentiation for the provenances under study. The overall mean of 4.0 demonstrates that the oak trees are still more or less crooked and bent at this young age. Therefore, the stem form assessment has to be repeated at a later age.

GENETIC DIVERSITY IN THE PROVENANCE TRIALS OF *QUERCUS ROBUR* AND *QUERCUS PETRAEA*

The hypothetical gametic multilocus diversities calculated for the different pedunculate and sessile oak provenance samples are presented in Figure 2 and Figure 3, respectively. This variation parameter reflects the genetic diversity present in each provenance and quantifies the potential of each provenance sample to form the given number of genetically different multilocus gametes (Gregorius et al. 1986). This kind of quantification takes into account the fact that the adaptability of populations depends decisively on the ability to produce genetically different gametes and thus to form the succeeding generation via genetically heterogeneous forest reproductive material. The range of v_{gam} appears to be similar for both oak species tested in the provenance trials with maximum values around 25,000 each. It needs to be taken into account that the values for sessile oak refer to only 18 loci (20 loci in the case of pedunculate oak). In spite of this fact, the highest v_{gam}-value of more than 27,000 is reached by the sessile oak provenance 6 Peine (D/NI) follo-

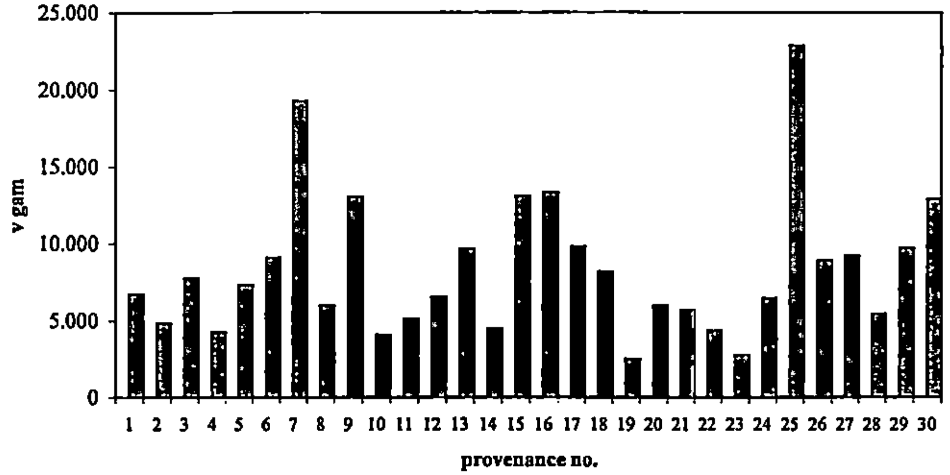

Figure 2. Hypothetical gametic multilocus diversity (V_{gam}) as obtained for the 30 pedunculate oak provenances under study

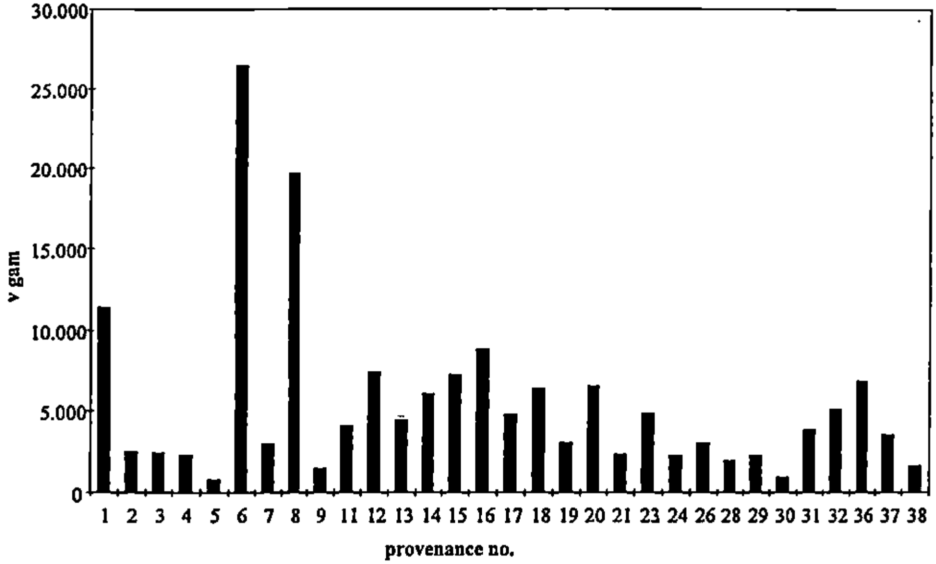

Figure 3. Hypothetical gametic multilocus-diversity (V_{gam}) as obtained for the 31 sessile oak provenances under study

wed by the Dutch pedunculate oak provenance no. 25 at 22,836. The lowest v_{gam}-values are 714 for the sessile oak provenance 5 Recklinghausen 1 (D/NW) and 2,492 for the pedunculate oak provenance 19 Schwerin (D/MV). Within each provenance trial, the v_{gam}-values deviate substantially from each other: in the case of pedunculate oak, 7 out of the 30 provenance samples reveal values smaller than 5,000, while the values of 6 samples considerably exceed 10,000. In the case of sessile oak, the corresponding values are 19 and 3, respectively, out of 31. Evidently, deviations among multilocus diversities are more pronounced among provenance samples of sessile oak as compared to pedunculate oak.

DISCUSSION

While in the Federal Republic of Germany oak covers a mean surface of approximately 8.6 %, it is about 15 % for the Federal State of Rhineland-Palatinate by considering a managed forested area (state and communal forests only) of approximately 527,000 hectares (Eder and Rose 1995). Oak occurring in the Rhineland-Palatinatian forests comes fourth in the tree species distribution Šafter Norway spruce *(Picea abies)* 26%, European beech *(Fagus sylvatica)* 24 % and Scots pine *(Pinus sylvestris)* 18 %Ć (Anonymus 1996). The oak surface is shared predominantly by sessile oak *(Quercus petraea)* comprising about 87 %, while pedunculate oak *(Quercus petraea)* covers the remaining 13 % of the oak surface. While coniferous forests were abundant in the past as compared to hardwood forests, the catastrophic windthrows in the past decade made necessary the change of the composition of the forests by raising the proportion of deciduous tree species, including oak. However, in the case of pedunculate oak, there are only a limited number of stands that are suitable to be approved seed stands. In particular, these concern the colline and submontane zonal ranges. What makes the situation even more complicated is the state of heath of oak: as pointed out by the recent report on the health of the Rhineland-Palatinatian forests, both oak species are still damaged to a very high level of 50 %, which is the highest for all tree species (Anonymus 1999).

As a consequence of this situation and the fact that, due to a temporary lack of suitable reproductive material, unsuitable provenances may be utilised, provenance trials were established for pedunculate oak in order to test selected provenances for their adaptedness to localities of different altitudinal zonation with respect to a variety of phenotypic traits. Moreover, in the framework of an international joint project on sessile oak provenance research, a trial was started at the very same time on an experimental site in the forest district of Eppenbrunn, thus located in the core area of the natural distribution range of sessile oak. From the Rhineland-Palatinate point of view, the results obtained by phenological, phenotypic and growth-related measurements in the trial should give valuable information on the status of the indigenous occurrences of sessile oak.

Characteristics from the early developmental stage of the oak plants included in this paper comprise growth, mortality and frost hardiness. Even in this early test phase, the studied provenances of both oak species exhibit a great variation with regard to mortality and frost hardiness as well as height growth reflecting differing adaptedness and performance. However, in general, it is too early to assess the oak provenances regarding clinal or ecotypic variation.

The great variation in sessile oak regarding frost damage, leaf flushing, lammas shoot formation and leaf coloring in fall was also studied in growth chambers as well as in field and greenhouse trials during the years 1991 and 1994 in Grosshansdorf (Stephan et al. 1994). Early flushing provenances have their origin particularly in southern regions and are therefore more affected by late frost than the late flushing ones, which come from Great Britain. Further development of the provenance trial at Eppenbrunn will therefore be of great interest.

To characterise precisely the provenances under study, surveys will have to be carried out at regular intervals concerning growth (height, form of stem and crown, crown development, diameter) and biotic and abiotic damage. Phenological surveys should be conducted regarding leaf flushing and termination, and for the case of nutrient contents. These data will be the base to supply supportive information for setting up scientifically-sound provenance and cultivation recommendations which should be used in the future to improve the productivity of oak in its function as renewable raw material, even though some results will only be obtained in the intermediate and long term.

Assessments of the genetic variation present in provenance samples contained in trials significantly contribute to the characterisation of provenances. Analysing isoenzyme gene markers has become a routine laboratory method now because of the availability of suitable enzyme systems and standardised methods. The quantification of genetic variation reveals substantial deviations among provenance samples of each of the studied oak species. In the case of calculated multilocus diversities, deviations among samples are particularly pronounced due to the multiplicative effect of this variation parameter. In spite of this tendency, diversities which exceed corresponding values by more than a factor of 30 (*e.g.* sessile oak provenance 6 Recklinghausen as compared to 5 Recklinghausen) must be considered as highly indicative.

Data clearly demonstrate that collections from neighbouring localities can result in strongly deviating values for genetic diversities. This particularly holds for the above-mentioned samples no. 5 and 6 which both originate from the forest district of Recklinghausen in North West Germany. On the other hand, samples which originate from mixtures of neighbouring localities do not necessarily reveal above-average diversities. For instance, in the case of pedunculate oak, the lowest multilocus diversity is indicated for sample 19 Schwerin (D/MV) in Northern Germany. In contrast, a mixture which originates from various pedunculate oak stands in the Netherlands reveals the maximum multilocus diversity within the samples of this species.

These findings are interpreted, for the present, to indicate both existing deviations among the genetic diversities of provenance samples and various environmental impacts following reproduction and the mode of collection of forest reproductive material. Further studies are required in order to specify corresponding statements.

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TESTOVI PROVENIJENCIJE NA VRSTAMA *QUERCUS ROBUR* L. I *QUERCUS PETRAEA* (MATT.) LIEBL. U REGIJI RHINELAND-PALATINATE (NJEMAČKA): PRELIMINARNI REZULTATI FENOTIPSKIH I GENETSKIH ISTRAŽIVANJA

I hrast lužnjak (*Quercus robur*) i hrast kitnjak (*Quercus petraea*), koji potječu s različitih njemačkih i europskih lokaliteta, trenutno se testiraju u odvojenim testovima provenijencije. Ti su pokusi počeli 1992. godine. Ovdje su predstavljeni neki rezultati koji se odnose na fenotipska svojstva u ranom stadiju razvoja biljke uključujući rast, smrtnost, otpornost na mraz i oblik debla. Štoviše, utvrđivanjem genotipova na osnovi 20, odnosno 18 enzimskih kodiranih genskih lokusa kvantificirana je genetska varijacija u obje vrste kao gametska višelokusna raznolikost. Razmatra se značenje tih pokusa za šumarstvo regije Rhineland-Palatinate.

Ključne riječi: *Quercus robur, Quercus petraea*, test provenijencije, fenotipska svojstva, genetska raznolikost, izoenzimski genski marker

UDK 630*165+232.3+931+(436) (Quercus robur L.)

OAK SEEDLOTS AND FOREST SEED TRADE REGULATIONS: AN INVESTIGATION USING MOLECULAR MARKERS

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The trade of forest tree seeds and plants is regulated internationally and nationally because trueness-of-type of the material, and the supply of appropriate material for each given site, are important. Especially in Central Europe, landscape topology (mountain ranges) creates diverse ecological conditions. A minimum genetic base for forest tree species can be provided by harvesting seed for afforestation purposes from many trees within a stand. In Austria, at least 20 trees have to be included in marketable seed harvests of *Quercus robur* and *Q. petraea*. To test for correct labelling, only lengthy growth tests have been available previously. Isozyme analysis has only rarely provided the necessary information. In a microsatellite marker pilot study we have shown that inferences on the number of seed parents and pollen donors included in seed harvests can be made using laboratory data obtained from individual tree seedlots. These two parameters are estimated utilising Mendelian inheritance of the markers and genetic map information. We close with an outlook into future applications of molecular genetics to forest seed material: provenance identification will probably be based on chloroplast and mitochondrial DNA, while analysis of the genetic composition and relatedness within seed material, and between the seedlot and its source, will take advantage of the high level of polymorphism offered by nuclear microsatellites.

Key words: *Quercus robur*, microsatellites, genetic diversity, forest seed trade, legislation

INTRODUCTION

Devastating deforestations in Central Europe in former centuries often triggered great efforts to re-establish healthy forests. Many such efforts failed completely because wrong seed provenances were employed. When it became apparent around 1900 that traits controlling the local adaptation of tree populations were genetically inherited, it was quickly suggested to introduce legislation to control the proper use of provenances. As the following decades were preoccupied by the ideas of genetic determinism, the idea was quickly taken up (e.g. in the German law on forest species in 1934). Ever since then, genetic issues have made a strong stance in forestry legislation. The European Communities introduced a directive in 1966 (Council of the European Economic Community 1966), and the Organization for Economic Co-operation and Development (OECD) established a scheme for the "control of forest reproductive material moving in international trade" in 1974 (OECD 1974). Many countries have similar legislation in force that incorporates the objectives of these international documents. The application of these schemes depends heavily on the guarantee that the quality of the seedlots is labelled correctly. Authorities have to implement a system of controls and checks that prevent forging of the labels. Up to now, this was only possible by trying to document each step in the seed supply chain. This is the case simply because testing the seed for actual growth performance would take too long - at least a few months if controlled environment chambers were used. Effective measures against mislabelling, however, require much faster methods of analysis.

In this situation, many are turning their eye to molecular genetics in the hope for quick screening methods that can accurately determine seed provenance and plant performance. In this paper, we review the importance of seed testing in the frame of international developments regarding forest reproductive material. To illustrate this, we summarise the results of a case study for the practical implementation of recently established seed trade regulations in Austria. In this pilot study, two intuitive genetic diversity parameters, the numbers of different seed parents and pollen donors contributing to a *Quercus robur* seedlot were analysed.

INTERNATIONAL REGULATIONS ON FOREST REPRODUCTIVE MATERIAL

The OECD scheme (OECD 1974) tries to ensure "trueness of name" for marketable plant material, the main objective being to *standardise terms of quality* ("to provide clear information for the customer") by introducing four broad categories aimed at unifying otherwise confusing labels and designations for forest seed and plants (reproductive material). The scheme only gives minimum quality requirements; its application in member countries (and others) is voluntary. However, the regulations have to be adopted as a whole if the OECD label is to be applied. The originally established categories of the certification are: "source-identified" (a minimum standard), "selected", "from untested seed orchards", and "tested". Material not qualifying for one of these categories has to be identified as such.

Moreover, the EC is very concerned about a *functional market* in this area (Council of the European Economic Community 1966), a market that does not compromise other goals, such as the maintenance of healthy forests with a high and sustainable production level, and the proper use of the material. The latter concern is not directly implemented in the directive, but many measures there try to encourage the user to buy material that is adequate not only for his or her individual needs, but also for the community's interest in the environment and the forests. This may even lead to member states imposing further regulations on basic material (material that is utilised to produce reproductive material) or restricting the use of material unsuitable for their territories.

These two multinational schemes have not been fully compatible in their original forms (see, for example, Nather 1992); furthermore there have been a number of amendments over the years in both of them. An IUFRO Working Party (2.10.00, chair: H.-J. Muhs, Großhansdorf, Germany; homepage: http://iufro.boku.ac.at/iufro/iufronet/d2/hp21000.htm) deals with issues of legislation on forest reproductive material. A further concern is that "unconventional", e.g. biotechnological, methods for seed and plant production require a flexible scheme. Otherwise, further amendments would be necessary with each technical advance. Therefore, in a continuing discussion, both schemes have been revised and proposals for new documents are on the table. The aim is to *unify labelling requirements* in such a way that one label fulfils the needs of both regulations. One point that has not yet been resolved is the marketing of genetically modified organisms. The EC approach to this problem is rather cautious, allowing additional regulations to be imposed on such material whenever scientific advice should suggest so (Commission of the European Communities 1999). In the discussion on revision of the OECD scheme, a consensus on this issue has not yet been achieved.

An important aspect in the context of this paper is the fact that there is - reading between the lines - a certain shift in these international regulations as compared to the past. *Verifying the quality* of reproductive material becomes more important. For a national market, customers will often be satisfied with their national authorities issuing a "stamp of approval" for the seedlots. Will they also accept such a "seal of quality" from another country? The feeling is there that more and more "paperwork" has to accompany the actual product (seeds and plants) so that no doubt remains on the reliability of the certificate. Methods of certification that are based on tests of a sample of the actual seedlot would hopefully raise customer confidence and ensure that both of the following objectives can be met: opening of markets *and* supply of seed that is suitable for a given country or region. What would be more appropriate today than turning to molecular genetics for an answer?

CENTRAL EUROPE AND THE IMPORTANCE OF PROVENANCES AND GENETIC DIVERSITY (MINIMUM GENETIC BASE)

A further issue is of great concern, especially for Central European countries: big emphasis is given here on the *provenance of a seedlot* (Table 1). Regions of provenances are carefully outlined on maps, and the exact geographical locations are cast in laws and bylaws, e.g., in Germany (Anonymous 1994) and Austria (Anonymous 1996). One reason for this great administrative and legislative effort is the importance of forests for the *protection of sensitive landscapes*, in this case, in the Alps and Carpathian Mountains. The use of wrong provenances in high mountain forests will often lead to a great risk of disasters like avalanches and mudslides. The general public, alarmed by the scientific debate on global warming, is even more sensitive in this area now than 30 years ago. Big mountain ranges like those in Central Europe have a particular feature that is important here, namely the great diversity of climatic and site conditions. Specific conditions often change abruptly over short geographic distances, as is the case for watersheds or changes in ground rock composition.

The practical administration of reproductive material for this mosaic of ecological conditions has been accomplished by the creation of *seed trade and elevation zones* (Table 1). Trading of seed is only encouraged within, not across, the geographical regions of provenances. Elevation, which is a prime determining factor of ecological conditions in mountain areas, has been shown to lead to genetic adaptation of tree populations. Numerous field trials have made this clear, and the growth difference between high and low elevation provenances of, for example, spruce (*Picea abies*) from Austria is clearly visible to a layman in the forest nursery. In the case of oaks, the differences in ecological profiles between the two species, *Q. petrea* and *Q. robur*, but also the intraspecific differences between provenances raise similar concerns for the maintenance of healthy and productive stands (Svolba and Kleinschmit 2000).

Table 1. Some regulations on forest reproductive material in Central Europe

country	regulations for provenances/stands	specific rules	reference
Austria	provenance and elevation zones; approval of stands	minimum genetic base: at least 20 seed parents	Müller in Geburek and Heinze (1998)
Germany	provenance and elevation zones; approval of stands	-	Stephan in Geburek and Heinze (1998)
Netherlands	provenance zones; list of recommended sources	-	de Vries in Geburek and Heinze (1998)
Switzerland	provenance zones	-	Bonfils & Finkeldey in Geburek and Heinze (1998)
Slovakia	provenance and elevation zones	rather strict rules on transfer across elevation zones	Paule in Geburek and Heinze (1998)
Czech Republic	provenance zones	use of material from same provenance compulsory	Vancura in Geburek and Heinze (1998)
Hungary	provenance zones	certificates required for marketing	Matyas in Geburek and Heinze (1998), Solymos (1995)

All of these considerations have resulted in *detailed regulations for seed harvesting, processing, and labelling* (Table 1). Some of these regulations also take account of another fact: *the variability between seedlots from single trees* of a stand or provenance. Field tests of single tree harvests of oak, like those initiated by Krahl-Urban in Germany (Krahl-Urban 1953), revealed that beside provenance differences, a large proportion of the variability can be attributed to the individual tree from which the seeds were harvested (Krahl-Urban 1959, p. 56; for a general discussion, see, for example, Kleinschmit et al. 1996a). Interestingly, the first provenance trial of oaks in Central Europe, that of Cieslar, located near Vienna and planted in 1905, was also based on single-tree harvests (Cieslar 1923). In other tree species, field tests have shown that the variability between single tree seedlots can be of the same order as the variability between provenances (e.g. *Fraxinus excelsior*, Kleinschmit et al. 1996b; *Prunus avium*, Weiser 1996a) and new provenance trials take account of this by carefully mixing equal amounts of seedlings from a number of single tree seedlots (20 in many cases) to make up the "provenance" in the trial (Weiser 1996b). To minimise the risk of bad performance, it is necessary to harvest from a high number of trees in each stand. Present regulations often require that stands approved for seed harvest are of a minimum size or consist of a minimum number of flowering trees. Likewise, seed orchards have to be composed of a minimum number of different clones. The flowering behaviour of seed orchard clones is subject to compulsory observations in Austria (Anonymous 1996). However, such detailed legal requirements introduce costs for all parties involved. There are concerns that such costs are avoided by breaking the rules, so that efficient control measures are needed.

CONTROL

As inherent traits of seeds, and to a little lesser extent, plants, cannot be judged quickly enough with field test methods, *strict control schemes* are in place. In Austria, stands for future seed harvest have to be approved after a visit by experts. When the harvest actually takes place, seeds have to be collected from at least 20 trees in the case of oaks (there is even a "premium" category of seedlots "with higher genetic diversity" for which seeds from 50 trees are required; Anonymous 1996). Separate samples of five acorns from each of these trees have to be shipped to the Austrian Federal Forest Research Centre for testing purposes. District administration authorities have to confirm that all legal requirements have been met - a difficult task to do, as there are numerous possibilities for unlawful manipulation of the seedlots. Permanent surveillance during all steps would be necessary - of course, this is not possible.

Over the last decades, research in biochemical and genetic variation of tree populations using laboratory methods has intensified. Isozyme genetic markers turned out to be of limited use for the purpose of provenance characterisation, especially on the rather fine scale required by legislation in many countries. Among the successful exceptions are species of fir (*Abies* sp.) in Europe and Western Asia (Hosius et al. 1996, Matschke and Bergmann 1998, Bergmann and Matschke 1998). However, variation between provenances as evident in common garden experiments must have a genetic base - therefore, attention now turns to molecular genetics, i.e., DNA analysis. It is hoped that one day markers or, indeed, genes are identified that either "fingerprint" each provenance or that are responsible for the growth differences observed. Examples of chloroplast DNA differentiation are encouraging - at least the descent from different glacial refugia can be traced in most species (Taberlet et al. 1998). However, even in European oaks, where a lot of data have accumulated, the scale of resolution achieved is not yet sufficient to meet the demands of European seed trade regulations. Presently, this topic is the subject of intensive studies in a number of laboratories

It is much more difficult to prove genetically whether a seedlot has been harvested from a particular (approved) stand or not. The main problem here is the high number of potential mothers (within the stand) and fathers (within and outside the stand), and their generally high within-stand genetic variability. Analysing whether the genetic composition of a seedlot conforms to the special legal requirements in Austria (to harvest seed from at least 20 trees) is also a demanding task, especially for hardwoods, but there are possibilities that should be given a trial. We have undertaken a pilot study in this direction that will be introduced in the following chapter.

MOLECULAR GENETIC MARKERS FOR ANALYSING GENETIC RELATEDNESS IN OAK SEEDLOTS: A PILOT STUDY BASED ON MICROSATELLITES

Microsatellites are currently the marker system of choice for this particular purpose for a number of reasons:

- a substantial number of microsatellite loci is available for analysis (Steinkellner et al. 1997, Kampfer et al. 1998)
- many of these have been mapped on a genetic map (Barreneche et al. 1998)
- they provide sufficient levels of codominant polymorphism to identify individual trees within a stand (Streiff et al. 1999).

In this study (Lexer et al. 1999, Lexer et al. in press), a model half-sib family (28 seedlings) and samples from six single tree harvests were genotyped at nine microsatellite loci. The model half-sib family was harvested from a single tree in an arboretum, whereas the single tree harvests were supplied to the Federal Forest Research Centre in Vienna in the course of the commercial seed harvest as required by the Austrian forest seed bylaw (Anonymous 1996). The acorns of these originally 20 lots (at least five acorns per lot) were sown in the experimental nursery;

only a limited number of those lots produced enough plants (at least four to five) to be included in the analysis.

Analysis of the model half-sib family revealed that the *maternal genotypes can be inferred from the offspring* simply on the basis of Mendelian inheritance of the polymporphic microsatellites (Figure 1A). Analysis of the single-tree harvests revealed contaminations with unrelated seedlings in four out of six families. This result was achieved by either clustering of allele-sharing data, where unrelated individuals were located in a distal position on the phenograms (Figure 1B), or by counting the number of "private" alleles for each seedling within a seedlot - again, unrelated individuals stood out against the remaining seedlings because of their unusually high number of private alleles not present in any other plant of the same lot. Average relatedness between the remaining individuals indicated that they were indeed half-sibs, probably with a proportion of full-sibs among them. For five samples the genotypes of the mother-trees were partially inferred from the offspring alone. The supposed number of five different mother trees was confirmed by direct comparison of the maternal genotypes and by pairwise Fst calculations between families. Our results also suggest that correct genotype reconstruction can be confirmed by monitoring recombination events between linked markers (Lexer et al. 1999).

Genetic linkage between microsatellite markers can also be exploited when focusing on the *paternal contribution to the seeds*. In order to deduce the number of pollen donors directly from genotype data of the offspring, three polymorphic loci, closely linked on the same chromosome, were analysed in an opened pollinated family. Matrices of the haplotypes of the seeds were compared with data obtained by simulating the allelic composition of such seedlots with different numbers of pollen donors after a phase of random mating over many generations. The results suggested that the number of diploid pollen donors can be expressed as an exponential function of the number of the deduced paternal chromosomes in the offspring (Figure 1C). The computer simulations certainly represent a simplification, as they include the assumption of random mating. In a real oak stand, some pollen donors may contribute over-proportionally to the pollen cloud (Streiff et al. 1999). Both of their chromosomes will be detected, while for others, only one chromosome will appear in the offspring. This affects the asymptotic behaviour of the curve (Figure 1C). However, based on the present poor knowledge of the mating system of *Q. robur*, our assumptions seem to be a fair working hypothesis.

Finally, we used a "real" open pollinated family to demonstrate the resolution obtained by genotyping linked haplotypes. Six independent (unlinked) microsatellites were analysed in pollen gametes sharing the same haplotype at three linked microsatellites. The results suggest that most of such gametes are identical by descent from the same father (Lexer et al. in press).

Our results demonstrate that microsatellites are a suitable tool in examining if seeds were harvested from a sufficient number of trees, as demanded by the legal regulations. Furthermore, microsatellites allow predictions on the number of pol-

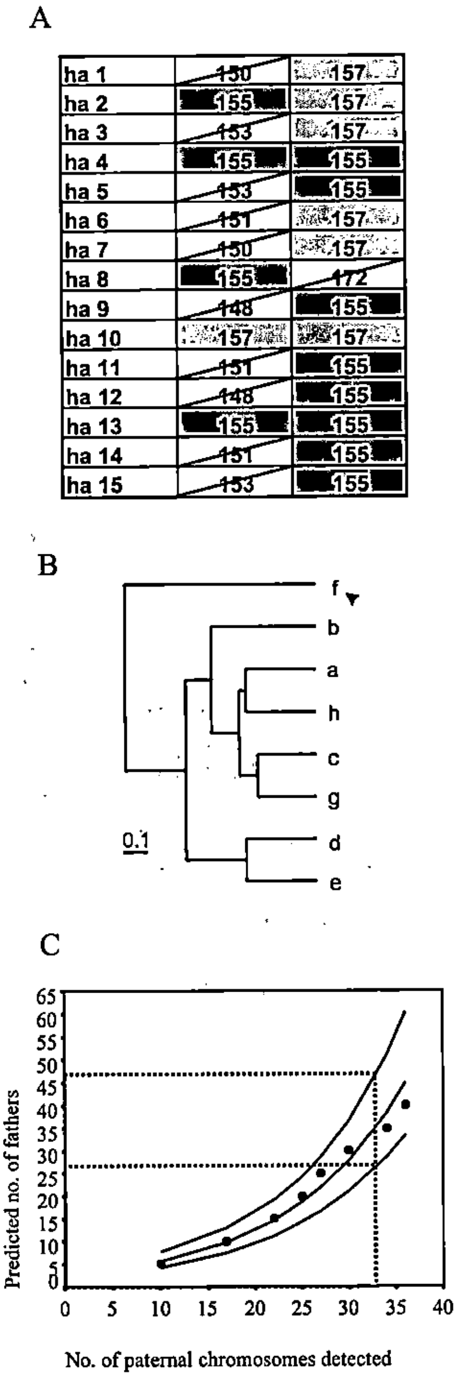

Figure 1. Microsatellite analysis of relatedness and descent in seedlot samples from oak

A) Example for *reconstruction of the maternal genotypes.* The figure shows the genotypes of 15 seedlings, derived from 1 single tree harvest, at one locus (ssrQpZAG 3/64). Alleles have been named according to their molecular size in basepairs. Alleles that are excluded as being of maternal origin have been crossed off the list. The maternal alleles – as inferred from the seedling genotypes – are shaded bright and dark.

B) Example for *detection of seed contaminations.* UPGMA phenogram revealing the genetic relationships between 8 seedlings derived from 1 single tree harvest (seedlings a - f). The phenogram is based on genetic distances calculated with 9 microsatellite markers. The unrelated seedling f is located in a distal position on the phenogram (see black arrowhead). After removing seedling f, the genotypes of the remaining seedlings were consistent with a half-sibling relationship (not shown).

C) Example for *inference of the number of pollen donors.* Regression curve and 95 % confidence intervals obtained with simulated data, relating the number of paternal chromosomes detected with 3 linked microsatellites to the number of fathers in simulated datasets. The regression curve was used to estimate the number of fathers in a real seedlot sample. 33 haplotypes of linked markers were counted in that sample (see x-axis), resulting in a lower 95% confidence limit of 27 fathers (see y-axis). For details see text.

len donors involved. The concept of ensuring a minimum genetic base in commercial acorn seedlots via demanding a minimum number of seed parents is intuitively simple; our results suggest that this can be tested with methods that may even hold in an eventual lawsuit.

OUTLOOK: IT'S ALL IN THE GENES ??

In view of the rapid advances in molecular marker technology and computation methods it seems probable that the next decade will bring a series of advances in molecular genetics of forest seed material. The *characterisation of provenances* may be further improved by introducing novel marker types. Assigning seed to its respective provenance requires markers that are able to detect geographic variation, i.e. this approach will only succeed if such genes or specific combinations of genes (and markers that trace them) really exist. Provenance experiments provide enough data to hold on to this working hypothesis. Maternally inherited DNA markers located in the oak chloroplast genome may be able to meet these demands to some degree (Ferris et al. 1993; Dumolin-Lapégue et al. 1997). In the meantime, there are further advances in chloroplast DNA analysis: microsatellite markers have been isolated from chloroplast DNA (Weising and Gardner 1999). These are expected to be more polymorphic than previously analysed chloroplast markers. Chloroplast data may also be combined with mitochondrial DNA data (Dumolin-Lapégue et al. 1996, Dumolin-Lapégue et al. 1998). Mitochondria are also maternally inherited in oaks (Dumolin et al. 1995). All this together may in the future make it possible to assign a seedlot to its geographical origin on a finer scale.

Tests for the identity of seed source and reproductive material may be feasible in the future with methods introduced in our case study, provided that seed samples from single trees are made available. For instance, maternal genotypes reconstructed from the seedlot and genotype data from the source stand could be compared. If the presumed maternal genotypes cannot be found in the stand, it will be difficult to argue against mislabelling. In seed orchards, where the number of clones is usually smaller than the number of trees in a stand, the task is even simpler. The approach can be quite easily implemented for conifers. A cone contains seed only from a single mother tree, and in many conifers, the haploid endosperm of the seed can be analysed with isozymes, which are often sufficiently variable for the purpose. In hardwoods beside oaks, the microsatellite approach is most promising, but it depends on the availability of primers. Such primers are increasingly being tested, for example for *Fraxinus* sp. (Brachet et al. 1999, Lefort et al. 1999), *Prunus avium* (Heinze unpublished), and *Fagus sylvatica* (Heinze et al. unpublished).

Genetic relatedness within and between seedlots may be elucidated with unprecedented resolution using nuclear microsatellite markers. The potential of the method has been demonstrated by Lexer et al. (1999) and Lexer et al. (in press), as summarised within the present contribution. However, the power of the approach may be further improved by increasing the number of markers employed. In total, 49 microsatellite markers have been isolated from *Q. petraea* (Steinkellner et al. 1997) and *Q. robur* (Kampfer et al. 1998). Preliminary genetic mapping studies show that the microsatellites are distributed over all 12 linkage groups of the oak genome (Lexer 1999), permitting the selection of a large number of unlinked (independent), highly polymorphic microsatellite markers for studies of genetic relatedness.

The genetic basis of economically and ecologically important traits may be dissected with increasing precision by analysing the distribution of quantitative trait loci (QTL) in the genome of various tree species (see). In oaks, the construction of a genetic linkage map based on RAPD, SCAR, microsatellite, minisatellite, isozyme and 5s rDNA markers has been prepared for future QTL studies (Barreneche et al. 1998). One of the primary goals in this context may be the characterisation of QTL controlling traits that are involved in adaptation to specific site conditions. Molecular markers that are linked to adaptive traits, or indeed, adaptive genes themselves, may contribute greatly to the selection of appropriate seed material in the future.

Given the developments outlined above, it can be foreseen today that molecular genetics will play an increasing rôle in maintaining (or even increasing) the quality of forest reproductive material. However, it is not a great act of prophecy to predict that once we have a detailed and structured picture of the components of tree genomes (like we begin to have for the model plant, *Arabidopsis thaliana* – Lin et al. 1999, The European Union Arabidopsis Genome Sequencing Consortium and The Cold Spring Harbor, Washington University in St Louis and PE Biosystems Arabidopsis Sequencing Consortium 1999, Meyerowitz 1999; see also), it will emerge that interaction between those components, and between them and the environment, also plays an important role in controlling tree growth. We are only beginning to understand how complex the various types of interactions can be. Predicting performance of reproductive material, therefore, will always remain a great challenge to science.

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HRASTOVE SJEMENSKE SASTOJINE I ODREDBE O TRGOVINI ŠUMSKIM SJEMENJEM: ISTRAŽIVANJE POMOĆU MOLEKULARNIH MARKERA

Trgovina sjemenjem šumskoga drveća i bilja regulirana je na međunarodnoj i nacionalnoj razini zato jer je vrlo važno da za svako pojedinačno stanište postoji točan tip materijala i ponuda odgovarajućega materijala. Zbog topologije terena (planinski lanci), osobito u središnjoj Europi, stvaraju se raznoliki ekološki uvjeti. Minimalna genetska baza za vrste šumskoga drveća dobiva se skupljanjem sjemena radi pošumljavanja s mnogih stabala u jednoj sastojini. U Austriji se sjeme za tržište mora uzimati s najmanje 20 stabala *Q. robur* i *Q. petraea.* Za testiranje istinitosti navoda prije su na raspolaganju bili samo dugotrajni testovi rasta. Potrebne su se informacije vrlo rijetko dobivale iz izozimske analize. U pilot-studiji mikrosatelitskih markera pokazali smo da se pomoću laboratorijskih podataka iz pojedinih stabala u sjemenskim sastojinama mogu izvesti zaključci o broju sjemenskih roditelja i davatelja peludi od kojih se prikuplja sjeme. Ta se dva parametra procjenjuju pomoću Mendelova pravila nasljeđivanja markera i informacije o genetskoj mapi. Završavamo s izgledima za buduću primjenu molekularne genetike na sjemenski materijal: identifikacija provenijencije vjerojatno će se temeljiti na kloroplastnoj i mitohondrijskoj DNA, dok će analiza genetskoga sastava i odnosa unutar sjemenskoga materijala i između sjemenske sastojine i njezina izvora koristiti visoku razinu polimorfizma koju nude nuklearni mikrosateliti.

Ključne riječi: *Quercur robur*, mikrosateliti, genetska raznolikost, trgovina šumskim sjemenjem, zakonodavstvo

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TAXONOMY AND GENETICS OF CHOSEN OAK POPULATIONS IN SLOVENIA

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Several morphological parameters and cpDNA variability were studied on selected oak populations in Slovenia. The morphological data were measured on leaves from two pedunculate oak (*Quercus robur* L.), two sessile oak (*Q. petraea* Matt. Lieb.), two mixed (*Q. robur* / *Q. petraea*) oak and one pubescent oak (*Q. pubescens* Willd.) populations. For this, 100 leaves were sampled from 5 trees on each location and 9 morphological characteristics were measured or estimated. By using multivariate statistical analysis it was possible to determine the taxonomic status of trees in the *Q. robur* / *Q. petraea* complex. In order to optimise future morphometric investigations in oak populations, results obtained on a large sample (100 leaves per tree) were compared with those from a small sample (5 leaves per tree). Since the quality of information decreased with the sample size, we propose to apply morphometric analyses for the Slovenian oak populations on large samples. For cpDNA analysis, the standardised method has shown no or very little polymorphism among the populations tested. However, the limited number of samples does not allow us to draw any definitive conclusions.

Key words: *Quercus robur*, *Quercus petraea*, *Quercus pubescens*, morphological variation, cpDNA analysis

INTRODUCTION

Forests cover 53% of Slovenia. They have not been influenced by human intervention to such an extent as in most Central European countries. The reason for this is in its mountainous and karst character, with the following consequence: a large proportion of not easily accessible forests.

However, lowland forests of oaks are the most changed forest ecosystems in Slovenia. Due to agricultural activities and urbanisation, they have been transformed into cultural steppes and urban areas. Only a few remnants of them have remained and even these suffer from various disturbances like a changed water table, the input of fertilisers, air pollution impact etc. There are seven (maybe only 6) indigenous oak species (Martinčič, Sušnik, 1984, Batič, 1996, Batič, 1997, Azarov, 1991) in Slovenia (Table 1) (the occurrence of *Q. virgiliana* has not been confirmed recently).

Table 1. Indigenous oak species in Slovenia, their status and share in growing stock of all oak species and the annual felling in 1996 (as compiled by Smolej et al., 1998; # marks endangered species in terms of IUCN categories, * marks the species being in its geographical borderline in Slovenia)

Latin name	Common name	Status	Annual felling in 1996 (m^3)
Quercus robur L.	common oak	7% of all oaks	10,913
Quercus petraea /Matt./ Liebl.	sessile oak	82% of all oaks	76,128
Quercus ilex L.	holm oak	#, *	0
Quercus cerris L.	turkey oak	8% of all oaks	6,260
Quercus pubescens Wild.	downy oak	2% of all oaks	328
Quercus crenata Lam.	false-cork oak	#, *	0
Quercus virgiliana Ten. (?)	Croatian oak	#, *	0

The major oak species in Slovenia have an outlined ecological role, while mainly common oak and sessile oak have also an economic importance. Downy oak is ecologically important in the reafforestation of the karst region. Different oak species in Slovenia often occupy the same ecological niches or, due to the high site diversity in a small area, different oak species can grow in a broad spectrum of ecological conditions. Only 45% of oak forest stands grow in žoak sites', such as *Querco Fagetum, Robori Carpinetum, Querco Ostryetum etc.*, and mixed type sites are frequent. Therefore, the movement of alleles between the populations in hybrid zones and inbreeding occur, while ecological specialisation might represent an obstacle to these processes (Stern, Roche 1974). Sessile oak grows mainly in the colline to montane region on dry sites with well-aerated soils, poor in minerals. Common oak grows on wet sites on soils rich in minerals along rivers and in some karst fields, but it also rises up the hills and becomes mixed with sessile oak. Downy oak is a thermophylic species, growing on dry, shallow or stony soils, especially in the Karst and several warm sites in mid Slovenia (Figure 1).

