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## LONG-TERM CHANGES IN TREE SPECIES COMPOSITION IN OLD-GROWTH DINARIC BEECH-FIR FOREST

DUGOROČNE PROMJENE U SASTAVU VRSTA DRVEĆA DINARSKIH  
BUKOVO-JELOVIH PRAŠUMA

JURIJ DIACI<sup>1</sup>, DUŠAN ROŽENBERGAR<sup>1</sup>, STJEPAN MIKAC<sup>2</sup>, IGOR ANIĆ<sup>2</sup>,  
TOMAŽ HARTMAN<sup>3</sup>, ANDREJ BONČINA<sup>1</sup>

<sup>1</sup> University of Ljubljana, Biotechnical Faculty, Department of Forestry and  
Renewable Forest Resources, Večna pot 83, 1000 Ljubljana, Slovenia

<sup>2</sup> University of Zagreb, Faculty of Forestry, Croatia

<sup>3</sup> Slovenia Forest Service

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Successive inventories of individual old-growth beech–fir forests from Dinaric mountains show structural changes during the last half a century. To be aware of these trends is important for general understanding of regeneration processes in old-growth forests, as well as for stating appropriate silvicultural aims. However, no study comparatively investigated data sets from several old-growth forests. We analyzed data from 31 inventories of growing stock in seven old-growth forests representing large area stretching from the north-west of the Dinaric mountain range in Slovenia to the central part in Croatia. All forests experienced a decrease in the proportion of silver fir in the growing stock. The decrease was of a different magnitude in individual old-growth forests. However, the overall growing stock in the majority of old-growth forests didn't fluctuate as expected due to the silver fir decline. The diameter distribution of five selected forests was closer to a rotated sigmoid than to a negative exponential distribution in spite of relatively large areas which were inventoried. The curves for growing stock according to dbh revealed, that beech and silver fir occupy different niche within ecosystem. In the lower diameters beech is more frequent and competitive, while silver fir compensates for this in larger diameters (and heights). Both curves from most reserves were not stable in time. The most apparent and worrying trend in Slovenia was the decrease of the silver fir curve over the entire range of the diameter distribution, with peaks in the lowest and largest

diameters. Moreover, the silver fir regeneration > 20 cm was almost completely absent due to high densities of large herbivores. While Čorkova Uvala appears to be a very balanced reserve in regard to all sampled parameters. The results revealed a general synchronous trend of silver fir replacement by beech on a broader geographical scale. The complex reasons for this are discussed and some general guidelines for the silviculture in managed beech fir forests are given.

**Keywords:** old-growth forest, beech-fir forest, virgin forest, diameter distribution, growing stock, species composition, alternation of tree species, long-term inventories.

## INTRODUCTION UVOD

Beech-fir forests form one of the largest areas of continuous forest in south-central Europe. In the north-western part of the Balkan Peninsula, they stretch over the Dinaric Mountain range along the Adriatic Sea coast, covering some 163.500 ha in Slovenia and 140.000 ha in Croatia. They serve as both an important wood source and a key habitat for several important and endangered animal species. During the last century the tree species composition of this forest changed dramatically, especially in Slovenia (Ficko in Bončina, 2006), where once silver fir (*Abies alba* Mill.) dominated forest is now in some areas dominated by beech (*Fagus sylvatica* L.). The mechanisms behind the alternation in dominance that occurred over the past century are not entirely clear. There are several possible reasons, including reintroduction of red deer in the late 19th century, silver fir decline, which started in the 50's (Bončina et al. 2003), different management regimes that changed the stand climate in favor of beech and natural processes of tree species replacement (Brinar 1969; Forcier 1975; Fox 1977; Gašperšič 1974; Mlinšek 1967). The silver fir decline in old-growth forests suggests that management was not the predominant factor triggering it. Although repetitive studies of structural changes of single old-growth forests from Dinaric mountains are frequent (e.g. (Hartman 1987; Turk et al. 1985; Roženbergar 2000)), there is no overview of structural changes in old-growth forest from several sites. In this study long-term data about structure and tree species composition of mature stands and regeneration was analyzed from several selected old-growth forest reserves in the area of Dinaric beech-fir forests in Slovenia and Croatia. The aims of the study were to: (1) examine if virgin forest from different geographical regions of Dinaric mountain chain show similar trends of structural changes over the time, (2) propose ecological reasoning for the changes, (3) identify possible future trends of forest structures and (4) develop general recommendations for managed forests.

## METHODS

### METODE

#### Research sites

#### Područje istraživanja

The research was performed in 7 natural old-growth forest reserves. Forest reserves Rajhenavski Rog (RR), Pečka (PE), Strmec (ST), Krokari (KR) and Bukov vrh (BV) are located in Slovenia, while Čorkova uvala (CU) and Devčića tavani (DT) in Croatia (Figure 1). In all cases the site conditions were similar (Table 1) and forests were dominated by beech - fir (*Fagus sylvatica* L. and *Abies alba* Mill.) communities, which are typically located between 700-1200 meters in the Dinaric mountain range. Other less abundant species were also present in forest stands, including sycamore maple (*Acer pseudoplatanus* L.), wych elm (*Ulmus glabra* Huds.), spruce (*Picea abies* (L.) Karsten), common ash (*Fraxinus excelsior* L.), and large-leaved lime (*Tilia platyphyllos* Scop.).

