UNIVERSITY OF LJUBLJANA
BIOTECHNICAL FACULTY

Srđan KEREN

COMPLEXITY OF STAND STRUCTURES IN TWO MIXED MOUNTAIN OLD-GROWTH FORESTS AND ADJACENT MANAGED FORESTS IN BOSNIA AND HERZEGOVINA

DOCTORAL DISSERTATION

Ljubljana, 2015

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DOCTORAL DISSERTATION

RAZNOLIKOST SESTOJNIH STRUKTUR V DVEH MEŠANIH GORSKIH PRAGOZDOVIH IN BLIŽNJIH GOSPODARSKIH GOZDOVIH V BOSNI IN HERCEGOVINI

DOKTORSKA DISERTACIJA

Ljubljana, 2015

This doctoral dissertation represents final part of doctoral program in biosciences, scientific field Management of Forest Ecosystems at the Biotechnical Faculty, University of Ljubljana.

The Senate of the Biotechnical Faculty approved the dissertation topic and appointed prof. dr. Jurij Diaci as a supervisor and prof. dr. Zoran Govedar as a co-supervisor on September 9, 2012.

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Defense date: February 19, 2015

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KEY WORDS DOCUMENTATION

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DC	FDC 23:228.81+188Piceo-Abieti-Fagetum Illyricum(497.6)(043.3)=111
CX	old-growth forests, managed forests, structural attributes, selection silviculture, climatic extremes, European beech, silver fir, Norway spruce, replacement patterns
CC	
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AB This study was conducted in Dinaric mixed mountain old-growth (OG) forests Janj and Lom and adjacent managed stands on the same site (*Piceo-Abieti-Fagetum illyricum*), which were managed with a selection (plenter) system for more than a century. The following attributes were examined: light climate, ground vegetation, regeneration, tree density, dbh distribution shapes, tree species composition, mean diameter, basal area (BA), growing stock (GS) and coarse woody debris (CWD). As expected, taller and larger trees, higher BA, higher share of senescent phase and more CWD were found in OG forests. Regeneration process in OG forests was characterized by lower levels and variability of light, lover ground vegetation coverage and vascular plant diversity, and the species composition was more dominated by beech. Beech seedling density indicated positive relation to beech BA, while all regeneration stages of fir showed negative relation with fir BA. Beech was significantly more represented in OG forests also in the middlestory. Dbh distributions in both managed and OG forests had shapes that indicate a demographic equilibrium, despite high values of GS. Most frequent species specific shapes indicated demographic stability or even progression of beech, and imbalance or regression of conifers. Despite significant shares of spruce and fir in the upperstory, their regeneration and small trees were given low chances to replace mature trees in OG forests in the near future. Similarly to the natural disturbance pattern in OG forests Janj and Lom, single tree selection in managed forests performed only slightly better regarding recruitment of spruce and maple into the stand middlestory. The long-term comparison of OG forest structure indicated decline of conifers (especially spruce). However, comparison of recent data in managed and OG forests indicated that silvicultural activities may hold back long-term conifer decline since managed forests exhibited greater compositional stability.

KLJUČNA DOKUMENTACIJSKA INFORMACIJA

ŠD	Dd
DK	GDK 23:228.81+188Piceo-Abieti-Fagetum Illyricum(497.6)(043.3)=111.6
KG	pragozdovi, gospodarski gozdovi, strukturne značilnosti, prebiralno gojenje gozdov, klimatski ekstremi, bukev, jelka, smreka, vzorci nadomeščanja
KK	
AV	KEREN, Srđan
SA	DIACI, Jurij (mentor), GOVEDAR, Zoran (so-mentor)
KZ	SI-1000 Ljubljana, Večna pot 83
ZA	Univerza v Ljubljani, Biotehniška fakulteta, Interdisciplinarni dokotrski študij Bioznanosti, področje Upravljanje gozdnih ekosistemov
LI	2015
IN	RAZNOLIKOST SESTOJNIH STRUKTUR V DVEH MEŠANIH GORSKIH PRAGOZDOVIH IN BLIŽNJIH GOSPODARSKIH GOZDOVIH V BOSNI IN HERCEGOVINI
TD	Doktorska disertacija
OP	X, 147 str., 54 pregl., 44 sl., 0 pril., 194 vir.
IJ	en
JI	sl/en