The size of oak populations in Slovenia is small. The biggest complex of common oak is Krakovski gozd, measuring 3000 ha. The other common oak forests do not exceed 500 ha. The populations of sessile oak grow in bigger areas, but, at least

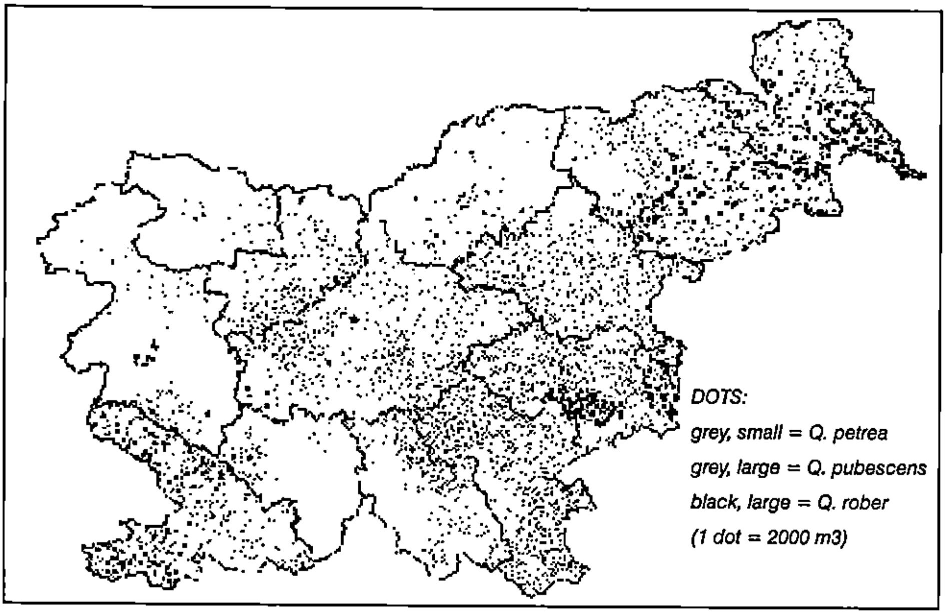


Figure 1. Distribution of *Q. robur, Q. petraea* and *Q. pubescens* in Slovenia

in the lower colline region, always mixed with common oak. Downy oak also grows in mixed stands with sessile oak (and other species) in thermopyllic submediterranean associations. Pure downy oak stands are rare.

Hybridisation between common, sessile and downy oaks in mixed local oak populations can be well adapted to the diversity of microsite conditions (Aas 1993, Kleinschmit 1993, Kleinschmit et. al. 1995, Bacilieri et al. 1995), but also to a high variability in morphological characteristics and unclear morphological differentiation between species. Taxonomical determination can cause problems resulting in rather doubtful knowledge on the distribution of different oak species in Slovenia and their share in the growing stock.

In recent years numerous molecular methods have been developed that enable the efficient detection of variation on the level of DNA. In plants, the study of chloroplast DNA variability is one of the most widely used approaches to study phylogeny or phylogeograpy. The development of universal primers for cpDNA that target variable, noncoding regions of the genome has proven to be of great value in such studies. The analysis of cpDNA has been applied to many different, broadly distributed tree species and has proven its usefulness also in oaks (*Quercus* spp.) (Petit et al., 1993, 1997).

In Slovenia, morphological and genetical studies of oaks started in the nineties (Azarov 1991, Batič et al 1994 etc.). In the last year we have intensified these studies with the application of new molecular methods and with a selection of a larger number of populations in the research. The main objective is to get an insight into genetic variability and to define the real ecological niches of the most widespread oak species in Slovenia. Through the analysis of the spatial distribution of different oak taxons we hope to be able to prepare a long-term concept for the protection of oak genetic resources, to intensify silvicultural measures and measures for the genetic improvement of oaks and to provide adequate advice and control of oak reproductive material in newly defined provenance regions.

In our preliminary study we decided to:

i) standardise the morphological analysis regarding the size of the samples with respect to the variability of the measured characteristics of leaves,

ii) standardise the molecular method in our conditions and survey cpDNA variability in a limited number of Slovenian oak populations to test the usefulness and applicability of this method on Slovenian samples.

The choice of populations tested depended on the regional climatic and local site gradients and the occurrence or absence of hybrids among the *Q. robur, Q. petraea* & *Q. pubescens.*

MATERIALS AND METHODS

For morphological studies, seven oak stands were included in the sampling in NE and in SW Slovenia: 2 *Q. robur* stands ((Zgornji log 1 & Hrastovec 1), 2 *Q. petraea* (Zgornji log 3 & Hrastovec 3), 2 mixed *Q. robur* / *Q. petraea* stands (Zgornji log 2 & Hrastovec 2) and in one *Q. pubescens* stand (Istra 2). The stands Zgornji log 1, 2 & 3 and on the other hand Hrastovec 1, 2 & 3 represent two transects along the ecological gradient.

In each stand we sampled 100 leaves from each of five trees, from the upper sunny side of the crown from the short fertile shoots. The number of measured leaves from each tree is presented in Table 2.

The measurements were done manually and with a digitiser. Hairiness was estimated at 50x magnification. For each tree we measured, estimated or calculated: the length of the leaf lamina (mm), lamina width (mm), length of petiole (mm), depth of the sinusoidal indentations under the maximal laminar width (mm), number of lobes on both sides of the leaf, the presence of intercallary veins (4 ranks: 1 = one, 2 = two, 3 = several single, 4 = several in pairs), the shape of the leaf base (4 ranks: 1 heart-like, 2 = assimetrical with ears, 3 = assimetrical without ears, 4 = clinal), hairiness of the underside of leaf lamina (5 ranks depending on the occurrence 0 – 4) and the ratio between the depth of sinus and laminar width.

Statistical analyses (descriptive statistics, ANOVA, discriminative analysis) were done by "Statistics for Windows 5.0". For the discriminative analysis of the complex *Q. robur* / *Q. petraea* only the characteristics that showed statistically significant impacts on differentiation between the two species were taken into account.

For optimisation of further morphometrical analyses of oak populations in Slovenia we compared the statistical significance of measurements, done on five leaves per tree (small sample) with measurements done on 70 - 100 leaves per tree (big sample).

For cpDNA analysis 2 to 5 trees from four geographically distinct oak populations (including *Q. robur, Q. petraea* & *Q. pubescens*) were included in the analysis. We analysed 5 samples of *Q. robur* from Murska šuma, 2 samples (*Q. robur / Q. petraea*) from Ljubljana, 3 to 5 samples (*Q. pubescens & Q. petraea*) from Kras, Komen pri Devici Mariji, and five samples (*Q. pubescens*) from Istra, Ankaran.

Two methods were used for the extraction of total DNA. The standard CTAB method (Saghai Maroof et al. 1984) with modifications was used for the isolation of DNA from dormant buds, herbarium material and frozen leaves, while isolation using DNAeasy Plant mini kit (Qiagen) was used only for the isolation of DNA from frozen leaves.

The amplification of two chloroplast DNA fragments (CD and DT) was done according to Demesure et al. (1995) using primers trnC [tRNA-Cys(GCA)] and trnD [tRNA-Asp(GUC)] for CD fragment and trnD [tRNA-Asp(GUC)] and trnT [tRNA-Thr(GGU)] for DT fragment. Amplified fragments were restricted with TaqI. For the separation of restriction fragments, two systems were used: 3% agarose (FMC) gels and 8% polyacrylamide (Roth) gels. Agarose gels were stained with ethidium bromide (Sigma) and polyacrylamide gels were silverstained.

RESULTS AND DISCUSSION

MORPHOLOGICAL VARIABILITY

The taxonomic status of trees in the complex *Q. petraea / Q. robur* was determined by discriminative analysis based on the local reference population characteristics. These were measured on trees no. 12, 13 & 14 for common oak and on trees no. 32, 34 & 35 for sessile oak. All other trees were classified by discriminative analysis as follows: 6 were common oak, 11 sessile oak, 3 were hybrids. Trees no. 71, 72, 73, 74 & 75 were not classified since these were the reference trees for downy oak (Figures 2 and 3).

Hybrids occur only in the transect Zgornji log. We suppose this might be due to a continuous shift in site conditions on this plot.

In Table 2 the arithmetic mean values and parameters of the analysis of variance are represented for measured or estimated parameters in different oak taxons.

The most recognisable differences between common & sessile oak are the length of petiole, intercalary veins, hairiness of leaf lower lamina and the shape of the leaf base. The leaves of sessile oak and downy oak are morphologically similar,

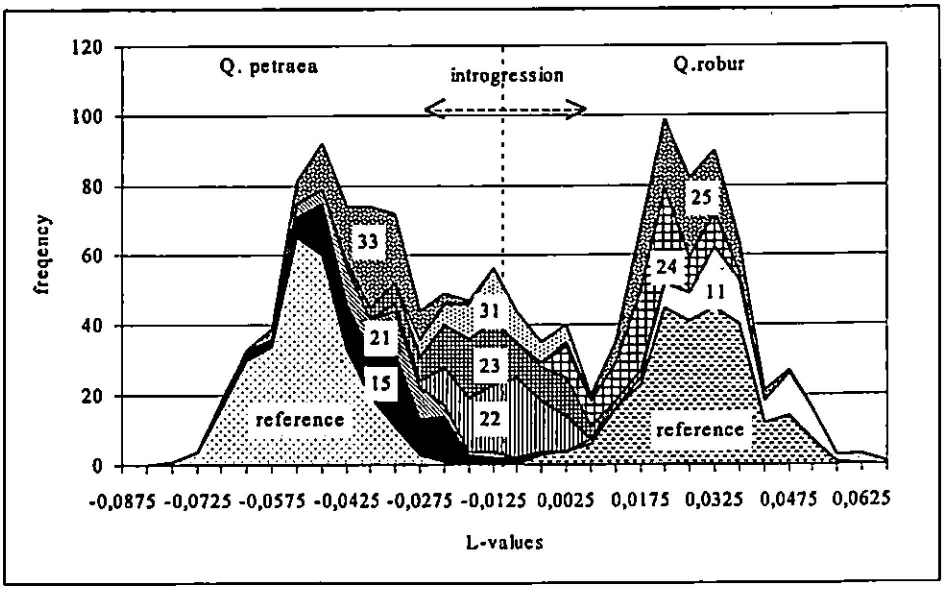


Figure 2. Distribution of the discriminant values (L) for leaves from trees no. 11, 15, 21, 22, 23, 24, 25, 31, and 33 from stands Zgornji log 1, 2 and 3 (transect Zgornji log)

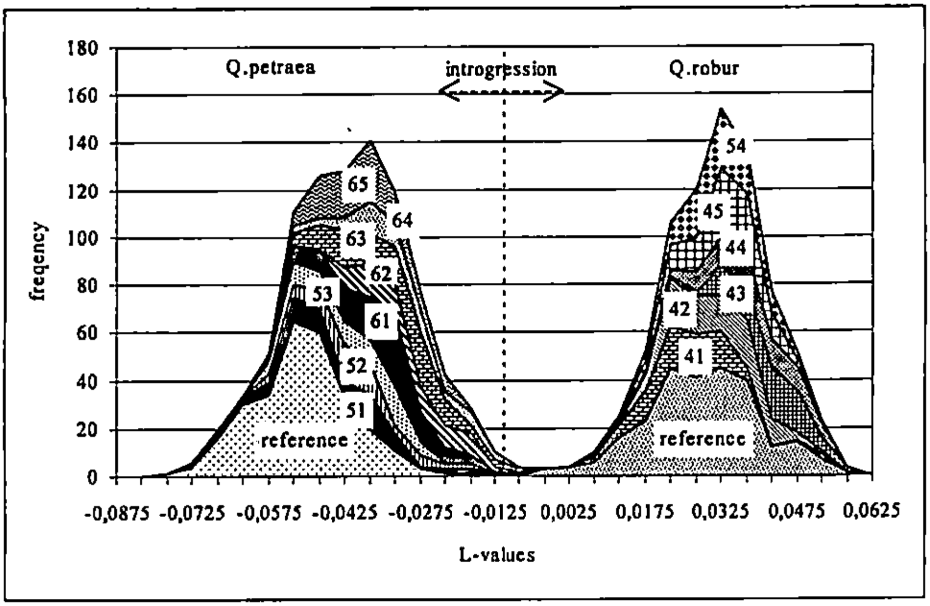


Figure 3. Distribution of the discriminant values (L) for leaves from trees no. 41, 42, 43, 44, 45, 51, 52, 53, 54, 61, 62, 63, 64 and 65 from stands Hrastovec 1, 2 and 3 (transect Hrastovec)

with differences occurring in the size of leaves (length & width), the length of petiole and depth of simuses. The shape of hairs were not considered here. The differences between the aritmetic mean values were statistically evaluated by a non-parametric test after Kruskal-Wallis. All differences are statistical significant at a probability of error below 0.001.

Table 2. Comparison of 4 oak taxons: mean values and χ^2 values of the analysis of variance between groups (Kruskal – Wallis test)

	Group1	Group 2	Group 3	Group 4	χ^2 value
Oak species	*Q. robur*	*Q. robur* X *Q. petraea*	*Q. petraea*	*Q. pubescens*	
No. of trees	6	3	11	5	
No. of leaves	1045	257	1158	500	
DP–petiole length (mm)	6,6	14,5	19,3	9,6	2170,54
IZ – intercalary veins	2,9	1,3	0,5	0,5	1349,25
OD-Leaf base	1,7	2,9	3,2	3,0	1071,99
GS-depth of sinuses (mm)	20,4	16,8	16,5	9,1	700,99
PU-pubescence	0,23	1,89	3,24	3,34	642,10
DL–length of lamina (mm)	92,5	93,5	96,5	52,3	610,85
SL-width of lamina (mm)	65,0	65,2	66,7	38,1	605,07
K-number of lobes	9,8	12,1	12,1	9,8	563,38
LDR-Lobe depth ratio	0,62	0,51	0,48	0,47	507,86

OPTIMISATION OF SAMPLING PROCEDURES

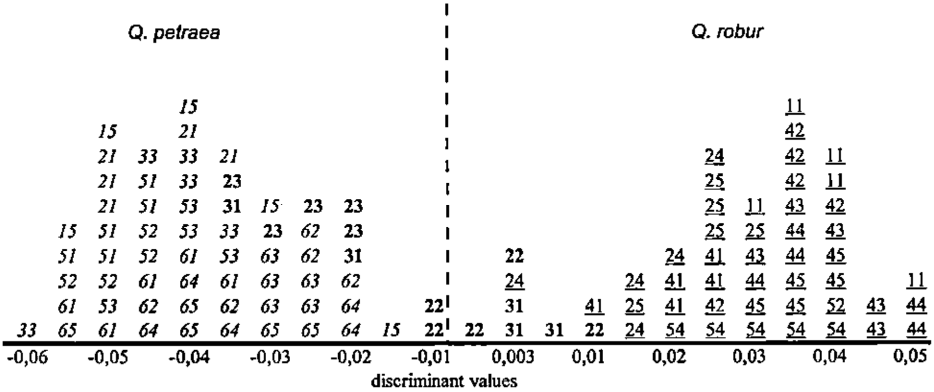
The classification of leaves based on equal discriminative analysis was also done on a small sample of 5 leaves per tree. In this case the taxonomical status of oak trees is less clear and can lead to false conclusions (Fig. 4).

Using the same sets of data we also made a comparison of the quality of measured parameters depending on the size of sample for numerical characteristics. The quality of results is represented by the relative error of mean values (Table 3), as calculated after the following formula:

$$D\% = Z * KV\%/\mathrm{sqrt}(n)$$

The relative error depends on the size of the sample and the variability of each characteristic. For the big sample it is 2.5 to 6% , for the small sample it reaches 10 to 30%. A large error means less confidence with respect to the arithmetic mean and in accepting hypotheses on the differences among the mean values, the variability of characteristics, etc. In our samples the highest relative errors can be found for the depth of sinuses

In Table 4 the needed number of leaves per tree is calculated in order to reach the chosen value of the relative error of the arithmetic mean value (D% = 5% and D% = 10%).



*(italic = Q.petraea; bold = hybrid foms; underlined = Q. robur)**

* - according to previos clasification, based on large sample

Figure 4. Distribution of discriminant values for leaves, based on a sample of 5 leaves per tree (each number represent one leaf from the tree with the same number)

In order to reach 5% relative error of the estimated arithmetic mean, we need ca. 4 times bigger sample than for a relative error of 10%. Therefore, the necessary sample size should be 50 to 100 leaves per tree.

cpDNA VARIABILITY

The standard CTAB procedure was used for the isolation of DNA from three different types of starting material: fresh dormant buds, frozen leaves and dry leaves from the herbarium. DNA isolated from fresh dormant buds was of high quality and was later successfully used for amplification. DNA extracted from frozen leaves was also of high enough quality to give us the amplification in almost all samples, but DNA from the herbarium material failed to amplify. DNAeasy Plant mini kit proved to be more efficient for the extraction of DNA from frozen leaves than the CTAB method and gave high quality DNA from almost all properly frozen samples. The quality of extracted DNA from different starting materials showed that both the used methods, CTAB and DNAeasy Plant mini kit, can be efficiently used for DNA extraction from frozen leaves. The quality of the frozen material proved to be crucial for successful DNA isolation. Dormant buds appeared to be very appropriate material for DNA extraction and can be of especially important use during the winter when fresh material is not available.

Two pairs of primers sucessfully amplified cpDNA. The length of the CD fragment was about 3000 bp and DT fragment was about 1800 bp. CD and DT products were of the same length in all analysed individuals.

The restriction fragments, separated on agarose gels, showed no polymorphism. The separation of CD-TaqI restricted fragments on polyacrylamide gels

Table 3. Comparison of two sampling models (large and small sample size) according to the relative error of the mean value (D%)

Tree No.	Sp.	Sample size		Lamina lenght (DL)		Lamina width (SL)		Petiole lenght (DP)		Depth of sinuses (GS)		Lobe depth ratio (LDR)	
		n_1	n_2	D% (n_1)	D% (n_2)	D% (n_1)	D% (n_2)	D% (n_1)	D% (n_2)	D% (n_1)	D% (n_2)	D% (n_1)	D% (n_2)
Zgornji log 1:													
11	*rob.*	81	5	4,7	17,1	5,3	13,7	5,1	16,5	6,8	18,7	3,5	8,1
12	*rob.*	57	5	4,2	10,8	5,2	11,4	5,6	11,2	8,2	14,8	5,2	13,9
13	*rob.*	100	5	3,6	17,1	4,0	22,6	4,8	28,5	5,6	26,5	4,2	6,9
14	*rob.*	100	5	3,7	7,3	3,9	16,3	4,9	26,2	6,4	43,2	3,5	27,7
15	*pet.*	100	5	3,1	18,4	3,6	23,1	4,0	19,5	5,6	38,0	3,5	18,9
Zgornji log 2:													
21	*pet.*	59	5	3,7	8	4,4	10,5	5,5	16,9	6,8	13,2	4,3	9,0
22	*hyb.*	100	5	3,4	12,5	3,6	4,5	4,4	21,9	5,8	10,6	3,4	9,3
23	*hyb.*	100	5	3,4	16,3	4,1	16,7	3,7	9,4	5,6	23,3	3,2	13,0
24	*rob.*	100	5	2,7	10,6	3,0	19,5	4,3	17,8	6,2	47,9	5,0	39,1
25	*rob.*	100	5	2,9	8,3	3,7	9,8	6,3	24,4	5,1	8,0	3,0	9,2
Zgornji log 3:													
31	*hyb.*	57	5	4,4	5,2	5,3	5,3	5,6	29,0	7,7	19,0	5,6	18,8
32	*pet.*	100	5	4,0	16,5	3,9	16,9	4,7	29,3	5,8	17,1	3,4	8,4
33	*pet.*	100	5	3,3	17,3	4,1	22,2	4,2	25,9	7,1	28,4	4,4	7,6
34	*pet.*	100	5	3,5	15,7	3,6	20,5	3,6	10,3	5,8	31,4	3,6	24,0
35	*pet.*	78	5	3,7	17,6	4,2	26,6	4,0	18,1	7,8	59,3	5,3	40,5
Hrastovec 1:													
41	*rob.*	77	5	4,3	14,2	4,5	26,2	4,8	15,6	6,8	19,9	4,3	7,7
42	*rob.*	95	5	2,8	10,7	3,6	12,5	4,8	12,0	5,6	22,8	3,9	13,6
43	*rob.*	75	5	2,9	7,3	3,1	7,7	5,1	27,6	4,4	4,3	3,2	9,4
r44	*rob.*	67	5	4,1	16,3	5,3	25,2	6,3	11,2	7,2	28,4	4,0	12,8
45	*rob.*	100	5	2,7	14,7	3,5	12,6	5,3	16,4	5,2	18,7	3,3	11,2
Hrastovec 2:													
51	*pet.*	63	5	4,9	25,2	6,1	25,1	5,4	19,8	8,7	28,4	5,4	18,6
52	*pet.*	62	5	4,4	10,0	6,6	17,4	6,6	42,4	10,5	31,4	5,7	26,6
53	*pet.*	69	5	4,1	12,3	5,3	17,3	5,2	13,7	8,9	24,5	5,2	20,9
54	*rob.*	93	5	3,4	13,2	3,9	16,3	5,8	15,8	5,2	20,0	3,6	11,3
Hrastovec 3:													
61	*pet.*	100	5	3,8	13,9	4,2	8,1	3,2	11,7	5,5	16,1	3,5	14,5
62	*pet.*	68	5	3,0	13,8	4,4	22,5	4,7	9,8	6,5	28,0	3,9	10,9
63	*pet.*	100	5	3,4	10,2	3,8	10,7	3,6	7,1	5,7	13,9	3,1	13,1
64	*pet.*	59	5	4,7	15,3	5,8	22,7	4,7	27,4	8,6	34,8	4,2	18,9
65	*pet.*	100	5	2,8	12,2	3,0	13,2	3,8	21,8	4,6	30,3	2,7	22,5
Istra 2:													
71	*pub.*	100	5	3,3	12,8	3,5	18,4	5,7	28,4	7,3	38,1	6,2	24,2
72	*pub.*	100	5	2,3	11,2	2,4	16,6	4,3	21,2	5,4	22,5	4,9	14,2
73	*pub.*	100	5	2,8	6,4	3,4	18,3	4,4	10,4	5,8	36,1	4,7	42,1
74	*pub.*	100	5	2,7	15,4	2,6	11,4	3,7	13,3	5,2	11,9	4,1	11,3
75	*pub.*	100	5	2,1	7,5	2,9	9,9	4,7	24,0	5,3	22,8	6,2	29,2

Table 4. Estimated number of leaves per tree in a sample (n) required to reach specified criteria for the relative error of mean value (D%)

Tree No.	Sp.	Lamina length (DL)		Lamina width (SL)		Petiole length (DP)		Depth of sinuses (GS)		Lobe depth ratio (LDR	
	-	n(5)	n(10)	n(5)	n(10)	n(5)	n(10)	n(5)	n(10)	n(5)	n(10)
Zgornji log 1:											
11	*rob.*	72	18	93	23	84	21	152	38	41	10
12	*rob.*	41	10	62	15	72	18	153	38	61	15
13	*rob.*	51	13	63	16	93	23	127	32	72	18
14	*rob.*	55	14	62	16	98	24	166	42	50	13
15	*pet.*	39	10	52	13	64	16	124	31	48	12
Zgornji log 2:											
21	*pet.*	32	8	46	12	71	18	108	27	43	11
22	*hyb.*	48	12	52	13	76	19	133	33	46	12
23	*hyb.*	46	11	66	16	56	14	125	31	41	10
24	*rob.*	29	7	37	9	74	19	154	38	100	25
25	*rob.*	33	8	55	14	157	39	102	26	35	9
Zgornji log 3:											
31	*hyb.*	44	11	63	16	72	18	135	34	71	18
32	*pet.*	64	16	62	15	88	22	136	34	46	11
33	*pet.*	45	11	68	17	69	17	199	50	77	19
34	*pet.*	50	12	53	13	51	13	134	34	51	13
35	*pet.*	43	11	56	14	49	12	188	47	86	22
Hrastovec 1:											
41	*rob.*	57	14	61	15	70	17	143	36	58	14
42	*rob.*	29	7	50	12	88	22	121	30	59	15
43	*rob.*	25	6	28	7	78	20	57	14	31	8
44	*rob.*	46	11	76	19	106	27	139	35	43	11
45	*rob.*	30	7	49	12	112	28	108	27	43	11
Hrastovec 2:											
51	*pet.*	62	15	95	24	73	18	191.	48	73	18
52	*pet.*	48	12	107	27	107	27	274	68	79	20
53	*pet.*	46	12	76	19	75	19	219	55	76	19
54	*rob.*	42	11	57	14	125	31	99	25	47	12
Hrastovec 3:											
61	*pet.*	57	14	71	18	42	10	122	31	49	12
62	*pet.*	25	6	52	13	59	15	117	29	41	10
63	*pet.*	47	12	59	15	51	13	132	33	39	10
64	*pet.*	52	13	80	20	52	13	176	44	42	11
65	*pet.*	32	8	35	9	58	15	85	21	30	7
Istra 2:											
71	*pub.*	43	11	50	13	132	33	216	54	152	38
72	*pub.*	21	5	24	6	74	18	115	29	97	24
73	*pub.*	31	8	45	11	77	19	135	34	89	22
74	*pub.*	29	7	27	7	54	14	110	27	68	17
75	*pub.*	17	4	34	9	88	22	112	28	155	39
Average value (column)		42	11	58	14	79	20	141	35	63	16

Note: n (5) = no. of leaves per tree in a sample to reach 5% relative error of mean (D%)
n (10) = no. of leaves per tree in a sample to reach 10% relative error of mean (D%)

also showed a monomorphic pattern for all analysed samples. Low variation was detected only in DT-TaqI restricted patterns. Two samples, one from Murska šuma and the other from Istra, Ankaran, exhibited a few polymorphic (additional or absent) bands.

A very low level of DNA variation was detected in the analysed oak samples. No polymorphism was detected between individuals of otherwise morphologically well defined (distinct) and geographically separate populations. The preliminary results indicate a surprisingly lower variation than suspected and cannot support the findings of Zanetto et al. 1994, who, on the basis of isozyme analysis, detected in Slovenian samples a much higher genetic distance between *Q. robur* and *Q. petraea*, as compared to inter-regional inter-specific genetic distances.

The limited number of analysed samples does not allow us to draw any definitive conclusions. The inclusion of additional samples and especially the analysis of additional cpDNA fragments would probably enable us to identify more useful polymorphisms. The use of microsatellite markers (Steilkellner et al., 1997) and sequencing also promise more efficient detection of variation which could all greatly improve the study of the genetic structure of oak populations in Slovenia and their postglacial migration routes.

CONCLUSIONS

The precise taxonomic classification of oaks is possible by use of characteristics which show the highest differentiation and multivariate statistical analyses. The occurrence of common and sessile oaks in mixed stands does not necessarily support their hybridization, which seems to depend more on site characteristics and their variation in the space.

Downy oak is morphologically, with respect to numerical characteristics, similar to sessile oak and the delimitation between these two species seems more difficult than between sessile oak and common oak. The main differential characteristic is the hairiness of the lower leaf lamina. The frequency of trichomes is similar, but their morphology is different.

The size of the sample in morphometrical studies defines the quality of the taxonomical classification of common and sessile oak and has a role in the analysis of the intra- and inter-populational variability of each oak species. An adequate sample size depends on the goals of the studies in Slovenia. For taxonomical studies the samples can be of medium size (10 - 50 leaves per sample), while for any estimation of the values of morphological characteristics (D% = 5%) biger samples are needed (n = 40 -100) .

In the cpDNA analysis, the method was sufficiently standardised. However, it showed no or very little polymorphism among the populations tested. So far, the limited number of samples does not allow us to draw any definitive conclusions.

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TAKSONOMIJA I GENETIKA IZABRANIH HRASTOVIH POPULACIJA U SLOVENIJI

Istraživano je nekoliko morfoloških parametara i varijabilnost kloroplastne DNA na izabranim hrastovim populacijama u Sloveniji. Morfološki su podaci mjereni na lišću populacija dvaju hrastova lužnjaka (*Quercus robur* L.), dvaju hrastova kitnjaka (*Q. petraea* /Matt./ Lieb.), dvaju mješovitih (*Q. robur* / *Q. petraea*) hrastova i jednoga hrasta medunca (*Q. pubescens* Willd.). U tu su svrhu prikupljeni uzorci 100 listova s 5 stabala na svakoj lokaciji i izmjereno je ili procijenjeno 9 morfoloških svojstava. Primjenjujući multivarijatnu statističku analizu, odredili smo taksonomski status stabala u kompleksu *Q. robur* / *Q. petraea*. Radi optimizacije budućih morfometričkih istraživanja u hrastovim populacijama rezultati dobiveni na velikom uzorku (100 listova po stablu) uspoređeni su s rezultatima dobivenim iz maloga uzorka (5 listova po stablu). Budući da se kakvoća informacije smanjuje s veličinom uzorka, predlažemo da se za slovenske populacije hrastova primjenjuje morfometrička analiza na velikim uzorcima. Za analizu kloroplastne DNA standardna je metoda pokazala nikakav ili vrlo mali polimorfizam u ispitanim populacijama. Međutim, ograničeni broj uzoraka ne dopušta nam da izvedemo neke određene zaključke.

Ključne riječi: *Quercus robur, Quercus petraea, Quercus pubescens*, morfološka varijacija, analiza kloroplastne DNA

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UDK 630*165 (Quercus robur L.)

ESTIMATION OF GENETIC GAIN IN A PROGENY TRIAL OF PEDUNCULATE OAK (*QUERCUS ROBUR* L.)

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In the central Podravina seed region (Croatia), phenotypic selection of pedunculate oak (*Quercus robur* L.) was made and an experimental clone seed orchard with 40 clones was founded. During 1992, a test consisting of 21 half-sib progenies was established. The progeny trial involved the families from the selected mother trees included in the clonal seed orchards and belonging to the central Drava River seed region, with two populations (Donji Miholjac and Slatina). Total heights were measured at the plantation age of 2 + 3, 2 + 4, 2 + 6 and 2 + 7 years. An estimation of genetic parameters (heritability and genetic gain) was made for in total 21 half-sib progenies, as well as separately for half-sib progenies from each population.

Key words: *Quercus robur*, progeny trial, genetic parameters.

INTRODUCTION

In the Republic of Croatia the pedunculate oak occupies large areas as one of the most important and the most valuable forest tree species. Although the pedunculate oak forests are of high quality, efforts are being made to improve their management, especially due to problems of natural regeneration manifested in the last few decades. The acorn yield is no longer regular, and for a high acorn yield ten years or even more of waiting is required. For this reason there are problems not only in natural regeneration, but also in the filling up of the partly naturally regenerated areas as well as in the afforestation of clearings. To avoid or to reduce this problem, the raising of clonal seed orchards started to enable the control of production concerning both the genetic quality and the acorn yield (Vidaković

1996). Thus, the half-sib progeny trial of pedunculate oak was established with plants raised from selected open-pollinated plus trees, for the purpose of determining the genetic quality of our mother trees.

To ensure the maximum possible objectivity in the genetic gain estimation for the generative progenies grown in the future clonal seed orchard, it is necessary to test the selected plus trees by genotype. On the basis of the growth of their progenies, an estimation as objective as possible of their heritability (h^2) would be made and then, based on their general combining ability (GCA), the secondary selection of mothers in the established clonal seed orchard would be made.

The progeny trial involved the families from the selected mother trees included in the clonal seed orchards and belonging to the central Drava River seed region, with two populations (Donji Miholjac and Slatina).

MATERIAL AND METHODS

In 1988, the work on the establishment of an experimental pedunculate oak clonal seed orchard started in the Forest District Našice. As a part of this work, in 1989, seeds from the selected plus trees were harvested, and in the following years the plants, the half-sib progenies of open-pollinated plus trees, were grown for the purpose of the establishment of a plus tree half-sib progeny trial. The percentage of germinated acorns ranged between 20 and 73 %, the average for all samples being 50.3 % (Vidaković et al. 1992).

Of 40 selected plus trees, aged from 75 to 120 years, twenty-one yielded enough acorns from which plants for the establishment of the field experiment were grown. The amount of acorns borne by another six plus trees was so low that we could not grow a sufficient number of plants, while the remaining 13 plus trees did not fructify at all.

The experiment was established in spring 1992, in the forest unit Krndija, in the locality of Vukojevački Šikar, with plants aged 2 + 0 years. In addition to the acorns from plus trees, acorns were also harvested as a random sample from the Donji Miholjac (DM) and Slatina (S) stands, from where the selected plus trees come, too (Vidaković 1996).

The experiment was established in a random plant distribution with a total of 25 treatments in five blocks, with four plants in a plot. Heights were measured at the plantation age of 2 + 3, 2 + 4, 2 + 6 and 2 + 7 years.

The estimation of genetic parameters (heritability and genetic gain) was made for in total 21 half-sib progenies, as well as separately for half-sib progenies from each population (eight from the Donji Miholjac population and thirteen from the Slatina population).

The statistical model is as follows:

$$Y_{ijk} = \mu + Block_i + Female_j + BF_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the k^th^ tree of the j^th^ female in the i^th^ block, μ is the experiment mean, $block_i$ is the i^th^ block, $female_j$ is the j^th^ female, BF is the interaction of the i^th^ block and j^th^ female, ε_{ijk} is random error.

Formulas for family heritability and gain are:

$h^2 = \frac{\frac{1}{4}\,\delta^2_{fam}}{\delta^2_p}$ and $\Delta G = i\,h^2\,\delta_p$ respectively (van Buijtenen & Yeiser 1989).

The calculation of genetic gain for the selection by phenotype was made according to the formula $\Delta G = i\,h^2$, and for the selection intensity by the genotype 10/21 for the expected genetic gain (Becker 1984).

RESULTS AND DISCUSSION

By the analysis of variances, the statistically significant differences for the height increment trait between the pedunculate oak half-sib progenies were obtained, and this at the population level as well as inside the investigated seed region (Table 1). This indicates the existence of a distinctly marked genetic differentiation inside individual populations (Donji Miholjac, Slatina), that is, in the investigated central Drava River seed region.

The estimated heritability value (h^2) for the total height trait in all half-sib progenies was between 0.74 and 0.87, depending on the year in which the investigation was carried out, which suggests that this trait should be under high genetic control (Table 1). The heritability values in the investigated half-sib progenies from individual stands were also high, from $h^2 = 0.70$ (the Slatina population) to $h^2 = 0.90$ (the D. Miholjac population), depending on the population age, too. The reason for such obtained values is the fact that the pedunculate oak stands underwent several thinnings by which minus trees were eliminated, thus reducing the selection differential. This resulted in an increase in the average total height value in the populations where the selection had been made. The high heritability values for the total height were obtained at the juvenile age in other oak species, too, as stated by Min (1992), Struve & McKeand (1994), Jensen et al. (1997).

The heritability values (h^2) changed at various half-sib progeny ages, but, with the increase of age, mostly the higher estimated values were obtained (Table 1). This referred to the estimation of genetic heterogeneity for both the half-sib progenies inside individual populations (Donji Miholjac, Slatina) and to all tested half-sib progenies inside the seed region. The value was increased because, with ontogenetic ageing, the genetic heterogeneity of the half-sib progenies from the selected trees becomes more distinctive, showing the differences in phenotypical expression during ageing. Estimations of the genetic heterogeneity values (h^2), for the total height trait in *Q. acutissima*, rose with the increase of age in the research made by Toda et al. (1994), too.

From the obtained results of the genetic gain estimations (ΔG), it can be seen that, because of the very early age, they were somewhat lower than the expected genetic gains, in relation to the control from the seed region. The controls consisted of plants grown from a random sample from the individual populations and from the seed region. The achieved genetic gain in half-sib progenies was lower, in some cases even negative (the Slatina population), than the expected genetic gain in the populations. Although the achieved genetic gain at this juvenile age is lower than the estimated one, the obtained real values are explainable by the fact that the selected plus trees belonged to various populations, which resulted in an increase in genetic heterogeneity value (h^2) and a decrease in genetic differential in the progenies. The average of the grown progenies achieved after the selection criteria (x > + 2 s) of mother (plus) trees, between the phenotypically superior trees only, made it possible to obtain such achieved genetic gain. In relation to the control, the achieved genetic gain in particular populations ranges between negative values and 6.0 % or in total from 1.0 to 2.0 % for the seed region, depending on the stand age (Table 1).

Table 1. Estimation of genetic parameters for the total heights in the progeny trial of *Quercus robur*

Half-sib progenies	F value	Heritability (h^2)	expected ΔG		realised ΔG	
			cm	%	cm	%
1995th Year – Plantation age 2 + 3 yrs						
Seed region Srednja Podravina	3.85**	0.74	12.4	13.0	1.8	2.0
Population Donji Miholjac	6.56**	0.85	14.6	15.0	0.8	1.0
Population Slatina	3.32**	0.70	12.0	13.0	2.8	3.0
Selected half-sibs (10/21)	-	-	10.0	10.5	10.3	11.0
1996th Year - Plantation age 2 + 4 yrs						
Seed region Srednja Podravina	4.63**	0.78	23.0	12.0	2.7	1.5
Population Donji Miholjac	8.47**	0.88	30.4	15.0	4.4	2.0
Population Slatina	3.72**	0.73	19.6	10.0	2.9	1.5
Selected half-sibs (10/21)	-	-	18.5	9.5	18.6	9.7
1998th Year - Plantation age 2 + 6 yrs						
Seed region Srednja Podravina	5.92**	0.87	42.9	15.0	3.0	1.0
Population Donji Miholjac	9.50**	0.89	53.7	20.0	16.0	6.0
Population Slatina	4.52**	0.78	32.6	11.0	-5.5	-2.0
Selected half-sibs (10/21)	-	-	34.6	12.5	34.5	12.4
1999th Year - Plantation age 2 + 7 yrs						
Seed region Srednja Podravina	5.76**	0.83	46.3	13.5	3.3	1.0
Population Donji Miholjac	9.71**	0.90	63.9	20.5	20.2	6.0
Population Slatina	3.80**	0.74	32.6	9.5	-5.9	-2.0
Selected half-sibs (10/21)	-	-	37.3	11.0	37.8	11.0

** significant at 0.01 level

From these results it can be seen that the achievement of a significant genetic gain for the height increment trait is possible, which means a significant improvement of wood mass production, assuming however that there is no change in the height increment dynamics in the progenies (Zobel & Talbert 1984).

On the assumption that the selection intensity is increased by the selection of the best ten half-sib progenies, based on the GCA ability of their mother trees, the achievement of an additional genetic gain from 9.7 to 12.4 % is possible, as seen in Table 1. The estimated genetic gain values corresponded to the obtained ones, so the estimation of selection intensity by Becker (1985) proved to be very accurate.

The achieved additional genetic gain at this age is relatively lower than the expected one, because of the additional selection made with a relatively low selection intensity, but also because of the small number of tested progenies of the selected mother trees. This intensity can be increased by the participation of a larger number of clones in the clonal seed orchard, with an increase in genetic gain, since the selected plus trees will then figure not only as female parents but partially as male ones, too. As the clonal seed orchards serve also for further breeding, as well as for gene preservation, the number of mother trees in an orchard should be higher (at least fifty), and that is our objective. The flowering of the pedunculate oak clones in the orchard will not be synchronised by years either, but also because of the determined significant differences regarding the participation of male and female flowers in particular clones, sterile clones and "transitus" clones as found by Bordasc (1997). It can be expected that some genotypes will prevail as functionally male or female, but a small number of clones with a balanced proportion of female and male flowers can appear, which may also have an effect on the future pedunculate oak plantation from the aspect of ecosystem stability.