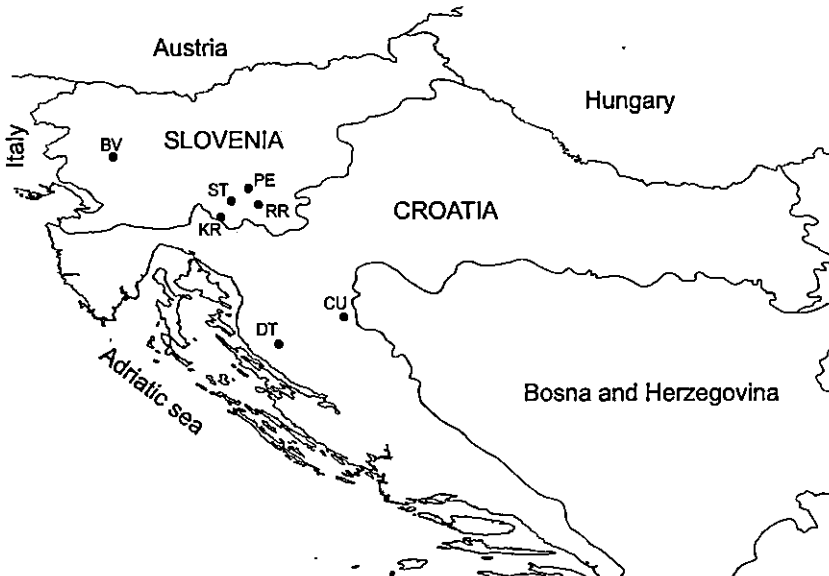


Figure 1: Locations of the old-growth beech-fir forest reserves included in the research (Rajhenavski Rog – RR, Pečka – PE, Strmec – ST, Krokari – KR, Bukov vrh – BV, Čorkova uvala – CU and Devčića tavani – DT)

Slika 1. Bukovo-jelove prašume uključene u istraživanje (Rajhenavski Rog – RR, Pečka – PE, Strmec – ST, Krokari – KR, Bukov vrh – BV, Čorkova uvala – CU i Devčića tavani – DT)

Two of the selected research sites, namely Krokari and Bukov vrh, are located on the edge of beech-fir forest distribution area. The conditions are not as favorable for silver fir growth as in other cases; therefore the proportion of silver fir on these locations is by nature lower compared to other analyzed forest reserves (Kordiš, 1985). Krokari is situated on a plateau just above the Kolpa river with more intensive

exposure to warm air which is lifting up along the cliffs above the river. The large area of the reserve is also covered with dolomite parent material changing to some extent the soil conditions to more uniform which promotes beech as dominant tree species (Zeibig, 2001). Bukov vrh on the other hand is close to altitude border of silver fir distribution with colder mountain climate.

Typically Dinaric Mountains consist of dolomite and limestone parent material; therefore the soils are in all cases free draining, ranging from rendzinas to calcareous brown soils (calcocambisol) of variable depths. Macro- and microtopography of the research sites are diverse, changing the site conditions significantly over very small spatial scales. Karst phenomena such as sinkholes and rock outcrops at or close to the surface are common on all sites.

Table 1. Basic data of the research sites (RR – Rajhenavski rog, PE – Pečka, KR – Krokari, ST – Strmec, BV – Bukov vrh, DT – Devčića tavani, CU – Čorkova uvala)

Tablica 1. Osnovni podaci o istraživanim lokalitetima (RR – Rajhenavski rog, PE – Pečka, KR – Krokari, ST – Strmec, BV – Bukov vrh, DT – Devčića tavani, CU – Čorkova uvala)

Research site / Lokalitet	RR	PE	KR	ST	BV	DT	CU
Area / Površina [ha]	52.1	59.5	74.5	15.6	9.3	100	79.5
Location Položaj	45°40'N 15°01'E	45°46'N 15°00'E	45°33'N 14°47'E	45°38'N 14°49'E	46°00'N 13°53'E	44°88'N 15°04'E	44°55'N 15°32'E
Altitude Nadm. vis.	740-880	795-910	840-1170	840-940	1200- 1313	1192- 1295	860-1030
Annual precipitation God. padal. [mm]	~1650	~1220	~1526	~1556	~3000	1875	~1650
Average annual temperature Pros. god. temp. [°C]	7	14.3	8.4	8.3	6.2	5	7
Meteorological station Meteor. postaja	Kočevoje, Žaga Rog	Novo mesto	-	GGN Koče	Vojsko	Zavižan	Plitvička jezera
Forest site classification Šumarska zajednica	<i>Omphalo-</i> <i>lodo-</i> <i>Fagetum</i>	<i>Omphalo-</i> <i>lodo-</i> <i>Fagetum</i>	<i>Omphalodo-</i> <i>Fagetum</i> , <i>Lamio orva-</i> <i>lae-Arunco-</i> <i>Fagetum</i>	<i>Omphalo-</i> <i>lodo-Fa-</i> <i>getum</i>	<i>Omphalo-</i> <i>lodo-Fa-</i> <i>getum</i>	<i>Omphalo-</i> <i>lodo-Fa-</i> <i>getum</i>	<i>Omphalo-</i> <i>lodo-Fa-</i> <i>getum</i>
Country / Država	SLO	SLO	SLO	SLO	SLO	CRO	CRO