AI Raziskava je bila izpeljana v Dinarskih jelovo-bukovih pragozdovih Janj in Lom (OG) ter gospodarskih gozdovih v bližini (MF) na primerljivih rastiščih (*Piceo-Abieti-Fagetum illyricum*), kjer že več kot stoletje prebiralno gospodarijo. Proučevale so se naslednje značilnosti gozdov: svetlobne in zeliščne razmere, pomlajevanje, drevesna sestava, gostota, temeljnica in debelinska struktura sestojev ter veliki drevesni ostanki. Kot je bilo pričakovati, so značilnosti OG: višja in večja drevesa, višje temeljnice, večji deleži terminalne faze in več drevesnih ostankov. Za ekologijo pomlajevanja v OG je bila značilna manjša količina in variabilnost svetlobe, manjša pokrovnost in raznovrstnost vaskularnih rastlin, v zmesi mladja pa je bolj prevladovala bukev kot v MF. Gostota manjšega bukovega mladja je bila v pozitivni povezavi s temeljnico bukve, medtem ko so vse razvojne faze jelovega mladja nakazovale negativno povezavo s temeljnico jelke. Bukev je tudi značilno prevladovala v srednji drevesni plasti pragozdov v primerjavi z MF. Porazdelitve prsnih premerov OG in MF so, kljub visokim lesnim zalogam, nakazovale demografsko ravnotežje. Najpogostejše vrstno specifične oblike porazdelitev so nakazovale demografsko stabilnost ali napredovanje bukve in demografsko neravnovesje ali nazadovanje iglavcev. Kljub znatnim deležem smreke in jelke v zgornji plasti, so njuni čakalci v spodnji plasti nakazovali slabe možnosti za nadomestitev odraslih dreves v OG. Podobno kot pri naravnem vzorcu motenj v OG Janj in Lom, prebiralno gospodarjenje ni bistveno izboljšalo deleža smreke in javorja v srednji plasti. Dolgoročna primerjava strukture OG je nakazala nazadovanje iglavcev (predvsem smreke). Vendar pa primerjalna analiza zadnjih podatkov v OG in MF nakazuje, da lahko gojenje gozdov prispeva k zadrževanju dolgoročnega nazadovanja iglavcev, kajti gospodarski gozdovi izkazujejo večjo stabilnost zmesi.

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List of acronyms

OGF	Old-growth forest (used for singular old-growth forest, e.g., OGF Janj, OGF Lom, etc.)
OG	Old-growth (used only as an adjective two describe two or more old-growth forests, e.g., OG forests Janj and Lom)
MF	Managed forest (used for singular managed forest, e.g., MF Janj, MF Lom; in plural full expression managed forests was used)
LCR	Live crown ratio
ADR	Apical dominance ratio (ratio between apical and lateral shoot)
BA	Basal area
GS	Growing stock
CWD	Coarse woody debris
PCoA	Principal coordinate analysis
DIR	Direct component of sunlight transmitted to forest understory
DIF	Diffuse component of sunlight transmitted to forest understory
LAI	Leaf area index
DBH, dbh	Tree diameter at breast height (1.3 m above ground)
RS	Rotated sigmoid dbh distribution
NE	Negative exponential dbh distribution
IQ	Increasing-*q* dbh distribution
UNI	Uniform or convex dbh distribution
CO	Concave dbh distribution
VAR	Variable dbh distribution
BiH	Bosnia and Herzegovina