CONCLUSIONS

1. By the phenotypical selection of pedunculate oak plus trees and by the progeny trial, the genetic gain (Δ G) for the height increment can be achieved inside the investigated central Drava River seed region as well as in the half-sib progenies from particular populations. The achieved genetic gain at the orchard age from two to seven years was lower than the expected one (Δ G) due to the decreased selection differential in the old pedunculate oak stands.

2. Estimations of heritability values (h^2) were increased with orchard age, and in the tested half-sib progenies these values ranged from 0.74 to 0.87, which suggests that this trait is under a high genetic control level.

3. The statistically significant differences were also obtained for total heights between half-sib progenies inside the investigated populations and the seed region, which indicates the existence of a very marked genetic differentiation in the pedunculate oak populations.

4. By increasing the selection intensity on the basis of mother GCA abilities, it is possible to achieve an additional genetic gain, taking care however of the stability of future pedunculate oak plantations.

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PROCJENA GENETSKOGA POBOLJŠANJA U TESTU POLUSRODNIKA HRASTA LUŽNJAKA (*QUERCUS ROBUR* L.)

Na području sjemenskoga rajona srednje Podravine (Hrvatska) izvršena je fenotipska selekcija stabala hrasta lužnjaka (*Quercus robur* L.) i osnovana je eksperimentalna klonska sjemenska plantaža s ukupno 40 klonova. Tijekom 1992. godine osnovan je test u koji je uključena 21 familija polusrodnika. U testu potomstva uvrštene su familije sa selekcioniranih majčinskih stabala uključenih u klonske sjemenske plantaže, koje pripadaju sjemenskom rajonu srednje Podravine, s dvije populacije (Donji Miholjac i Slatina). Totalne visine izmjerene su kod plantažne dobi 2 + 3, 2 + 4, 2 + 6 i 2 + 7 godina. Procjena genetskih parametara (nasljednosti i genetske dobiti) rađena je za ukupno 21 polusrodnika te odvojeno za polusrodnike iz svake populacije.

Ključne riječi: *Quercus robur*, test potomstva, genetski parametri

S. Bordacs: Assessing cpDNA diversity in hungarian oak populations and its sylvicultural aspects
Glas. šum. pokuse 37: 383–393, Zagreb, 2000.

UDK 630*165+583+(439) (Quercus sp.)

ASSESSING CPDNA DIVERSITY IN HUNGARIAN OAK POPULATIONS AND ITS SYLVICULTURAL ASPECTS

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Autochthonous populations of different white oak taxa were sampled on a basis of a 50 x 50 km grid system. The chloroplast DNA of the samples was analysed by 4 specific primer pairs and restriction enzymes (PCR-RFLP) and silver staining PAGE. Each haplotype was drawn with different colours which resulted in a synthetic map of cpDNA polymorphism for white oak taxa. In total, 9 haplotypes were found in 53 oak populations of Hungary. Haplotypes 2, 4, 5, 6, 7, 17, 32 were revealed which might originate from the Balkan and Apennine peninsulas. No taxon specific or Western-European haplotypes could be found. Additionally, 2 newly described haplotypes were found in several populations. Artificially planted stands revealed a mixture of different haplotypes because of their different origin. It is supposed that the long-term utilisation of nonautochthonous reproductive materials might confuse the natural genetic structure.

In general, the geographic patterns of the haplotypes in Hungary correlated to the present legal system of regions of provenances for oak species. Both this system of the regions of provenances and natural regeneration might be effective tools to preserve the natural genetic structure of white oak taxa.

Key words: Quercus, chloroplast DNA, haplotypes, provenances

INTRODUCTION

Quercus taxa are the most relevant forest tree species in Hungary. Approximately 35% of Hungarian forests are composed of stands of these oak species. Similar to the European situation, the hybridisation and differentiation of oak taxa cause difficulties in clarifying taxonomic or silvicultural status (Bordacs and Burg 1997). Oak taxa of the Balkan-Mediterranean region (*Q. cerris, Q. dalechampii, Q. polycarpa, Q. frainetto, Q. pubescens and Q. virgiliana)* form natural mixed forest stands with the widely distributed *Q.petraea* and *Q. robur* (Schwarz 1936-37, Tutin 1964, Jalas and Suominen 1976). *Q. petraea* and *Q. dalechampii* usually grow together in mixed stands on dry, acidic or neutral soils of the hill sides (200-1000 m latitude). However, *Q. dalechampii* is reported to colonise mostly with *Q. cerris* (Querceto petreae-cerris) (Gencsi and Vancsura 1992). Autochthonous populations of *Q. robur* (Querceto roboris) can be found mostly on wet lowlands of the Carpathian Basin, at most at 300 m above sea level but a large number of populations in the Carpathian Basin have also been reported on sandy soils (Gencsi and Vancsura 1992). Pubescent oaks (Q. pubescens, Q. virgiliana) are distributed on extremely dry, calcareous hill slopes mixed with *Q. polycarpa* or on forest-steppe areas in the lowlands mixed with *Q. robur*. The oak forests on these sites were mostly changed for vineyards, fruit orchards and pastures in the past. The remaining pubescent oak populations are mostly coppice stands (Gencsi and Vancsura 1992), supposedly as autochthonous populations. Hungarian oak (Quercus frainetto) populations are located primarily in the South-Carpathians and further southwards. Only a few populations in the Basin are probably autochthonous. In the nineteenth century and later, Hungarian oak was planted in the region because of its attractive crown and appearance (Gencsi and Vancsura 1992).

The naturalness of each oak species is different in Hungary. The pedunculate oak was intensively managed in the past. Most of the pedunculate oak stands have been artificially reforested in Hungary in the last 150-200 years. A well-known example is the Slavonian oak which is reported to have a segregated area in the Carpathian Basin (Matyas 1972). At the end of the last century, Slavonian oak (*Q. robur ssp. slavonica* /Gay/ Maty) was propagated throughout the Carpathian Basin and nowadays 2500 ha of Slavonian oak stands are estimated to be planted in Hungary (Koloszar 1982). Most of the populations of the sessile oak taxa (*Quercus petraea, Q. dalechampii, Q. polycarpa*) and pubescent oaks (*Q. pubescens, Q. virgiliana*) have been naturally reforested or traditionally coppice regenerated in the past. These stands are supposed to be autochthonous with only a few stands having been planted, as proved by historical, sylvicultural documents.

In mixed populations, the chloroplast genome of the white oak species has proved to be the same (Petit et al. 1993, Petit et al. 1996) and, generally, cpDNA polymorphism has shown no species differentiation (Kremer and Petit 1993). Several studies have shown that the investigation of specific regions of chloroplast DNA (cpDNA) is helpful in estimating the colonisation routes of plant species or in estimating the maternal origin of the populations (Ferris et al 1993, Ferris et al 1995, Petit et al. 1996, King and Ferris 1998). cpDNA diversity, based on restriction digestion of 4 cpDNA regions of different oak taxa, has been studied throughout Europe (Dumolin-Lapegue et al 1997). This study has identified 23 different cpDNA haplotypes and pointed out 3 refugial areas (Iberian, Italian and Balkans) in Europe. The results of the cpDNA studies have not been able to reveal any significance between the cpDNA haplotypes and oak species. The cpDNA diversity seems to be independent of the taxonomic status of oaks (Dumolin-Lapegue et al. in press).

The present study of cpDNA diversity was started in 1998 to make a genetic survey on oak populations in Hungary and to review the present legal status of the region of provenances for oak species. The cpDNA haplotypes are supposed to indicate both the natural or artificial origin and the natural areas of each population. These additional genetic data might be useful both for practical silviculture and for the legal control system of the reproductive material of oak. Presently, the naturalness of social broadleaves, especially of oaks, is increasingly requested for forest owners and nature protectors. The knowledge of the origin (provenance information) of reproductive materials therefore provides useful information for the regeneration of ecologically stabile forest stands.

MATERIALS AND METHODS

The method was developed by an EU funded (FAIR1-CT95-0297) project (Petit et al., in press). In order to collect plant material, a 50 x 50 km grid system was used, considering the natural forest areas composed by oak species. Within a population, the distance between the sampled trees was at least 50 metres. The main aspects of the sampling of the populations were the following:

1. Natural origin supposed by age (>100 years) or coppice forest stands.
2. Known origin based on forestry or historical documents (see Slavonian oak).
3. Mixed stands composed by several oak taxa.

At least 5 trees were sampled in a population. Additionally, some single, very old žrelict' trees were sampled in Hungary, mostly in the Great Hungarian Plain as a remainder of forest-steppe vegetation. Here, the oak forests were cut down in the Middle Ages and natural forests can hardly be found. The sampled populations are summarised in Table 1. The trees were classified by morphological characters of leaves and also by bark, branches and acorns using the characterisation system of Matyas, 1970. Fresh summer leaves were sampled and stored at -20 °C. The DNA of leaves was extracted using QIAGEN DNAeasy Plant Mini Kit. The samples were analysed by PCR-RFLP using 4 specific cpDNA primer pairs and restriction enzymes described by Dumolin-Lapegue et al. (1997). The samples were run on 26 cm long 8% polyacrylamid gel stained with silver-nitrate. The individual samples were classified for cpDNA haplotypes based on the presence or absence of DNA fragments. Haplotype frequencies of the samples were plotted using MapInfo Professional Version 4.1 (MapInfo Corporation).

RESULTS AND DISCUSSION

In total, 53 populations and 260 trees were analysed. For the distribution maps of cpDNA haplotypes, see Figure 1. In total, 9 haplotypes were found in the

Table 1.

LOCALITY	SPECIES	LONG	LAT	ALT	ORIGIN	STAND
Aggtelek	pubescens	20.50	48.47	370	dubious	Forest
Albertirsa	mix	19.62	47.25	200	autochthonous	Forest
Arlo	mix	20.25	48.18	230	autochthonous	Forest
Bakony-Kabhegy	mix	17.65	47.03	570	autochthonous	Forest
Baktalórántháza	robur	22.08	48.00	150	autochthonous	Forest
Bánokszentgyörgy	robur	16.78	46.55	260	dubious	Forest
Barabás-Kaszonyi hegy	mix	22.50	48.25	160	autochthonous	Forest
Bélavár	robur	17.20	46.12	240	autochthonous	Forest
Budakeszi	pubescens	18.92	47.50	310	autochthonous	Forest
Budapest-Jánoshegy	petraea	19.00	47.50	500	autochthonous	Forest
Bugac	robur	19.78	46.63	120	autochthonous	Pasture-Forest
Bükk-Szarvaskö	mix	20.37	48.00	350	autochthonous	Forest
Csákberény	mix	16.50	47.35	430	autochthonous	Forest
Csévharaszt	pubescens	19.42	47.28	120	autochthonous	Forest
Debrecen	robur	21.80	47.50	140	autochthonous	Forest
Demjén-Kerecsend	pubescens	20.35	47.80	180	autochthonous	Forest
Demjén	pubescens	20.33	47.83	200	autochthonous	Forest
Diosjenö	mix	19.03	47.95	340	dubious	Forest
Domoszlo	petraea	20.12	47.83	540	autochthonous	Forest
Érpatak	robur	21.77	47.82	150	autochthonous	Forest
Felsöszenterzsébet	petraea	16.45	46.73	200	autochthonous	Forest
Felsötárkány	mix	20.40	48.00	290	autochthonous	Forest
Gemenc	robur	18.90	46.32	100	autochthonous	Forest
Gerecse	mix	18.47	47.67	380	autochthonous	Forest
Gyenesdiás	mix	17.25	46.77	290	autochthonous	Forest
Káld	mix	17.05	47.17	210	autochthonous	Forest
Kemence	robur	18.88	48.00	350	dubious	Forest
Kerkafalva	robur	16.48	46.77	200	autochthonous	Pasture-Forest
Kimle	robur	17.35	47.82	110	autochthonous	Forest
Kölcse	robur	22.72	48.05	110	autochthonous	Pasture-Forest
Lengyeltoti	hyb	17.62	46.67	180	autochthonous	Forest
Mázaszászvár	petraea	18.37	46.27	480	autochthonous	Forest
Mohács	robur	18.68	45.92	90	dubious	Forest
Nádasd	mix	16.62	46.97	210	dubious	Forest
Nagybörzsöny	mix	18.83	47.93	420	autochthonous	Forest
Nagykörös	mix	19.78	47.03	150	autochthonous	Forest
Ohuta	mix	21.37	48.40	400	autochthonous	Forest
Pécs-Jakabhegy	mix	18.12	46.12	550	autochthonous	Forest
Sasrét	robur	17.90	46.22	230	autochthonous	Forest
Sellye	robur	17.85	45.83	100	dubious	Forest
Sellye-Körcsönye	robur	17.83	45.87	100	dubious	Forest
Sikáros	mix	19.00	47.70	360	autochthonous	Forest
Sopron	mix	16.67	47.67	190	autochthonous	Forest
Szalafö	mix	16.35	46.87	230	autochthonous	Forest
Tiszaigar	robur	20.80	47.53	100	autochthonous	Forest
Tokaj	mix	21.40	48.12	510	autochthonous	Forest
Ugod	mix	17.60	47.32	300	autochthonous	Forest
Ujszentmargita	mix	21.10	47.73	100	dubious	Forest
Vámosatya	robur	22.40	48.20	110	autochthonous	Forest
Velem	mix	16.50	47.35	520	autochthonous	Forest
Visegrád	petraea	18.97	47.78	350	autochthonous	Forest
Zala-Kiscsehi	mix	16.67	46.52	240	dubious	Forest
Zamárdi	pubescens	17.97	46.88	200	autochthonous	Forest

List of sampled populations in Hungary

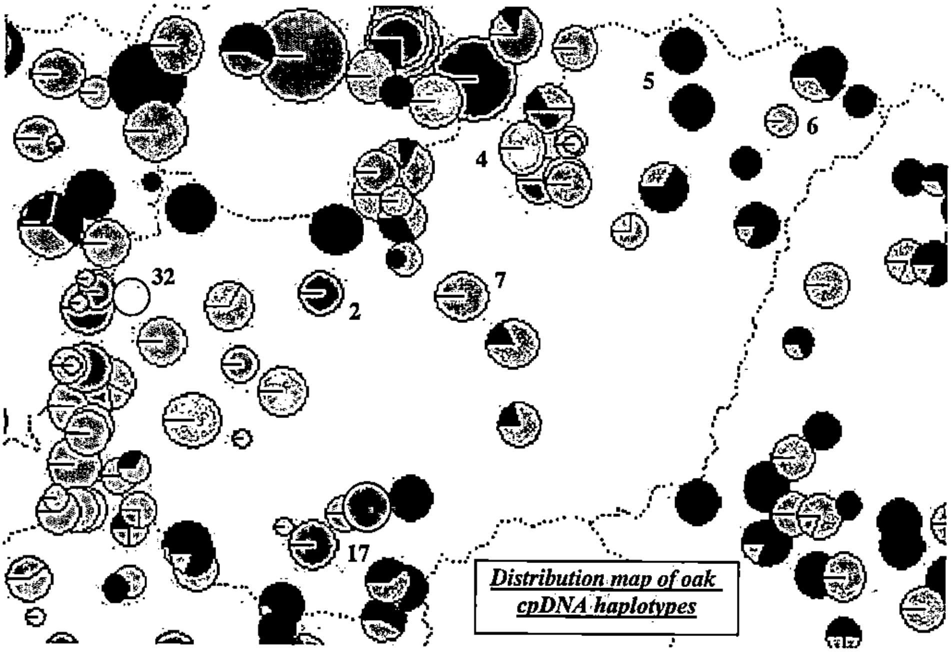

Figure 1. The distribution of sampled oak populations marked by different colours of each haplotype numbered by type. The polymorphic populations marked by colours of each presented haplotype

studied populations (Table 2). Haplotype 2, 4, 5, 6, 7, 17, 32 were described in previous studies (Dumolin-Lapegue et al. 1997, Petit et al., in press). Two 'new' haplotypes were found and described in the present study. These 'new' types showed a segregated and restricted distribution area within the studied region in contrast to the widely distributed types like Haplotype 5 or 7.The haplotypes distributed on the Atlantic Coast are not naturally present in Hungary. Practically, the haplotypes found in the region are supposed to have an Italian and/or Balkan - Black Sea Basin refugial origin. On the basis of the distribution map of haplotypes, the region of the Carpathian Basin is supposed to be a crossing point of different colonisation routes (Csaikl et al., in press).

The presence of each haplotype seems to be patchy and restricted to distances of 30-100 km. Comparing general European trends, the diversity of cpDNA haplotypes is relatively high in Hungary. This fact suggests strong ecological competition between different oak populations (taxa) naturally present in forest stands. The ecological conditions are very mosaic-like throughout Hungary. The soil types generally determine the forest associations and indirectly the oak species which can be successful on each site. This can be the reason that Haplotype 2 was only found in pure or mixed pubescent oak stands. This haplotype is quite common in Italian oak stands but could not be found in the Hungarian Great Plain on sandy or salt-affected (alkaline) soils.

Table 2.

LOCALITY	H 2	H 4	H 5	H 6	H 7	H 17	H 32	NEW	NEW	Ro	Pe	Pu	Fr	Total
Aggtelek	*	*	*	*	5	*	*	*	*	*	*	5	*	5
Albertirśa	*	*	*	5	*	*	*	*	*	3	*	2	*	5
Arlo	*	*	6	*	*	*	*	*	*	3	3	*	*	6
Bakony-Kabhegy	*	2	*	*	4	*	*	*	*	*	4	2	*	6
Baktalórántháza	*	*	*	3	*	*	*	*	*	3	*	*	*	3
Bánokszentgyörgy	*	*	1	*	2	*	*	2	*	5	*	*	*	5
Barabás-Kaszonyi hegy	*	*	4	*	*	*	*	*	*	2	2	*	*	4
Bélavár	*	*	4	*	*	*	*	*	*	4	*	*	*	4
Budakeszi	*	*	1	*	*	*	*	*	*	*	*	1	*	1
Budapest-Jánoshegy	*	4	*	*	*	*	*	*	*	*	4	*	*	4
Bugac	*	*	1	4	*	*	*	*	*	5	*	*	*	5
Bükk-Szarvaskö	*	*	*	*	*	2	*	*	*	*	*	2	*	2
Csákberény	8	*	*	*	*	*	*	*	*	*	3	5	*	8
Csévharaszt	*	*	*	*	6	*	*	*	*	*	*	6	*	6
Debrecen	*	*	4	1	*	*	*	*	*	5	*	*	*	5
Demjén-Kerecsend	*	*	*	5	*	*	*	*	*	*	*	5	*	5
Demjén	*	*	*	5	*	*	*	*	*	*	*	5	*	5
Diosjenö	1	1	1	6	*	*	*	*	*	2	2	*	5	9
Domoszlo	*	*	*	*	*	6	*	*	*	*	6	*	*	6
Érpatak	*	*	3	*	*	*	*	*	*	3	*	*	*	3
Felsöszenterzsébet	*	*	*	*	4	*	*	*	*	*	4	*	*	4
Felsötárkány	*	*	1	2	*	3	*	*	*	3	3	*	*	6
Gemenc	*	*	5	*	*	*	*	*	*	5	*	*	*	5
Gerecse	5	*	*	*	*	*	*	*	*	1	2	2	*	5
Gyenesdiás	*	*	1	*	6	*	*	*	*	1	4	2	*	7
Káld	*	*	*	*	4	*	1	*	*	2	3	*	*	5
Kemence	*	*	*	*	*	*	1	*	1	2	*	*	*	2
Kerkafalva	*	*	*	*	5	*	*	*	*	5	*	*	*	5
Kimle	*	*	4	*	1	*	*	*	*	5	*	*	*	5
Kölcse	*	*	3	*	*	*	*	*	*	3	*	*	*	3
Lengyeltoti	1	*	*	*	*	*	*	*	*	*	*	1	*	1
Mázaszászvár	*	*	*	*	*	4	*	*	*	*	4	*	*	4
Mohács	*	*	2	3	*	*	*	*	*	5	*	*	*	5
Nádasd	*	*	*	4	1	2	*	*	*	2	1	*	4	7
Nagybörzsöny	*	2	1	*	*	*	2	*	*	*	3	2	*	5
Nagykörös	*	*	1	5	*	*	*	*	*	3	*	3	*	6
Ohuta	*	*	5	*	*	*	*	*	*	2	3	*	*	5
Pécs-Jakabhegy	*	*	*	*	*	6	*	*	*	*	3	3	*	6
Sasrét	*	*	*	*	1	*	*	*	*	1	*	*	*	1
Sellye	*	*	4	*	*	1	*	*	*	5	*	*	*	5
Sellye-Körcsönye	*	*	2	*	*	*	*	*	*	2	*	*	*	2
Sikáros	*	4	2	*	*	*	*	*	*	4	2	*	*	6
Sopron	*	*	6	*	*	*	*	*	*	*	3	3	*	6
Szalafö	*	*	*	*	8	*	*	*	*	3	5	*	*	8
Tiszaigar	*	1	*	*	3	*	*	*	*	4	*	*	*	4
Tokaj	*	*	5	*	*	*	*	*	*	1	2	2	*	5
Ugod	*	*	*	*	6	*	*	*	*	1	2	3	*	6
Ujszentmargita	*	2	4	*	*	*	*	*	*	3	1	2	*	6
Vámosatya	*	*	4	2	*	*	*	*	*	6	*	*	*	6
Velem	*	*	*	*	*	*	*	*	7	*	4	3	*	7
Visegrád	*	3	*	*	*	*	*	*	*	*	3	*	*	3
Zala-Kiscsehi	*	*	*	*	6	*	*	*	*	2	4	*	*	6
Zamárdi	*	6	*	*	*	*	*	*	*	*	*	6	*	6
TOTAL	15	25	75	45	62	24	4	2	8	106	80	65	9	260

List of haplotypes in the sampled populations and sampled oak species. Ro.: Robur, Pe.: Petraea, Pu.: Pubescens, Fr.: Frainetto

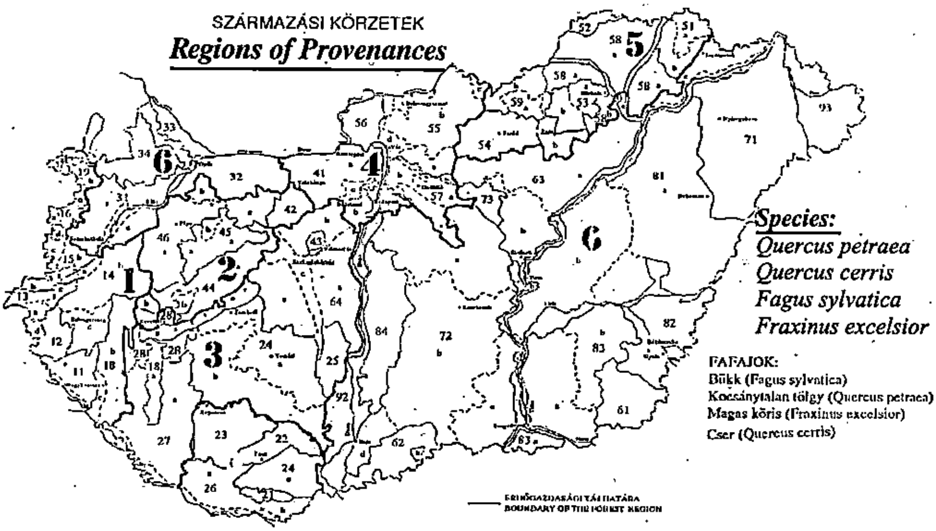

Figure 2. The map of the legal system of regions of provenances for *Quercus petraea* in Hungary

Haplotype 4, described in Hungary as practically a subhaplotype (Haplotype 4a), could be found only in the Carpathian Basin and is not present south- or eastwards (Csaikl et al., in press). The distributional area of Haplotype 4 is practically restricted to the lower mountains in Central-Hungary and is not present southwards or eastwards. Similarly, the 2 newly described haplotypes were found in the mountainous regions. Some micro-refugial oak populations could be the theoretical explanation of populations which could survive the glacial periods and could be more successful on special sites in the Postglacials (hypothesis of žhills up and down', Zolyomi 1958, Borhidi 1997).

The distributional map of the haplotypes (Figure 1) shows that the line of the Danube practically stopped the natural spreading of Haplotype 7. This haplotype was not found in the Hungarian Great Plain (East-Hungary) or further eastwards. In eastern areas, the possibly Balkan originating haplotypes (Haplotype 5 and 6) were dominant. This area might be strongly connected to the Transylvanian regions from where rivers flow to East-Hungary and where the oak populations could easily have spread by river floods during the Postglacials. Similarly to European trends, the different oak taxa within an autochthonous population share the same haplotype (Dumolin-Lapegue et al. 1997, Csaikl et al., in press). The monomorphic cpDNA pattern within a stand is generally supposed to be an autochthonous population (Petit et al. 1993, Petit et al. 1996) and the polymorphic cpDNA structure might have originated from artificial reforestation. Simultaneously, several populations (Debrecen, Tiszaigar, Vámosatya) seemed to be autochthonous in spite of polymorphic cpDNA patterns, on the basis of forest construction, plant association, age of the stand and historical documents. (For example, some areas were covered by swamp-forest up to the end of the nineteenth century and wood-harvesting was the first infrastructural activity proven by documents.) In Hungary - generally in the former Austro-Hungarian Monarchy - intensive silvicultural activity started in the nineteenth century. Natural reforestation using coppice technologies was common on oak forest sites, while plantations of oaks were hardly used. The majority of coppice and coppice with standard oak forests should therefore be autochthonous in Hungary.

Based on the cpDNA results, the white oak populations in Hungary have been in a different status of naturalness. Most of the sessile oak (*Q. petraea, Q. dalechampii, Q. policarpa*) and pubescent oak (*Q. pubescens, Q. virgiliana*) populations have resulted in monomorphic cpDNA patterns. These populations must be autochthonous. In contrast, the pedunculate oak (*Q. robur and Q. r. ssp. Slavonica*) stands are polymorphic and are supposed to be highly influenced by silvicultural activities.

Historical documents prove that acorn was collected all over Slavonia at the end of the nineteenth century and transported by coaches or train to distribution centres in Hungary where the acorn was mixed and stored. These centres distributed the reproductive materials throughout Hungary (Kolossvary 1975). All of the studied Slavonian oak stands (Bánokszentgyörgy, Körcsönye, Sellye, Nádasd) show polymorphic patterns which support the hypothesis of mixed origin and artificial planting. Interestingly, the Croatian populations of Slavonian oak usually result in similar polymorphic patterns (Csaikl et al., in press). Two planted populations of Hungarian oak (Q. frainetto) which were also sampled (Diosjenö, Nádasd) showed polymorphic cpDNA patterns, similarly to the Slavonian oak stands.

CONCLUSIONS

The provenance information of reproductive materials has been increasingly important for foresters to plant new forests or to make reforestations. Hungary has been part of the OECD system of forest reproductive materials since 1989. Regions of provenances have been described for the main forest tree species like oaks, mainly based on ecological and plant association characteristics of forested areas. The legal provenance system of sessile oak can be seen in Figure 2. (Turkey oak and beech were included in the same map.) In comparison with the 50 regions of the previous provenance system, only 6 regions were described for sessile oaks. The boundaries of each region were determined both by using scientific information and by considering practical aspects. For example, regions 4 and 5 were cut from each other by using soil maps and genetic information of the isozyme database and by considering the boundaries of different state forest companies managing the forests in North Hungary.

The present cpDNA study has resulted in additional genetic information on maternal effects within and between the regions of provenance. Haplotype 4 is dominant in Region 4 and is in effect restricted only in this area. Practically, the oak populations of the region have the same maternal origin. In West Hungary (Region 1), Haplotypes 2 and 7 were dominant. Both haplotypes were found sporadically in other regions. The separation of Region 1 seems therefore to be realistic. The populations of the Mecsek region (marked 3a) presented Haplotype 17 in a large number. Earlier, based on the special morphological characters of oak populations, a subregion was supposed to have been outlined. Based on the cpDNA data, a new (sub)region is worth being considered.

Generally, the cpDNA data might confirm the previous hypotheses. The present legal system of sessile (and pubescent) oak provenances seems to be realistic and sufficiently genetically based. The Hungarian system of provenances can only recommend the utilisation of each provenance and does not oblige forest owners to use native reproductive materials. The increase in the artificial planting of oaks might involve the risk that nonautochthonous oak provenances (genotypes) could be dominant in Hungary, thus endangering the natural genetic and ecological structure. The natural regeneration of oak forests and generally nature-friendly management methods can be the most sure and useful tools to preserve ecologically stabile oak forests.

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PROCJENA RAZNOLIKOSTI KLOROPLASTNE DNA U POPULACIJAMA MAĐARSKOGA HRASTA I NJEGOVI UZGOJNI ASPEKTI

Ispitane su autohtone populacije različitih taksona bijeloga hrasta na osnovi mrežnoga sustava od 50 x 50 km. Kloroplastni uzorak DNA analiziran je pomoću četiri specifična para *primera* i restriktivnih enzima (PCR-RFLP) metodom PAGE. Svaki je haplotip označen različitom bojom, što je rezultiralo sintetskom kartom polimorfizma kloroplastne DNA za taksone bijeloga hrasta. Ukupno je nađeno 9 haplotipova u 53 hrastove populacije u Mađarskoj. Otkriveni su haplotipovi 2, 4, 5, 6, 7, 17, 32, koji su možda porijeklom s balkanskoga i apeninskoga poluotoka. Nije nađen ni jedan specifičan takson ili zapadnoeuropski haplotip. Usto su u nekoliko populacija pronađena dva novoopisana haplotipa. Na umjetno podignutim sastojinama pronađene su mješavine različitih haplotipova zbog njihova različita porijekla. Pretpostavlja se da je dugotrajna upotreba neautohtonoga reproduktivnoga materijala pomiješala prirodnu genetsku strukturu.

Općenito, geografski obrasci haplotipova u Mađarskoj koreliraju sa sadašnjim zakonskim sustavom regija provenijencija hrastovih vrsta. I ovaj bi se sustav regija provenijencija i prirodna obnova mogli pokazati učinkovitim oruđem za očuvanje prirodne genetske strukture taksona bijeloga hrasta.

Ključne riječi: *Quercus*, kloroplastna DNA, haplotipovi, provenijencije

S. Perić, et al.: Flushing variability of pedunculate oak (*Quercus robur* L.) in the provenance experiment in Croatia. Glas. šum. pokuse 37: 395–412, Zagreb, 2000.

UDK 630*165+181.8 (Quercus robur L.)

FLUSHING VARIABILITY OF PEDUNCULATE OAK (*QUERCUS ROBUR* L.) IN THE PROVENANCE EXPERIMENT IN CROATIA

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The provenance experiment of Pedunculate Oak, with a total of 16 provenances, was established in spring 1988 in the Gajno locality, in the Forest Office Karlovac. The experiment was established in a completely randomised block design in four repetitions with 400 2+0 old seedlings per provenance. The flushing investigation of Pedunculate Oak started in spring 1992. Monitoring was repeated in 1993 and 1994. Significant differences in the flushing variability range were observed between and within provenances. The variability of flushing in 1992 was three weeks, in 1993 four weeks, and in 1994 it was six weeks. A more detailed research of the flushing of Pedunculate Oak started in 1996, in seven flushing phases. The results of this research have shown the existence of differences in flushing time between and within provenances in all seven phases.

Key words: Pedunculate Oak provenances, variability of flushing phases, Croatia

INTRODUCTION

Pedunculate Oak (*Quercus robur* L.) is one of the most valuable and most important broadleaf tree species, not only in Croatia but in Europe as well. Of the total forested areas of Croatia, 1/10 are Pedunculate Oak forests and those located in the eastern part of Croatia achieve their optimum. A large area of dispersion as well as an extensive variability of edaphic and hydrological conditions under which the Pedunculate Oak grows have caused significant variability in its morphological and physiological characteristics (Krstinić 1996). Research on the growth success of different provenances of Pedunculate Oak in European countries (Germany, Austria, Denmark) began as early as the start of the twentieth century (Birger 1921, Ciesler 1923), whereas in Croatia they began much later (Gračan 1986, Gračan and Perić 1993, Gračan and others 1995). Flushing as a feature of the physiological character has been studied by many scientists (Nikodem 1977, Hayek 1909, Hesmer 1955, Šafar 1966, Stojković 1991, Gračan and others 1991, 1993, 1995). Literature contains various data on the beginning of flushing in provenance tests. For instance, the difference in the beginning of flushing in early and late Pedunculate Oak vary from 7 days (Hendrich 1973) to 2-4 weeks (Šafar 1966).

The aim of the research is to monitor the survival and growth success of different Pedunculate Oak provenance's in Croatia as well as to monitor flushing in seven phenophases[1] in order to establish the time difference of flushing in early and late Pedunculate Oak.

MATERIAL AND METHODS

Pedunculate Oak flushing was monitored in a test including 16 provenances. The test was established in the spring of 1988 at the Gajno locality (Karlovac Forest Administration, Forest Office Jastrebarsko) in a randomised block design in four replications with 400 plants per provenance, i.e. 100 per replication. Basic data on the Pedunculate Oak provenance are shown in Table 1. Survival registra-

Table 1. The general data about Oak provenances

Number	Provenances	Altitude	Longitude	Elevation
1	Motovun	45°20′	13°50′	90
2	Skakavac	45°29′	15°42′	112
3	Orlovac	45°33′	15°44′	112
4	Velika Gorica	45°40′	16°10′	98
5	Novska	45°02′	16°55′	143
6	Lipovljani	45°26′	16°49′	143
7	Okučani	45°11′	17°10′	95
8	Đurđenovac	45°34′	18°08′	97
9	Guševac	45°13′	18°29′	96
10	Spačva	44°56′	18°50′	85
11	Gunja	44°57′	18°49′	86
12	Moroviæ	45°02′	19°11′	82-85
13	Dubica	45°17′	16°44′	98
14	Zdenački gaj	45°37′	17°04′	160
15	Ključevi	45°11′	17°21′	95
16	Vrbanja	45°01′	18°59′	85

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[1] Further on "phase"

Photo 1. Phases of Pedunculate Oak flushing (Photo: S. Perić)

tion as well as diameter and height measurements were conducted during the spring of 1988. The data were processed using the variance analysis method and

Table 2. Mean, maximum and minimum monthly and annual air temperatures (Meteorological Station Jastrebarsko)

Temperatures in °C	Year	Months												
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Yearly
Mean	1997	-1.2	3.2	5.9	7.2	16.1	19.3	19.7	19.5	15.2	8.6	4.9	2.3	10.1
	1998	2.6	4.3	4.7	11.9	15.2	19.9	20.7	21.6	15.2	10.8	3.2	-3.9	10.5
	1999	1.7	0.8	7.6	11.1	16.1	19.2	20.8	20.3	17.8	11.3	3.1	0.5	10.6
Maximum	1997	5.0	18.5	21.5	20.5	30.0	31.0	31.5	30.0	30.0	26.2	22.5	12.6	31.5
	1998	15.5	23.0	20.5	25.6	29.1	34.2	32.5	34.0	29.0	22.0	19.0	5.4	34.2
	1999	13.0	19.1	20.5	25.0	31.0	30.0	34.5	33.0	29.5	25.5	21.0	13.0	34.5
Minimum	1997	-10.6	10.5	-3.5	-4.5	2.1	4.0	9.2	9.0	2.0	-3.0	-7.5	-6.5	-10.6
	1998	-8.7	-9.5	-6.0	-1.5	3.2	5.5	7.3	5.0	3.5	-0.4	-8.5	-16.5	-16.5
	1999	-6.0	-14.5	-2.0	0.6	6.2	7.6	12.5	10.0	8.8	1.0	-11.2	-14.0	-14.5

the F – test. Monitoring of the flushing of the Pedunculate Oak plants began in spring 1992 and was continued in the following years. Since 1997 the flushing of plants of different provenances has been monitored in seven phases. The first phase is the phase of overwintering, characterised by sleeping buds. In the second phase the buds are swollen and prolonged, whereas in the third phase they begin to open and the first green is visible. The fourth phase is characterised by the appearance of the first bent leaves which are more clearly visible in the fifth phase. In the sixth phase the leaves are formed but still obviously twisted lengthwise and in the seventh phase they become completely developed, smooth and wide. The 7 phases of Pedunculate Oak flushing is shown in Photograph 1. Monitoring of the Pedunculate Oak flushing from beginning to end in seven phases was conducted in 1997 starting on April 7 until May 28 (11 times), in 1998 from April 6 to May 5 (11 times) and in 1999 from March 22 to May 31 (12 times). In every monitoring the plants were categorised into flushing phases. The monitoring was conducted every 4-8 days. The data were sorted by provenance, blocks, phases and time of monitoring. During the three years of monitoring, a total of 16,500 tests were conducted.

Since the data acquired are very complex and numerous, tests were conducted for the data acquired for phases 1 - 2 and 6 – 7 for 1997, 1998 and 1999. The monitoring results are shown in diagrams (method of descriptive statistics) so as to enable better visibility of certain tendencies and the definition of a correct statistical hypothesis. The percentage of polylinear charts for plants in phases 1, 2, 6 and 7 are shown by year and monitoring time for all provenances. After the descriptive statistics, we began to conduct the analysis by monitoring phases 1 and 2, i.e. the end of phase 1 and the entering into phase 2 which represents the start of the flushing process. The polylinear charts which represent the transition from phase 1 to phase 2 and phase 6 into phase 7 are similar to the distribution of the survival function which was the basis for using the survival analysis. Because of its relative simplicity, the parameterless Kaplan-Meir method was chosen to evaluate the survival distribution function. This method is based on the time distribution function of phase 2 (i.e. the number of days elapsed from the beginning of the monitoring – April 7 1997; April 4 1998; March 22 1999). This number of elapsed days is marked with "t", and $S_i(t)$ is the probability that the monitored (i-t) provenance is still in phenophase 1 after "t" or more days since the beginning of monitoring. The advantage of this method lies in the possibility of testing the equality hypothesis $S_i(t)$, i=1....16, i.e. on the equality of the survival function by provenance. The statistical hypothesis on the equality of the probability that phase 2 begins "t" days from the beginning of monitoring (March 22 1999) was, for all 16 provenances, tested using the Log-rank and Wilcoxon tests. The assumption was that all provenances were to start flushing at the same time. Because of the connection of flushing with air temperature, Table 2 shows the maximum, minimum and mean values of air temperature by month for 1997, 1998 and 1999. The data were registered in the meteorological station in Jastrebarsko.

RESULTS AND DISCUSSION

Table 3 shows the survival results of Pedunculate Oak provenances in 1998. The average percentage of survival was relatively high at 86.78%, and in absolute terms varies from 77.75% in the Ključevi provenance to 93.0% in the Orlovac provenance. Alongside Orlovac, a high survival percentage is noted in the Guševac

Table 3. Survival of Pedunculate Oak plants at Gajno locality (1998)

No.	Provenances	Blocks				Mean value
		I	II	III	IV	
1	Motovun	92	93	82	77	86.00
2	Skakavac	89	79	92	93	88.25
3	Orlovac	97	87	94	94	93.00
4	Velika Gorica	84	91	92	80	86.75
5	Novska	96	99	89	75	89.75
6	Lipovljani	90	94	97	79	90.00
7	Okučani	77	93	81	94	86.25
8	Đurđenovac	83	89	81	82	83.75
9	Guševac	93	91	85	95	91.00
10	Spačva	85	89	82	74	82.50
11	Gunja	83	96	91	87	89.25
12	Mitrovica	90	89	94	76	87.25
13	Dubica	89	94	75	90	87.00
14	Zdenački gaj	88	98	79	79	86.00
15	Ključevi	69	96	84	62	77.75
16	Vrbanja	87	89	83	77	84.00
Mean values		87.00	91.69	86.31	82.13	86.78

(91%), Lipovljani (90%) and Novska (89.75%) provenances. Table 4 shows the results of the diameter and height measurement for 1998. According to these data the largest mean diameter was recorded in the provenances Đurđenovac (41.4 mm), Okučani (40.9 mm), Spačva (40.9 mm) and the largest mean height was recorded in the Spačva (397.7 cm), Đurđenovac (394.6 cm) and Okučani (392.3 cm) provenances. Table 5 shows the F – test results for diameter and height measurements by provenance. The F – test results for the diameter is 1.89. Since this is identical to the value of the F – distribution for 5% taken from the Tables, we can discard the hypothesis of diameter equality with a 5% risk. Significant differences have been noted in the 5% margin between the mean heights in different provenances. Since the p- value is 1.3%, we can consider the height differences to be significant. Knowledge acquired from forest tree breeding confirms these data, since plant height is under stricter genetic control than diameter which is largely influenced by planting density.