### Field methods and data analyses

#### Prikupljanje i analiza podataka

Three basic approaches were used in this study. First was the analysis of changes in the total volume and beech and silver fir proportion over the research period, which was completed for 7 locations (Table 1). The second was the examination of the long term data on number of trees and living volume according to the diameter at breast height (dbh) performed for 5 research sites and the third was the analysis of regeneration in two selected old-growth forest reserves.

First information about the tree species composition in Rajhenavski rog and Pečka dates back to 1883 and 1893 respectively, when the first management plans for the area were done (Hufnagel, 1893). All the rest of the long term data were gathered as a part of management activities after year 1950 with 10 years period between the measurements until today. In most of the cases dbh was measured and tree species defined for all trees in the reserve (full callipering). In the case of Čorkova uvala measurements were made on a systematic grid over the whole area of the reserve two times. Also the data gathered on 1 ha plots in most representative part of the reserve in CU and DT are included in this analysis, but just to observe the changes in tree species composition. In all cases only trees above 10 cm in diameter were included in the analysis. 5 cm diameter classes (up to 100 cm diameter) were used to show the distribution of number of trees and volume per hectare according to dbh. In cases where previous measurements were performed only up to certain dbh, all trees above that dbh were put together in the last diameter class in all following data sets.

Between 2001 and 2004, under different light conditions in gaps, under stands surrounding the gaps, and under the closed canopy a N-S oriented 5x5 m grid was established and 773 - 1,5 x 1,5 m plots were established on the grid intersections. On each plot all seedlings of each tree species were counted and categorized within several height classes: 1 year-old seedlings, <20 cm height, 21 - 50 cm, 51 - 90 cm, 91 - 130 cm, 131 - 200 cm, 201 - 300 cm and >300 cm.

## RESULTS REZULTATI

### Long-term changes in tree species composition and growing stock Dugoročne promjene smjese vrsta drveća i drvne zalihe

Seven old-growth forest under investigation cover substantial range from the very start of the Dinaric mountain range in Trnovski gozd Slovenia, represented by Bukov vrh, to the core area in Croatia, represented by Čorkova Uvala and Devčića tavani. In the 50' the share of silver fir in growing stock of all live trees amounted on average between 50-65% (Figure 2). Values below 30% were measured in Krokari and Bukov vrh. First is only partly covered by beech-fir ecosystem, while Bukov vrh represents a transition towards high mountain beech forests. However, from 1950 on, all old-growth forests demonstrate a decrease of silver fir share in the growing stock of all live trees. This reduction is less pronounced in Croatia compared to Slovenia. Still, also within countries significant differences in decrease exist. The steepest decrease took place in Pečka in Slovenia, where silver fir share declined from 58 % in 1893 to 17 % in 2003, which represents a 41 % decrease in about 100 years. It appears that old-growth forest at the edge of Dinaric mountain chain (for example Pečka with 20 % decrease over the last 20 years) or at the edge of the beech-fir ecosystems within the Dinaric mountains (Krokari with 17 % decrease in the last 40 years) demonstrate a more noticeable decrease. The decrease of the silver fir was not constant over the

time. Two old-growth forests show a more pronounced decrease in the last interval between the measurements, namely Pečka and Devčića tavani, while the change is not so evident in case of Bukov vrh and Rajhenavski Rog. The majority of others show a decrease of ca. 5 %. Observing longer periods of time we can see different patterns, as for example a relatively constant and lately accelerated decrease in Pecka and an increase until 50' followed by a gradual decrease in Rajhenavski Rog.