1 INTRODUCTION

Silviculture in Europe was mostly based on wood production until the mid 20th century and such management had significant implications for complexity of forest structure. According to Johann (2006), during the last 500 years a sharp reduction in the complexity of forest structure has occurred at all spatial scales. Tree planting was quite welcomed from 1820 onwards (Thomasius, 2001b). It usually followed clear cutting. In this way tree species replacement took place where broadleaved species, especially European beech (*Fagus sylvatica* L.), were artificially replaced by conifers. This kind of forest management is known as a "German classic school of forestry" and was promoted by the German forester and teacher at the Forest Academy in Tharandt, Heinrich Cotta. Afforestation in the 19th century was also influenced by the doctrine of Pressler, which promoted silvicultural techniques to gain the highest financial yield. Good example of such management is Germany and some other countries of Central Europe with extensive Norway spruce monocultures. Broadleaved species were virtually eliminated from the 1860s onwards. The purpose of this kind of forestry was purely economic, while natural processes and structures were not taken into consideration (Johann, 2006). As a result, not only did forested landscape change and tree species diversity reduce, but the stability of newly formed forests decreased as well, especially due to insect infestations and fungi attacks over larger areas. As often is said that good plan means half job done, here foresters were unable to develop reliable management plans as forest stability was constantly threatened. Monocultures were often disturbed, and sometimes even completely destroyed due to wind, snow, insects, and fungi, so the constant flow of desirable wood products was broken. At the end of 19th century only few foresters like K. Gayer, B. Borggreve, L. Hufnagel, etc. (see Mlinsek, 1996) realized that different approach in forest management is needed, if the forests are to be managed in a sustainable long-term way.

Science-based management of forest ecosystems in Central Europe came into view in the period of transition from 19th to 20th century when exploitive harvesting was replaced by silvicultural techniques that aimed at maintaining a constant flow of harvestable products, and which foresters called the sustained yield approach. Just when Bosnia and Herzegovina (BiH) was annexed by Austro-Hungarian empire in 1908, over 50 % of the area in BiH was covered by old-growth forests (Froehlich, 1954). Insufficient forest accessibility was the main cause why these forests had remained intact. There are numerous documents from the Austro-Hungarian period reflecting forest management activities in the area of research, mostly relating to the issue of exploitation of forests (Begovic, 1960, 1978). However, very few papers relate to the issue of forest structure, composition and natural regeneration of mixed beech-fir-spruce forests providing only for indirect inference about it. What is known is that their main feature was very high share of very thick and over-mature trees, which however had poor quality. Due to poor forest road network at the time, the conversion of these forests into economic form proceeded very slowly. During the Austro-Hungarian Empire in BiH railroads were built, whereas management ranged from clear-cutting in some stands to selection system in the other. However, historical data do not provide comprehensive answer to this question, but current structure in some areas today indicate application of both systems. Intact to this day remained only small complexes of valuable mixed forests in Janj, Lom and Perucica. First sawmill in BiH was started in the year 1889 by German entrepreneur Otto Steinbach, and afterwards many other, of domestic and foreign origin, occurred. Norway spruce (*Picea abies* (L.) Karst) and silver fir (*Abies alba* Mill.) were target species for cutting since wood processing technologies at the time were more adapted to conifers. Though beech was considered as undesirable at the time and used mostly for firewood, it was not spared from cutting since it was treated as undesirable species. In some cases cutting intensities were as high as 70 to 80 % considering trees with dbh above 30 cm (Begovic, 1978). This often impaired forming of selection stands. Also Matic (1963) indicated that principles of German classic school of forestry were partly applied in the process of transformation of OG forests into managed forests or cutting intensities were so high that they led to degradation of forest stands. The negative effects were alike those seen in Central Europe. Following World War II clearcut-plant system was also applied; however, as time went the sustained yield approach and selection system application in forests composed of shade-tolerant species were gaining more and more attention by Bosnian foresters. This management system is today the most preferred by foresters in BiH. Regulation of species composition and tending below inventory threshold (7 cm dbh) is not performed, which means that regeneration develops "freely". However, it is important to emphasize that within plenter system in Bosnian forests not only mature but also young beech trees having 7-25(30) cm dbh are often used for firewood (Figure 1).

Figure 1. Utilization of young beech trees for firewood in managed beech-fir-spruce forests in study areas.