Table 4. Diameter and heights growth of Pedunculate Oak at Gajno locality (1998)

No.	Provenances	Diameter, (mm)					Heights (cm)				Mean value
		Bloks				Mean value	Bloks				
		I	II	III	IV		1	II	III	IV	
1	Motovun	24.18	28.00	34.13	27.97	28.57	234.14	292.22	326.96	245.32	274.66
2	Skakavac	32.78	28.25	36.73	34.85	33.15	292.62	263.13	350.43	338.14	311.08
3	Orlovac	38.81	42.18	38.14	39.47	39.65	365.56	383.22	362.35	383.47	373.65
4	Velika Gorica	40.16	41.00	35.21	32.71	37.27	351.45	374.37	365.92	340.51	358.06
5	Novska	31.63	41.87	46.32	30.51	37.58	319.70	411.07	415.52	280.95	356.81
6	Lipovljani	42.77	30.99	41.39	40.89	39.01	401.28	319.23	404.49	400.03	381.26
7	Okučani	55.33	31.33	38.53	38.54	40.93	482.48	331.11	355.98	399.56	392.28
8	Đurđenovac	48.94	43.01	35.77	37.75	41.37	441.30	417.37	372.94	346.94	394.64
9	Guševac	28.54	35.43	38.77	38.95	35.42	284.27	341.73	370.66	359.49	339.04
10	Spačva	43.33	41.05	42.50	36.61	40.87	397.28	407.47	415.76	358.22	394.68
11	Gunja	47.30	41.04	32.54	39.02	39.98	479.14	364.54	337.10	379.26	390.01
12	Mitrovica	39.71	26.71	40.19	32.41	34.76	370.00	236.03	400.16	312.64	329.71
13	Dubica	29.45	29.51	34.65	33.86	31.87	280.56	298.30	349.79	351.62	320.07
14	Zdenački gaj	40.97	39.89	37.73	34.00	38.15	371.56	421.43	398.39	328.85	380.06
15	Ključevi	41.91	36.77	31.11	36.34	36.53	412.43	383.31	343.14	314.39	363.32
16	Vrbanja	46.20	32.37	35.43	35.38	37.35	404.54	304.52	324.41	295.79	332.32
mean		39.50	35.59	37.45	35.58	37.03	368.02	346.82	368.38	339.70	355.73

Table 5. F-test values of diameter and heights for Pedunculate Oak, locality Gajno (1998)

Source of variability	Degrees of freedom	F-values	
		Diameter, mm	Heights, cm
Provenances	15	1.89	2.37
Blocks	3		
Error	45		

*F 5% =1.89

**F 1%= 2.46

The research results of flushing variability through phases (1-7) are shown through descriptive statistics and the function of survival distribution. The graphical illustration of the percentage values of phases 1 and 2 in Figures 1, 2 and 3 show transition tendencies from phase 1 to phase 2 for individual provenances for 1997, 1998 and 1999. This shows a divergence for the provenances Gunja, Velika Gorica and Novska from the other 13 provenances. The Gunja provenance remains in phase 1 the longest. 98% of the plants of the Gunja provenance were still in phase 1 on April 30 1997, 82% on April 28 1998 and 81% on April 26 1999. During the monitored years the Gunja provenance shows a mild transition from phase 1 to phase 2 by the end of April. A homogeneus transition in a very short interval (5 to 7 days) is visible from April 30 to May 5 in 1997, April 28 to May 5 in 1998 and April 26 to May 3 in 1999. The Velika Gorica and Novksa provenances have an oscillation in the transition from phase 1 to phase 2. From the polylinear charts for the monitored years, it is visible that the Velika Gorica provenance has a slower transition into phase 2 than the Novska provenance. The shortest transition into phase 2 for all three years is present in the Đurđenovac provenance. Over 90% of all plants from this provenance entered phase 2 from April 7 to March 30 in 1997 (23 days), April 6 to April 28 in 1998 (18 days) and from March 22 to April 7 in 1999 (17 days). Figures 1, 2 and 3 show the flushing variability in the transition from phase 1 to phase 2. According to Stojković (1997), variability can be of a continued or discontinued nature. With continued variability, the transition is gradual, whereas with discontinued variability the transition is sharp. Gradual transi-

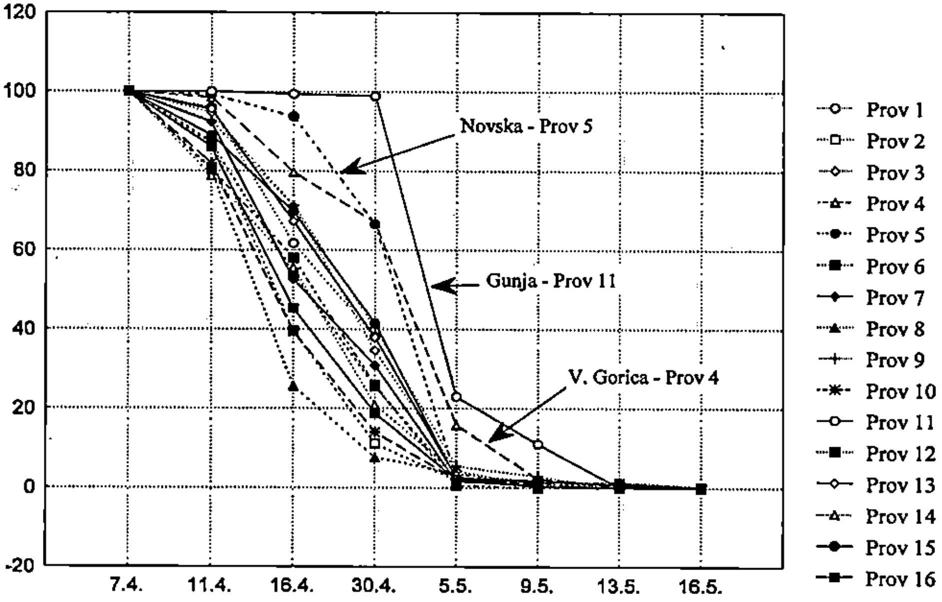

Figure 1. Percentage by provenances entering into phase 2 (1997)

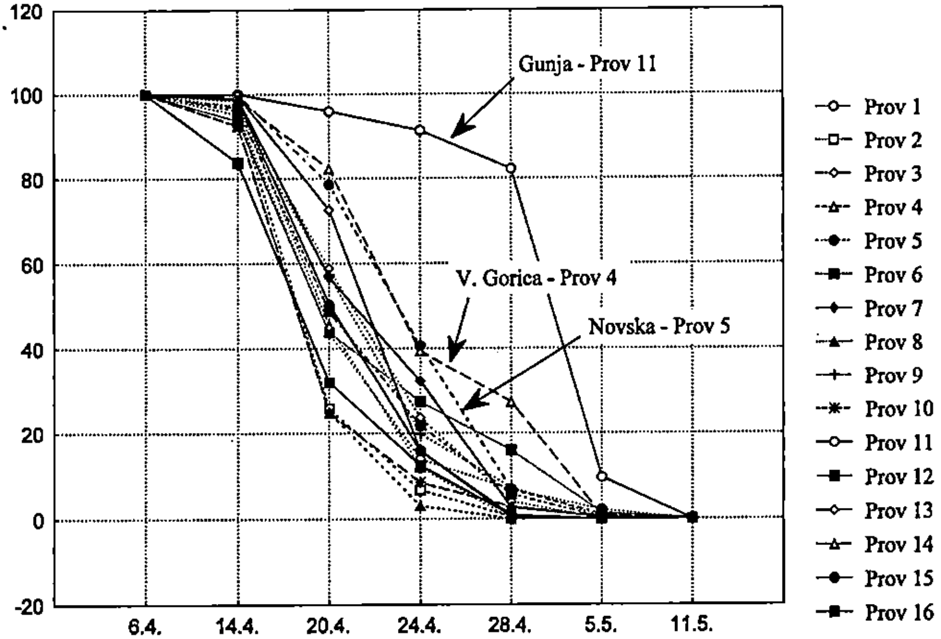

Figure 2. Percentage by provenances entering into phase 2 (1998)

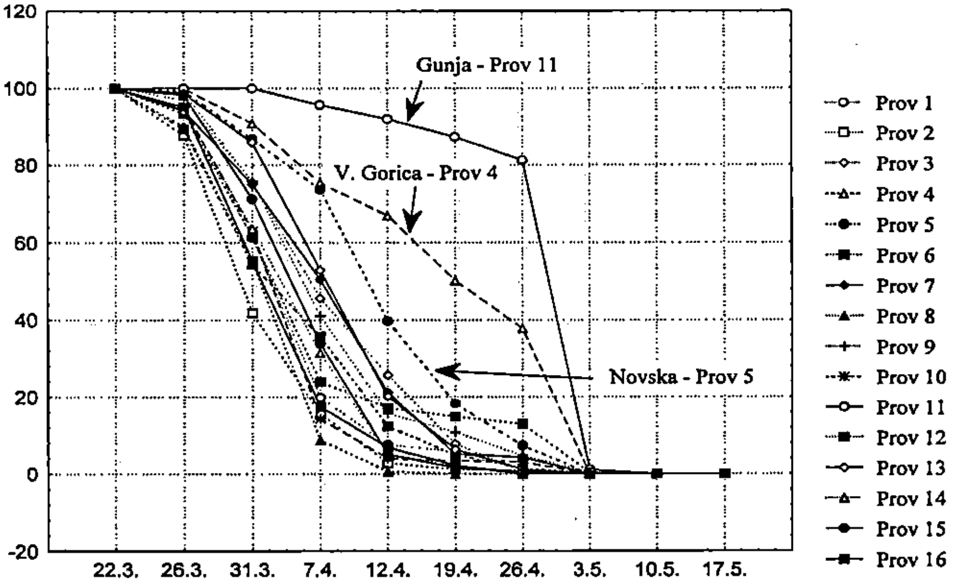

Figure 3. Percentage by provenances entering into phase 2 (1999)

tion indicates quantitative variability where the issue may be a larger number of genes which define a certain characteristic or this characteristic may be due to a lesser degree of heritability. The charts for Gunja and Đurđenovac provenances have abrupt, sharp transitions from phase 1 to phase 2 which indicate discontinued flushing variability for these provenances. The flushing is influenced by the smaller number of genes, i.e. the heritability feature is more prominent. According to the charts, the Velika Gorica and Novska provenances fall under the group of late flushing provenances, but they are a mixture of early and late genotypes where the late genotype prevails.

Figures 4, 5 and 6 show the tendencies in the transition from phase 6 to phase 7 for Pedunculate Oak provenances by year. The earliest start of the process of transition into phase 7 occurred after April 19 1999, and the latest only after May 9 1997. The Đurđevac and Spačva provenances have the earliest and shortest transition into phase 7. For this transition, they needed only 11 days in 1997, 17 days in 1998 and as many as 28 days in 1999. The latest transition into phase 7 was noted in the Gunja, Velika Gorica and Novska provenances. In early May until May 16 in 1997, May 15 in 1998 and May 10 in 1999, over 90% of the plants from these provenances were still in phase 6. After these dates a sharp transition into phase 7 began. The Gunja provenance has the steepest chart line and the most homogenous transition which confirms the discontinued flushing variability for this provenance. Figures 7, 8 and 9 show the percentage in flushing phases by provenance for May 5 1997, May 5 1998 and May 3 1999. A significantly narrower span of flushing phases in 1997 is noticed (1 to 5). This is directly connected to the air temperatures in March, April and May. Data shown in Table 2 on the mean maximum and minimum temperatures recorded at the meteorological station in Jastrebarsko confirm this. April 1997 had much lower air temperature values. The mean temperature was 7.2 °C, the maximum being 20.5 °C and the minimum –4.5°C. 1998 and 1999 had almost equal temperature values (mean value of 11.9°C and 11.1°C, a maximum monthly value of 25.6°C and 25°C and a minimum monthly value of –1.5°C and 0.6°C). The appearance of phases 1 to 7 on May 5 1998 and May 3 1999 shows quicker flushing dynamics in comparison with May 5 1997 where only 5 phases were recorded (1-5). The average intensity of the presence of the individual phases varies significantly through the monitored years. On May 5 1997 the dominant phase was phase 3, on May 5 1999 it was phase 5 and on May 3 1998 phase 6. The largest deviation from the average phase presence was noted in the Gunja, Velika Gorica, Spačva and Đurđenovac provenances. In the Gunja and Velika Gorica provenances, on May 5 1997 and May 5 1998 phase 2 was dominant, whereas on May 3 1999 the dominant phase was 3. In the Spačva and Đurđenovac provenances on May 5 1997 phase 4 was dominant and on May 5 1998 phase 6 was dominant, whereas on May 3 1999 the dominant phase was 7. Throughout the three year monitoring period with monitoring times being almost identical (May 5 1997, May 5 1998, May 3 1999), the Gunja and Velika Gorica provenances show clear late flushing characteristics, whereas the Spačva and

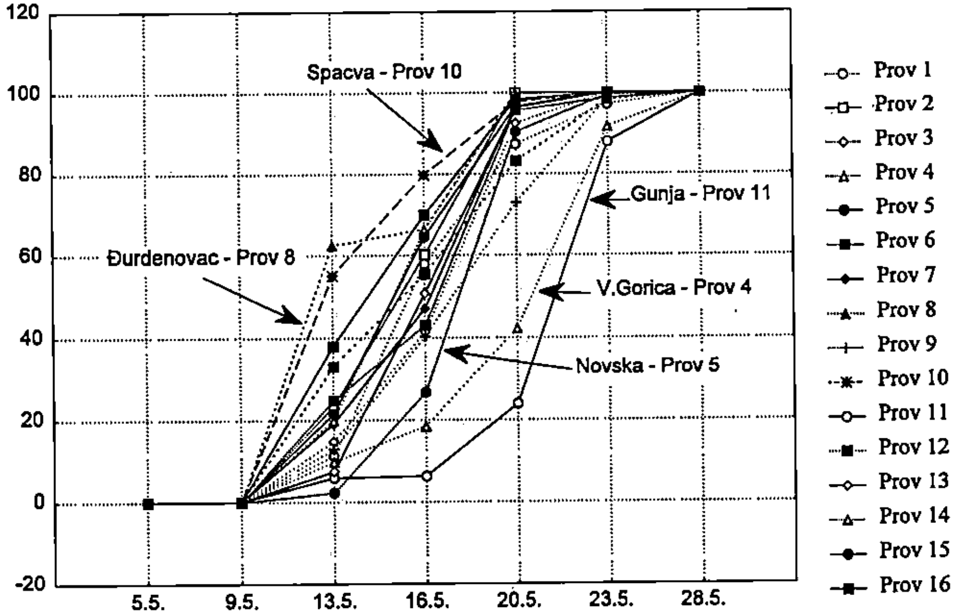

Figure 4. Percentage by provenances entering into phase 7 (1997)

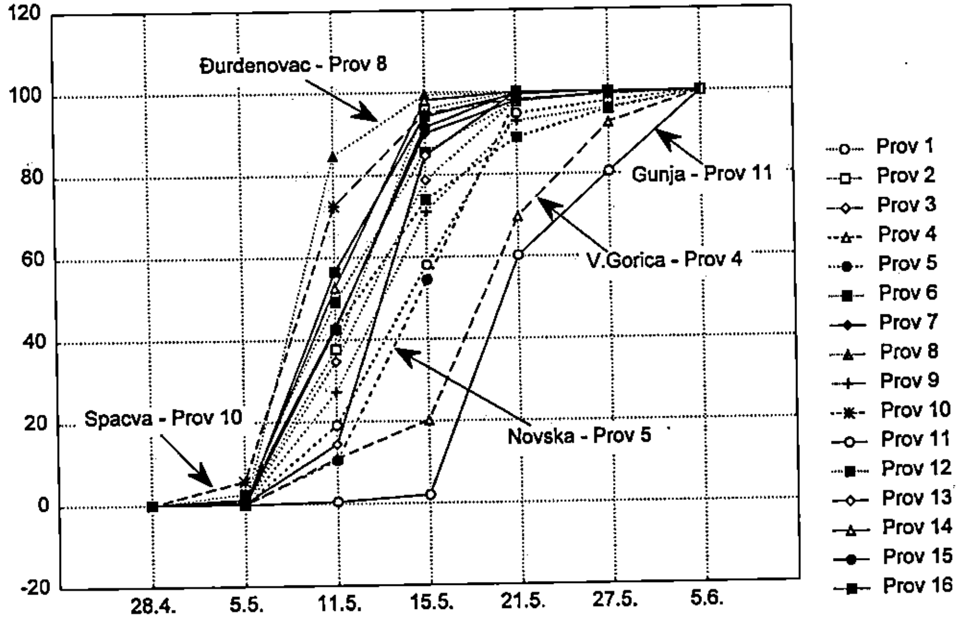

Figure 5. Percentage by provenances entering into phase 7 (1998)

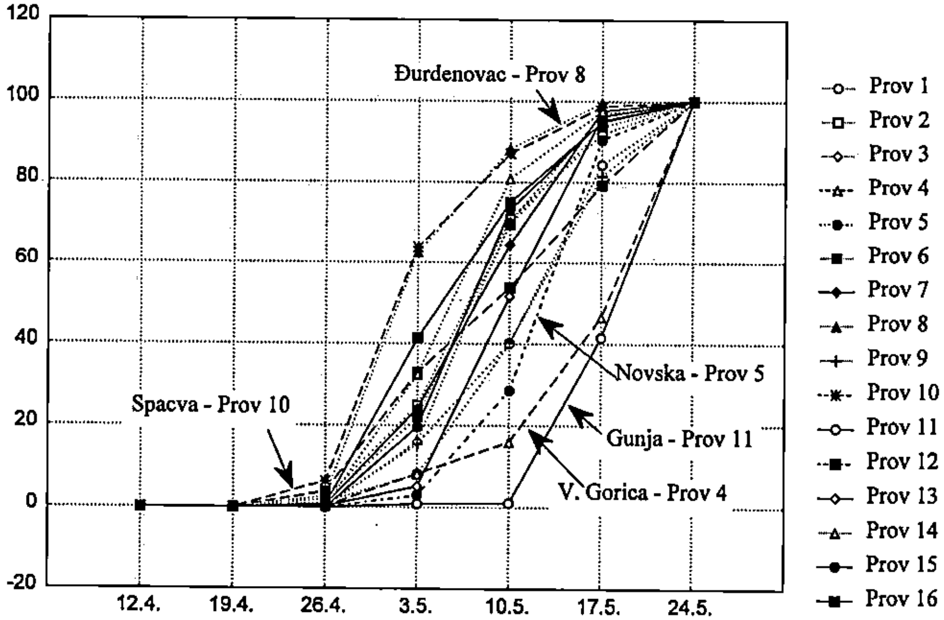

Figure 6. Percentage by provenances entering into phase 7 (1999)

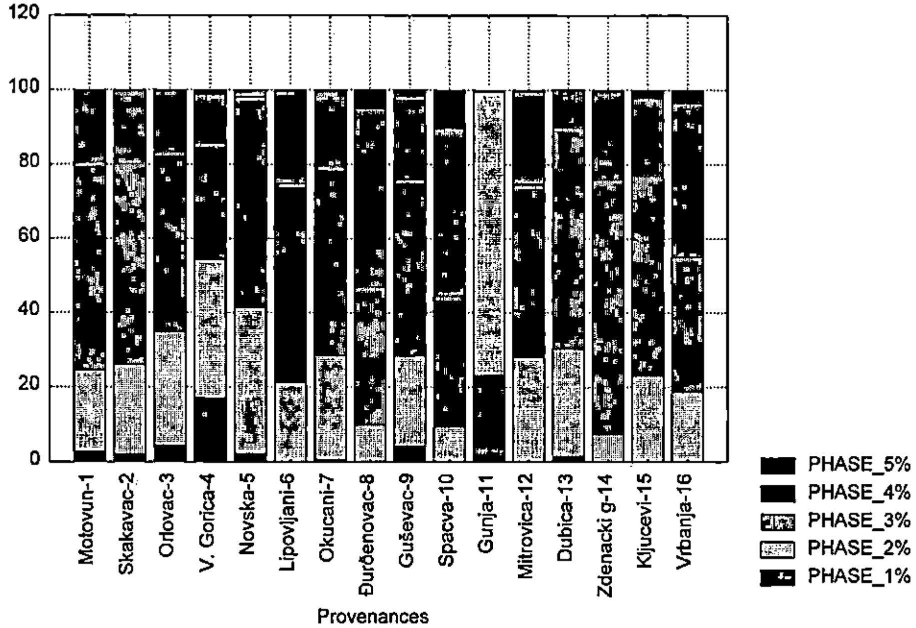

Figure 7. Number of plants in different flushing phases on May 5, 1997

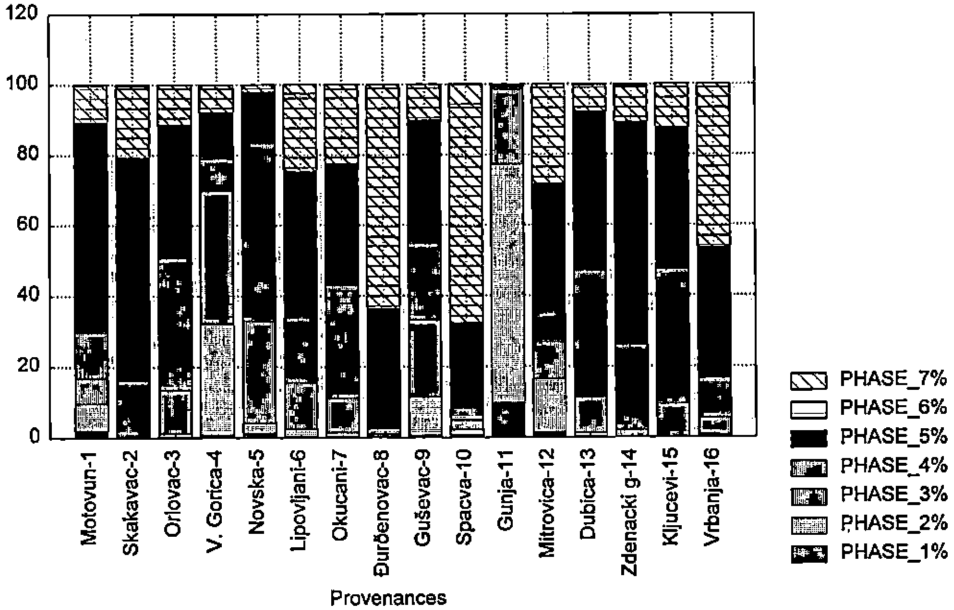

Figure 8. Number of plants in different flushing phases on May 5, 1998

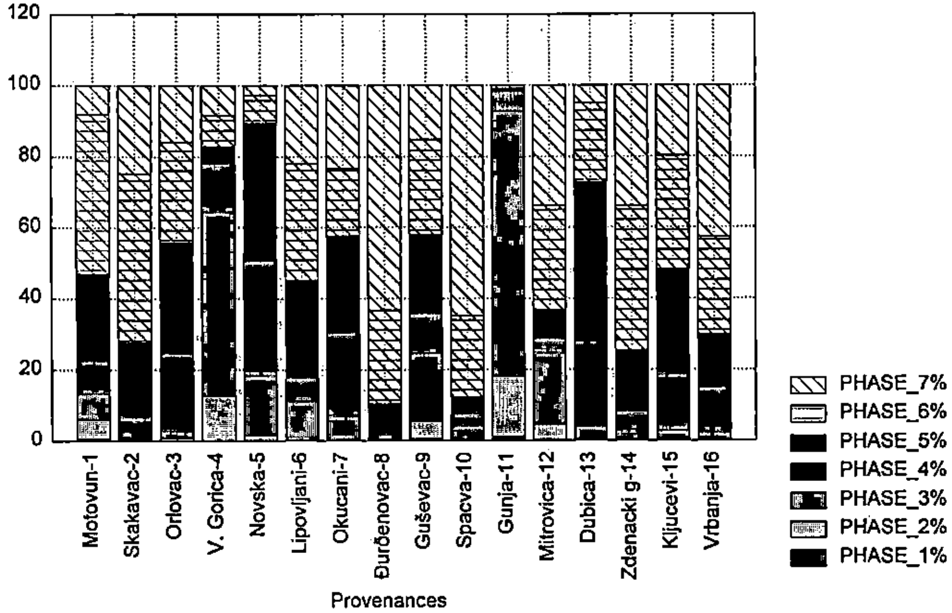

Figure 9. Number of plants in different flushing phases on May 3, 1999

Đurđenovac provenances show clear early flushing characteristics. These data prove a time difference in the flushing of early and late Pedunculate Oak. The temperatures during this three-year period influence the dynamics of flushing but the results indicate the existence of larger genetic variability which influences this characteristic.

The existence of early and late flushing in Pedunculate Oak is especially important for the Oak itself. Therefore, special forms of Oak have been given names: ***tarda*** Nordel, ***tardissima*** Sim and ***tardiflora*** Czern. for late flushers and ***praecox*** Czern for early flushers. Flushing is inherited polygenously, with three pairs of genes where the early form is semi-dominant (Stojković 1978, 1991). Research on the differences in the beginning of flushing in the provenance tests started early. According to Krahl-Urban (1959), there is a three-week difference in flushing between the late Slavonian provenance and the German provenance. Literature contains different information, stating that the differences range from 7 days (Hendrich 1973) to 2-4 weeks (Šafar 1966).

The research on the flushing variability in the Pedunculate Oak provenance test has defined the range of variability for 1997, 1998 and 1999 as well as the range of the variability of phases 1, 2 and 7. The range of flushing variability for 1997 equals 51 days, while for 1998 and 1999 it equals 60 days. If compared to the data given by Stojković (1991) which defines the range of variability at 54 days, we can notice a prolongment of 6 days for 1999.

Monitoring flushing by provenance and phases has provided an insight into the range of the variability of individual phases. The range of variability for phase 1 for the Đurđenovac and Skakavac provenance is 32 days, for the Gunja provenance 20 days and for the Moravić provenance as much as 32 days. The variability range for phase 2 ranges from 18 days for the Đurđenovac provenance to 34 days for the Velika Gorica and Guševac provenances. In phase 7 the shortest variability of 7 days is recorded for the Gunja provenance, while the range for the provenance Spačva is 22 days. By observing the very beginning of flushing in the Pedunculate Oak provenances we can notice a significant difference between Gunja and Velika Gorica provenances and the Spačva and Đurđenovac provenances. The provenances which transform in the shortest time and are earliest from phase 1 to phase 2, i.e. are the first to start the flushing process, show the same trend in the transition from phase 6 to phase 7.

Table 6 gives information on the average number of days in which 25%, 50% and 75% of the plants entered phase 2. The data for 1995 show an even transformation into phase 2. Information regarding the moment when 25% of the plants are in transition shows that this occurs on the 28th day for the Gunja provenance, on the 23rd day for the Velika Gorica and Novska provenances, and on the 9th day from the start of the monitoring (April 7, 1997) for all the other provenances. In the 75% transition into phase 2, two groups are distinguishable. The first is comprised of the Skakavac, Đurđenovac, Spačva, Zdenački Gaj and Vrbanja provenances where 75% of the plants enter phase 2 on the 23rd day. The second group is the

Table 6. The averge number of days for flushing entering into phase two

Prove-nances	The averge number of days for flushing change to phase two														
	7.4.1997.					6.4.1998.					22.3.1999.				
	25% plants	50% plants	75% plants	Mean	Standard error	25% plants	50% plants	75% plants	Mean	Standard error	25% plants	50% plants	75% plants	Mean	Standard error
1	9	23	28	19.47	0.48	14	14	18	16.62	0.26	9	16	16	15.41	0.43
2	9	9	23	14.63	0.46	14	14	18	15.11	0.16	9	9	16	12.40	0.34
3	9	23	28	20.62	0.44	14	18	18	17.42	0.21	16	16	28	18.97	0.42
4	23	28	28	24.18	0.44	18	18	29	20.77	0.31	21	28	42	29.87	0.62
5	23	28	28	25.61	0.28	18	18	22	19.33	0.22	18	21	28	23.34	0.46
6	9	23	28	17.45	0.50	14	14	18	17.05	0.23	9	16	21	15.38	0.45
7	9	23	28	17.63	0.50	14	18	22	17.72	0.22	9	21	21	18.53	0.46
8	9	9	23	12.19	0.44	14	14	16	14.67	0.15	9	16	16	12.89	0.27
9	9	23	28	20.94	0.47	14	18	18	17.33	0.25	16	16	21	18.40	0.46
10	9	9	23	14.49	0.48	14	14	14	15.10	0.21	9	16	16	14.64	0.37
11	28	28	28	29.23	0.17	29	29	29	27.83	0.25	42	42	42	49.14	0.37
12	9	23	28	17.30	0.50	14	14	22	17.66	0.33	9	16	16	17.36	0.60
13	9	23	28	20.26	0.47	14	18	18	17.58	0.15	16	21	21	19.60	0.38
14	9	23	23	17.03	0.53	14	14	18	16.19	0.16	9	16	21	15.20	0.35
15	9	23	28	20.37	0.51	14	18	18	16.60	0.18	9	16	21	16.36	0.34
16	9	9	23	15.75	0.50	14	14	18	14.86	0.23	9	16	16	14.09	0.34

Table 7. Test of Equality over Strata

Test	1997			1998			1999		
	Chi-Square	DF	Pr > Chi-Square	Chi-Square	DF	Pr > Chi-Square	Chi-Square	DF	Pr > Chi-Square
Log-Rank	1209.287	15	0.0001	1620.342	15	0.0001	2015.657	15	0.0001
Wilcoxon	1277.508	15	0.0001	1383.436	15	0.0001	1618.753	15	0.0001
-2Log (LR)	270.538	15	0.0001	139.650	15	0.0001	540.206	15	0.0001

Motovun, Orlovac, Velika Gorica, Novska, Lipovljani, Okučani, Guševac, Gunja, Morović, Dubica and Ključevi provenances where 75% of the plants enter phase 2 on the 28th day. From the data collected for 1998 it is visible that the Gunja provenance has 25% of plants in phase 2 on the 29th day, Velika Gorica and Novska on the 18th day and the other provenances on the 14th day from the first day of monitoring (April 4 1998). For a percentage of 75%, only plants from the Gunja and Velika Gorica provenances entered phase 2 on the 29th day, which once again confirms the late flushing of these provenances. Data for 1999 show that the Gunja and Velika Gorica provenances differ from the rest of the provenances. The Velika Gorica provenance has 25% of its plants in phase 2 on the 21st day from the beginning of monitoring, 50% on the 28th day and 75% on day 42. If we observe the transition of 15% of the plants into phase 2, we can see that the Motovun, Skakavac, Lipovljani, Okučani, Đurđenovac, Spačva, Morović, Zdenački Gaj, Ključevi and Vrbanja provenances act in the same way. Already on the 9th day from the beginning of monitoring 25% of all plants have entered phase 2, while this transition in the Gunja provenance occurs on the 42nd day. It is also interesting to note that the transition into phase 2 for 15% to 75% of the plants of the Gunja provenance happens on the 42nd day. This sharp transition can be seen in Chart 1 where we can see the steep fall of the line between April 24 and May 3. Between these two dates comes the 42nd day of monitoring. A large deviation of the mean value from the median represents an unequal transition from phase 1 to phase 2. An example of this is the Gunja and Đurđenovac provenances. The Đurđenovac provenance has a median significantly lower than the mean value which indicates a sharp transition into phase 2 in the first days of monitoring, while the Gunja provenance has a median significantly higher than the mean value and its plants remain in phase 1 longer and then rapidly enter into phase 2.

The differences in the time distribution for the beginning of phase 2 by provenance have been tested in parameterless tests shown in Table 9. These two tests (log-rank and Wilcoxon) indicate the differences in time distribution of the beginning of phase 2 by provenance. Both tests are equally significant ($p< .001$).

On the basis of the given facts we can categorise all the provenances into 3 groups. The first group consists of the provenances which enter phase 7 the soonest – the early flushing provenances of Đurđenovac and Spačva. The second group consists of those which enter phase 7 at a medium speed – the Motovun, Sklakavac, Orlovac, Lipovljani, Okučani, Guševac, Morović, Dubica, Zdenački Gaj, Ključevi and Vrbanja provenances, and the third group consists of the provenances which enter phase 7 the latest – the late flushing provenances of Gunja, Velika Gorica and Novska.

CONCLUSIONS

On the basis of the results of this research on the growth success of Pedunculate Oak provenances and the flushing monitoring at the Gajno locality, we can conclude:

The highest survival percentage is found in the Orlovac (93%), Guševac (91%) and Lipovljani (90%) provenances and the lowest in the Ključevi (77.75%) provenance. The results of the diameter and height measurements indicate the best growth success in the Spačva, Đurđenovac, Okučani and Gunja provenances, while the worst is for provenance Motovun.

We can divide all provenances into three groups according to the speed and way of flushing. The first consists of the early flushing provenances (Đurđenovac and Spačva), the second of the medium flushing provenances (Motovun, Skakavac, Orlovac, Lipovljani, Okučani, Guševac, Morović, Dubica, Zdenački Gaj, Ključevi and Vrbanja) and the third group of the late flushing provenances (Gunja, Velika Gorica and Novska). The Novska provenance falls under the group of late flushing provenances with a mixture of early and late genotypes where the late genotype prevails.

Monitoring of the Pedunculate Oak flushing in 7 phases during 1997, 1998 and 1999 indicates a trend of flushing in each of the 16 provenances and the existence of high variability regardless of the identical beginning and conclusion of flushing. In the three year research with an almost identical time of monitoring (May 5, 1997; May 5 1998; May 3 1999), the Gunja and Velika Gorica provenances show distinctive late flushing characteristics and the Spačva and Đurđenovac provenances distinctive early flushing characteristics. This information indicates a shift in flushing time between the early and late Pedunculate Oak. The average number of days when 75% of the plants enter into flushing phase 2 for the Gunja provenance is 28 in 1997, 29 in 1998 and 42 in 1999. For the Đurđenovac provenance it equals 23 days in 1997, 14 in 1998 and 16 in 1999.

The scale of flushing variability for 1997 is 51 days and for 1998 and 1999 it is 60 days. The scale of phase 1 variability in 1999 for the Đurđenovac and Skakavac provenances is only 13 days, for the Gunja provenance 20 days and for the Morović provenance as high as 32 days. The scale of phase 2 variability is from 18 days for the Đurđenovac provenance to 32 days for the Velika Gorica and Guševac provenances. In phase 7 the Gunja provenance has the lowest variability scale of only 7 days while the Spačva provenance has a variability scale of 22 days. The parameterless tests (Log-rank and Wilcoxon) indicate differences in the time distribution of the beginning of phase 2 by provenance for years 1997, 1998 and 1999. Both tests are highly significant.

The temperature during the monitored years influences the flushing dynamics, but the results indicate the existence of higher genetic variability for this characteristic.

The results of this research indicate the existence of three types of Pedunculate Oak flushing in Croatia. Because of the importance of this research we recommend that it be continued.

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VARIJABILNOST LISTANJA HRASTA LUŽNJAKA (*QUERCUS ROBUR* L.) U POKUSU PROVENIJENCIJA U POKUPLJU

Pokus provenijencija hrasta lužnjaka, s ukupno 16 provenijencija, osnovan je u proljeće 1988. godine na lokalitetu Gajno, u Pokuplju. Pokus je osnovan kao randomizirani blok-sustav u četiri ponavljanja s ukupno 400 dvogodišnjih sadnica po provenijenciji. Izučavanje početka listanja hrasta lužnjaka (*Quercus robur* L.) po provenijencijama i ponavljanjima počelo je u proljeće 1992. godine i nastavilo se tijekom 1993. i 1994. godine. Uočene su znatne razlike u širini varijabilnosti ovoga svojstva. Širina varijabilnosti listanja tijekom 1992. godine iznosila je tri tjedna, 1993. četiri tjedna, a 1994. šest tjedana. Detaljnije izučavanje svojstva listanja hrasta lužnjaka počelo je 1997. godine, a provodi se u sedam faza. Rezultati ovih istraživanja upućuju na varijabilnost listanja po provenijencijama i ponavljanjima za svaku od sedam promatranih faza.

Ključne riječi: provenijencije hrasta lužnjaka, varijabilnost faza listanja, Hrvatska

M. Liesebach, et al.: Development of provenances of *Quercus petraea* and *Quercus robur* from acorns to six-year old plants in relation to species specific traits. Glas. šum. pokuse 37: 413–423, Zagreb, 2000.

UDK 630*232.1+164+165+ (430) (Qurcus robur L., Q. petraea Liebl.)

DEVELOPMENT OF PROVENANCES OF *QUERCUS PETRAEA* AND *QUERCUS ROBUR* FROM ACORNS TO SIX-YEAR OLD PLANTS IN RELATION TO SPECIES SPECIFIC TRAITS

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Seed samples were collected in 14 pure or mixed stands of the two European white oak species *Quercus petraea* and *Q. robur* in autumn 1992. Each acorn of a seed sample was labelled and classified in relation to the presence or absence of vertical stripes by three persons. The independent classification agreed in about 80 % of cases. The labelled acorns were sown in 1993 and from the developing plants leaf samples were collected annually for assessments and measurements. Growth traits, flushing and attack by mildew were also investigated. The data of the leaf characters were used in multivariate analysis. A precise distinction of the two oak species was uncertain if only annual measurements or assessments of leaf traits were used. If the measurements and assessments of six years observation were put together for analysis, two clouds of data points could be separated. The distinguished clouds showed a rather good accordance with the acorn trait striping considered as a typical character for the two oak species. The striping of acorns can be one of the differentiating traits, even if a precise decision is sometimes not easy, while its expression can vary and is often very indistinct.

Keywords: *Quercus*, sessile oak, pedunculate oak, phenotypic variation, differentiation of species

INTRODUCTION

Sessile oak (*Quercus petraea* [Mattuschka] Liebl.) and pedunculate oak (*Quercus robur* L.) can be considered taxonomically as two separate species. Both species occur sympatrically, and intermediate forms can be found. In crossing experiments, hybrids can be achieved (Steinhoff 1998). The two species can be distinguished by the morphological characters of their acorns and leaves. But it could be shown in the past that the two species can be distinguished only by a simultaneous observation of several characters. Single traits are not sufficient for the distinction. The present study continues investigations in 14 pure and mixed oak stands, on which some results have already been published (Liesebach and Stephan 1998).

The aim of the following investigations was focused on the questions:

- whether the traits of acorns, particularly the striping, can be used as a distinguishing feature or whether independently observing persons come to different results,
- whether there were differences between the morphological characters of the leaves sampled from the same plants in the course of the subsequent six years after sowing, and
- whether there were correlations between acorn stripes and leaf characters which allow an unequivocal association to one or the other species.