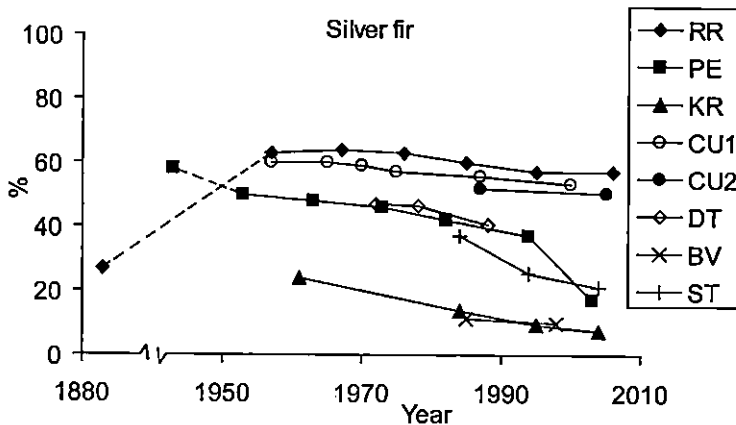


Figure 2: Long-term changes in proportion of silver fir in living volume in seven beech-fir old-growth forests in Dinaric mountains

Slika 2. Dugoročne promjene volumnog udjela obične jele u sedam dinarskih bukovo-jelovih prašuma

The most important species competing with silver fir is beech, all the remaining species from Norway spruce to sycamore maple represent a minor share of maximum 5 % in some reserves. The trends of beech proportion in the growing stock of all live trees were reciprocal to those demonstrated by silver fir (Figure 3), as expected. The beech share in all old-growth forests exceeds 40 %. The most silver fir dominant forests remain Corkova Uvala and Rajhenavski Rog.

The growing stock of old-growth forest was in an interval form slightly above 500 m<sup>3</sup>/ha on more extreme sites as Bukov vrh, to 942 m<sup>3</sup>/ha in Pecka in 50' (Figure 4). The average value of most representative beech-fir old-growth forests was about 800 m<sup>3</sup>/ha (RR, PE, CU), the rest of old-growth forest with lower growing-stock include also additional less productive sites in inventoried protected compartments. Most of the variation intervals of growing stock in the observed time are close to 100 m<sup>3</sup>/ha, which seems reasonable in regard to relative large areas under investigation (from 10 to 100 ha). The maximal decrease of growing stock was observed in Pecka. Here it declined from 942 m<sup>3</sup>/ha in 1953 to 698 m<sup>3</sup>/ha in 2003. The highest increase of almost 150 m<sup>3</sup>/ha over 45 years was recorded in Krokari. In some old-growth forests (e.g. RR) the growing stock remained relatively constant over almost 60 years. In the period between last two measurements there is a noticeable trend of growing stock decrease in all forest reserves with the exception of CU2.

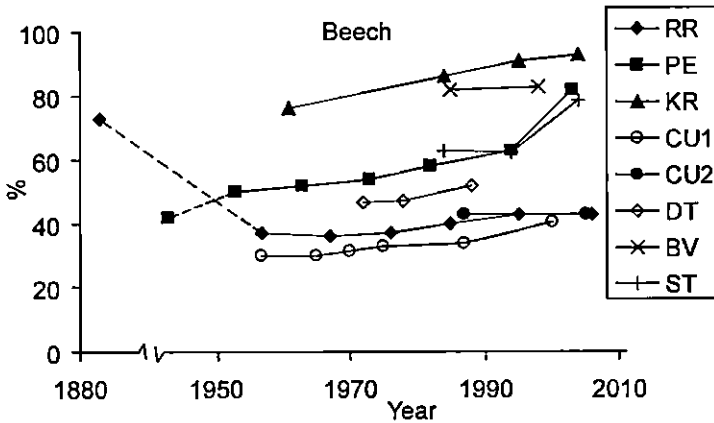


Figure 3: Long-term changes in share of beech in living volume in seven beech–fir old-growth forests in Dinaric mountains

Slika 3. Dugoročne promjene volumnog udjela obične bukve u sedam dinarskih bukovo-jelovih prašuma

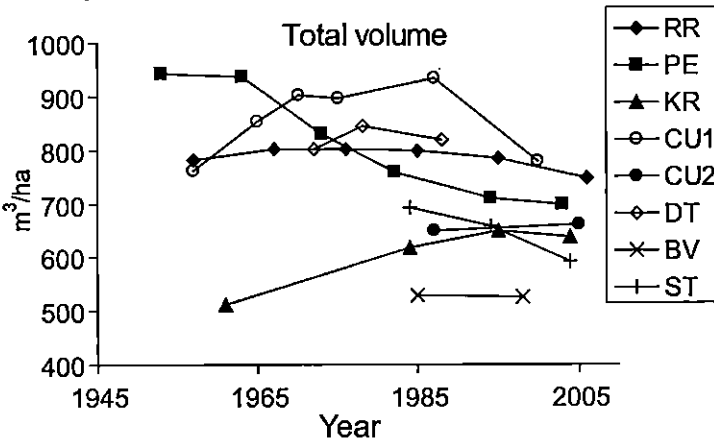


Figure 4: Long-term changes in amount of growing stock of live trees in seven beech–fir old-growth forests in Dinaric mountains

Slika 4. Dugoročne promjene prosječne drvene zalihe živih stabala u sedam dinarskih bukovo-jelovih prašuma