In some countries in Central Europe quite a lot of attention has been given recently to a „new" approach that is called nature-based silviculture. In the year 1968 professor Mlinsek described a system called "freestyle silvicultural technique" which assumes that forester in his work follows natural processes rather than any other principles. Why? Because naturalness proved to ensure stability. And where this naturalness could have been investigated? Not in managed forests or artificially grown cultures but in virgin forests as they serve as references for studying naturalness, complexity, diversity and stability, and even climate change.

Many genuine foresters are nowadays disposed towards the idea of nature-based silviculture. It is consequently of vital importance for forestry practice to get insight into the structure and development of natural forests. In that sense, forest reserves are justifiably more and more used as reference sites in the process of silvicultural planning as they provide the answer on what is possible and expectable in managed forest if certain structures, species mixtures, and disturbance patterns are followed. Moreover, forest reserves can serve as suitable reference sites when assessing the efficiency of nature-based silviculture.

In BiH, despite the presence of notable areas of virgin forests, nature-based forestry has never gained sufficient attention in its original form as foresters and decision-makers rather stayed loyal to the traditional selection system. Single-tree selection cutting is sometimes believed to be similar to the natural gap disturbance regime, but few studies have specifically compared the compositional and structural characteristics of OG stands, undergoing natural gap dynamics and stands previously subjected to partial cuts (Boncina, 2000; Angers *et al.*, 2005). Though selection system has provided sustained yield so far, following the Rio summit in 1992 the sustained yield approach has been widely replaced by concern over sustainability of the entire ecological system, consisting of ecosystem structures, functions, goods and services (Kimmins *et al*., 2007). Since nowadays forest managers are facing old and new demands, the old approach may be relevant to some areas and irrelevant to some other. Therefore, nature-based silviculture comes in play as case specific because its principles may differ from place to place, and from site to site. Due to this fact, comparison of live as well as dead dendromass structure, species diversity and ecological conditions (especially light conditions) between a virgin forest and adjacent managed forest can give answer to what extent and if at all the applied system goes along with nature or not. By doing so new conclusions come to the table. The solutions to mentioned problems within silviculture include: (1) improvement of traditional tending and (2) development of new silvicultural models; consequently, the existing silvicultural models can be improved with consistent use of all processes compatible with our aims, and the so called employment of "natural automation" (Schütz, 1999; Diaci, 2006).

Concrete problems arise owing to the lack of natural forest remnants, which often inhibits management planning based on comparison between managed and unmanaged forests. Therefore, it has become desirable from a scientific and practical point of view to partly embed nature conservation into forest management so that sufficient information on similarities and differences between managed and unmanaged forests can be drawn and used for better planning of silvicultural activities. However, it is necessary to be rational with demands regarding total conservation. Because total protection only secures a certain number of habitats and rare species at a very local scale, silviculture is essential for maintaining large-scale biodiversity in production forests, regionally (Parviainen, 1999). This author set an interesting hypothesis, namely, that more natural management activities are in production forests, the less there is a need for total conservation of forests. This question encompasses not only biodiversity but also climate change and sustainable wood production. So, whenever there is necessity to reconcile different views, the best answer on how to manage forest ecosystems in a sustainable manner seems to come from comparison of managed and unmanaged forests.

1.1 EXPECTED RESULTS

The goals of this research are to provide better understanding of structure, dynamics, and developmental stages of virgin forests Janj and Lom and comparable managed forest stands. As significant data was already collected from virgin forest Lom, the new task was to depict and compare managed stands with virgin forests in terms of live and dead dendromass structure, regeneration, light conditions, ground vegetation, etc. This type of research that is based on comparison of managed and unmanaged forests was carried out for the first time in BiH. Coexistence of beech and fir was partly explained in previous studies; however, the puzzle for forest managers seems to be even more complex in higher altitudes where European beech and silver fir are usually accompanied by Norway spruce. The results of research shall contribute to a better understanding of the ecology and coexistence of these tree species and other species, such as sycamore maple (*Acer pseudoplatanus* L.), especially because these species play a major ecological and economic role in forests of the Republic of Srpska (BiH), as well as in some other countries of south-eastern and central Europe.