Finally, it should be found out which characters were most suitable for the distinction between *Q. petraea* and *Q. robur.*

MATERIALS AND METHODS

SEED SAMPLES, FIELD TRIAL AND EVALUATION METHODS

In autumn 1992 a total of 14 seed samples were collected both in pure stands of *Q. robur* and *Q. petraea* as well as in mixed stands in northern, western and southwestern Germany. Three persons without information about the origin or species belonging of the material classified in a random order 200 labelled acorns of each of the 14 seed samples in relation to the presence or absence of small dark vertical stripes. The stripes can be recognised clearly only in fresh acorns. The stripes can disappear during storage or drying. Three groups were distinguished: with distinct stripes (s-group), without stripes (t-group), and with weak or indistinct stripes (u-group) depending on the three evaluations which differed in some cases (for details see Liesebach and Stephan 1998). Stripes are considered typical for *Q. robur.* In *Q. petraea* they are normally missing. The number of stripes was of no consideration.

The individually labelled acorns were sown in spring 1993 in the nursery of the institute. After three years the oaks were transplanted in spring 1996. The recorded morphological acorn characters were kept for each plant. From a random sample of 420 plants (about 14 %) in each year from 1993 to 1998 two leaves from each tree were collected for assessments and measurements. 15 traits of the leaves (for details see Liesebach and Stephan 1998) were assessed or measured or calculated according to the modified scales of Rushton (1983), Aas (1988) and Elsner (1993). Additionally, some traits regarding growth (total height, annual increment), phenology (flushing) or attack by mildew (*Microsphaera alphitoides* Griff. et Maubl.) were also measured or evaluated in the course of the years.

STATISTICAL ANALYSIS

Statistical evaluation was done with the help of the SAS software package (SAS 1989, 1990). At first, the homogeneity of the classification of acorns among the three persons was tested by the means of a contingency table.

For the 15 leaf characters, mean values were calculated on the basis of two randomly sampled leaves per year and tree. 10 of the 15 leaf characters which show differences between the groups of distinct, weak or unstriped acorns were used in multivariate analysis for examining relationships. For this purpose the data were standardised with a mean of zero and a standard deviation of one. Standardisation of taxonomic data is normally obligatory, since characters are usually a combination of length, indices, etc. (Jeffers 1964). The standardised data were used in a factor analysis which performs a component analysis and an orthogonal varimax rotation. The method of factor extraction was a principal component analysis and the number of components was specified with three. The principal component analysis is a method employed to describe patterns among trees in a multidimensional space. In this space, principal axes are aligned sequentially in the direction of greatest variance. During the analyses, the trait striping of the acorns was not taken into consideration. The three dimensional scatter plots were posteriorly assigned according to the striping of the acorns. By this procedure it was possible to check if group formation on the basis of leaf traits coincides with the striping of the acorns.

For each plant and leaf trait, analyses of variance were run, variance components were estimated, and least-squares means (LSM) were computed for the three striping groups. These groups were used for the multiple comparisons with the combined evaluations of the three persons.

RESULTS

COMPARISON BETWEEN THREE INDEPENDENT EVALUATIONS OF ACORNS

The striping of acorns varied between and within the investigated seed samples. Regarding the stripes, the evaluations of 2,794 acorns of totally 14 seed samples resulted in the three main groups mentioned above (see also Liesebach and Stephan 1998).

The independent assessments of the three persons varied, but agreed in about 80 % of the cases. The differences between the three assessments varied between about 7 % and 9 % (Table 1). The deviations were similar when the comparison was restricted to the random sample of 420 oak plants, from which the leaves were collected annually. The chi-square test resulted in significant differences.

Table 1. Differences between the evaluations of the striping of acorns of 14 oak seed samples by three independent persons in absolute numbers and in %.

Person	Group 1: acorns without stripes	Group 2: acorns with distinct stripes	Group 3: acorns with weak or indistinct striping
1	1,147 (41.1 %)	1,423 (50.9 %)	224 (8.0 %)
2	907 (32.5 %)	1,503 (53.8 %)	384 (13.7 %)
3	1,050 (37.6 %)	1,293 (46.3 %)	451 (16.1 %)
mean (%)	(37.03 %)	(50.34 %)	(12.63 %)

In order to check the quality of the assessment, 250 acorns of the overall seed sample were repeatedly assessed by the same three persons in a new order. Surprisingly, the repeated assessments showed differences. In the repeated assessment between 85 % and 94 % of the acorns of group 1 and between 85 % and 92 % of those of group 2 were assigned to the same group. Only between 22 % and 30 % of the acorns were assigned twice to group 3. Most of the acorns classified first as weak or indistinct striped were assigned in the repeated assessment to group 1.

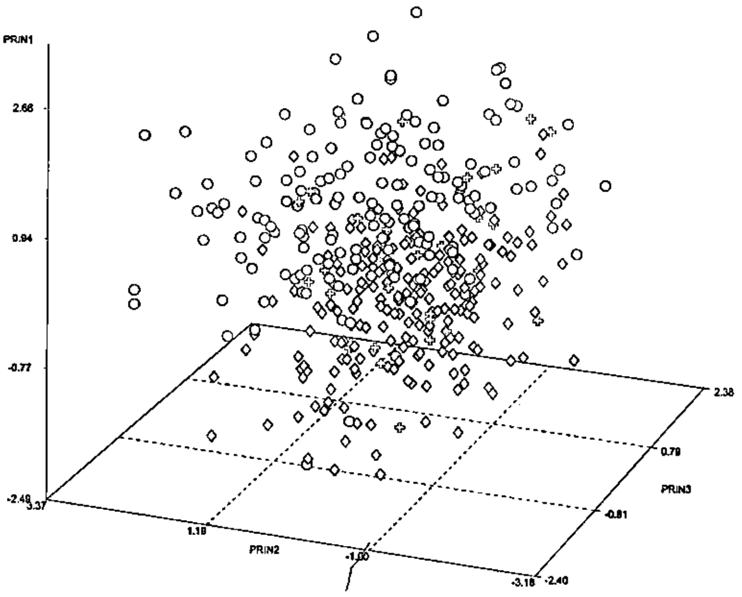
To summarise, it can be stated that the striping of acorns can be a differentiating trait, but its expression can vary and is often very indistinct. Therefore, a precise decision is sometimes not easy.

COMPARISON ON THE BASIS OF ANNUAL DATA OF TRAITS

The 15 leaf traits of the random sample of 420 oak plants were assessed or measured annually between 1993 and 1998, in total six times. For the same plant, the traits were relatively constant in the various years. A multivariate analysis of the annual data was used. The factor analyses using ten leaf traits resulted in a more or less dense cloud, as illustrated in Figure 1 for the first (1993) and the last year (1998). If the data points are given different symbols according to grouping with regard to striping, a certain structure of the cloud can be observed. The presentation is based here on the assessment of one person. A higher number of plants with unstriped acorns is visible in the upper part of the cloud (circle as symbol), whereas a higher number of plants with distinctly striped acorns occurs in the lower part of the cloud (rhomb as symbol). But in each part of the cloud symbols of other groups also occur. To summarise the results, one can state that a precise distinction of the two oak species is uncertain if only annual measurements and assessments of leaf traits are used.

COMPARISON ON THE BASIS OF ANNUALLY REPEATED DATA

As the evaluation of data of single years gave no clear picture for a distinction of the two oak species, the factor analysis was run with all annual data of the leaf characters, together 60 data. This resulted in a high differentiation of two clouds



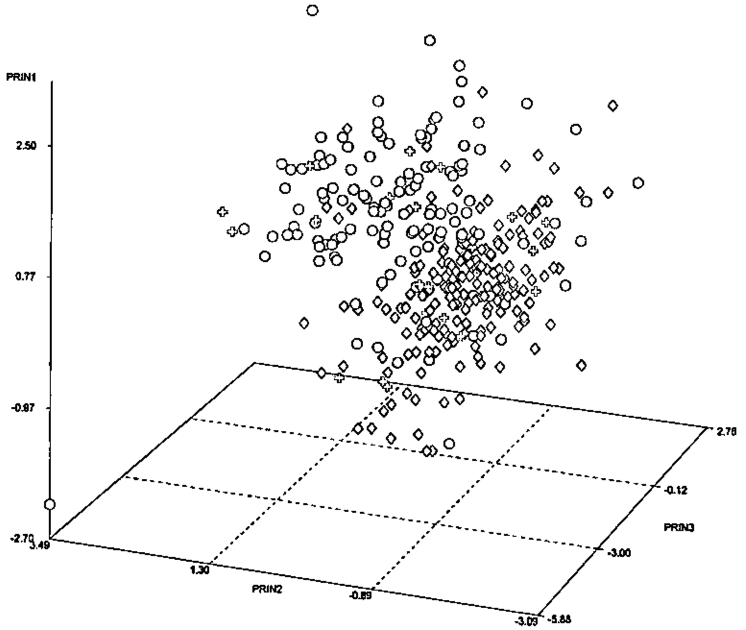


Figure 1. Scatter plots of the principal component analysis using 10 leaf characters of the year 1993 (above) and the year 1998 (below). The symbols are assigned according to the assessment of one person (circle = without stripes; rhomb = distinct stripes; cross = weak or indistinct stripes). In 1993 the three main components explain in total 70.9 % of the variance (Prin1: 35.0 %, Prin2: 21.7 % and Prin3: 14.2 %), in 1998 in total 75.2 % (Prin1: 47.7 %, Prin2: 15.2 % and Prin3: 12.3 %).

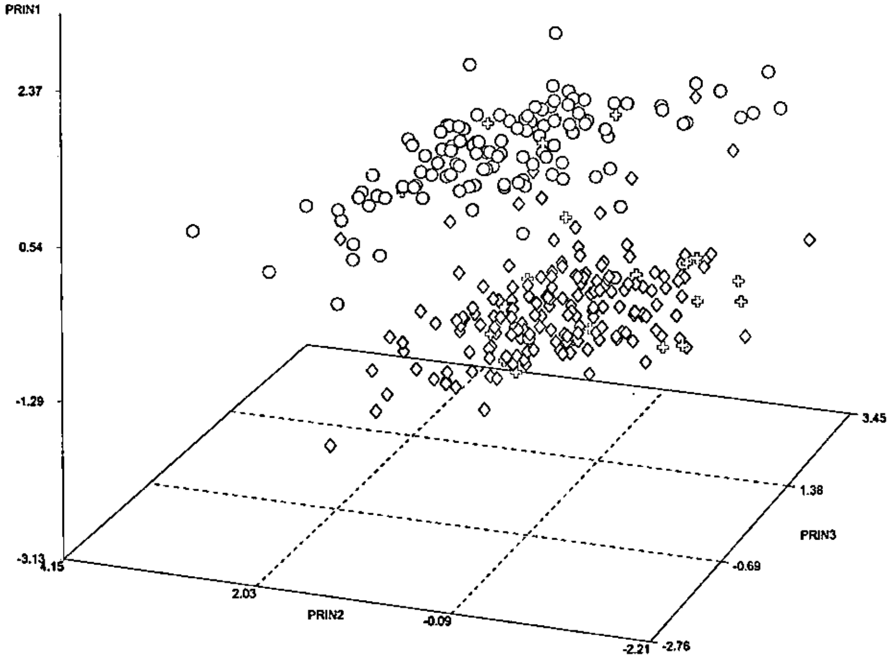


Figure 2. Scatter plot of the principal component analysis using 60 leaf trait data assessed from 1993 to 1998. The symbols are assigned according to the assessment of one person (circle = without stripes; rhomb = distinct stripes; cross = weak or indistinct stripes). The three main components explain in total 46.8 % of the variance (Prin1: 35.4 %, Prin2: 6.3 % and Prin3: 5.1 %).

as shown in Figure 2. If again the data points of the clouds were assigned with the trait striping of acorns, the two separate clouds are in good accordance with the distinction between oak types. The upper cloud represents the leaf traits of *Q. petraea* type with unstriped acorns. The lower cloud comprises the leaf traits of *Q. robur* type with distinctly striped acorns. Nevertheless, some opposite symbols and individuals with indistinctly striped acorns occur in each cloud. It was not investigated whether they were intermediate oak forms or hybrids. In summary, it could be demonstrated that a distinction of the two oak species is obviously more precise if the measurements and assessments of a longer observation period are put together for analysis.

IMPORTANCE OF TRAITS FOR THE DIFFERENTIATION OF THE TWO OAK SPECIES

In addition to the leaf characters, total height and annual increment were also measured, and flushing and mildew attack assessed for all plants in the respective years. The results of multiple comparison tests on the basis of adjusted means are given in Table 2. The flushing of plants varied between the years. The differences between early and late flushing were generally low, which can explain that in the years 1996 and 1997 differences between population means were not significant. In some years plants of the *Q. petraea* type flushed earlier, and in other years plants of the *Q. robur* type. Total height was in all years high, and significantly taller in plants of the *Q. robur* type than in those of the *Q. petraea* type. Not surprising was the fact that the annual increment was also significantly higher in plants of the *Q. robur* type than of the *Q. petraea* type. The exception in 1996 and the lower significant level in 1997 can be explained by the planting shock after the transplantation in spring 1996. Also for the attack by mildew, significant differences between the two oak types could be observed in most of the years. In 1995 the infection rate was very high. Therefore, the attack was relatively uniform on all plants of the trial. Nevertheless, the plants of the *Q. robur* type were generally more severely attacked.

Table 2. Differences between plants of the *Q. petraea* and the *Q. robur* type, respectively, on the basis of traits of growth and phenology measured or assessed from 1993 to 1998. (Significances: * = 5 %, ** = 1 %, *** = 0.1 %, ns = not significant, - = not observed)

trait	1993	1994	1995	1996 1)	1997	1998	1999
flushing	-	***	*	ns	ns	***	***
height	***	***	***	***	***	***	-
increment	-	***	***	ns	*	-	-
mildew	-	***	ns	***	**	***	-

1) the oaks were transplanted in spring 1996

In the previous chapters all leaf traits of the random sample of 420 oak plants were investigated by combined analysis. But it was also of great interest to check how the individual leaf traits contribute to the distinction between the two oak species. As already shown in a previous paper (Liesebach and Stephan 1998), 10 of 15 leaf traits contributed highly significantly to the differences between species in all years. This was also observed in the years 1997 and 1998, which had not then been evaluated in the mentioned publication. The remaining five leaf traits (lamina length, lobe width, length of lamina from the lamina base of the widest part, lamina shape, and total leaf length) varied between different levels of significance and lack of significance depending on the year.

Of particular interest was the question which leaf traits contributed most strongly to a differentiation between the striping groups of acorns. Therefore, the individual variance components were calculated for each year and for each leaf trait. The annual variance components of the ten leaf traits which can be explained by the striping of acorns are demonstrated in Figure 3. The values varied between the years, some remained more or less stable, some values increased in the course of

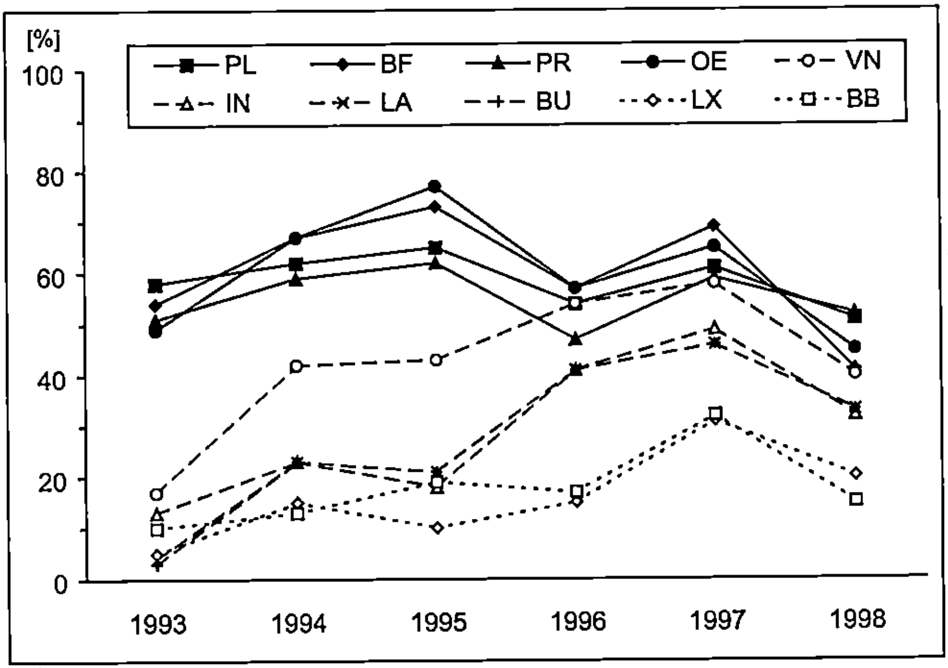


Figure 3. Annual values of the estimated variance components for the leaf traits (for abbreviations see text) from 1993 (age 1) to 1998 (age 6). Lines are only connections between the data points.

the years. For 1998, a general decrease could be observed for all values. Leaf traits with a relatively high contribution (40 % to 80 %) were the following: auricle development (OE), basal shape of lamina (BF), length of petiole (PL), ratio of petiole to total leaf length (PR). Low values (about 8 %) in the first years and increasing values (up to 60 %) in the following years were calculated for the traits: portion of veins (VN), number of lobe pairs (LA) and number of lamina sinuses (BU), number of intercalary veins (IN). The least values (5 % to about 30 %) were given by the traits: lobe depth ratio (BB) and lamina width (midrib to base of sinus) (LX).

DISCUSSION AND CONCLUSION

A precise distinction of the two white oak species, sessile oak (*Quercus petraea*) and pedunculate oak (*Q. robur*), is not only interesting from the taxonomic point of view, but is above all a necessity in connection with the national and international seed trade on the basis of European directives, national laws and regulations for forest reproductive material (see, for example, Anonymous 1979/94, Council of the European Union 2000). Seed samples should comprise pure species and impurities should be low. In the past, many studies were conducted to find traits or markers for a clear and distinct differentiation of the two above-mentioned oak species. Up to now, no single biochemical and molecular marker or morphological character has been suitable to differentiate the two species with absolute certainty. Both species seem to be related to such a degree that some authors have concluded that pedunculate oak and sessile oak may represent different ecotypes of the same species (Kleinschmit *et al.* 1995).

The most valuable results for the differentiation of species have been found by morphological studies on leaf and acorn traits. Therefore, in the present investigations more details should be clarified in this direction. The same morphological leaf traits were investigated as performed by other authors (e.g. Aas 1988, Elsner 1993, Rushton 1983). But these authors calculated discriminance analyses and compared the data with the characters of plants which they considered as typical for one or the other of the respective oak species. The aim of our study was to start without knowing to which species the various plants belong, to assess or measure as many acorn and leaf traits as possible, to add several growth and phenological traits, and to try to separate the material by multivariate analysis. Two separate groups could be distinguished which showed a rather good accordance with the acorn trait striping considered as a typical character of the respective oak species. Problematical was the fact that annual evaluations of investigated leaf traits are obviously not sufficient for clear differentiations. Only the factor analysis which combined the traits of all years led to a clearer separation. In this connection, a few leaf traits together with growth traits are of significant importance.

Although some individual plants did not fit into one of the groups which seem to correspond to one of the investigated oak species, we can conclude that *Q. petraea* and *Q. robur* are obviously two separate species, probably with some intermediate or hybrid forms.

Acknowledgements: We want to thank for the seed material the colleagues of the Research Stations in Escherode and Trippstadt. The skilful and laborious work of Silke Pohrt and Katrin Groppe during the establishment of the trial and the following measurements and evaluations are gratefully acknowledged. We are also very grateful to Klaus Liepe, Heiner Venne and Birgit Ziegenhagen for their valuable cooperation in the beginning of these investigations. Many thanks also to Armin König for comments on a previous version of the manuscript.

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RAZVOJ PROVENIJENCIJA *QUERCUS PETRAEA* I *QUERCUS ROBUR* IZ ŽIRA DO ŠESTOGODIŠNJIH BILJAKA U ODNOSU NA SPECIFIČNA SVOJSTVA VRSTE

U jesen 1992. godine prikupljeni su uzorci sjemena iz 14 čistih ili mješovitih sastojina dviju europskih bijelih vrsta hrastova *Quercus petraea* i *Q. robur*. Tri su osobe označile i klasificirale svaki žir uzorka u odnosu na prisutnost ili odsutnost vertikalnih pruga. Neovisna se razredba podudarala u oko 80 %. Označeni su žirevi posađeni 1993. i svake su godine prikupljani uzorci listova od rastućih biljaka radi procjene i mjerenja. Također su ispitana svojstva rasta, početak listanja i napadi plijesni. Podaci o svojstvima lista upotrijebljeni su za multivarijantnu analizu. Pri godišnjim mjerenjima ili procjeni svojstava listova nije se mogla točno utvrditi razlika između tih dviju vrsta hrasta. Ako se za analizu primjenjuju i mjerenja i procjene šestogodišnjega praćenja, mogu se izdvojiti dvije skupine podataka. Izrazite skupine (oblaci) pokazuju prilično dobru podudarnost svojstva žirovih pruga koje se smatraju tipičnim svojstvom dviju vrsta hrasta. Pruge na žirevima mogu predstavljati jedno od razlikovnih svojstava, čak i ako donošenje točne odluke ponekad nije lagano jer se ispruganost razlikuje i često je vrlo nejasna.

Ključne riječi: *Quercus*, hrast kitnjak, hrast lužnjak, fenotipska varijacija, diferencijacija vrsta

Ž. Borzan: Hermaphroditic, unseasonal flowering in the "green oak", growing in northern Dalmatia, Croatia. Glas. šum. pokuse 37: 425–439, Zagreb, 2000.

UDK 630*174+181.5+(4-015) (Quercus × viridis Trin.)

HERMAPHRODITIC, UNSEASONAL FLOWERING IN THE "GREEN OAK", GROWING IN NORTHERN DALMATIA, CROATIA

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Hermaphroditic flowering has been observed on a single tree, the "green oak", a supposed hybrid between *Quercus cerris* and *Q. ilex*. This tree has been systematically defined as *Quercus* × *viridis* Trinajstić, but it is unlikely that a hybrid of two species where acorns mature in the second year (*Q. cerris* L.) and in the first year (*Q. ilex* L.) could be found. For that reason, a new investigation of this tree was conducted. In late autumn, on 3 November 1998, during acorn collection from the crown, unseasonal flowering was discovered on two branches. Flowers appeared to be stiff, like female inflorescences, more elongated and with more flowers than normal. At first glance, the presence of numerous stamens in the inflorescence was evident. Under a hand lens, 4–6 stamens could be seen, surrounding a pistillate flower with well-developed stigmas. Inflorescences and individual flowers were photographed. Pollen from hermaphroditic flowers was photographed by a scanning microscope. In spring, on 26 April, abundant flowering of normal male and female flowers was observed, photographed and analysed. No aberrant morphology similar to the flowers discovered in November 1998 could be seen in the crown of the "green oak". Papers describing the occurrence of hermaphroditic flowering in some American oaks, especially the Gambel oak (*Q. gambelii* Nutt.), are discussed. Unseasonal flowering in "green oak" and the appearance of hermaphroditic flowers could not be explained by unusual climatic changes in the area. It could be speculated only that hermaphroditic flowering represents a primitive ancestral condition in the *Fagaceae*, as suggested by some of the authors discussed in the paper.

Key words: *Quercus* L., hermaphroditic flowering, unseasonal flowering

INTRODUCTION

In the village of Islam Latinski, Latitude 44° 12' N, Longitude 15° 26' E, 15 km NE from Zadar, Northern Dalmatia, Croatia, there grows a particular oak tree of impressive dimensions (Figure 1). This tree grows near the intersection of the main roads. Being so dominant in its size and habit, people used it as a focal point to measure distance and time to or form that tree. It is legendary because of its dimensions. It seemed that it has been part of this landscape from ancient time. Local inhabitants still claim that the tree is over 700 years old. The tree is different from other local oak species by its morphology, thicker bark, and its being covered with green leaves deep into the winter, hence people named it the "green oak". It is distinct in the environment of low growing degraded thermophilous, deciduous forests of the downy oak (*Q. pubescens* Willd.) and the Oriental hornbeam (*Carpinus orientalis* Mill.) where downy oak and Turkey oak (*Q. cerris* L.) are an integral part of that vegetation.

Figure 1. Older "green oak" near the village of Islam Latinski. Estimated age by use of the resistograph is 200 years. August 27th, 1995.

The evidence in literature, in which Trinajstić (1974) described the "green oak", prompted this research. He presumed that the "green oak" is a hybrid of "... = ? *Q. cerris* f. *austriaca* × *Q. ilex*". He gave a name to that tree *Quercus* × *viridis* Trinajstić, hibr. nov. Although hybrids between two oak species where acorns mature in the second year (*Q. cerris* L.) and in the first year (*Q. ilex* L.) are doubtful, in Trinajstić's paper the explanation or research which could support such a possibility is missing. That triggered our detailed biological and morphological investigation of the "green oak", supported by the local municipal organization "Nasadi" in Zadar (Siegert 1995, Vranković and Pernar 1995, Borzan *et al.* 1997, Borzan and Pfeifhofer 1998).

MATERIALS AND METHODS

The "green oak" tree was visited repeatedly several times a year. In autumn, on November 3rd, 1998, during the acorn collection from the crown, on two branches, freshly developed flowers were observed. The branches were cut off and examined the next day in the laboratory. The flowers were photographed and the pollen collected. Pollen grains from unseasonal flowering "green oak" inflorescences and from the regular flowering period next spring (April 26th, 1999) were collected from the "green oak", from *Q. cerris* and from *Q. ilex* trees. Pollen grains were photographed by means of a scanning electron microscope. In spring, on April 26th, 1999, abundant flowering of normal male and female flowers was observed, branches with flowers were cut off and details photographed and analysed in the laboratory. The same day, three km from the "green oak", another, but younger tree with similar morphological traits, was found (Figure 2). In autumn, on October 31st, 1999, both "green oak" trees were inspected again and searched for possible unseasonal flowers in the crown.

RESULTS

The "green oak" is approximately 200 years old, 20.2 m high and has a diameter of 1.6 m at breast height (Siegert 1995, Borzan *et al.* 1997). In late autumn, on November 3rd, 1998, during acorn collection from the crown of the "green oak", unseasonal flowering was discovered on two branches. Flowers were on 3-5 clustered inflorescences, arising on branches from the lowest spring shoot axils (Figure 3). Inflorescences were elongated, 2-5 cm long, stiff, much longer than normal female inflorescences, and shorter, but thicker than regular male inflorescences, densely covered with hairs (Figures 3-10). The presence of numerous stamens in the inflorescence was evident at first glance. Under a dissecting microscope, four to six stamens could be seen, surrounding a pistillate flower with well-developed stigmas. Opened anthers contained abundant well-developed pollen grains. Pistillate flowers were surrounded along the rachis with more stamens present on the top of the inflorescence and fewer or none in the proximal part (Figure 4). Each inflorescence had abundant hermaphroditic flowers.

Pollen from the hermaphroditic flowers (Figure 13) and the normal spring pollen grains (Figures 14-16) collected in 1999 were photographed by a scanning electron microscope. No difference in the pollen size or shape was observed. Scanned pollen grains collected in spring 1999 were considerably smaller in the *Q. ilex* when compared to the pollen grains of the "green oak" and *Q. cerris*. The "green oak" and *Q. cerris* had pollen grains of the same size.

In spring of 26th April, 1999, abundant flowering of normal male and female flowers (Figures 7-10) was observed, photographed and analysed. No aberrant morphology similar to the flowers discovered in November 1998 could be seen in the crown of the "green oak".

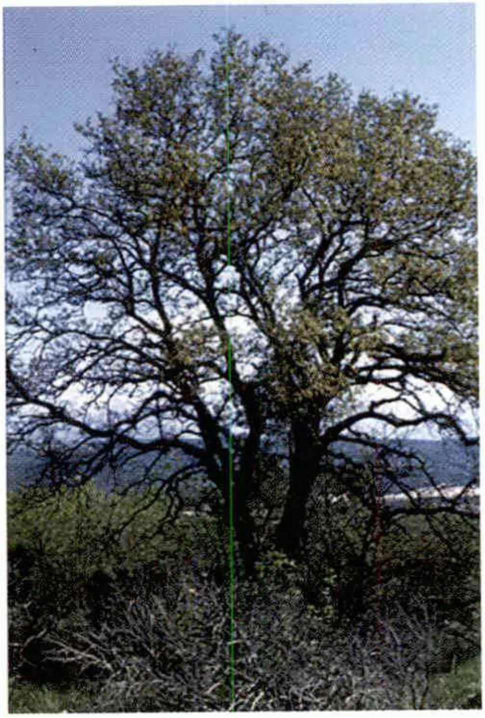

Figure 2. Younger "green oak" is approximately 70-80 years old. April 26th, 1999.

In April 1999 another "green oak" tree, located three km from the original "green oak", was found (Figure 2). That tree is younger, and is approximately 80 years old.

In autumn, on October 31st, 1999, after a careful search within the crown of the "green oak" unseasonal flowering was not observed. In the crown of another, younger "green oak" tree, 6 branches with unseasonal flowers were observed. They were male catkins only (Figure 11), and no female or perfect flowers were found.

DISCUSSION

The morphology of the "green oak" has been described several times (Jedlowski 1955, Trinajstić 1974, Borzan at al. 1997). In each of those papers, additional traits were described. Jedlowski (1955) stated that the acorns fell before ripening. As a result of such an opinion he drew the scaly cup with a partially developed acorn. For that reason, in this paper the photograph of fully developed acorns of

Figure 3. Inflorescences with hermaphroditic flowers on branchlet of the "green oak". November 3rd, 1998.

the "green oak", collected on November 3rd, 1998, with scaly cup is shown. Acorns are 3-5 cm long and 1.5-2.3 cm thick (Figure 12).

The total number of fully developed acorns of the "green oak" tree in the last three years has not been more than 500 per year. That number is what we could

Figure 4. Female flowers are located on the rachis in the proximal part of the hermaphroditic inflorescence. Perfect flowers cover main part of the rachis, with more stamens in the distal region.

Figure 5. Part of the inflorescence with hermaphroditic flowers. Most of the anthers are open.

Figure 6. Part of the inflorescence with pistillate flowers. Pistills have 3-4 stigmas.

Figure 7. Normal, male aments in the crown of the "green oak". April 26th, 1999.

Figure 8. Close up of the normal, male ament of the "green oak". April 26th, 1999.

observe from the total number of collected acorns from the ground and from the crown. We collected them within a period of one month (between November 1st and 30th), once a month from the crown and once a week from the ground. It is believed that the total number of acorns is much greater, considering that local inhabitants and visitors who stop by that tree collect acorns too and take them away. Most of the acorna from the ground (ca 90 %) are infected by acorn weevils (*Curculio* L. spp.), with 2-5 larvae in each acorn.

Normal male and female flowers of the "green oak" have not been described yet. In Figure 7 normal male inflorescences are shown within the tree crown, and in Figure 8 one close up of the male inflorescence is presented. Figures 9 and 10 show normal spring female inflorescences born in the axils of the upper leaves on terminal shoots. Each inflorescence has 2-5 pistillate flowers; three on average.

The unseasonal flowering on November 3rd, 1998., showed aberrant flower morphology similar to that described by Tucker (1972), Tucker *et al.* (1980) and Scaramuzzi (1958). Tucker (1972) found hermaphroditic flowers on a specimen of *Q. turbinella* Greene ssp. *californica* Tucker on August 9th, 1941, and on one specimen of *Q. durata* Jeps. on August 31st, 1947, in California. In their paper, Tuc-

Figure 9. Normal female inflorescence of the "green oak" born in the axils of the upper leaves on young shoots of the current season. April 26th, 1999.

Figure 10. Typical, female inflorescence of the "green oak" with expressed stigmas. April 26th, 1999.

ker *et al.* (1980) describe another finding, this time on August 2nd and 3rd, 1978, on two plants of Gambel oak clones (*Q. gambelii* Nutt.) along a streamside in Utah. By the description, these hermaphroditic flowers resemble the hermaphroditic flowers of the "green oak". In the American oaks they appeared two to three months earlier than on the "green oak". Apart from the time variation in the formation of the hermaphroditic flowers, their location on the shoots differs in comparison to the American oaks too. Inflorescences with hermaphroditic flowers in the American oaks were born in positions where next year's catkins are normally initiated, i.e. around the base of the new emerging shoot. In the "green oak" they grew from axils of a spring woody shoot (Figure 3), so one could speak of a sort of cauliflorous occurrence. Fall mail flowers were also found on the younger "green oak" on October 31st, 1999. They grew in the area of a shoot where next spring growth is normally expected, on the tip of the fall shoots (Figure 11).

It is worth mentioning an additional variation that exists between the American oaks and the "green oak". In the American species the acorns ripen in the first year, whereas in the "green oak" the acorns ripen in the second year. However, hermaphroditic flowers on *Q. coccifera* L. on which the acorns ripen in the second year were discovered during mid May 1954, and described by Scaramuzzi (1958).

Hermaphroditic flowers on the inflorescence are considerably longer than normal female spring inflorescences. Emphasising this fact, Tucker (1972) indicates that some oaks posses the potentiality for bearing a greater number of pistillate flowers, but the growth hormones most likely suppress their development in the upper part of the rachis. Thus, one to three female flowers ripen in the proximal part only. He continues: "If, then, the "normal" auxin regime were upset on rare occasions by a marked change in environmental conditions, perhaps this potential would be realized and ancestral gene combinations still in the code, but long suppressed, would be re-activated to produce not only elongated, multi-flowered inflorescences but hermaphroditic flowers as well. Tucker *et al.* (1980) suggest that "multi-flowered inflorescences containing hermaphroditic flowers represent a primitive ancestral condition in the *Fagaceae*, still present in the genome, but normally suppressed, which may be evoked by unusual environmental condition".

In the spring of 1999, in the crown of the "green oak", hermaphroditic flowers were not detected and that tree did not bloom in the fall of 1999. During May of 1999 severe attack of gypsy moth (*Lymantria dispar* L.) was detected. It caused detaliation on the "specimen" oak and even more drastic defoliation on the younger "green oak". Both trees recovered relatively quickly, hence by mid fall the effects of defoliation were not noticeable.

The formation of hermaphroditic flowers in oaks will most probably be researched for a duration of time before it can be defined with certainty. The "Green oak" will have to be visited, observed and studied continuosly over several years. Only then will one be able to conclude if the out of the season and aberational bloom is cyclical or if the aberational bloom in fall of 1998 was an isolated case.

Figure 11. Male inflorescences from the crown of the younger "green oak" blooming in the fall. Flowers were found on October 31st, 1999, photographed 6 days later, after ripening in a container with water.

Figure 12. Acorns of the "green oak". November 3rd, 1998.

Taxonomical status of the "green oak" has not been completed. Trinajstić (1974) named it as hybrid of Turkey and holm oak, without the experimental pro-

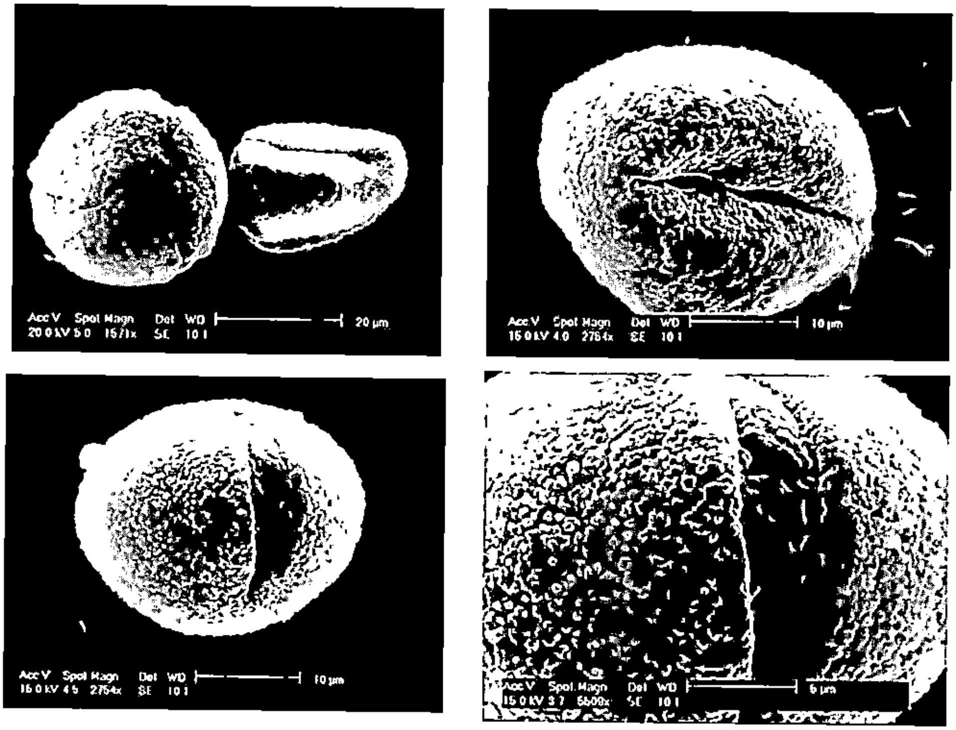

Figure 13. Pollen from hermaphroditic flowers of the "green oak" taken by scanning electron microscope.

of of hybridisation or the explanation of how these two species could be hybridised. Furthermore, he stated that the "green oak" is an evergreen. However, the "green oak" is not an evergreen tree. It does not bear foliage on biannual shoots. In the winters of 1994/1995 until 1999/2000 it was void of foliage. Lovrić (1981) also considers it as a "hybrid of holm and Turkey oaks (Q. × *ambrozyana* Simk.)", and states "that it appears in the eastern Adriatic coastal region in submediterranean forests of parental species as a sporadic and solitary specimen". However, in Krüssmann (1978) Q. × *ambrozyana* Simk. is mentioned as a synonym of cultivar Q. *cerris* 'Ambrozyana' and is believed to be a hybrid between Turkey oak and the cork oak (Q. *suber* L.). Jedlowski (1955) thinks that "according to its morphological traits, the "green oak" appears to be a hybrid of Turkey and cork oak". Borzan and Pfeifhofer (1998) analysed volatile compounds obtained by steam distillation of the "green oak", the Turkey oak and of the holm oak leaves. After gas chromatography and gas chromatography/mass spectrometry analysis, a cluster analysis of the patterns of the volatile substances in the leaves did not support the assumption that the green oak is a hybrid between the Turkey and holm oaks. Their opinion is "that the "green oak" could be a progeny of a back-crossed hybrid between Q. *cerris*

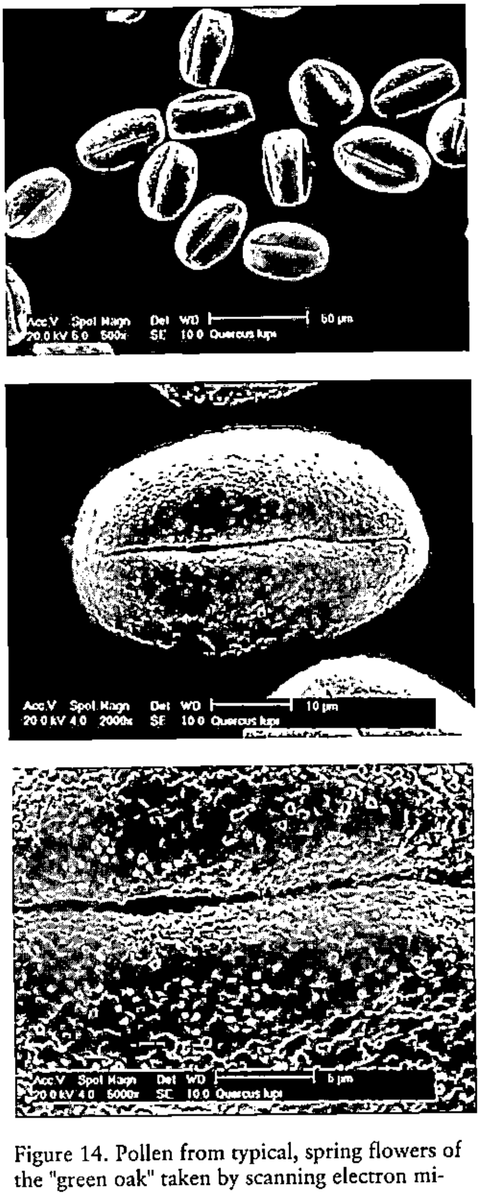

Figure 14. Pollen from typical, spring flowers of the "green oak" taken by scanning electron microscope.