### Changes in tree species frequency and growing stock distributions according to dbh

Promjene distribucija vrsta drveća i drvene zalihe s obzirom na prsni promjer

From seven old-growth forests, five with complete data sets for the last two inventories in 1980' and 2000', respectively were selected for a detailed analysis of diameter and growing stock distributions. The diameter distributions including all trees showed more tendency towards the rotated sigmoid than the negative expo-



nential distribution (Figure 5). The closest to the reverse J-shaped curve was the distribution from Čorkova Uvala and Strmec, if we neglect the larger diameter sizes above 19 dbh. The curve from Čorkova uvala was also the most stable in time, while the curves from Slovenian old-growth forest showed changes in the shape of the curve. However, this was different from forest to forest. For example, in Pečka, Strmec and Krokár we noticed a decrease in small diameters and an increase in large ones, while in Rajhenavski rog there was a decrease in the middle diameters. The closer look into the diameter distribution of each species reveals the nature of changes for the curve of total stems in reserve. There are differences between countries and among individual reserves. The curves for both species seem to be relatively stable for both species in Čorkova uvala, while in Slovenia the curves for species show significant differences in time. The most apparent and worrying trend is the decrease of the silver fir curve along whole range of the diameter distribution. Still, this is most pronounced in the lowest and largest diameters. On the other hand the beech shows a decrease of curves among the youngest diameters and increase among the largest. This trend points to the severe mortality among the young beech generation which competed for space in the gaps created after the most severe decline of silver fir, which was followed by two successive windthrows. The gaps were partially closed by the growth of the advanced regeneration and partially by lateral extensions of the crowns of surrounding trees. The exception is Rajhenavski rog where the decrease of silver fir and increase of beech in the low diameter classes seem to be slow and thus synchronous. In all reserves the inverse sigmoid curve was more expressed with beech than with silver fir.

In the last two decades the growing stock curve for all live trees has shifted towards right hand side of the figure in all Slovenian old-growth forests, whilst it stayed relatively stable in Čorkova uvala (Figure 6). This is probably due to more pronounced silver fir decline in Slovenia, which triggered lush ingrowth of beech. This phenomenon is more pronounced if we analyze growing stock distributions per dbh for beech and silver fir separately. The beech curve had the strongest shift towards right in Pečka, followed by Krokár and Strmec. This curve seems relatively stable in Rajhenavski rog and Čorkova uvala. However, the silver fir curve showed the strongest decrease in Pečka, followed by Strmec and Krokár. In Rajhenavski rog and Čorkova uvala it stayed stable with a slight move to the right hand side. To allow comparability the diameters above dbh class 20 were merged into 20th dbh class for Pečka, Rajhenavski rog and Čorkova uvala. For Krokár and Strmec all higher diameters were merged into 16th dbh class. Still, from the graphs we could see the general rule that beech and silver fir supplement each other within the curves. In the lower diameters beech is more frequent and competitive, while silver fir compensates for this in larger diameters (and heights). The beech curve usually finishes with 19th dbh class, while silver fir often attains diameters up to 24th dbh class, with individual trees up to 32th class.