There is a lack of comparative type of (managed *vs.* unmanaged forests) research, and thus we are currently lacking the knowledge on natural development of virgin forests as well as differences between nature-based and selection silviculture. Since we are on the look for sustainable solutions, the overall goal of this dissertation is actually to diminish the lack of knowledge. As it is known, certain level of coarse woody debris storage is a requirement for close-to-nature forest management and certification of forests, so the comparable research can certainly contribute to better management of live dendro-mass and coarse woody debris. The results shall finally show the similarities and differences between managed and OG forests in terms of diameter distributions, light regime, ground vegetation and tree species composition. Consequently, the proposals for forestry practice shall be given on how natural features of self-sufficient virgin forests can be transferred through silvicultural practice into managed forests.

2 REVIEW OF PUBLISHED PAPERS

2.1 STAND STRUCTURES AND MIXTURES

Mixed forests of beech, fir and spruce forests occupy an area of about 220 000 ha or 47.0 % of the total growing stock of high forests in the Republic of Srpska (the entity in BiH in which study areas are located). Most of the research in mixed stands of beech, fir and spruce in BiH was related to the application of management systems encompassing elements of structure and productivity of stands (Matic, 1963; Drinic, 1984; Pintaric, 1991; Stojanovic and Krstic, 2000). Most authors in their research point out a huge variety of site and stand conditions in these mixed forests. The studied stands were found out to be characterized by different structural forms, which range from selection, over varied uneven-aged forms to even-aged stands. The latter usually appear where dominance of spruce was pronounced. Stefanovic (1981) observed that classical selection system did not fit in these mixed forests, hence especially spruce regeneration was afflicted. Stojanovic and Krstic (2000) came to the same conclusion as regards spruce, and thus pointed out that the renewal through group selection cutting could be more convenient approach that can provide abundant regeneration of all constituent species.

According to Mlinsek (1999) virgin forest as a teacher is the approach that takes effort to be promoted, not only among scientists, forest managers and decision-makers, but also among broader civil communities. Nature-based silviculture and forest planning that conserve natural stand dynamics, respect the local site conditions, monitor forest ecosystems and their conservation status, and harmonize suitable measures addressed to management objectives and nature conservation standards are crucial for integrating nature conservation into forest management (Boncina, 2011). However, due to very restricted areas of forest reserves in Europe investigations on nature-based silviculture have been more rarity than rule. Several articles on virgin forests of BiH date back as to mid 20th century (Drinic, 1956; Fukarek *et al*., 1958; Manuseva *et al*., 1967) but, the issues in domestic forestry at that time differed from current challenges, so new studies seem to be a necessity. After disastrous consequences that followed application of clear cuttings all across Europe, many forest scientists shifted their work toward the research on suitability of silvicultural systems in varied forest types. One answer to previous mistakes is selection (plenter) system as it allows for demographic sustainability on a very small scale, namely on a stand level. Demographic sustainability is achieved when an adequate (i.e. balanced) distribution of trees over diameter class is established in relation to growth and disappearance (mortality) rates; however, these structures appear only temporary and are not naturally sustainable in the long run (Schütz, 2001). For example, in primeval beech-fir forests, typical selection stand structures appear to be relatively infrequent, comprising at most 14 % of the forest area (Schrempf, 1986). As a general rule, selection silviculture is a man-made system, which needs either man's intervention in the form of structure regulation, or spontaneous small scale natural disturbances to maintain it in the long run (Schütz, 2001).

In uneven-aged silviculture, diameter frequency distributions have been the most common technique for describing stand structure (O'Hara and Gersonde, 2004). Spatiotemporal changes in diameter distributions are important in old-growth research since they help to trace past disturbances; understand regeneration, growth and mortality patterns; predict future development of stands and reveal the competitive relationship between tree species (Goff and West, 1975; Aldrich *et al.*, 2005; Diaci *et al.*, 2011). Namely, in tree populations, size, social status and age considerably influence demographic processes. For dbh distributions of OG forests close to their demographic equilibrium, several shapes can be characteristic (Leak, 1996; Shimano, 2000; Schwartz *et al.* (2005), Westphal, *et al.*, 2006): negative exponential, negative power function, increasing-*q* and rotated sigmoid. Increasing-*q* and rotated sigmoid shapes could indicate past disturbances or management (Leak, 1996), while UNI shape indicates heavier disturbance or succession (Aldrich *et al.*, 2005; Janowiak *et al.*, 2008). OG stands are often composed of several species, which may add to the complexity of distribution shapes (Diaci *et al.*, 2011). Detailed descriptions of diameter distributions comparing managed and unmanaged forests were given in the articles by Janowiak *et al.* (2008) and Schwartz *et al.* (2005).