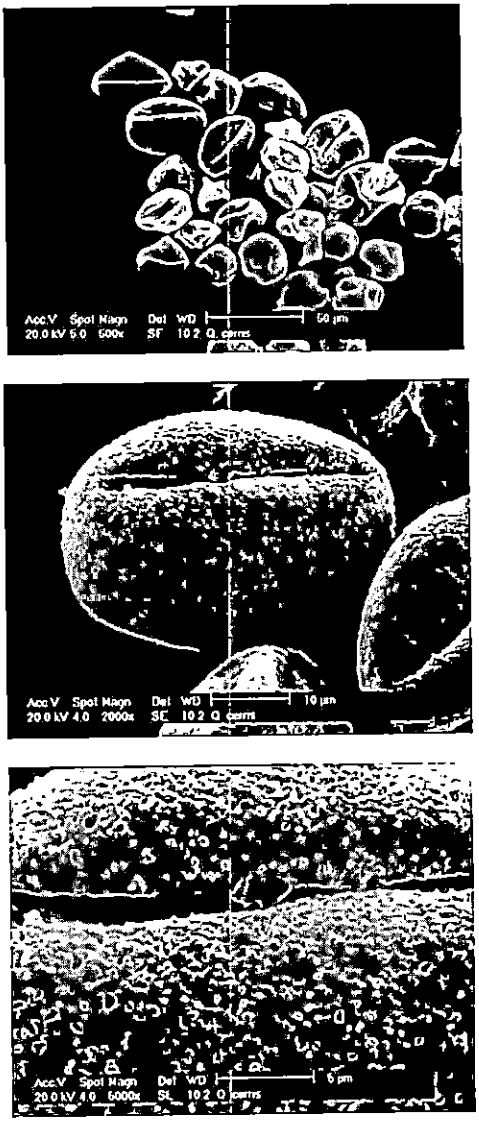

Figure 15. Pollen from spring flowers of the Turkey oak (*Quercus cerris* L.) taken by scanning electron microscope.

and *Q. suber* or a variety of *Q. cerris* restricted to a small area of distribution in Ravni kotari, Croatia". Without cytological and molecular research, or without a conducted hybridisation of the "green oak" and other submediterranean and Mediterranean oaks, it will be, difficult to define its taxonomical status.

Though it is difficult to believe that oak in which acorns mature in a single season could be hybridised with oaks whose acorns mature in two seasons, Cottam *et al.* (1982) cite the example of a successful by controlled hybridisation of three such crosses: *Q. turbinella* × *Q. cerris*, *Q. turbinella* × *Q. suber* and *Q. turbinella* × *Q. marilandica*. In those crosses the female parent was always *Q. turbinella*, whose acorns ripen during the first year. It is significant that for progenies from those crosses they gave a credible verification of their hybridity. Their morphological traits were intermediate to parental species and they have also been proved by the use of biochemical methods. Consequently they write: "Thus, whatever the genetic control may be of the timing of reproductive events, this difference in fruit maturation is not necessarily a major barrier to intercrossing". In the "green oak", however, if it is a hybrid, it is clear that the intermediary character toward *Q. ilex* is missing, since by its morphological traits it resembles Turkey oak but with smaller and more downy leaves, a thicker and corky bark red in furrows, and the ability to retain green foliage deep into winter.

The region of Ravni Kotari should be systematically explored to find all the samples of "green oak", to identify and protect them. Unfortunately, this region is covered with mines, as a residue of the 1991–1995 war, so at this time it is impossible to find and how many and how frequent the "green oak" specimens appear in this area. Considering that in April of 1999 we found one more "green oak", one may assume that more could be found, as is also believed by local inhabitants.

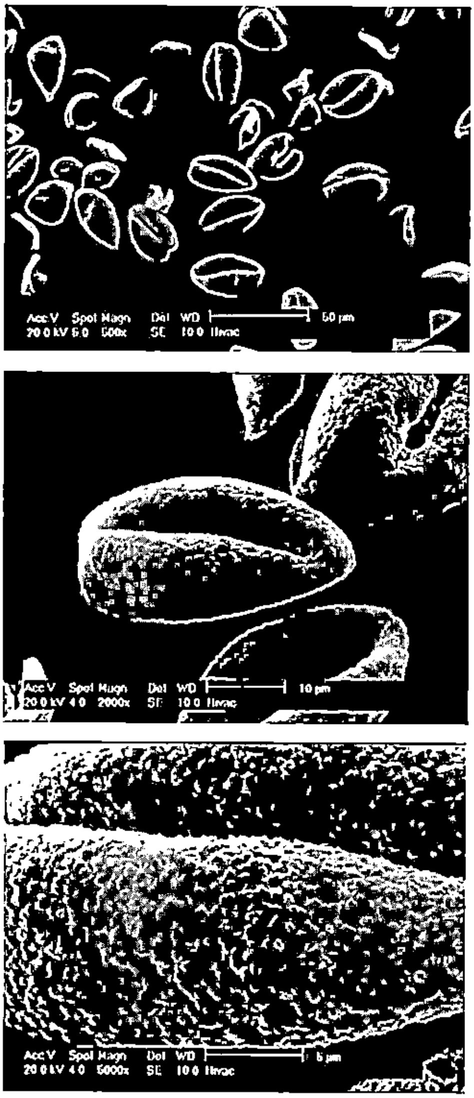

Figure 16. Pollen from spring flowers of the holm oak (*Quercus ilex* L.) taken by scanning electron microscope.

ACKNOWLEDGEMENTS

Appreciation is extended to Dr. Edith Stabentheiner for work with scanning electron microscope scanning of the oak pollen grains and to my colleagues at the Department of Plant Physiology, University of Graz Dr. H. Guttenberger and Hartwig W. Pfeifhofer for providing the laboratory facilities and the sophisticated photo equipment. Thanks are given to my friend Charles D. Holetich for reviewing the manuscript. The research was financially supported by Croatian Forests Inc., Zagreb, and by the municipal organization "Nasadi" Zadar, Croatia.

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HERMAFRODITSKO, IZVANSEZONSKO CVJETANJE "ZELENOGA HRASTA" KOJI RASTE U SJEVERNOJ DALMACIJI U HRVATSKOJ

Primijećeno je hermafroditsko cvjetanje na jednom stablu, "zelenom hrastu", pretpostavljenom hibridu između *Quercus cerris* i *Q. ilex*. To se stablo sustavno definiralo kao *Quercus* x *viridis* Trinajstić, ali je malo vjerojatno da postoji hibrid dviju vrsta u kojemu žirevi sazrijevaju u drugoj godini (*Q. cerris* L.) i u prvoj godini (*Q. ilex* L.). Iz toga su razloga poduzeta nova istraživanja toga stabla. Kasne jeseni, 3. studenoga 1998. godine, tijekom skupljanja žireva iz krošnje, na dvije je grane primijećeno izvansezonsko cvjetanje. Cjetovi su izgledali kruti kao ženski cvat, duži i s više cvjetova nego što je normalno. Na prvi se pogled u cvatu vidjela prisutnost brojnih stamena. Pod ručnim su se povećalom mogla vidjeti 4–6 stamena koji su okruživali muški cvijet s dobro razvijenim stigmama. Napravljene su fotografije cvata i pojedinih cvjetova. Pelud je iz hermafroditskih cvjetova fotografiran skenirajućim mikroskopom. U proljeće, 26. travnja, primijećeno je, fotografirano i analizirano bogato cvjetanje normalnih muških i ženskih cvjetova. U krošnji "zelenoga hrasta" nije zamijećena nikakva devijantna morfologija slična cvjetovima otkrivenim u studenome 1998. Razmatraju se radovi u kojima se opisuje pojava hermafroditskoga cvjetanja na nekim američkim hrastovima, posebno na gambelu (*Q. gambellii* Nutt.). Izvansezonsko cvjetanje "zelenoga hrasta" i pojava hermafroditskih cvjetova ne može se objasniti neobičnim klimatskim promjenama u ovom području. Može se samo pretpostaviti da hermafroditsko cvjetanje predstavlja primitivno naslijeđeno stanje u porodici *Fagaceae*, kao što sugeriraju neki autori o kojima se u ovom radu govori.

Ključne riječi: *Quercus* L., hermafroditsko cvjetanje, izvansezonsko cvjetanje

J. Kleinschmit, J. G. R. Kleinschmit: *Quercus robur – Quercus petraea*: a critical review of the species concept. Glas. šum. pokuse 37: 441–452, Zagreb, 2000.

UDK 630*164+165+181 (Quercus robur L., Q. petraea Liebl.)

QUERCUS ROBUR – QUERCUS PETRAEA: A CRITICAL REVIEW OF THE SPECIES CONCEPT

KLEINSCHMIT J., KLEINSCHMIT J.G.R.

This paper summarises the results of studies on the differentiation of pedunculate (*Quercus robur* L., ssp. *robur*) and sessile (*Quercus robur* L., ssp. *petraea*) oak and discusses these results in the light of hypotheses on the evolutionary status of the two oaks with special reference to implications for a sustainable treatment of the natural resource "oak".

The early descriptions of *Q. robur* and *Q. petraea* focus on the morphological and ecological differences of what was considered to be a good species. Species discrimination based on morphological differences relies on the taxonomic species concept. According to the biological species concept, two individuals belong to the same species if environmental conditions exist where they are part of the same population, i.e. where they might have common descendants. Thus, if we take a complex like the oaks, which are not completely reproductively isolated, the question arises where the evolutionary process is leading to? To species differentiation, to a reunion of two already distinct species, or to an equilibrium where sessile and pedunculate oak are kept by both gene flow and selection? This question has to be answered to be able to work in accordance with the adaptational evolutionary processes without risking the adaptability of the oaks.

This paper summarises the results of morphological, phenological, physiological and biochemical genetic studies and of controlled crosses. Results are discussed referring to the above-mentioned hypotheses on the evolutionary status of oaks. The evolutionary status cannot finally be answered. Nevertheless, some implications for future research and practical actions are discussed.

INTRODUCTION

Oak species are arousing increasing interest for economical and ecological reasons. In many countries of Central Europe, forest policy favours hardwoods in silviculture. This has stimulated research on these species, both on a European and on a national level.

In the field of forest genetics as a special area of research activities, the question of species differentiation plays a central role. The aim of discriminating species is twofold:

1. finding easily distinguishable units to work efficiently;

2. understanding the biology of evolutionary units and deducing biologically meaningful strategies for human action.

The complex of the genus "Quercus" is a good example to show that both aims can produce conflicting results (Muller 1952, Burger 1975, Aas 1998).

The differentiation of oaks has been studied using traits with different degrees of environmental and genetic control: morphological, phenological, physiological and genetic traits. The objects of study have been different genetic units like species, provenances, progenies or controlled crosses.

Morphological studies can help in understanding the differentiation and adaptational situation.

Genetic traits like isozyme or DNA markers – nuclear as well as extranuclear – give information about the genetic structure (e.g. diversity, relatedness, genetic background) of different genetic units and the evolutionary processes (e.g. drift, selection, migration) acting on them.

The genetic units' norm of reaction of these traits can be inferred only by using experiments with different ecological conditions (e.g. climate chamber tests, multi-site tests).

Controlled crosses allow the study of:

1. genetic isolation/ fertility of genetic units,
2. the degree of genetic control of phenotypic traits and
3. hybrid morphology and performance.

All this information contributes to the knowledge of the species: how far the results of such studies influence the delineation of genetic units into different species depends very much on the species concept (Summary see: Ereshefsky 1992). We follow the biological species concept: the biological species concept defines that "species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1992, 1957).

INFORMATION BASE FOR PEDUNULATE AND SESSILE OAK

MORPHOLOGICAL INFORMATION

The two types "pedunculate oak" and *"sessile oak"* are botanically defined by morphological traits (Oelkers 1913; Schwarz 1937; Camus 1938 to 1939; Jones 1959; Krahl-Urban 1959; Tutin et al. 1964; Aas 1998) They have different ecological requirements; pedunulate oak is typical for rich, humid sites in the lowlands, sessile oak has its characteristic populations on less rich, warmer and drier sites. At first glance, this differentiation seems to conform with the aim to find easily distinguishable units.

For northern and western Germany the detailed morphological analysis of more than 1,400 stands showed that only 18 % of the stands consisted of only one of the types. All other stands included a certain percentage of intermediate forms and/or of the other type (Table 1) (Elsner 1993, Kleinschmit 1993). This seems to be especially true for sites with mosaics of humid and dry soil conditions. In these places intermediate morphological forms are found more or less frequently (Elsner 1993; AAS 1988; Krahl-Urban 1959; Kleinschmit et al. 1995). Similar results were found in other countries (e.g. Gathy 1970; Sutilov 1968; Benea 1960).

Table 1. Composition of 1,416 oak stands in North and West Germany (1999)

State	pedunculate oak number and percent of stands within a category sessile oak									Total
	+	A	B	C	D	C	B	A	+	
Schleswig-Holstein	42 17 %	102 40 %	45 18 %	24 10 %	13 5 %	12 5 %	6 2 %	8 3 %	-	252 18 %
Niedersachsen	71 8 %	231 27 %	97 12 %	47 6 %	79 9 %	49 6 %	55 7 %	113 14 %	94 11 %	836 59 %
Rheinland-Pfalz	5 2 %	8 3 %	7 2 %	18 5 %	13 4 %	37 11 %	61 19 %	129 39 %	50 15 %	328 23 %
Total	118 8 %	341 24 %	149 11 %	89 6 %	105 7 %	98 7 %	122 9 %	250 18 %	144 10 %	1416 100%

\+ = stands of pure ecotype
A = stands with a certain percentage of intermediate forms
B = stands with intermediate forms and up to 10% of the other ecotype
C = stands with intermediate forms and 10-50% of the other ecotype
D = stands with high percentage of intermediate forms and both ecotypes

Controlled crosses revealed that some of the morphological traits which had been used for the discrimination between pedunculate and sessile oak are strongly maternally inherited. This fact makes these traits unsuitable for discrimination of the two types.

PHENOLOGICAL INFORMATION

In phenological characters, no basic differences exist between pedunculate and sessile oak if they originate from the same region. However, between provenances drastic differences can occur. Thus, within a region, flower phenology does not constitute a reproductive barrier (Krahl-Urban 1959; Kleinschmit 1993; Bacilieri 1994).

ISOENZYMSTUDIES AND DNA-MARKERS

A recent summary of genetic studies in pedunculate and sessile oak is given by Herzog (1998) and Gehle (1999). They conclude that up to now neither morphological characters nor isozyme and DNA markers show disjunct distributions between both species. They follow the arguments of Kleinschmit et al. (1995) that these facts of limited genetic differentiation but different ecological requirements indicate that pedunculate and sessile oak are ecotypes of the same biological species. Finkeldey (2000) and Hertel (1998) found significant differences in the frequency of certain enzyme systems. Herzog (2000) describes significant differences between populations of pedunulate oak under different selection regimes.

A specific set of DNA markers, the chloroplast DNA (cp DNA), which are maternally inherited, allow the study of the recolonisation of oaks after the glaciation. For these markers, it is striking that both pedunculate and sessile oak have the same cp DNA haplotypes in the same geographical region (Petit et al. 1995; Finkeldey 2000).

PROVENANCE AND PROGENY TESTS

For a summary of the results of provenance/progeny tests, see Kleinschmit 1993. These results show that certain provenances are adaptable over a wide range of environments with low losses and excellent growth (e.g. Madsen et al. 2000). The variation in stem quality between provenances is quite high. There is no clear indication that pedunculate oak is superior to sessile oak on typical pedunculate oak sites (Jensen 1993; Svolba and Kleinschmit 1999). There seems to exist a higher resistance to stress induced by defoliation in sessile oak if grown under the same site condition. However, the variation between provenances within pedunculate or sessile oak by far exceeds the differences between the ecotypes (Svolba and Kleinschmit 1999).

CONTROLLED CROSSES

Artificial hybridisation between the two species is possible (Dengler 1941; Rushton 1977; AAS 1988; Steinhoff 1993, 1997). The rates of acorn production for interspecific crosses with pedunculate oak as the seed tree and sessile oak as the pollen tree showed about 60 % success compared to the intraspecific crosses of pedunculate oak. For sessile oak as a seed tree, the interspecific crosses had only 8 % success in single tree crosses and 54 % in crosses with pollen mix as compared to within-species crosses (Fig. 1). Isozyme analysis in a mixed French oak stand with natural regeneration supports these results (Bacilieri 1994).

The intermediate forms are fully fertile and the progenies perform as well as pedunculate oak and are superior to sessile oak at a young age (Kleinschmit and Svolba 1979; Steinhoff 1997). Up to the age of seven, the hybrid families of the two types grow in the nursery as well as families of the seed parent type (Steinhoff 1997).

DISCUSSION

From the above findings it is clear that pedunculate and sessile oak are actually or potentially interbreeding populations. According to AAS (1998) there also

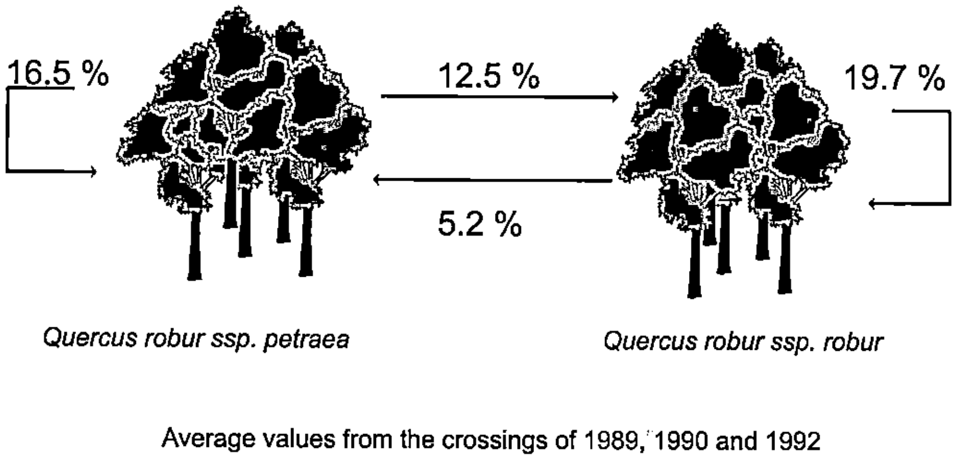


Fig.1. Fertility rates of controlled crosses

exists a broad hybrid zone between sessile oak and Q. pubescens. We tend to look at pedunculate and sessile oak as a dynamic system in time and space with an asymmetric gene flow, favouring hybridisation in the direction of pedunculate oak as a mother species.

With the knowledge of all the results, we have to look at the two types of oak as a single though complex biological species whose delineation, from other oak species, has not been finished yet.

Three hypotheses on the actual status of the oaks within the evolutionary process seem to be possible.

1. We are looking at a formerly single species from which have evolved two partly new, completely separated species.
2. We have a stable equilibrium between convergence by gene flow and divergence due to adaptation to different ecological conditions.
3. Two formerly separate species are converging to a single species.

The last hypothesis seems to be unrealistic because of the shared cp-DNA variation of both oak types when they are sympatric (Petit et al. 1995).

POSTGLACIAL RECOLONISATION

The analysis of the postglacial recolonisation of Central Europe might give some hints about which of the hypotheses should be favoured. The western part of the glacial refugia is located in the Mediterranean region. During recolonisation, not all variability from the south of Europe arrived in the north (Zanetto and Kremer 1995). Local patterns of variation for chloroplast DNA type can be random due to founder trees (Petit et al. 1995). This can explain some of the ecotypic variation found in provenance experiments for adaptive traits. However, 90 % of diversity in chloroplast DNA exists between populations, and only 3 % of nuclear diversity (Kremer and Petit 1993). The latter should be responsible for adaptive traits.

Petit et al. (1995) argue that the recolonisation was strongly supported by water and birds, especially by the jay (Garrulus glandarius) which prefers the bigger acorns of pedunculate oak. Therefore, pedunculate oak was the coloniser by seed and sessile oak followed by pollen. Gene flow was a precondition for sessile oak to migrate by pollen into pedunculate pioneer stands (Petit et al. 1995). There must be a strong selection pressure under specific site conditions to reconstitute sessile oak by recombination and stronger isolation against pedunulate oak.

Another scenario would be the regionally repeated local differentiation of sessile oak from the genepool of pedunculate oak under specific site conditions. This would imply that the genepool of pedunculate oak always includes the potential for differentiation into the other ecotype. The second scenario implies a very strong and globally uniform acting disruptive selection pressure.

Postglacial recolonisation has not finished yet. We do not expect a stabile equilibrium on all sites. Local provenances are not necessarily the best adapted, due to founder effects.

STRATEGIES FOR HUMAN ACTION

The typical ecotypes are found under the typical ecological situations (humid and rich versus warmer, drier, less rich) (Fig. 2). There exists, however, a broad zone where both ecotypes, including intermediate forms, exist side by side. These sites are characterised by a mixture of ecological conditions. Under these condi-

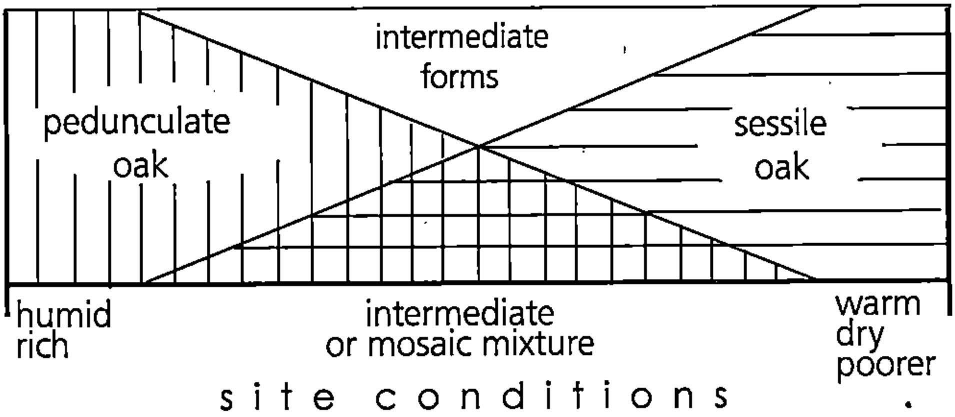


Fig. 2. Shematic situation of pedunculate and sessile oak depending on site conditions

tions hybridisation can occur. Some stands show a high percentage of intermediate forms. These forms seem to have a selection advantage under certain site conditions (Kleinschmit and Svolba 1979). Here an equilibrium between recombination and selection could be established, or evolution is moving the system in one direction.

Silviculture

For management decisions, the results of field testing are at the moment easier to interpret than those from genetic studies. Both must be combined, though. There also exists a considerable variation for adaptive traits between populations within ecotypes, which is not reflected in biochemical-genetic markers. This could be explained by random distribution of genetic information in the founder populations. If these had time to establish dense forests before the migration of seed and pollen could change the genetic structure, this situation may be nearly fixed or changed only very slowly (Petit et al. 1995), especially if there exists no continuous stand structure. This situation is typical for oak. Ecophysiological studies with genetically clearly defined material could help to better understand the evolutionary forces acting on the oaks. One necessary analysis will be to check the hybrid advantage /disadvantage in comparison with the pure ecotypes under different site conditions (Fig. 3).

If we take the fact of asymmetric gene flow as an evolutionary result, human activities should be in accordance! We would expect the more isolated unit – here sessile oak – to be found under more extreme environmental conditions. Seed transfer should not be done with "pedunculate oak" type material to typical sessile oak sites. The transfer of seed material in the opposite direction should be less critical or even supporting evolutionary forces if we accept the first scenario of postglacial recolonisation.

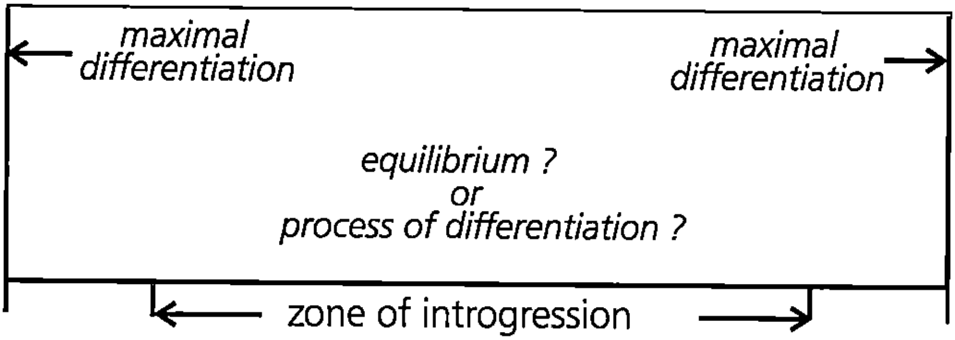


Fig. 3. Evolutionary processes behind the pattern of distribution

Table 2. Hypotheses on the evolutionary status of pedunculate and sessile oak: indicators, necessary analysis, and strategies for human action

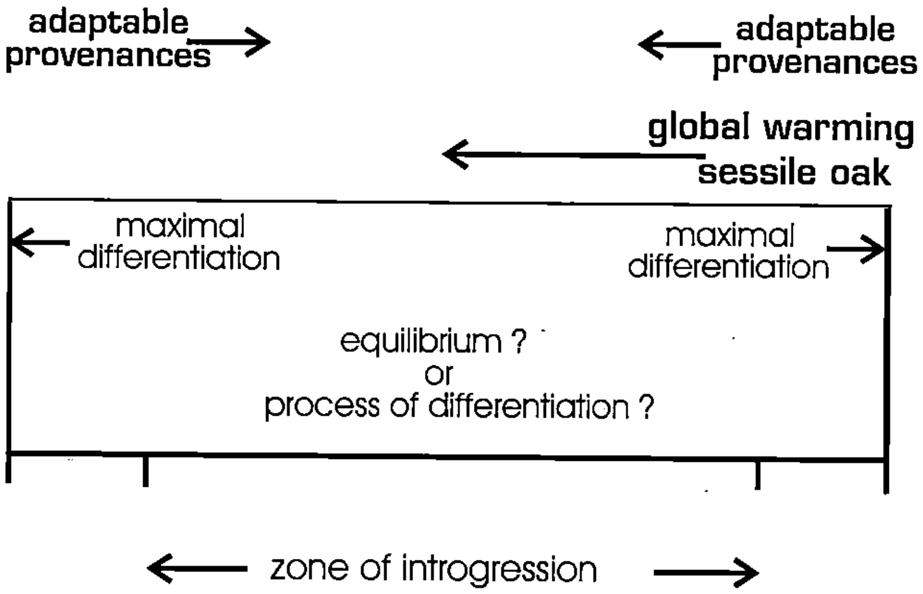
	1 Disruptive selection producing two separated species	2 Balance between gene-flow and disruptive selection	3 Stabilising selection producing one single species
Indicator / Necessary analysis	- Different ecological requirements - Same cp-DNA types - Disruptive selection / specialists	- Gene flow - Same cp-DNA types - Local hybrid advantage - On extreme sites selection against hybrids	- Gene flow - Global hybrid advantage - Stabilising selection
Strategies for human action for A: seed-transfer B: selection of uniform types	Use only "pure types' seed" Choose type according to site condition	Use seed from comparable site conditions Prefer sessile oak on intermediate sites	Mix seed as much as possible Take only intermediate forms / hybrids

Global warming

Since environmental conditions change (e.g. global warming) a selective advantage for sessile oak seems to be probable in future. Some results of oak decline point in this direction (Svolba and Kleinschmit 2000). Zaspel and Hertel (1999) demonstrated that tolerant individuals have a higher heterozygosity and a higher multilocus diversity irrespective of the ecotype. From field experiments we know certain provenances which show high adaptability under a wide range of site conditions. How far this is reflected in genetic markers is not known.

CONCLUSION

Pedunculate and sessile oak are connected in an evolutionary process, which has a different stage of development in space. The process of differentiation is locally finished and distinct populations exist; at other locations, this process is actively going on with all intermediate steps of differentiation (Table 1). Whether this is an equilibrium under such site conditions or a directional process cannot be answered finally. However, the intermediate and/or mosaic site conditions indicate an equilibrium situation, which, however, can be altered by changing environmental conditions and by the introduction of different (more adaptable) provenances as well (Figure 4):



LITERATURE

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QUERCUS ROBUR – QUERCUS PETRAEA: KRITIČKI OSVRT NA KONCEPT VRSTA

U ovom su radu sumirani rezultati proučavanja diferencijacije hrasta lužnjaka (*Quercus robur* L., ssp. *robur*) i hrasta kitnjaka (*Quercus robur* L., ssp. *petraea*) i razmatrani su dobiveni rezultati u svjetlu hipoteze o evolucijskom statusu tih dviju vrsta uz poseban osvrt na implikacije za potrajni tretman prirodnoga resursa "hrasta".

Rani su opisi *Q. robur i Q. petraea* bili usmjereni na morfološke i ekološke razlike onoga što se smatralo dobrim vrstama. Razlikovanje vrsta temeljeno na morfološkim razlikama oslanja se na koncept taksonomskih vrsta. Prema konceptu bioloških vrsta dvije jedinke pripadaju istoj vrsti ako postoje okolišni uvjeti u kojima su one dio iste populacije, to jest u kojima mogu imati zajedničke potomke. Tako, ako uzmemo kompleks kao što su vrste hrasta, koje nisu potpuno reproduktivno izolirane, postavlja se pitanje kamo vodi evolucijski proces. Vodi li prema diferencijaciji vrsta, prema ponovnom sjedinjenju dviju već različitih vrsta ili prema ravnoteži u kojoj se hrast kitnjak i hrast lužnjak održavaju i pomoću genskoga tijeka i pomoću selekcije? Na to je pitanje potrebno naći odgovor kako bismo mogli raditi u skladu s adaptacijskim evolucijskim procesima, a da pritom ne riskiramo adaptabilnost hrastova.

U ovom su radu sumirani rezultati morfoloških, fenoloških, fizioloških i biokemijskih genetičkih proučavanja i kontroliranoga križanja. Rezultati se razmatraju u skladu s gore spomenutom hipotezom o evolucijskom statusu hrasta. Ne postoji konačan odgovor na evolucijski status. Ipak, razmatraju se neke implikacije za buduća istraživanja i praktične radnje.

I. Yakovlev: Genetic diversity of pedunculate oak (*Quercus robur L.*) in the middle near volga region of Russia. Glas. šum. pokuse 37: 453–468, Zagreb, 2000.

UDK 630*165+181.8+(47) (Quercus robur L.)

GENETIC DIVERSITY OF PEDUNCULATE OAK (*QUERCUS ROBUR L.*) IN THE MIDDLE NEAR VOLGA REGION OF RUSSIA

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Pedunculate oak *(Quercus robur* L.) in the Middle Volga region grows here on the North–Eastern boundary of the natural range of pedunculate oak in Europe. Oaks in the region are characterised by some peculiarities in intraspecific variability and genetic structure. Here oaks have three phenological forms in terms of autumn coloration and shedding of leaves: early-shedding form, late-shedding form and intermediate forms. There exist a high diversity of trunk, crown, leaf and acorn characters. On the basis of the study of leaf morphological trait variations, oak populations were subdivided into *Volga forest* and *Transvolga forest–steppe* groups, the latter including two population subgroups growing in the forest–steppe zone: Mokshansko–Surskaya (plain mountain) and Transvolga (flatland). Based on isozyme analysis at 10 loci, the genetic variability of 14 natural populations of pedunculate oak spreading throughout the region was studied. A high variability of pedunculate oak populations was shown: 60–83% of genes were in a polymorphic state; the average number of alleles per locus was 1.8–2.5. The observed and expected heterozygosities varied from 9.9% to 17.1% and from 11.9–18.4%, respectively. The populations share a common gene pool with intensive gene exchange between populations.

Key word: Pedunculate oak, intraspecific diversity, phenological forms, populations, isoenzymes

INTRODUCTION

The Middle Near Volga (Middle Povolzhje) is a region situated in the central–eastern part of European Russia. It includes the Chuvash republic, the Republics Tatarstan, Mordovia and Mary El, and Kirov, Nizhegorodskaya, Ulyanovskaja, Penzenskaya and Samarskaja provinces (oblasti) located in the basin of the River Volga (FIG. 3). Pedunculate oak *(Quercus robur* L.) is one of the main forest–forming species in the region. The oak forests here cover 934.1 thousand ha (5% of the forested area of the region and 25% of total oak forest area of Russia) and are of high environmental importance for water and soil protection and recreation. The oak forests of the region are growing in four natural zones: coniferous–broad-leaved forests, broad–leaved forests, and forest–steppe and steppe zones. A wide spectrum of climatic and soil conditions within the region determine a very diverse species composition and structure of oak forest ecosystems.

In the Middle Near Volga region oak forests grow on the northeastern limits of their natural range in Europe and are characterised by particular intraspecific variability and special physiological, biological and ecological peculiarities. Their formation has proceeded for a long period of time, which has determined the specific phytocenotic and genotypic structure of *Q. robur* populations. The monophyletic origin of pedunculate oak and the existence of phylogenetic relationships between the modern oak forests of the Middle Near Volga region and the ancient preglacial large oak forests have been postulated (Semerikov 1986). In the Pleiostocene epoch of the Quaternary period characterised by periodic glaciations, oak was kept in refuges on the territory of the Central Povolzhje in the vicinity of the glacier, namely, in the southern part of the Volga Upland, Southern Urals Mountains, and the eastern part of Obshchij Syrt Upland (Semerikov 1986, Denisov 1980). Later, after the glaciations, pedunculate oak spread from these refuges to the north and northeast within the modern boundaries of its range.

Oak forests were highly exploited over a long period of time. Since the first quarter of the 18th century, due to the development of shipbuilding, the oak forests in the Middle Near Volga region (former Kazanskaja and Simbirskaja provinces) and the central part of Russia were proclaimed as reserved, “ship” oak groves and served exclusively for the supply of oak wood for Baltic and Black Sea shipyards. A special management regime was established and only selective cuttings of the best oak trees were allowed. Multiple selective cuttings have led to intensive "negative selection" and the deterioration of the genetic potential of oak forests (Red’ko et al. 1997). The result of intensive cuttings and clearance was that from an initially common extended oak forest many small, isolated oak stands were formed.

INTRASPECIFIC VARIABILITY OF PEDUNCULATE OAK IN THE MIDDLE NEAR VOLGA REGION BY MORPHOLOGICAL TRAITS

Growing in different, frequently contrasting conditions of relief, soils and climate, the oaks are characterised by an extremely high interspecific polymorphism and a distinct variability of morphological and physiological characters, due to adaptation to variable environmental growing conditions. Oaks form a number of forms and types – geographical, ecological, phenological and morphological.

A considerable amount of studies on the intraspecific variability of pedunculate oak exists both in Russia and abroad. In the Middle Near Volga region, studies have been conducted by Danilov (1969, 1975) and Gurjev (1970) and in the present time by A. Yakovlev and I. Yakovlev (1995, 1999). Due to the limited size of this article, some tables and figures confirming the drawn conclusions are not shown.

EDAPHICAL ECOTYPES (EDAPHOTYPES) OF PEDUNCULATE OAK

Edaphical ecotype is defined as the groups of populations within the limits of a climatype, whose singularities are developed by the relief and soil–hydrological conditions of the places of growth. The considerable influence of edaphical conditions on the bio–ecological properties of oak, both on character, productivity and quality of stands and their stability, is marked. In the Middle Near Volga region, in the zones of mixed coniferous broad–leaved forests and the northern forest–steppe, three edaphical ecotypes of oak have been identified (Denisov 1965):

1) Low mountain (nagornij) ecotype – growing on the right bank of the Volga river, on high, plain areas and low–grade slopes of ravines and watersheds, on rich, drained soils;

2) Plateau (plakornij) ecotype – growing on the left bank of the Volga and Kama rivers, on flat, drained, non–swampy watershed plains, mostly on soddy podzolic humused loamy or loamy–carbonaceous soils;

3) Floodplain ecotype – growing on the floodplain terraces of the rivers, in specific soil–hydrological conditions with periodic flooding and a high level of ground waters on alluvial soils.

PHENOLOGICAL FORMS OF PEDUNCULATE OAK

The existence of two phenological forms of oak in the terms of spring leaf flushing – early and late - are described in many pieces of research for the central and western part of Russia (Lukjanetc 1979, Patlaj 1977, etc.). These forms are considered as genetically determining and are characterised by different ecological and growth requirements.

But in the northeast and eastern parts of the habitat range, i.e. to the east of the line Tula – Voronezh, the phenological forms of pedunculate oak in the periods of flushing are not determined. The variability of flushing time is only 5–10 days. At the same time, the duration of autumn coloration and shedding of leaves covers 55–75 days (Gurjev 1970, Danilov et al. 1975, Antciferov and Chemarina 1988, A. Yakovlev and I. Yakovlev, 1999). Due to such prolonged terms it is possible to determine quite clearly the trees whose leaves are shed comparatively early and the trees which shed their leaves later than all the others. The difference between these two groups of trees is 20 – 30 days. All this allow us to divide the trees into three phenological forms (phenoforms) in the terms of autumn coloration and shedding of leaves: the early-shedding (ES) form, the late-shedding (LS) and intermediate (IR) form.).

It is considered that the differences between the autumn phenological forms are genetically controlled because the trees of different phenoforms growing in the same stand keep the timing of leaf shedding from year to year which is also due to inheritance in progeny tests and correspondence of progeny to the Hardy–Weinberg equilibrium

It has been established that the phenological forms of oak exist in all edaphical ecotypes and that trees of different phenological forms have different physiological and morphological peculiarities. By the growth traits in stands, the group of trees of the late-shedding form have a statistically significant higher medium diameter and height and a higher rank than the group of early-shedding form of trees and are presumably more competitive. The late-shedding trees, in comparison with those of the early-shedding form, are characterised by straighter trunks and good clearance from branches, and by a higher quality of timber due to their lower susceptibility to damaging factors, diseases and especially frost shakes, but the difference is statistically non–significant. The trees of the intermediate form have intermediate values of traits or have values equal to those of the late-shedding form.

An average share of trees by autumn phenoforms was assessed in all edaphical ecotypes. Normally, in stands of all ages, trees of the intermediate form (IR) prevail with a share between 34 and 60 %, the share of trees of the early-shedding form is between 10% and 38%, with their share decreasing with the increase in the medium age of the stand, and the late form has a share between about 16 and 44 %, increasing with age (Fig. 1).