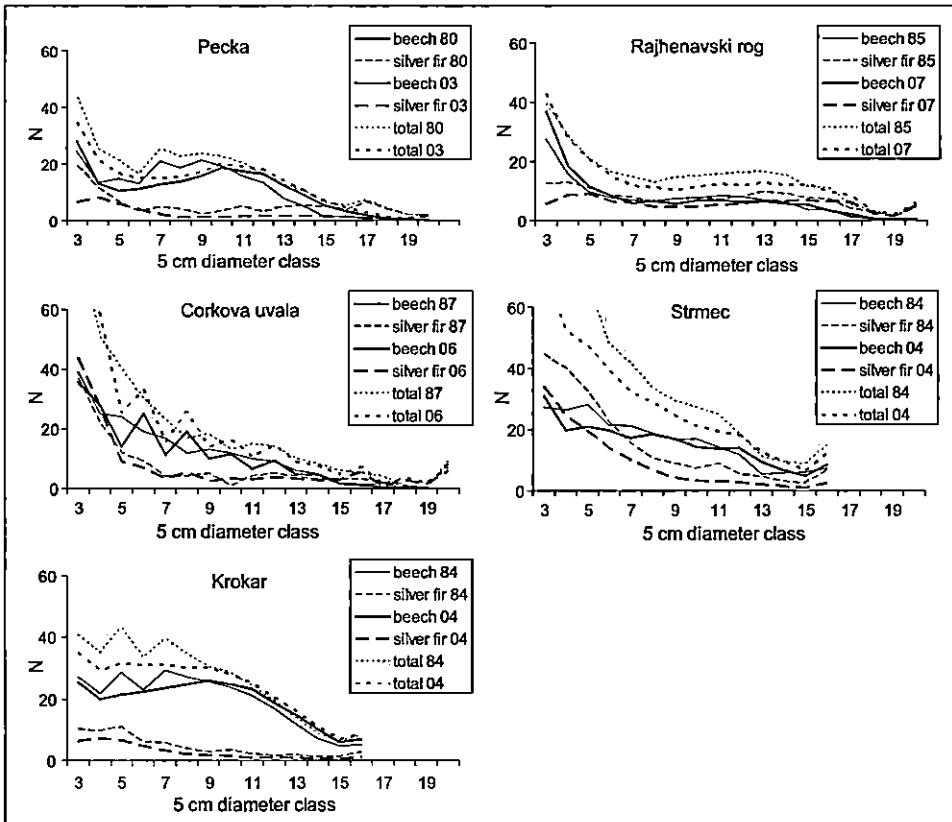


Figure 5: Comparison of diameter distributions of five beech–fir old-growth forests according to tree species between the last two inventories

Slika 5. Usporedba distribucija prsnih promjera za posljednje dvije inventure na primjeru pet bukovo-jelovih prašuma

### Regeneration tree species composition and height distribution Struktura pomlatka po vrstama drveća i visinama

The density of regeneration in total was almost five times higher (62.066 per ha) in Rajhenav compared to the Čorkova uvala (13.083 per ha) forest reserve ( $t = 19,4586$ ,  $p = 0,0000$ ), which is mostly due to an almost ten-fold increase (54.699 versus 5588 per ha) in the density of beech at Rajhenav (Figure 1 right). However, the total density of silver fir was more than twice as high (6312 versus 3187 per ha) in Čorkova uvala ( $t = -5,7711$ ,  $p = 0,0000$ ). In spite of the fact that there was much less silver fir in the upper storey, the density of one year old and up to 20 cm tall silver fir seedlings in Rajhenav was higher than in Čorkova uvala. However, the density of silver fir seedlings taller than 20 cm was higher in Čorkova uvala, as there were no seedlings taller than 50 cm in the Rajhenav old-growth forest reserve (Figure 1 left). Lower densities of beech seedlings in Čorkova uvala could be explained by lower radiation levels

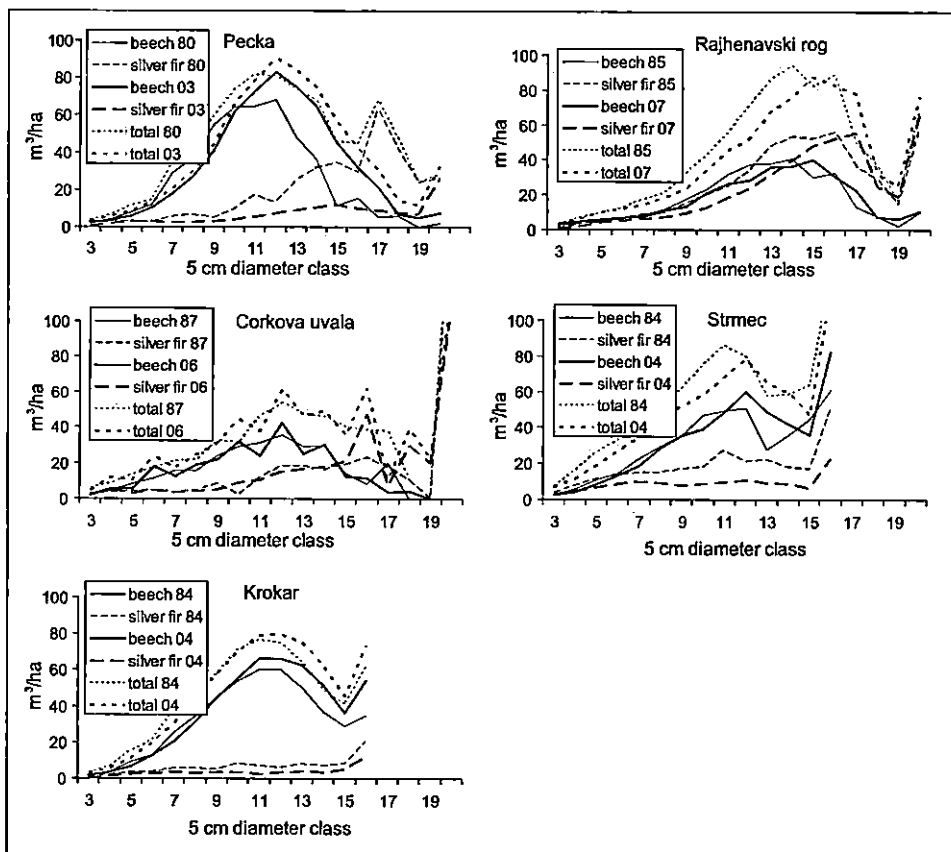


Figure 6: Comparison of distributions of growing stock in relation to DBH of five beech-fir old-growth forests between the last two inventories

Slika 6. Usporedba distribucija drvene zalihe za posljednje dvije inventure na primjeru pet bukovo-jelovih prašuma

and smaller gaps compared to Rajhenav, and also by much more intensive competition from the herb layer in Čorkova uvala. The main reason for the dramatically low density of fir seedlings above 20 cm tall in Rajhenav is the heavy browsing pressure, due to a high population density of red and roe deer in the Dinaric mountains in Slovenia. This also explains the much denser coverage of ground vegetation in Čorkova uvala, especially *Rubus* species, which is highly desired by deer.

## DISCUSSION RASPRAVA

Seven examined beech-fir old-growth forests covering broader geographical scale from north-west to central Dinaric Mountains showed a significant decrease

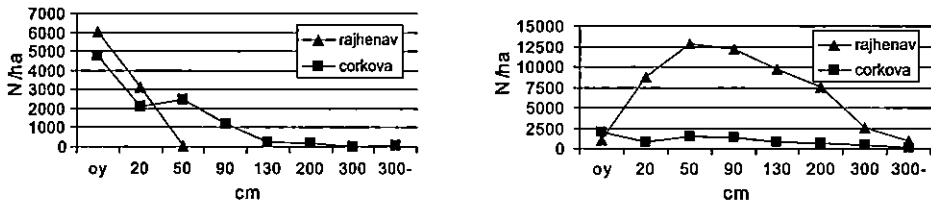


Figure 7: Density ( $n \text{ ha}^{-1}$ ) of fir (left) and beech (right) one year old (oy) and older seedlings in different height classes (cm) in Rajhenav and Čorkova uvala

Slika 7. Gustoća ( $n \text{ ha}^{-1}$ ) jelovog (lijevo) i bukovog (desno) ponika i pomlatka po visinskim klasama (cm) u prašumama Rajhenav i Čorkova uvala

of silver fir share in growing stock in the last half of the century. Similar trends were reported for managed forests many times during the period of acute silver fir decline from 1950' to mid 80' (Šafar 1964; Kandler 1992; Korpel 1985; Larsen 1986; Leibundgut 1974; Mlinšek 1964). The decrease of silver fir in growing stock was of a different magnitude among individual virgin forests, still it appears to slow down in recent decades. This is conform with the findings from managed forests were first observations of improved health status of silver fir were reported in the last decades (Dobrowolska 1998). The exceptions were Devčića tavani and Pečka, the last being hit by two successive windstorms (Nagel and Diaci 2006; Nagel et al. 2006).

In all studied forests silver fir was replaced by the beech. This is a common trend often reported for individual reserves and managed forests (Bončina et al. 2003; Diaci 1994). In spite of significant tree species replacement the overall growing stock in the majority of old-growth forests didn't fluctuate as expected. Exception was the old-growth Pečka, due to above mentioned reasons.

The causes for silver fir decline are complex, however they are of natural, anthropogenic and mixed origin. The anthropogenic reasons include the pollution of ecosystems on a local and global scale, climate change, high densities of the ungulates and non adapted silvicultural systems to the silver fir ecology. The last, appears not to be one of the primary causes due to the silver fir decline in old-growth forests. However, forestry might have an effect, through building of fine forest road network and thus changing the local forest climate, removal of CWD on which silver fir often regenerates and changing from single tree selection to irregular shelterwood system in Slovenia.

The most important natural cause of silver fir decline is the tree species alternation in persistent (climax) communities. The word alternation of species was proposed by a French forester in 1905 (Schaeffer and Moreau 1958) and then often observed or researched in temperate forests (Forcier 1975; Fox 1977; Watt 1947), including Croatia and Slovenia (Šafar 1967; Gašperšič 1974). Initially, the alternation was understood mostly on the local scale, from one or to at most few large canopy trees. Here, most processes affecting density and species composition operate, except dispersal (Fox 1977). (Watt 1947) was the first wrote about this issue; the alternation was reflected in the spatial mosaic of the community. Later (Fox 1977) found that sapling abundance was lower beneath the canopies of the same species.

Similar results were reported also for Dinaric beech–fir forests (Gašperšič 1974). There are several mechanisms behind the alternation (Fox 1977):

1. The substrate and micro-relief variability could be important on the diverse carstic conditions of Dinaric Alps. Short (climate, seed bed) and long-term (nutrients, chemical properties) influences of CWD could be added to this group, although they operate also tree species specific.
2. Demographic causes of alternation - each species inhibits the survival and growth of its own species most severely (autoinhibition):
  - parent tree is a source of predators and pathogens: herbivorous insects, other predators, toxins
  - conspecific trees may be thinned more severely: similar niche and need for resources, e.g. soil, light with temporal variability, variability in quality
  - other reasons: lower abundance of long living species - they take long to pass a certain dangerous height range
  - tolerance relations: adaptation to specific disturbance regime (small and large gaps); expected crown diameter at death is favoring another species; different crown size between conifers and broadleaves (silver fir - beech)
  - better growth of evergreens underneath of broadleaves
  - plants create individual microhabitats (light, precipitation).