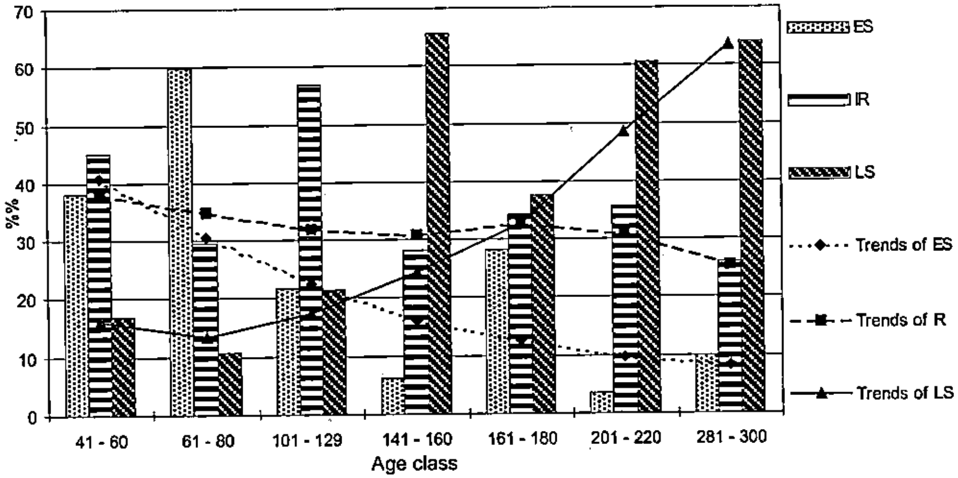

Fig. 1. Dynamics of shares and trends of trees of different phenological forms in oak stands of different age (low mountain ecotype)

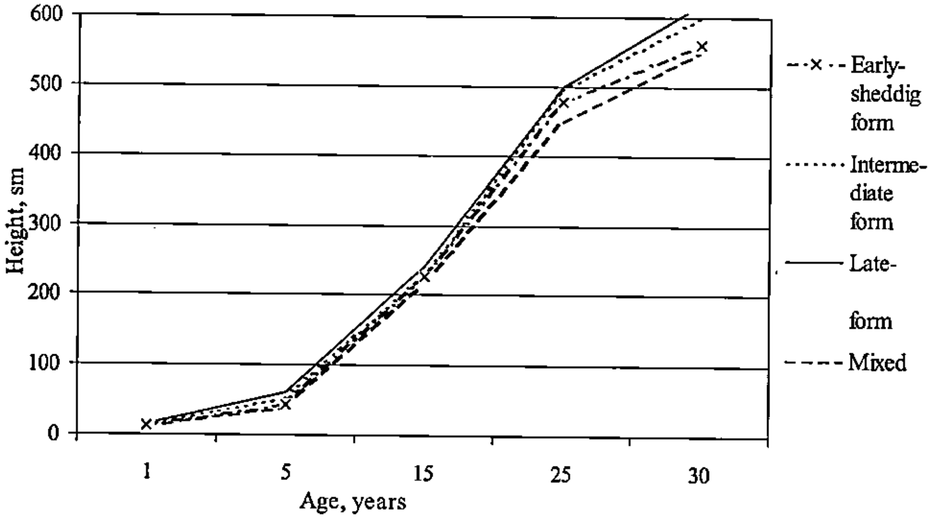

Fig. 2. Growth of progenies of trees of different phenological forms in progeny test

It is clear from the Figure 1 that in young and middle–age stands the trees of the early-shedding form prevail, but their share decreases with age and in mature and over–mature stands the share of ES trees is less than 10%, while the opposite trend is determined for trees of the late-shedding form and in mature and over–mature stands LS trees prevail. In the floodplain edaphotype, the share of the ES form is higher than in other edaphical ecotypes of oak.

The study of the growth of progenies from tress of different phenoforms over a period of 30 years shows a difference in growth rates between the forms in the early stages of development (Fig. 2).

The progenies from trees of the late-shedding form grew faster during the whole test and demonstrated lower susceptibility to damaging factors. The progenies from trees of the early-shedding form had lower growth rates and were more vulnerable to diseases. The intermediate form had an intermediate growth rate. But progenies from mixed acorns showed the highest losses in the first two years and the worst growth rate during the whole test period. This might be explained by higher competition between the progenies of different phenoforms in comparison with pure groups.

The prevailing nature of the early-shedding form in young stands is a little bit strange due to its lower competitive ability. However, this could be explained by the fact that the early-shedding form is more successful in propagation, and perhaps flowers better and produces more healthy acorns than other forms. Nevertheless this theory should be tested.

VARIABILITY OF TRUNKS AND BRANCHING

During our studies we tried to assess the intraspecific variability of oak by the morphological traits of trunks (straightness, clearance from branches, epicormic shoot spreading) and crowns (shape, types of branches).

There is a prevalence of trees with straight trunks, but at the same time with medium and bad clearance from branches and intensive development of epicormics (Table 1). But in the plateau and floodplain ecotypes, the share of straight trees and clearance from branches is lower than in the low mountain edaphotype. With increasing age, clearance from branches became worse due to intensive epicormic growth and sparser growing of trees. Regarding the branching and the form of tree crown, there is a prevalence of trees with a mixed type of branching and oval–broom (triangle) or broom–like form of crown.

Table 1. Structure of oak stands in the Middle Povolzhje by traits of stems

Character	Share of trees, %%						
	Low mountain (nagornij)					Plateau (plakornij)	Flood – plain
	Medium age of stands						
	60–100	60–100*	101–140	141–180	181 and older	81–140	81–140
Number of observed trees	960	540	456	251	79	171	194
Straightness of trunks							
Straight	56,5	61,3	66,8	70,1	76	48	50,6
Slightly crooked	18,8	16,5	15,5	14,3	5,0	20,5	23,4
Crooked	19,1	17,2	13,1	7,2	7,6	27,5	20,2
Very crooked and prong–shape	5,6	5,0	4,6	8,4	11,4	4,0	5,8
Clearance from branches							
Good	14,2	42,2	3,6	3,6	1,3	3,0	1,0
Medium	42,8	19,5	54,8	27	56,4	33,7	10,3
Bad	43,0	38,3	41,6	69,4	42,3	63,3	88,7
Epicormics	78,0	74,3	82,7	60,7	76,0	78,6	46,4
Basic angle of branching (form of crown)							
70–90° (oval)	31,0	35,4	16,8	7,3	–	31,0	43,0
60–75° (oval–triangle)	41,2	39	43,5	52,4	–	45,4	31,4
45–60° (triangle, broom–like)	16,6	17,3	24	20,7	–	13,6	15,1
Irregular (Dichotomic)	11,2	8,3	15,7	19,6	–	10,0	10,5

* – Forest plantation

VARIABILITY OF OAK BY CHARACTERS OF ACORNS

A high intraspecific variability of trees exists in the shape and dimensions of acorns. The variability of the dimensions of acorns in stands corresponds to the normal distribution. But for breeding aims, the grouping of acorns by weights and dimensions and in shape has been developed. There are three clearly identified forms in acorn shape: typical – ovoid, with a medium coefficient of shape (ratio of length to width) of 2.01 and more, long–acorn (oblong) with a medium coefficient of shape of between 1.51 and 2.0, and broad–acorn (broad–elliptic), up to 1.50. Also there are three forms by acorn weight: large – with a medium weight of 4.1 g and more, medium – 2.1 to 4.0 g, and small – up to 2.0 g. The size and shape of acorns are genetically controlled; in many cases it is easy to differentiate neighboring trees by their acorns.

No correlation has been established between the coefficient of shape and the time of coloration and shedding of leaves. The correlation between the width and length and the weight of acorns is direct and high. The shape of acorns does not correlate with their dimensions. The variability of the dimensions and weight of acorns in populations is high, while the shape of acorns has the lowest variability. In all oak edaphotypes, oaks trees with acorns of a typical shape (52 – 69%) prevail. Trees with broad–acorns are more rare than those with long–acorns: the share of trees with long–acorn varies from 19% to 28%, while the share of trees with broad–acorns (broad–elliptic) varies from 12 – 22%.

The influence of the shape and dimensions of acorns to the growth success of young trees has been analysed. It was established that acorns of a broad–elliptic form germinate earlier and with a higher energy of germination in comparison with others forms. In addition, acorns from trees of a late-shedding form have a lower energy and longer time of germination. In the trial tests of acorn form, the medium height of progenies from acorns of long–acorn form was higher than that of the progenies from acorns of broad–acorn form. This difference was maintained for the whole period of the test until the age of 15.

Therefore, these groups have an important value for forest tree breeding, especially for the organisation of a seed production base according to some peculiarity features. By the complex of growth and quality traits, the late-shedding form, and the long–acorn (oblong) and large–acorn forms were determined as the most valuable economically.

VARIABILITY OF OAK BY LEAF MORPHOLOGICAL TRAITS

The variability of oak leaf morphological traits was studied during an analysis of the spatial–population structure of oak forests of the Middle Near Volga region (I. Yakovlev 1999). The samples of leaves were taken from 37 populations throughout the region (Fig. 3). The leaves were collected from 40–50 trees in each population, 1 leaf per tree. The method of leaf sampling was based on the theoretical principles described by Semerikov (1986).

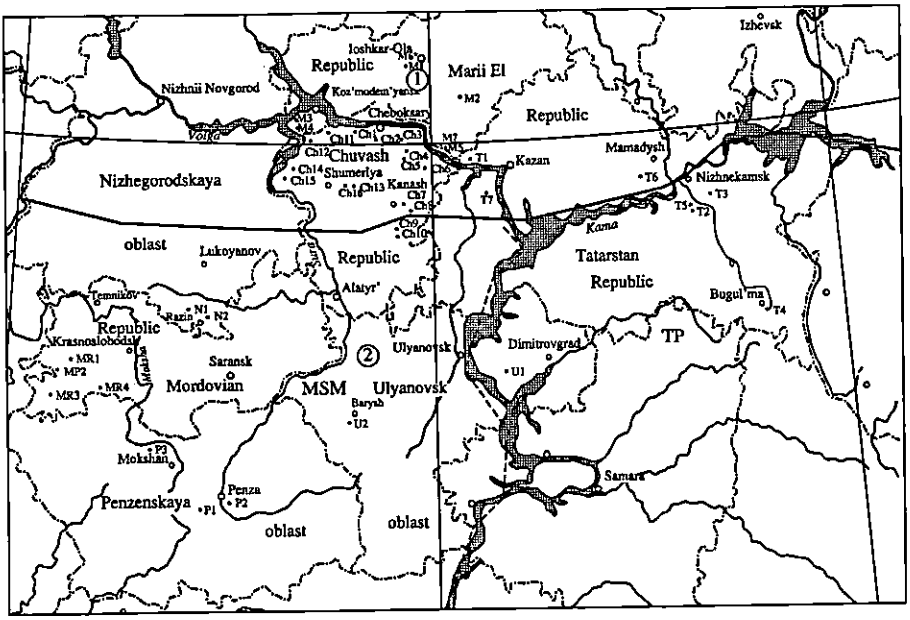

Fig. 3. Sampling sites and ranges of pedunculate oak population groups in the Middle Volga region: *M1–...–*Ch15 are samples from populations; 1 – the Volga forest group of populations, 2– the Transvolga forest–steppe group of populations; MSM - Mokshansko–Surskaya (mountain) subgroup, TP - Transvolga (flatland) subgroup of populations (Yakovlev I. 1999).

In each leaf, the following parameters were determined: (1) leaf length, mm, (2) petiole length, mm, (3) leaf width by lobes, mm, (4) leaf width by excisions, mm, (5) length of the leaf top, mm, (6) number of lobes; (7) tangent of veining, (8) form coefficient (the ratio between leaf length and width in the widest part), (9) form index (the ratio between the length of the leaf top and total leaf length), (10) average lobe length, (11) dissection coefficient (the ratio of the difference between leaf width by lobes and by excisions to leaf width by lobes). The presence of secondary lobes and the pubescence of blades were also checked. For each population, the mean values for all 11 traits, their average error, variations and frequency of qualitative traits were calculated. Due to limited space, the data of processing are not given in this paper.

Data analysis shows some trends in the variability of leaf morphological traits. A clear trend of increasing leaf dimensions (lamina length and width, petiole length, etc.) from populations of southern and southeastern parts of the Middle Near Volga region to populations of the northern and north–eastern part of the region exist. So, the largest leaves originate from the populations of the northern part of the Privolzhskaja upland and from the left Volga river bank area (that is, along the Volga river). Smaller leaves are found in the populations of the southern part of the Privolzhskaja upland (south of the Chuvash Republics, the Mordovia

Republics and the Penza province). A quite clear trend in the change of shape of leaves with a more oval lamina and apex (oval and obovate shape) of the northern populations to a narrower elliptic and spiky shape with a sharper angle of primary veins of the southern and southeast populations has been established.

The variability of lamina length is low, within the limits 11–13 %. The mean petiole length in the eastern range of oak distribution is 6 – 9 mm, a little smaller in southern and eastern parts of the region (6 – 6.8 mm), gradually increasing to the north and reaching 8.7 mm. However, the variability of this trait is high, the fluctuations of absolute means are from 4 up to 20 mm. The variability of size traits of leaves – maximal width of a leaf and lamina width, length of an apex and average height of blades – is high and medium, with a significant amplitude of fluctuations. The average number of lobes on a leaf is about 11–13 (5–7 pair blades). By this trait, the distinctions between samples of populations from different natural–geographical zones are insignificant and doubtful. By ratio traits – the coefficient of the form, lamina shape, and the lobe depth ratio – the distinctions between various samples are also insignificant.

Through qualitative traits, it has appeared that all leaves in the investigated region have pubescence and secondary lobes.

POPULATION STRUCTURE OF PEDUNCULATE OAK IN THE MIDDLE NEAR VOLGA REGION

Population structure was investigated for the purpose of a substantiation of genetic reserve allocation. For the analysis of the spatial–population structure of oak forests, the characteristics of samplings from various oak populations of the region by 11 quantitative traits of leaves were used. The consecutive application of multivariate procedures of the representation of data (factor analysis), classification (cluster analysis) and discrimination analyses have allowed us to carry out a division of populations into similar groups of individuals and to obtain a clear estimation of such a division.

It was established that significant variations of edaphic and climatic conditions in the Middle Near Volga region, the presence of the powerful isolation barrier - Volga River - and numerous oak forms and varieties has not resulted in a significant differentiation of populations.

A cluster analysis by Ward's method provided reliable evidence that the initial aggregation of samples from populations forms two distinct groups of clusters *(A* and *B*) subdivided into smaller subgroups (Fig. 4). The two large cluster trees join at the level of 39.9 in D^2 units, which suggests that they are genotypically remote from one another. At the same time, every large cluster consists of three groups of smaller clusters that join at levels of 6.33–9.05 units. It is surprising that the strong variation of edaphic and climatic conditions in the Middle Volga region, the presence of the efficient isolating barrier (the Volga River), and the existence of nu-

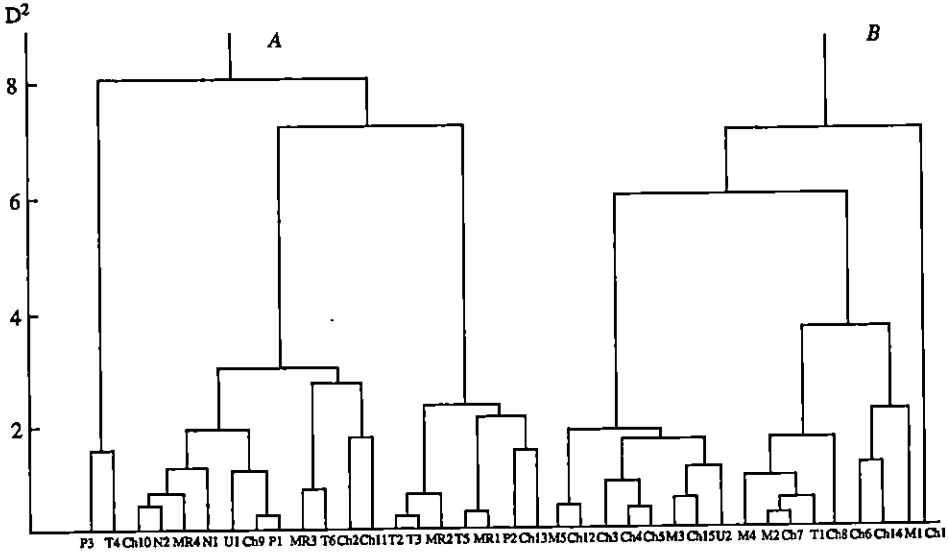

Fig. 4 Dendrogram plotted by Ward method for samples from pedunculate oak populations of the Middle Volga region.

merous oak forms did not result in any significant differentiation of populations. It is also possible, however, that the resolving capacity of markers (characters) and statistical methods used in the study were insufficient for revealing this differentiation.

To test the distribution of samples over possible groups, a discriminant analysis was used. The procedure of discrimination consisted in obtaining canonical equations allowing the attribution of an individual to a certain group or series. Taking into account the spatial distribution of populations and the results of cluster analysis (the levels at which subgroups are arranged into larger clusters), discriminant functions were calculated for two and three possible groups of populations. In the former case, the results showed a distinct subdivision of all populations into two non-overlapping groups. Discrimination by three groups and the analysis of relative positions of populations in the plane of canonical axes 1–2–3 also demonstrated their segregation into two large groups *A* and *B*, which virtually did not overlap. Moreover, the group *B* appeared to be subdivided into two slightly overlapping subgroups b_1 and b_2.

Thus, two groups of populations are revealed. 1. Volga forest – unites the populations of Common Oak of the forest zone of Zavolzhje (Forest Low Zavolzhje and Vjatka – Kamskaja highland area) and the zone of mixed coniferous–broad–leaved forests of the northern part of the Privolzhskaja highland area. 2. Transvolga (Sursko–Kamskaja) forest–steppe – unites two subgroups of oak populations, growing in a forest–steppe zone of the region. The 1st subgroup Mokshansko–Surskaja ("nagornaja" – low mountain) – occupies the whole of the central and south–western part of the Privolzhskaja highland area, the 2nd subgroup – Transvolga ("plakornaja" – plateau) – is located on the leached chernozems and gray forest soils of Low Zavolzhje and on the stony rendzina soils of High Zavolzhje. The border between the two groups of populations is allocated on the Privolzhskaja upland and passing along the line Ardatov – Arzamas – Poretskoe – Kanash – the mouth of the Kama river and further along the Kama river. The border between the subgroups passes along the Volga from the mouth of the Kama river and further down. The distinction of these subgroups is also caused by the set of their morphological traits as well as by their significant geographical distance from each other (Fig. 3).

ISOENZYME VARIABILITY OF PEDUNCULATE OAK IN THE MIDDLE NEAR VOLGA REGION

Here we present the results of the study of isoenzyme variation within and among the oak populations of the region by means of electrophoresis. The objectives of this research were the assessment of the level of genetic variation within the oak populations and the determination of the degree of genetic differentiation between different stands and edaphotypes of oak for the substantiation of measures on the conservation of oak genetic resources and the creation of a forest seeds basis.

Additionally to four earlier studied populations (I. Yakovlev et al. 1999), ten more indigenous populations of pedunculate oak of all edaphotypes in the Republics Mari El, Chuvashija and Tatarstan were investigated. All isoenzyme analyses were done in the Technical University of Zvolen (Slovakia) together with L. Paule and D. Gömöry. Placement and geographical coordinates are shown in Figure 3 and Table 2.

The extraction, migration and staining of gels were done as described in I. Yakovlev et al. 1999. Eleven enzyme systems controlled by 13 loci were analysed by standard starch gel electrophoresis in 3 buffer systems, but for further analyses only 10 loci were used (*Gdh–2, Got–1, Idh–1, Mdh–1, Me–1, Mnr–1, Pgi–1, Pgi–2, Skdh–1, Fest–1),* which were clearly interpreted for all populations (Table 2).

Only one of the 10 loci examined (*Pgi–1*) appeared to be monomorphic in all investigated populations. However, the mean percentage of polymorphic loci by no criterion ranged from 60 % to 83 % (Table 3, by 0.95 criteria – from 30 % (Jantikovo) to 50 % (most of population) and by 0.99 criteria from 50 % to 70 %.

The levels of gene diversity at the population level differed markedly among loci. These variations were mostly due to differences in frequency profiles. The availability of one more frequent (predominant) allele is characteristic to all loci. Three possible classes of loci by frequency structures could be identified. Class 1 includes monomorphic loci (only *Pgi–1*). Class 2 – weakly polymorphic loci – is characterised by one predominant allele (frequency > 0.85) and other rare alleles

Table 2. The main parameters of genetic variability of pedunculate oak populations

N	Population	Mean sample size per locus	Mean no of alleles per locus	Percentage of loci poly-morphic*	Mean heterozygosity	
					Observed (H_o)	Expected (H_e)
M7	Volzsk pojma	52,8±0,1	2,5±0,4	75	0,161±0,049	0,162±0,045
M1	Korta plakor	50,3±0,3	2,4±0,3	75	0,171±0,043	0,184±0,045
M6	Dub roscha	50,5±0,3	2,4±0,4	75	0,171±0,046	0,170±0,047
M5	Volzhsk plakor	50,0±0,0	2,5±0,3	75	0,178±0,051	0,183±0,052
M2	Ilet	47,8±0,1	2,3±0,3	83	0,150±0,042	0,163±0,049
T7	Kajbitskaja	51,3±0,3	2,2±0,2	80	0,130±0,050	0,133±0,050
Ch14	Pandikovo	47,0±2,1	2,2±0,5	60	0,163±0,057	0,169±0,060
Ch4	Marposad	45,4±5,2	2,2±0,4	70	0,163±0,047	0,161±0,048
Ch16	Babeevo	39,4±5,1	1,8±0,3	50	0,170±0,072	0,152±0,062
Ch15	Atnari	40,7±6,0	2,0±0,3	70	0,154±0,069	0,141±0,061
Ch13	Shorkistri	48,2±2,3	2,0±0,4	60	0,154±0,058	0,155±0,055
Ch1	Karachuri	51,9±0,8	2,0±0,3	60	0,152±0,060	0,138±0,054
Ch8	Jantikovo	36,9±5,1	1,9±0,3	60	0,099±0,043	0,119±0,052
Ch7	Kanash	45,2±4,1	2,0±0,3	60	0,125±0,045	0,131±0,050

* A locus is considered polymorphic if more than one allele was detected

(*Mdh–1, Me–1, Mnr–1, Skdh–1, Got–1, Pgi–2*). Even if the numbers of alleles per loci in these systems are 3 or 4, one allele predominated, while other alleles were rare or in some populations were absent. Class 3 – highly polymorphic loci – comprises loci with several rather frequent alleles (*Fest–1, Idh–1, Gdh–2*).

The mean number of alleles per population ranged for different populations from 1.8 (Babeevo) to 2.5 (Volzsk pojma and plakor) (Table 2).

On the basis of the allelic frequencies of all genes, the main parameters of the genetic diversity of populations were calculated (Table 2). The observed heterozygosity in population samples varied to an insignificant degree and ranged from 0.099 to 0.171. At the same time, the expected heterozygosity ranged from 0.119 to 0.184. Thus, the differences between the observed and expected heterozygosity is very low and insignificant. This can testify to an equilibrium state of populations of oak.

The genetic differentiation between pairs of studied populations of pedunculate oak was quantified by means of Nei's (1978) genetic distance coefficients. The calculated genetic distance coefficients are quite low and ranged from only 0.000 to 0.010. The highest difference was between Babeevo and Volzsk pojma and between Jantikovo and Babeevo–Atnari. The geographical remoteness, i.e. the distance between populations, seems to affect the differentiation of populations more

Table 3. Values of Wright's *F*–statistics and level of gene flow N_em for 9 polymorphic loci in populations of pedunculate oak in the Middle Povolzhje

Locus	F_{IS}	F_{IT}	F_{ST}	N_em
Fest	–0,104	–0,060	0,040	6,016
Mnr	0,086	0,103	0,019	12,952
Idh	0,009	0,017	0,007	33,737
Mdh	–0,010	–0,001	0,009	27,731
Me	–0,037	–0,004	0,032	7,501
Skdh	0,027	0,065	0,039	6,201
Got–B	–0,078	–0,042	0,033	7,263
Pgi–B	–0,032	–0,016	0,016	15,017
Gdh–B	0,022	0,054	0,033	7,267
Mean	–0,001	0,024	0,025	9,690

than the edaphical difference. However, because of quite a small number of the studied populations, it is difficult to make any more authentic conclusions.

By means of Wright's *F*–statistics, an attempt was made to determine the population structure of pedunculate oak. The calculated values are shown in Table 3. The values of the inbreeding coefficient F_{IS} vary from –0.104 for *Fest–1* to 0.086 for *Mnr–1*, on average – 0.001. The negative value indicates an insignificant (0.1 %) excess of heterozygosis in an average oak population in the region. Low values of coefficients of inbreeding confirm the equilibrium state of oak populations. The parameter of oak population differentiation – F_{ST}, ranged for polymorphic loci from 0.007 for *Idh–1* to 0.040 for *Fest–1*. The average value of F_{ST} for all investigated loci is 0.025. This means that 97.5 % of the whole diversity is distributed within populations of oak, and that a diversity of only 2.5 % is found in population variability.

The parameter F_{ST} allows us to evaluate the level of gene flow (N_em) – number of migrants per generation. From the data obtained, N_em appeared as nearly 10. This means that in each of the studied oak populations with an effective population size N_e, nearly 10 trees have genomes originating from adjacent populations. The transfer of this genetic material can be performed by the transport of pollen by wind and of acorns by jays. Thus, it is possible to assume that the oak populations exchange genetic material rather actively and, consequently, have similar gene pools.

. The data obtained in our research correspond with the patterns of diversity of pedunculate oaks obtained by other researchers (Kleinschmit et al 1995, Mattila et al.1994, Müller–Stark et al. 1993). But to confirm a possible pattern of genetic differentiation in different parts of the oak range, more populations throughout the Middle Near Volga region of Russia should be analysed.

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GENETSKA RAZNOLIKOST HRASTA LUŽNJAKA (*QUERCUS ROBUR* L.) U SREDIŠNJEM DIJELU RUSIJE UZ RIJEKU VOLGU

Hrast lužnjak (*Quercus robur* L.) u središnjem području uz rijeku Volgu uspijeva na sjeveroistočnoj granici svoga prirodnoga područja rasprostranjenosti u Europi. Hrast u ovoj regiji ima neke posebnosti u međuvrsnoj varijabilnosti i genetskoj strukturi. Ovdje hrastovi imaju tri fenološka oblika u smislu jesenskih boja i otpadanja lišća: oblik ranoga otpadanja lišća, kasnoga otpadanja lišća i prijelazni oblik između tih dvaju. Postoji velika raznolikost u svojstvima debla, krošnje, lista i žira. Na osnovi istraživanja varijacija morfologije lista populacije hrasta su podijeljene na grupe *šume Volge* i *šumostepe Zavolžja,* a ova posljednja obuhvaća dvije populacije podgrupa koje rastu u zoni šumostepe: Mokšansko-Surskaja (planine) i Zavolžje (nizine). Na osnovi izozimske analize na 10 mjesta istraživana je genetska varijabilnost 14 prirodnih populacija hrasta lužnjaka koji je rasprostranjen po čitavoj regiji. Utvrđena je visoka varijabilnost populacija hrasta lužnjaka: 60 – 83 % gena su bili u polimorfnom stanju; prosječni broj alela po lokaciji je iznosio 1,8–2,5. Promatrana i očekivana heterozigoitnost kreće se od 9,9 % do 17 %, odnosno od 11,9–18,4 %. Populacije imaju zajednički genetski pul uz intenzivnu razmjenu gena među populacijama.

Ključne riječi: hrast lužnjak, međuvrsna raznolikost, fenološki oblici, populacije, izoenzimi

J. Franjić, et al.: Multivariate analysis of leaf shape of the common oak (*Quercus robur* L.) in the "Gajno" provenance test (Croatia). Glas. šum. pokuse 37: 469–479, Zagreb, 2000.

UDK 630*165+232.1 (Quercus robur L.)

MULTIVARIATE ANALYSIS OF LEAF SHAPE OF THE COMMON OAK (*QUERCUS ROBUR* L.) IN THE "GAJNO" PROVENANCE TEST (CROATIA)

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In this work, the results of morphological research of the common oak (*Quercus robur*) leaf shape in the provenance test in the locality of Gajno (Jastrebarsko, Croatia) are given. The provenance test was established in autumn 1987 with annual seedlings. The test included in total 16 provenances (15 from Croatia and one from Vojvodina) belonging to various bioclimatic regions. The plot was arranged in the form of a randomised block system with 100 plants per each repetition. The leaf sample for analysis was picked in July 1998, and 200 leaves of each provenance (50 per repetition) were analysed. On each leaf five traits (leaf blade length, leaf blade width, petiole length, number of lobes on the leaf blade left side and number of lobes on the leaf blade right side) were measured. Regularities in the variability of particular traits under identical stand conditions corresponding to genetic differences were determined. All measured parameters were submitted to the description and regression analysis, the variance analysis and the multivariate analysis from which the differences between the studied provenances can be clearly seen. The results of this research will be very useful in the artificial regeneration of common oak forests, which is nowadays becoming more and more important and in which the selection of adequate regeneration material is of major importance, since the microsite conditions are fundamental to adequate decision making. Besides this, the quantity of acorns per area unit would be considerably reduced.

Key words: *Quercus robur*, leaf variability, provenance test

INTRODUCTION

The common oak forests in Croatia are generally regenerated naturally. However, for reasons of a poor and irregular acorn yield in the last few decades, artificial regeneration with acorns and seedlings has been applied in addition to natural regeneration. In this process, very often seedlings which do not belong to the domicile population are used. To avoid mistakes in the common oak stand through artificial regeneration by using inadequate seedling material, intensive research of the local population genetic variability has been made in the last decade (cf. Gračan et al. 1991; Stojković 1991; Franjić 1993, 1994, 1994a, 1996, 1996a; Gračan 1993, 1993a; Gračan & Perić 1993; Krstinić et al. 1996). Since the common oak is an endangered species, it is absolutely necessary to preserve the gene pool of this species. To do this, knowledge of the genetic differentiation at the individual and population level is extremely important. Data on the genetic differentiation of local populations can generally be obtained by researching the phenotypic and genetic variability. On the basis of the phenotypic variability of local populations, conclusions can be made as to the variability type, which can be of a continuous or a discontinuous character (cf. Krstinić et al. 1996).

Continuous variability is typical of compact populations and is generally expressed as a clinal variability. Through research of phenotypic variability, the clinal variability of morphological leaf traits in Croatia has been determined (cf. Franjić 1994), although discontinuous populations were involved, but their compactness has been affected anthropogenically by the large felling of forests in the Sava River region where the research was carried out.

Discontinuous variability suggests the existence of morphological and physiological races, known by the name of geographical variability. This type of variability is the consequence of changed macroecological conditions in the area where a species grows, as well as of the spatial isolation of local populations. Through earlier morphometric research of discontinuous populations belonging to various climatic regions, a very strong resemblance of populations with similar microsite characteristics was determined (Franjić 1993, 1994, 1996, 1996a, 1996b; Franjić et al. 1999).

In his research of the common oak populations in the Sava River and the Drava River regions in Croatia, Franjić (1993a, 1994, 1996, 1996a) arrived at the conclusion that each population has approximately the same number of genotypes, and the only difference occurs in the frequency of particular genotypes in the respective population. Either by ignorance or because the common oak variability and adaptability were not taken into account sufficiently, acorns were very often transported and planted in unsuitable sites and in this way the regeneration or refilling of the common oak stands was made. Today we are in a situation where the common oak is endangered and where considerable funds are earmarked for the regeneration of its forests and the preservation of its gene pool. But in spite of that, control of its regeneration is still inadequate. The problem is that the consequences cannot be seen immediately and that very often they coincide with other causes (such as acid rain, heavy defoliation and the like), that makes identification of the real cause of common oak withering rather difficult.

For all these reasons, it is necessary to determine experimentally and as soon as possible the genetic differentiation of local populations (provenances) and this by (generative or vegetative) progeny testing under the same conditions. Such research is important for all exploitable species, and in particular for the common oak as the most important exploitable tree species in Croatia.

The purpose of this research is to obtain a clearer picture of the genetic structure of each researched provenance. On the basis of such research, for artificial regeneration it will be possible to use a considerably smaller number of plants per

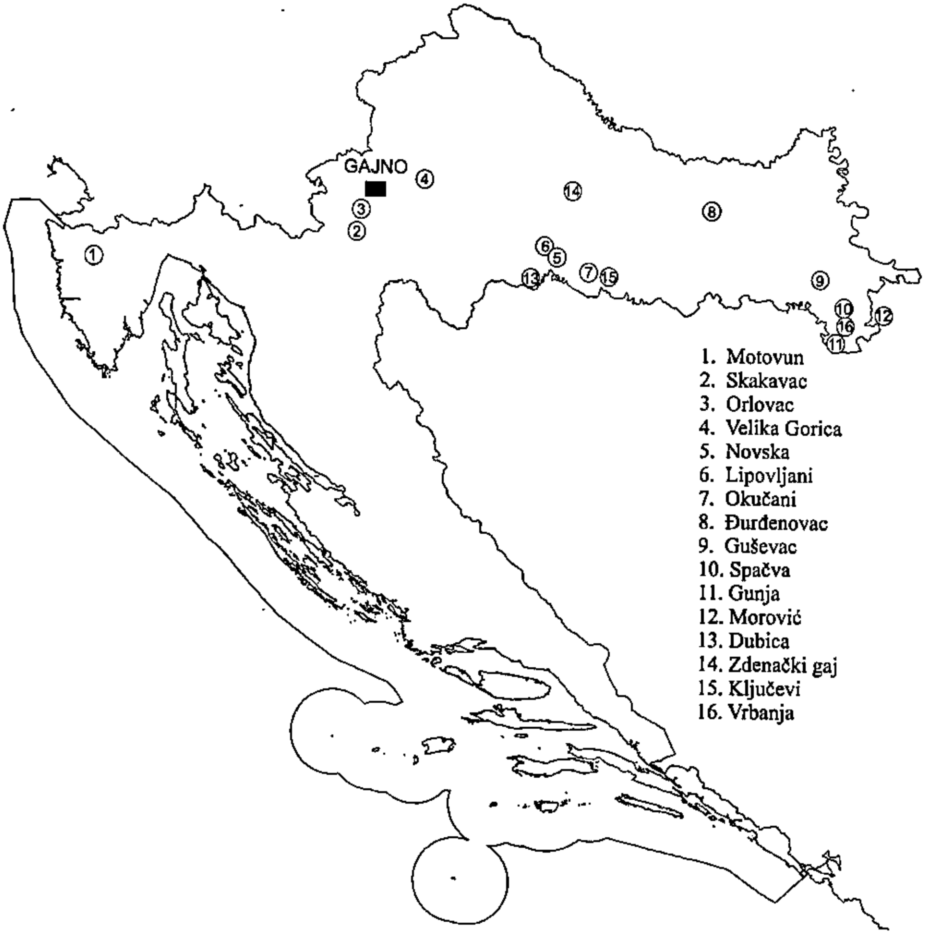

Figure 1. Distribution of 16 provenances of common oak (*Quercus robur* L.) in field trialy "Gajno" (Croatia)

area unit, thus reducing substantially the costs of artificial regeneration of the common oak forests.

MATERIAL AND METHODS

Acorns necessary for the establishment of provenance tests were harvested in common oak seed stands in autumn 1985 (cf. Gradečki & Poštenjak 1987; Gračan et al. 1991). The provenance test "Gajno" was established in autumn 1987 and in spring 1988. In the provenance test, there are in total 16 provenances (15 from Croatia and 1 from Vojvodina) belonging to various bioclimatic regions (cf. Fig.1). The plot was arranged in the form of a randomised block system with 100 plants in each repetition. The soil in the "Gajno" plot was marshy-amphigley-mineral-clay soil over clay deposits of the Okičnica and Gonjeva streams, at an elevation of 115 m (cf. Mayer 1989; Gračan et al. 1991). The leaf sample for analysis was picked in

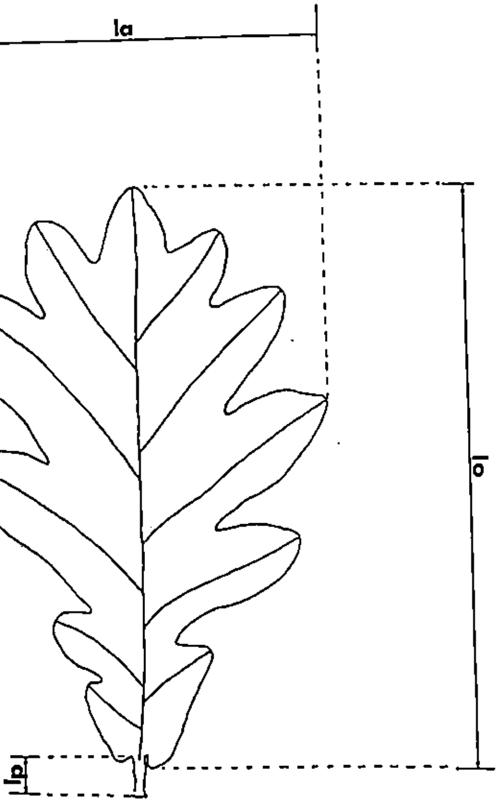

Figure 2. Representation of the measured leaf parameters (la - leaf blade width; lo - leaf blade lenght; lp - petiole lenght)

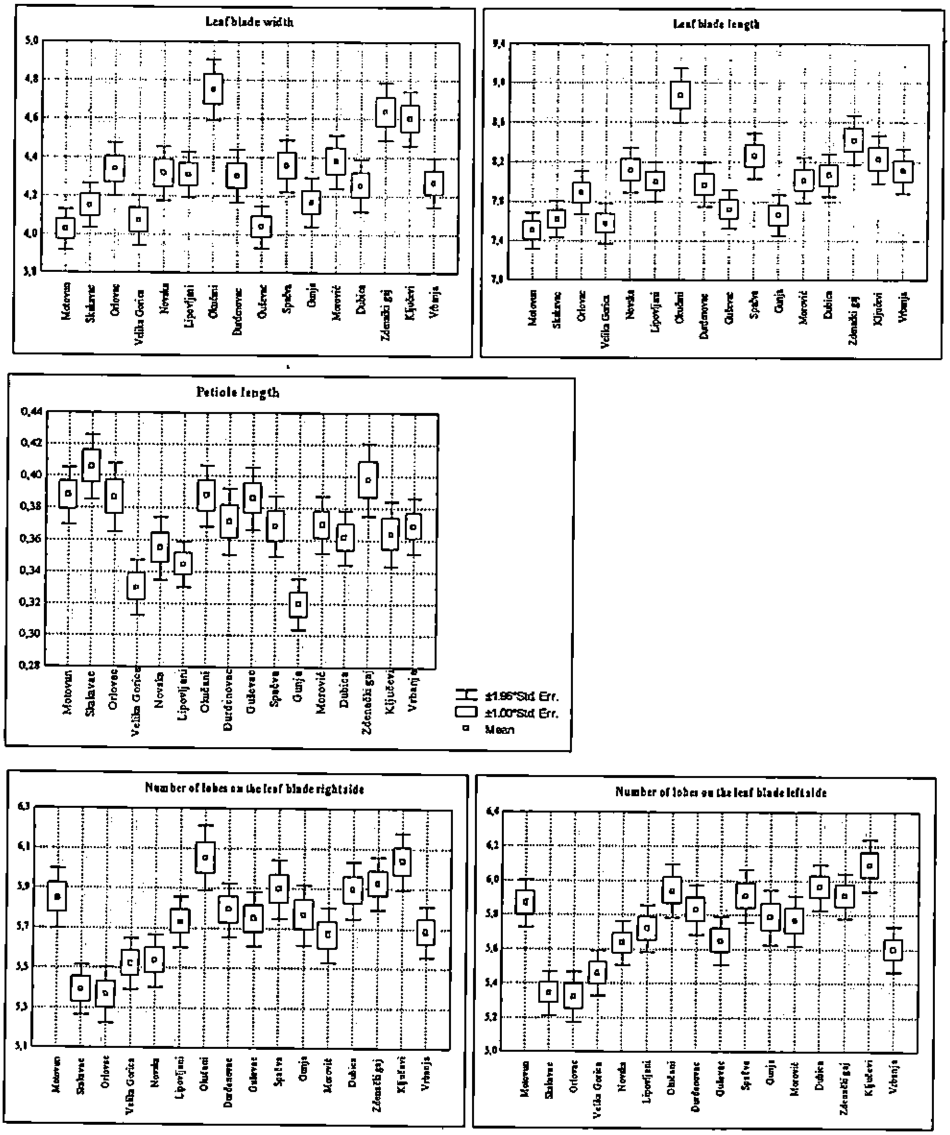

Figure 3. 95 % confidence interval (Box & Whisker Plot) of means by provenances for all five traits

July 1998 and put in the herbarium. Measuring was made immediately after herbarising and included 200 healthy and fully developed leaves of each provenance (50 per repetition). On each leaf five traits were measured (leaf blade length, leaf blade width, petiole length, number of lobes on the left side and number of lobes on the right side of leaf blade; cf. Fig. 2). Measuring was made with an accuracy of 1 mm.

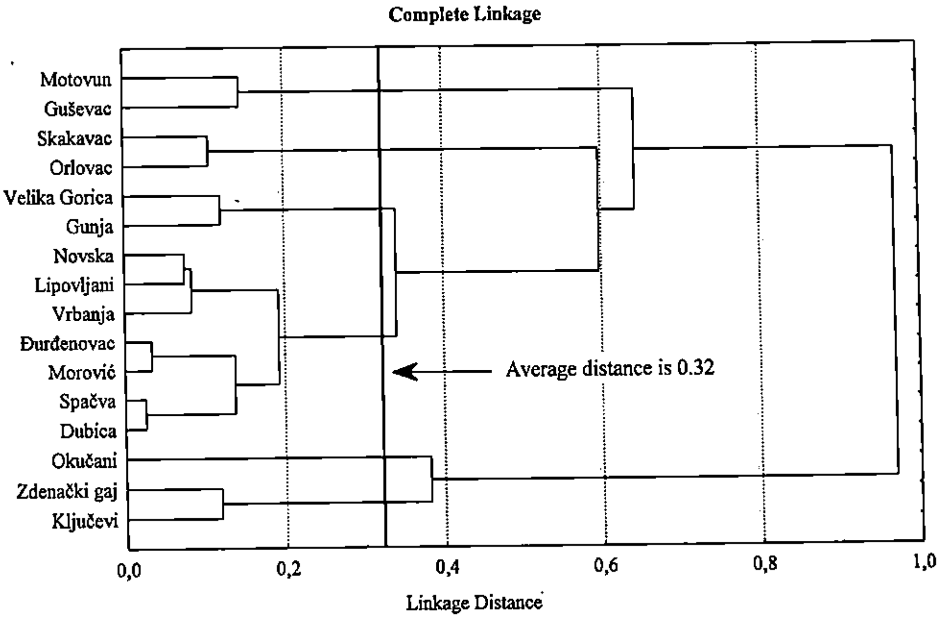

Figure 4. Dendrogram obtained by the Complete Linkage method

The measured traits were analysed in detail using descriptive statistics. The variance univariant analysis (ANOVA) for particular leaf traits (cf. Fig. 3), the variance multivariate analysis (MANOVA) and the multivariate cluster analysis were made. For this, algorithms for Ward's Complete Linkage method were used, namely Unweighted Pair Group Average (UPGMA), Weighted Pair Group Average (WPGMA), Unweighted Pair Group Centroid (WPGMC), and Weighted Pair Group Centroid (WPGMC), (cf. McClare & Dietrich 1988; Sharma 1996; Johnson 1998). All methods show a similar form and regularity of provenance linkage, but, since in this particular case the "Complete Linkage" method has the highest cophenetic correlation coefficient, this method was used for interpretation purposes (cf. Fig. 4). All used statistical data processing methods were done in the program package Statistics for Windows 4.5 (cf. StatSoft™ 1994).

ANALYSIS OF THE RESEARCH RESULTS AND DISCUSSION

The analysed provenances belong to various bioclimatic regions (areas) which differ between them very much by their macroecological characteristics (cf. Gračan et al. 1999). The common oak is a species very sensitive to changes in its site, so during evolution this species has undergone a fine adaptation to microsite conditions that has resulted in its differentiation into a series of ecotypes (cf. Trinajstić 1974, 1988; Franjić 1993, 1993a, 1994, 1996, 1996a, 1996b; Trinajstić & Krstinić 1993). For the territory of Croatia, the common oak differs very clearly, both morphologically and ecologically, from other oak species, because it occupies floodplain and, for other oaks, very selective sites. The only problem is introgression, where one or more nonselective traits of another congenial oak species (such as the sessile oak or bitter oak) can enter the common oak genom, which can cause great difficulties in the determination of the common oak (cf. Franjić 1993, 1993a, 1994).

From the results of the descriptive analysis, it can be seen that the researched provenances link between them into certain groups, and in these the form and the regularity of linkages do not depend on the macroecological belonging of the provenances (belonging to a certain area), (cf. Gračan 1996; Gračan et al. 1999). However, as stated in the introduction, this linkage certainly depends on the microsite conditions (cf. Franjić 1993, 1994, 1996, 1996a; Franjić et al 1999). Moreover, through the descriptive analysis at a very high level, for all researched properties and for all researched provenances, the right hand (+) asymmetry and the positive (+) flatness have been determined, which corresponds to the research made by Franjić (1996, 1996a, 1996b) on adult plants. The arithmetical average absolute values for all researched traits and all provenances in certain parts of the range in Croatia show a tendency of an increase or a decrease in the east→west direction that can be connected with clinal variability. Such a tendency is disturbed, however, by some provenances, which suggests ecotypical differences under the influence of microsites.

The multivariate analysis (MANOVA) confirmed the existence of significant differences in the researched traits between the provenances. Differences in traits for particular provenances can also be seen in the descriptive statistics graphs. For reasons of limited space, we shall present here the 95% confidence interval (Box & Whisker Plot) of the means by provenances for all five traits (cf. Fig. 3).

Considering that the statistically significant difference of provenances was obtained, various cluster analysis methods were used. All methods show a similar form and regularity of provenance linkage, and since in this particular case the "Complete Linkage" method has the highest cophenetic correlation coefficient, this was used for interpretation purposes (cf. Fig. 4).

In Fig. 4, six clusters which differ at a very high level can be clearly seen. The number of clusters was determined on the basis of the average distance which is 0.32 (cf. Fig. 4; Mahalanobis 1936), and the provenances are linked into clusters in the following way:

1. To the first cluster belong the provenances Motovun and Guševac
2. To the second cluster belong the provenances Skakavac and Orlovac
3. To the third cluster belong the provenances Velika Gorica and Gunja
4. To the fourth cluster belong the provenances Novska, Lipovljani, Vrbanja, Đurđenovac, Morović, Spačva and Dubica
5. To the fifth cluster belongs the provenance Okučani

6. To the sixth cluster belong the provenances Zdenački gaj and Ključevi.

From the mentioned clusters, it can be seen that very rarely do the provenances belonging to the same area link together (cf. Fig. 1 and 4), which, in practice, is the basis for seed (acorn) distribution. Such a situation is absolutely logical and expected, since, as said before, similar results have already been obtained (cf. Franjić 1993, 1994, 1996, 1996a, 1999) where it was emphasised that for seed distribution the most important factor is to determine the compatibility of microsites and not the geographical belonging. Thus, for instance, there is a linkage between:

- Motovun (Istria) and Guševac (Lower Posavina)
- Velika Gorica (the Upper Sava Region) and Gunja (Lower Posavina)
- Novska and Lipovljani (Central Posavina), Vrbanja and Spačva (Lower Posavina); Đurđenovac (Podravina), Morović (Srijem) and Dubica (Upper Posavina).

Although almost no regional links exist here, the soil and phytosociological belonging are basic properties linking these provenances into certain entities (cf. Gradečki & Poštenjak 1987; Gračan et al. 1991; Gračan & Perić 1993).

The provenances are very rarely linked according to their geographical belonging, such as:

- Skakavac and Orlovac (Upper Posavina)
- Zdenački gaj and Ključevi (Central Posavina), to which, at a somewhat higher level, the Okučani provenance belonging to Central Posavina is also linked.

All this can be connected to the accidental selection of provenances during the establishment of the tests, as well as to the coincidence of the soil type and the phytosociological belonging. By statistical analysis, it was again determined on this material, similar to earlier research (cf. Franjić 1993, 1994, 1996, 1996a, 1999), that in each common oak population in Croatia there is an approximately identical number of genotypes, and that the proportion of genotypes in the respective population depends on the microecological properties of the site.

CONCLUSION

The common oak forests in Croatia are generally regenerated naturally, but for reasons of a poor and irregular acorn yield during the last few decades, in addition to natural regeneration, artificial regeneration with acorns and seedlings has also been applied. By doing this, very often the seedling material which does not belong to the domicile population has been used. To avoid mistakes in the artificial regeneration of the common oak stands by using inadequate seedling material, intensive research of the genetic variability of local populations has been done in Croatia in the last decade.

Thus, in autumn 1987 and in spring 1988, the provenance test "Gajno" was established with a total of 16 provenances (15 from Croatia and 1 from Vojvodina) belonging to various bioclimatic regions (cf. Fig. 1; Gračan et al. 1991, 1999; Gračan 1996). In this test, a leaf sample for morphometrical analysis was harvested. In total, 200 fully developed and healthy leaves of each provenance were analysed and on each leaf five traits (leaf blade length, leaf blade width, petiole length, number of lobes on the leaf blade left side and number of lobes on the leaf blade right side cf. Fig. 2) were measured. The purpose of this research was to obtain a clearer picture of the genetic structure of each researched provenance.

All measured parameters were analysed. From the results of the analysis it can be seen that the researched provenances link between themselves into certain groups (cf. Fig. 3 and 4), and the form and the regularity of this linkage of provenances do not depend on their macroecological belonging (area belonging) but (cf. Gračan 1996; Gračan et. al. 1999), as pointed out in the introduction, the linkage of provenances undoubtedly depends on the microsite conditions (cf. Franjić 1993, 1994, 1996, 1996a; Franjić et al. 1999). From the given results (cf. Fig. 1 and 4), it can be seen that the linkage of provenances belonging to the same area, which in practice is the basis for seed (acorn) distribution, is very rare. Such a situation is absolutely logical and expected, since earlier research has given similar results (cf. Franjić 1993, 1994, 1996, 1996a; Franjić et al. 1999). Attention was then brought to the fact that of greatest importance in seed distribution is to determine the compatibility of microsites, not the geographical belonging.

By statistical analysis it was determined that on this material, similar to earlier research (cf. Franjić 1993, 1994, 1996, 1996a; Franjić et al. 1999), in each common oak population in Croatia there is approximately the same number of genotypes, and that the proportion of genotypes in the respective population depends on the microecological properties of the site.

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MULTIVARIJATNA ANALIZA OBLIKA LISTA HRASTA LUŽNJAKA (*QUERCUS ROBUR* L.) U TESTU PROVENIJENCIJA GAJNO (HRVATSKA)

U radu će biti prikazani rezultati morfometrijskih istraživanja oblika lista hrasta lužnjaka (*Quercus robur*) u testu provenijencija na lokalitetu Gajno. Test provenijencija osnovan je u jesen 1987. godine s jednogodišnjim sadnicama. Testom je obuhvaćeno ukupno 16 provenijencija (15 iz Hrvatske i 1 iz Vojvodine), koje pripadaju različitim bioklimatskim područjima. Pokusna je ploha postavljena u obliku nasumce izabranoga blok-sustava sa 100 biljaka po svakome ponavljanju. Uzorak lišća za analizu ubran je u srpnju 1998. godine, a analizirano je po 200 listova svake provenijencije (50 po ponavljanju). Na svakom listu mjereno je 5 svojstava (duljina i širina plojke, duljina peteljke, broj režnjeva s lijeve i s desne strane plojke). Istraživanjima se nastoji utvrditi zakonitost varijabilnosti pojedinih svojstava u identičnim stanišnim uvjetima, koji bi odgovarali genetskim razlikama. Svi izmjereni parametri podvrgnuti su deskriptivnoj, neparametrijskoj i multivarijatnoj analizi iz koje se mogu jasno uočiti sličnosti i razlike među istraživanim provenijencijama. Rezultati će ovih istraživanja biti veoma korisni pri umjetnoj obnovi šuma hrasta lužnjaka, koja danas sve više dobiva na značenju. Prilivno je važan izbor odgovarajućega materijala za obnovu jer su mikrostanišni uvjeti od izuzetnoga značenja pri toj odluci. Prethodnim je istraživanjima utvrđeno da svaka populacija ima po prilici isti broj genotipova, a razlika se javlja jedino u preživljavanju pojedinih genotipova. Rezultatima ovih istraživanja dobit će se jasnija slika genetske strukture svake istraživane provenijencije, a pri umjetnoj će se obnovi moći ići s manjim brojem jedinki po jedinici površine, čime će se znatno smanjiti troškovi umjetne obnove lužnjakovih šuma.

Ključne riječi: *Quercus robur*, varijabilnost lista, test provenijencija

I. Glaz: Genetic cartography of oaks in Poland using pcr-rflp markers of the chloroplast DNA
Glas. šum. pokuse 37: 481–487, Zagreb, 2000.

UDK 630*165+168+583+(438) (Quercus robur L., Q. petraea Liebl.)

GENETIC CARTOGRAPHY OF OAKS IN POLAND USING PCR-RFLP MARKERS OF THE CHLOROPLAST DNA

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The main aim of this project was to increase knowledge about the genetic diversity of oaks from Poland, ecologically and economically very important species in this country, and to establish a geographic map of genetic diversity of these species in Poland. The material for analysis was sampled from 33 populations (168 trees) of *Quercus petraea* and *Quercus robur* distributed over most of the territory of Poland. The PCR-RFLP method was used to analyse DNA. Nine different haplotypes were identified in the studied populations, four of which were detected for the first time and five have been found in other countries. Some haplotypes appear to have a patchy distribution, whereas others are spread over a large area. This information may help to indicate probable routes of postglacial recolonisation or artificial introduction. The results will complete the current database concerning the genetic diversity of oak species and will be used to create a single European map of genetic variants. The statistical analysis of genetic diversity of all studied species resulted in a small (*hs*=0.215) diversity within populations and a rather high (*Gst*=0.700) diversity among populations. Additionally, the differentiation among populations was higher in *Quercus petraea* (*Gst*=0.77) than in *Quercus robur* (*Gst*=0.65).

Key words: Quercus robur, Quercus petrea, chloroplast DNA polymorphism, PCR-RFLP, map of genetic diversity.

INTRODUCTION

Pedonculate oak (*Quercus robur*) and sessile oak (*Quercus petrea*) are two of the most common deciduous forest species in Poland. They are very important in this country, both ecologically and economically. Generally, the oaks belong to the group of species which are characterised by broad and continuous spreading, which influences their high level of genetic diversity. Nowadays, the study of the relationship between the phylogeny of different genetic variants of oaks and their geographic distribution has become a popular field, especially in evolutionary sciences (Avise et al. 1987, Johnk and Siegismund 1997, Petit and Pineau and Demesure and Bacilieri and Ducousso 1997, Hevitt 1996). Among the historical factors which have probably determined the present pattern of genetic variation observed in natural populations of the Temperate Zone, the most important appears to be the last glacial period, and afterwards, the recolonisation by plants. According to fossil pollen data (Huntley & Birks 1983), the geographic distribution of oaks was established about 7000 years ago, as a result of the long-range recolonisation that followed the end of the last glaciation. Prior to climatic warming, the geographical distribution of oaks was restricted to three refugia, in southern Spain, southern Italy and the Balkans (Huntley and Birks 1983), from where recolonisation took place.

From previous research it is known that the chloroplast DNA of oaks is maternally inherited and transmitted, in the case of oaks, only by seeds (Dumolin et al. 1995). As a consequence of the reduced gene flow for this marker (Petit et al., 1993a,b), cpDNA polymorphism has appeared to be much more structured than nuclear polymorphism. In addition, cpDNA is characterised by no recombination and it possesses slow evolutionary changes, which is important to reconstruct historical events. All of these features can help to reflect past colonisation dynamics. So, chloroplast DNA data, according to some authors (Le Corre, Dumolin-Lapegue and Kremer, 1997), give much more precise information about the glacial origin of populations than paleobotanical data. A high amount of genetic differentiation, studied using chloroplast DNA, has already been detected in association with a strong phylogeographical structure (Petit et al. 1993a) from the results received so far from chloroplast DNA variation over the whole range of several European white oaks species. These results confirm that the isolation into separate refugia explains the observed divergence between chloroplast lineages: A-the Balkans, B-Spain, C-Italy (Le Corre, Dumolin-Lapegue and Kremer, 1997). Nevertheless, the evidence that there is an association between the geographic location of the haplotypes and their position within the phylogenetic tree now remains limited to casual observations of variants on geographic maps (Dumolin-Lapegue, Demesure, Fineschi, Le Corre, Petit, 1997).

This paper presents the cpDNA haplotypes of the two species of Quercus distributed in Poland and a map of the cpDNA variation of studied oaks.

MATERIAL AND METHODS

The material for analysis was taken mainly from two species of oaks (*Quercus petrea* and *Quercus robur*), distributed over most of Poland's territory (mainly the eastern, western, and southern part), so that the results could be particularly representative. Buds of oak trees were sampled in selected seed stands, registered seed stands and natural stands. The stands are approximately 50 km distant from each other. The location of each population was determined by GPS (latitude, longitude and altitude). From 5 trees of these populations, about 50 m apart from each other, branches with buds were harvested. Finally, material was sampled from 168 trees of 33 populations.

Harvested buds were kept at –80°C and total DNA from them was extracted in France according to the protocol used in the Laboratoire de Génétique et Amélioration des Arbres Forestiers, INRA-Cestas (adopted from Doyle and Doyle 1990). The following ingredients were used: extraction buffer (ATMAB, EDTA 0.5 M, Tris-HCl 1M, NaCl 5M, PVP soluble), 1.4 Ditiothreitol, dichloromethane, isopropanol, ethanol 76%. In order to receive the genetic differentiation of the studied material, the PCR-RFLP method was used. The first step was DNA amplification using the PCR technique, relying on the duplication of specified fragments of DNA, using four pairs of universal chloroplast DNA primers (DT (Demesure et al. 1995), CD (Demesure et al. 1995), AS (Demesure et al. 1995) and TF (Taberlet et al. 1991), previously known as those which give polymorphism (Dumolin-Lapègue et al.1997). The PCR ingredients were the following: 2xbuffer (10X buffer, $MgCl_2$ 25 mM, dNTP-5 mM of each dNTP, dH2O), Primer 1 (2 μM), Primer 2 (2 μM), Taq polymerase 5 U/μl. The next step was the digestion of the amplified cpDNA fragments, in specific nucleotide motifs, giving diversification through detecting mutations, carried out by two restriction enzymes (*Taq*I, *Hin*fI). Finally, the received fragments were separated on 8% polyacrylamide gel and stained with ethidium bromide.

The guidelines for harvesting the material in the field and the method of analysis were previously used in France and other European countries in a EU project (FAIR « Synthetic maps of gene diversity and provenance performance for utilisation and conservation of oak genetic resources in Europe »), in which one of the main aims was the realisation of a map of chloroplast variants in each European country, based on the same fragments utilised in my work. Hence all these results are comparable and will be used to produce a single European map of genetic variants.

RESULTS

Nine different haplotypes (marked using numbers: 1, 1', 1'', 4, 4', 5, 5', 7, 12), arising from the mutual arrangement of cpDNA fragments, were found in the studied populations. Five of them (1, 4, 5, 7, 12) were found earlier in other European countries and four of them (1', 1'', 4', 5') were detected for the first time. On this basis, a map of genetic diversity of the chloroplast DNA of oaks in Poland has been created, showing the arrangement of these haplotypes (Figure 1). Some of the

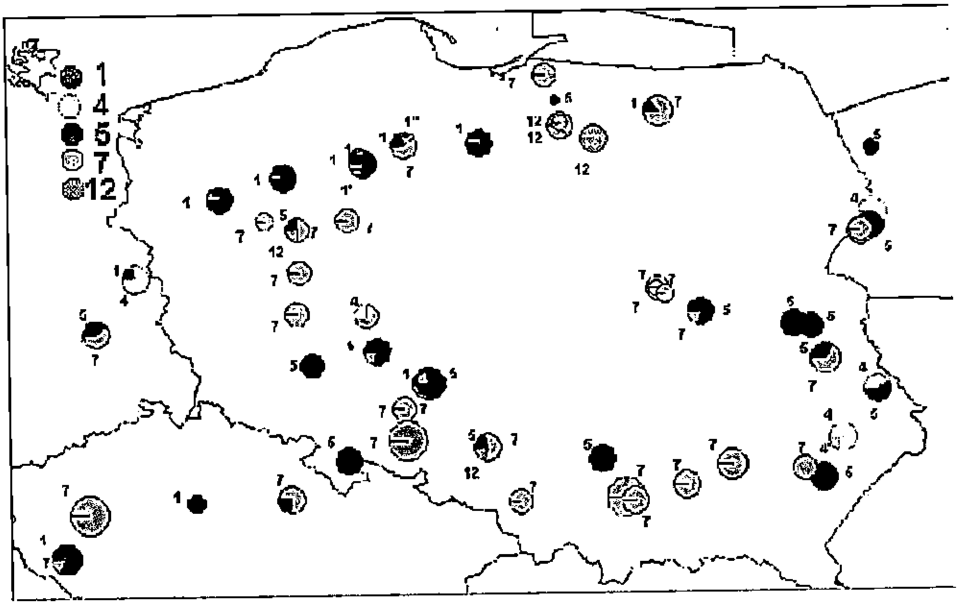

Figure 1. Geographical map of arrangement of chloroplast DNA of oaks in Poland.

haplotypes are arranged in groups on the studied area (haplotype 5-southern part of Poland, 1-north-west part and 4-eastern part), but some are spread over a broad area of Poland (7).

Table1. Calculations of genetic diversity using different parameters describing interpopulation (*GsthshT*)number of alleles=9, number of populations=32, mean=4.69, harmonic mean=4.59).

Parameters	Haplotypes									Total
	1	1'	1"	4	4'	5	5'	7	12	
Frequency	0.0938	0.0063	0.0063	0.0703	0.0063	0.2854	0.0078	0.4474	0.0766	1.0000
hS(Nei)	0.0256	0.0129	0.0128	0.0597	0.0128	0.1072	0.0150	0.1614	0.0278	0.2175
hS(Weir)	0.0271	0.0136	0.0136	0.0601	0.0136	0.1174	0.0127	0.1674	0.0263	0.2259
hS(Pons)	0.0250	0.0125	0.0125	0.0594	0.0125	0.1042	0.0156	0.1594	0.0281	0.2146
s.e. hS	0.0174	0.0125	0.0125	0.0287	0.0125	0.0362	0.0156	0.0436	0.0197	0.0493
hT(Nei)	0.1701	0.0125	0.0125	0.1311	0.0125	0.4086	0.0156	0.4956	0.1416	0.7001
hT(Weir)	0.0926	0.0067	0.0067	0.0694	0.0067	0.2125	0.0067	0.2503	0.0756	0.7270
hT(Pons)	0.1748	0.0125	0.0125	0.1335	0.0125	0.4184	0.0156	0.5063	0.1453	0.7157
s.e. hT	0.0799	0.0123	0.0123	0.0633	0.0123	0.0621	0.0154	0.0162	0.0744	0.0478
Gst(Nei)	0.8497	-0.0219	-0.0219	0.5446	-0.0219	0.7376	0.0400	0.6744	0.8039	0.6893
Gst(Neib)	0.8537	-0.0226	-0.0226	0.5525	-0.0226	0.7437	0.0413	0.6813	0.8089	0.6961
Gst(Pons)	0.8570	0.0000	0.0000	0.5551	0.0000	0.7510	0.0000	0.6852	0.8064	0.7002
s.e. Gst	0.0434	Nc	Nc	Nc	Nc	0.0220	Nc	Nc	Nc	0.0690
Covariance	0.0013	0.0008	0.0008	0.0033	0.0008	0.0029	0.0010	0.0031	0.0016	0.0003

Statistical analysis of genetic diversity, utilising parameters (Nei 1973, Pons and Petit 1995 and others) describing the structure of this diversity, such as: coefficient of interpopulation genetic diversity (*Gst)*, mean intrapopulation diversity (*hs)* and total diversity (*hT)*, on the basis of all data (combining the different species), resulted in a small (on average *hs*=0.215) diversity within populations and rather high (on average *Gst*=0.700) diversity among populations (Table1). Moreover, differentiation among populations appears to be higher in *Quercus petraea* (*Gst*=0.77) than in *Quercus robur* (*Gst*=0.65).

CONCLUSION

These results widen and complete the current database concerning the gene diversity of oak species by filling the missing places of the north-central part of Europe. The results may help to confirm the hypothesis of postglacial recolonisation routes in this part of Europe, through a comparison of haplotypes (haplotype 7, 5, 12, 1, 4) located in Poland with haplotypes found in neighbouring countries such as Germany (7, 1, 5, 12), France (7, 1, 12), Italy (1, 5), Spain (12, 1, 7) and others with different frequency and distribution. Taking into consideration the conducted investigations of the phylogeographical structure of oaks (Le Corre, Dumolin-Lapegue and Kremer, 1997, and others) most of the received haplotypes belong to lineage A (5, 4, 7), representing the Balkan refuge, the rest to B (12), representing the refuge of Spain, or C (1) representing the refuge of Italy. Nevertheless, it is necessary to take into consideration people's influence, which may disturb and modify the structure of genetic diversity through the transfer of seeds or seedlings (haplotype 12, 2), seen when haplotypes are mixed within populations or found in isolation. On the basis of these results, it was confirmed that chloroplast DNA is very suitable for this kind of research. Chloroplast DNA gives a higher diversity between, rather than within, populations of oaks, confirming previous results. Populations of sessile oak differ more from each other than populations of pedunculate oak. This trend was also been found in previous studies in France and Germany.

These results may have different practical applications, such as facilitating the evaluation of the arrangement of different provenance regions which exist in Poland, helping in the verification of the natural origin of stands, useful in the certification of the geographic origin of oak wood.

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GENETSKA KARTOGRAFIJA HRASTOVA U POLJSKOJ POMOĆU MARKERA PCR-RFLP DNA KLOROPLASTA

Izabela Glaz

Glavni se cilj ovoga projekta sastojao u proširenju znanja o genetskoj raznolikosti hrastova iz Poljske, ekološki i ekonomski važne vrste u ovoj zemlji, i izradi zemljopisne karte genetske raznolikosti ovih vrsta u Poljskoj. Materijal je za analizu prikupljen iz 33 populacije (168 stabala) *Quercus petraea* i *Quercus robur*, rasprostranjenih u gotovo cijeloj Poljskoj. Za analizu je DNA primijenjena metoda PCR-RFLP. U istraživanim je populacijama identificirano 9 različitih haplotipova, od kojih su četiri primijećena prvi put, a pet je pronađeno u drugim zemljama. Neki su haplotipovi rasprostranjeni mjestimično, dok su drugi rasprostranjeni u velikom području. Ova informacija može pomoći u identifikaciji vjerojatnih putova postglacijalne rekolonizacije ili umjetnoga uvođenja. Rezultati će dopuniti sadašnju bazu podataka o genetskoj raznolikosti hrastovih vrsta i koristit će se za stvaranje jedinstvene europske karte genetskih varijanata. Statistička analiza genetske raznolikosti svih istraživanih vrsta rezultirala je malom (hs = 0,215) raznolikošću unutar populacija i prilično visokom (Gst = 0,700) raznolikošću među populacijama. Usto je diferencijacija među populacijama bila viša kod vrste *Quercus petraea* (Gst = 0,77) nego kod vrste *Quercus robur* (Gst = 0,65).

Ključne riječi: *Quercus robur*, *Quercus petraea*, polimorfizam DNA kloroplasta, PCR-RFLP, karta genetske raznolikosti

UDK 630*232.3+(497.1) (Quercus robur L., Q. petraea Liebl.)

PHYSIOLOGY OF ACORNS DURING LONG-TERM STORAGE

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Acorns of common oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) are recalcitrant seeds, therefore they can only be stored with a high moisture content (40 - 45 %) at temperatures around 0 °C. At these conditions acorns can be stored successfully for only 1 - 2 years. Phytic acid could have an important role in preserving the vitality of acorns during storage. In 1997 acorns of sessile oak were collected on two different sites and stored for one year. The results suggest that the content of phytic acid in acorns could be correlated with the content of available phosphorus in soil and that phytic acid could have an influence on the vitality of acorns. The same year another lot of acorns of sessile oak were stored at three different temperatures (-3 °C, -6 °C, -9 °C) for one year. The results show that different temperatures of storage have no influence on the content of phytic acid in acorns. The content of some sugars (raffinose, stachyose) was also analysed in these acorns and the results show that higher contents of sugars at lower temperatures are in positive correlation with the higher vitality of acorns.

Keywords: oak, acorns, storage, phytic acid, sugars

INTRODUCTION

THE PROBLEMS OF STORING ACORNS OF COMMON AND SESSILE OAK

Acorns of common oak are recalcitrant seeds (Roberts 1973). Because of that, their moisture content must not be lower than 40 %. For storage, the acorns are dried to a moisture content between 40 and 48 %. Because the acorns have a high moisture content, we cannot store them at temperatures far below 0 °C, because at these temperatures water in the acorns would freeze and the acorns would lose their vitality. Therefore, they are stored at temperatures from -1 °C to -3 °C (Suszka et al 1996). Although at these temperatures the biochemical activities in the acorns and the development of pathogenic fungus (*Ciboria batschiana* (Zopf) Buchw.) are not stopped, they are slowed down, so the acorns lose their vitality during the storage. In these conditions it is possible to store the acorns for only 6 months or during one winter. Only if the crop is of very high quality, can the acorns be stored for 18 months or for two winters. Longer storage is impossible.

PHYTIC ACID AND THE VITALITY OF ACORNS DURING STORAGE

Several authors (i.e. Graf and Eaton 1990) have shown phytic acid (myo-inositol 1,2,3,4,5,6-hexakisphosphate) to be important in the vitality of seeds, because of its function as an antioxidant, in the storage of cations, P, proteins and potential energy. The inositol component of phytic acid is important for cell wall formation. Higher contents of phytic acid in seeds could improve their vitality during storage. Phytic acid in seeds probably increases with the content of total P in seeds (Raboy and Dickinson 1993). Furthemore, the P content of seeds could be positively correlated with available P in the soils (Miller et al. 1980, Raboy & Dickinson 1984, 1993, Lau and Stephenson 1994).

SUGARS AND THE VITALITY OF ACORNS DURING STORAGE AT LOW TEMPERATURES

The content of sugars in seeds changes during their development and germination. The content of monosaccharides decreases and the content of oligosaccharides increases during the maturation of seeds (Amuti and Pollard 1977). At germination the process is reversed (Koster and Leopold 1988). Recalcitrant seeds often have lower contents of oligosaccharides, especially stachyose and raffinose, when the maturation is completed (Brenac et al. 1997, Sun et al. 1994). The role of the above mentioned oligosaccharides could be in preserving cell membrane integrity, enabling the glass formation of cytoplasm and decreasing the content of injurious monosaccharides during the desiccation and freezing of seeds (Crowe et al. 1992, Leprince et al. 1992, Williams and Leopold 1989). Therefore, higher contents of oligosaccharids could improve the desiccation and frost tolerance of acorns.

OUR QUESTIONS

In our study we wanted to estimate the correlation of the contents of phytic acid and available soil P with the vitality of acorns during storage, and the correlation of phytic acid and sugars with the vitality of acorns during storage at low temperatures.

MATERIALS AND METHODS

ACORNS

For the selection of plots where the acorns were collected, the permanent oak research plots in Slovenia, which were established by the Slovenian Forestry Institute in co-operation with the Institut für Waldökologie-BOKU, were used (Smolej 1995). Two plots were selected. They differed essentially in the content of the total phosphorus in the leaves, which was taken as an indicator of the available phosphorus in the soil. Acorns were collected on the plots in October 1997, and stored for 9 months at -1 °C until August 1998 at the Slovenian Forestry institute. These acorns were only analysed for the content of phytic acid.

In 1997 acorns were also collected in France and then stored for one year at the INRA Center Nancy. They were stored at three different temperatures: -3 °C, -6 °C and - 9 °C. The temperature was lowered by 1 °C every two weeks. These acorns were analysed for their content of phytic acid and sugars.

THE DETERMINATION OF THE CONTENT OF PHYTIC ACID IN ACORNS

The content of phytic acid in acorns was determined by the m.d.d. (metal-dye detection) method (Mayr 1988) in combination with a spectrophotometer. This method was adapted for the purposes of the research, so that it was not used with the HPLC method but with a spectrophotometer instead. This adapted method was much quicker, cheaper and easier to use and at the same time it did not lose significantly in its accuracy (Zitnik et al. 1999). The samples of acorns were extracted by the following procedure (Crans et al. 1995): 18 ml of H_20 and 2 ml of 15% HCL (vol:vol) were added to 2 g ground acorns. The sample was stirred and after 30 min at room temperature the sample was filtered. Three samples of 2 μl were mixed with 1ml of reagent Š10 μM YCL_3 (Aldrich), 70 μM 4-(2-pyridylazo) resorcinol (Aldrich), 700 mM TRIS/HCL pH 8.5Ć and absorbance at 546 nm measured (Laussmann et al. 1996).

THE DETERMINATION OF THE CONTENT OF SUGARS IN ACORNS

The content of sugars in acorns was analysed with the enzymatic method for the determination of raffinose in foodstuffs and other materials (Boehringer Mannheim, Cat. No. 428 167). With this method, the content of raffinose, stachyose and some other á-galactosides (galactinol, melibiose...) was analysed together, without getting the content of each sugar apart. The samples of acorns were lyophilised (1 week at -50 °C and 3×10^{-2} mb) and then ground to powder. The samples were extracted by the following procedure (Schiweck and Büsching 1975): 2 g of the ground and homogenised sample were put into a 100 ml volumetric flask and heated with 50 ml water for 30 min in a water-bath at 60 °C. The sample was stirred and after 30 min at room temperature the sample was filtered.

RESULTS AND DISCUSSION

The results of the storage of acorns in Slovenia showed that the acorns from the plot which had a higher content of available phosphorus in the soil also had a higher content of phytic acid and their germination was higher (Zitnik et al. 1999). However, the difference was observed only at the beginning of the storage and it disappeared towards the end of the storage period. The conclusion of this research was that there are trends towards a positive correlation between the vitality of the acorns after long-term storage, the content of phytic acid in acorns and the content of available phosphorus in soil. However, the results of the research are not statistically significant to prove unequivocally that such a correlation exists. Further research will be needed to confirm or to disprove this possible correlation.

The results of the storage at the INRA Center Nancy showed that there are no differences regarding the content of phytic acid between different temperatures of storage. During storage, the content of phytic acid dropped. There was no correlation between the content of phytic acid and the germination of acorns. The level of phytic acid was the same in acorns with high germination and low germination. Therefore, phytic acid might not have any important role in the frost hardening of acorns.

The results of the storage at the INRA Center Nancy also show that the acorns that were stored at lower temperatures (-6 °C and -9°C) had higher levels of sugars (raffinose, stachyose) during storage than at the beginning of storage, while acorns stored at a temperature of -3°C retained the same level of sugars during storage. Therefore, lowering the temperature might induce higher levels of sugars in acorns. There was also a correlation between the content of sugars in acorns and their germination at the same temperature of storage. This correlation was observed only at temperatures of -6 °C and -9 °C, while at the temperature of -3 °C there was no correlation. The lower the temperature of storage, the higher the correlation was. The acorns that had higher germination during storage also had a higher content of sugars; therefore, the sugars could play an important role in the frost hardening of acorns.

Because of the interesting results of the influence of sugars on the frost hardening of acorns, we started in 1999 at the Slovenian Forestry Institute a new project on this subject. This time we will analyse the content of sugars in acorns with the HPLC method (Clement 1992): Refractive index detector (RI) and Aminex®

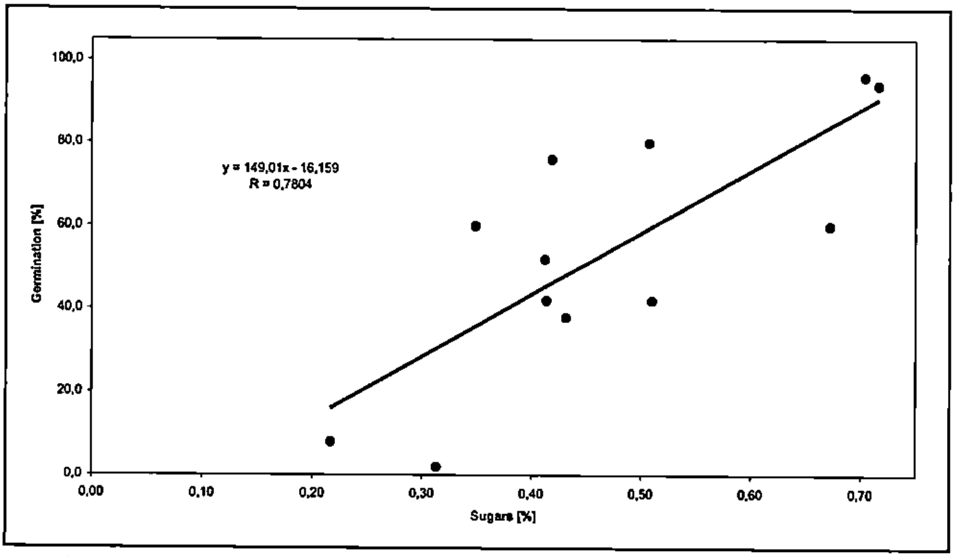

Figure 1. The correlation between the germination of acorns stored at temperature -9 °C and the content of sugars in them.

HPX-87P Column in collaboration with the INRA Center Nancy. We will analyse the content of several monosaccharides (glucose, fructose, galactose) and oligosaccharides (sucrose, raffinose, stachyose), and the content of starch in acorns with the enzymatic method. With the results of this research, we hope to better understand the physiological processes of different sugars in acorns at low temperatures.

CONCLUSIONS

In order to improve the long-term storage of acorns we should understand the physiological processes in acorns during storage. The results presented suggest that phytic acid and several sugars (raffinose, stachyose) might have an important influence on the vitality of stored acorns. Further research is needed to fully understand the processes by which they influence the vitality of stored acorns. Based on this knowledge we can then further develop better methods for the long-term storage of acorns.

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FIZIOLOGIJA ŽIREVA TIJEKOM DUGOTRAJNOGA ČUVANJA

Žirevi hrasta lužnjaka (*Quercus robur* L.) i hrasta kitnjaka (*Quercus petraea* /Matt./ Liebl.) sjeme su kratkoga vijeka trajanja, pa se prema tomu mogu skladištiti samo s visokim sadržajem vlage (40 – 45 %) na temperaturi od oko 0 °C. U takvim se uvjetima žirevi uspješno mogu čuvati samo 1 – 2 godine. Fitinska bi kiselina mogla igrati važnu ulogu u očuvanju vitalnosti žireva za vrijeme uskladištenja. U 1997. godini žirevi hrasta kitnjaka su skupljani na dva različita staništa i čuvani godinu dana. Rezultati pokazuju da količina fitinske kiseline u žirevima korelira s količinom dostupnoga fosfora u tlu i da fitinska kiselina utječe na vitalnost žireva. Te iste godine druga količina žireva hrasta kitnjaka skladištena je na tri različite temperature (-3 °C, -6 °C, -9 °C) na godinu dana. Rezultati pokazuju da različite temperature skladištenja nemaju nikakav utjecaj na količinu fitinske kiseline u žirevima. Analizirana je količina nekih šećera (rafinoze, stahioze) u ovim žirevima i rezultati pokazuju da su veće količine šećera na nižim temperaturama u pozitivnoj korelaciji s većom vitalnošću žireva.

Ključne riječi: hrast, žirevi, uskladištenje, fitinska kiselina, šećeri

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