However, also regional and global factors might have an important effect on the species alternation as shown in this study. For example different densities of ungulates, which hindered the regeneration of silver fir in Slovenia completely in last 30 years, and various silvicultural regimes operate on a regional scale. Moreover, the global climate change, with higher temperatures, more severe disturbance regime is less favorable for silver fir compared to beech. Similar replacements of both species have been found after the last ice ages (Andric and Willis 2003; Šercelj 1996). Finally, it appears very difficult to draw a line between different scales of operation of species alternation and natural versus anthropogenic factors.

The examined old-growth forest covered mainly large areas, however the diameter distribution of individual old-growth forest did not follow the negative exponential distribution as reported from many studies in old-growth forests (Lorimer 1980) (Leak 1996). The reverse negative exponential distribution suggest similar growth and mortality rates across the diameter range. The observed curves were closer to a rotated sigmoid distribution. This observation is not a new one (Goff and West 1975; Hartman 1987; Leibundgut 1982; Westphal et al. 2006). The deviation from the negative exponential curve might be due to higher mortality in lower and higher diameter classes and/or faster diameter growth in the mean classes. It is interesting that the rotated sigmoid distribution was found to provide the best fit also for managed equilibrium state plenter beech–fir forest in Switzerland (Schütz 2001).

The curves for growing stock per dbh revealed that beech and silver fir occupy different niche within ecosystem. In the lower diameters beech is more frequent and competitive, while silver fir compensates for this in larger diameters (and heights). This was already reported for two beech–fir old-growth forests in Slovenia (Hart-

man 1987; Turk et al. 1985). A general observation from most reserves was, that the diameter and volume curves were not stable in time.

A comparison of Slovenian old-growth forests with Čorkova Uvala in Croatia revealed a strong decrease of the silver fir curve in Slovenia along all the diameter distribution, with peaks in the lowest and largest diameters. If we add to this also the almost absent regeneration of silver fir in Slovenia, than it is obvious that silver fir is significantly more endangered in Slovenia than Croatia.

The worrying trends of silver fir decline in Slovenian old-growth forests require a continuation of special management procedures for controlling the roe and red deer density. The different niche occupation of silver fir and beech within the same ecosystem call for a individual silvicultural treatment of each species, e.g. different rotation periods, target diameters, modes of regeneration. Shaded silver fir regeneration and mature trees of high volume and age allow silver fir to develop the full competition potential. Still, the silver fir decline is partially also a natural phenomenon linked to species replacement, therefore more unpredictability and flexibility should be integrated in the silvicultural systems.

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## DUGOROČNE PROMJENE U SASTAVU VRSTA DRVEĆA DINARSKIH BUKOVO-JELOVIH PRAŠUMA

### SAŽETAK

Uzastopne inventure dinarskih bukovo-jelovih šuma tijekom prošlog stoljeća su pokazale promjene u njihovoj strukturi. Te su spoznaje važne za razumijevanje procesa pomlađivanja u prašumama i gospodarenje šumama. Ipak, nijedna studija nije uspoređivala nizove podataka iz nekoliko prašuma. Analizirali smo podatke o drvnjoj zalihi iz 31 inventure u sedam prašuma koje se prostiru od sjeverozapadnih Dinarida u Sloveniji do njihova središnjeg dijela u Hrvatskoj. U svim je šumama ustanovljeno smanjenje udjela obične jele u drvnjoj zalihi. Smanjenje udjela jele je različito među pojedinim prašumama. Ukupna drvena zaliha u većini prašuma ne pokazuje očekivane promjene s obzirom na odumiranje jele. Distribucija prsnih promjera u pet odabranih prašuma bliža je obrnuto sigmoidalnoj nego negativno eksponencijalnoj funkciji, unatoč relativno velikom području uzorkovanja. Distribucije volumena po debljinskim stupnjevima pokazuju kako bukva i jela zauzimaju različite niše unutar ekosustava. Bukva je više zastupljenija u nižim debljinskim stupnjevima, dok jela kompenzira taj prostor u višim debljinskim stupnjevima i visinama. Obje krivulje za sve istraživane rezervate pokazuju nestabilnost u vremenu. Najjasniji i zabrinjavajući trend u Sloveniji je opadanje udjela jele unutar čitavog opsega distribucije prsnih promjera, s najvišom točkom u nižim i višim stupnjevima. Osim toga, pomlatka jele iznad 20 cm visine nema zbog visoke gustoće populacije divljači. Čorkova uvala u odnosu na sve ostale istraživane prašume čini se najuravnoteženijom s obzirom na analizirane parametre. Rezultati pokazuju generalni istovremeni trend zamjene jele običnom bukvom na većoj geografskoj razdiobi. U radu su prikazani mogući razlozi tih promjena te su date preporuke za uzgajanje bukovo-jelovih šuma.

**Ključne riječi:** prašuma, bukovo-jelove šuma, distribucija prsnih promjera, drvena zaliha, sastojinski oblik, izmjena vrsta drveća, dugoročne izmjere.