Though many scientist realized importance of virgin forests, the research related to comparison between virgin forests and surrounding managed forests for the purpose of testing suitability of selection system and its adjustment to natural processes gained real momentum in the period of transition from 20th to 21th century. This type of research in BiH was conducted only by Govedar (2005) including virgin forests Janj and Lom and surrounding managed fir-spruce forests. This author used permanent field plots of 0.6 ha, one in each chosen managed stand, and by one plot 1.0 ha in size in each of OG forests. The results related mostly to live dendromass structure and forest productivity. Useful information was gathered for OG forests Janj and Lom as well, however, sampling pattern did not provide generalization of data for the whole areas of OG forests. Older research in Janj carried out by Drinic (1956) and newer research by Govedar (2002, 2003) showed significant increase of live wood volume during this period. Some other authors also surveyed virgin forests Janj and Lom (Maunaga *et al.*, 2005; Koprivica, 2006) but these examinations were focused mostly on structural elements, while ecological features were left out. On the other hand, Bucalo *et al.* (2008) made comprehensive phytocenological description of virgin forest Lom but the study did not include live and dead dendromass structure, light conditions, gap fraction, etc., so the interactions between mentioned elements were not examined.

Interesting observations were also made in Rajhenavski Rog, Slovenia. OGF Rajhenavski Rog went through major structural and compositional changes in the last 50 years. Changes in diameter structure, tree species composition, abundance and mixture of regeneration, as well as stand texture are typical of the natural stand dynamics of many silver fir-beech forests. However, it is interesting that in the observed period, the growing stock in Rajhenavski Rog remained high, and also the light levels at 2.5 m above ground stayed comparatively low. This was a result of reaction of canopy trees to silver fir decrease and recruitment of advance beech regeneration into the subcanopy. As a consequence, less shade-tolerant (e.g., *A. pseudoplatanus* L.) were not allowed to develop in the forest subcanopy and canopy strata. After 50 years of development, the overall density was slightly higher for trees with a dbh below 15 cm and above 65 cm, whereas there was a dramatic loss of trees with dbh between 15 and 65 cm. A strong decrease in the number of silver fir with dbh up to 75 cm was found, whereas two small increases were noted above this diameter. On the other hand, there was a sharp increase in beech with dbh up to 25 cm, whereas trees between 25 and 60 cm dbh showed a small decrease, and larger diameter trees increased slightly. The severe reduction of silver fir density up to 70 cm dbh with the peak of mortality in the period 1976–1985 can be attributed to air pollution, especially SO_2 emissions. Besides, silver fir decline linked with high browsing pressure has shifted the species composition in the last 50 years significantly towards beech. Due to the highly unbalanced species ratio in the height and dbh distribution of silver fir and beech, further replacement of silver fir with beech can be anticipated (Diaci *et al*., 2011).

However, this asynchronicity of the changes in species composition indicates the importance of additional factors such as reciprocal replacement (Fox 1977) and climate change (Wick and Möhl, 2006; Diaci *et al*., 2008). Fox (1977) stressed the local operational scale of reciprocal replacement (one or few large canopy trees) and the demographic causes - each species inhibits the survival and growth of its own species most severely (autoinhibition). However, the ecophysiological factors, such as the different use of light resources by beech and silver fir, might operate on larger scales. Moreover, synchronous decrease of silver fir in OG forests over larger geographic scales with different impact of air pollution (Diaci *et al*., 2008) might be caused by climate change, as already demonstrated in the past (Wick and Möhl, 2006).

A similar long-term change of silver fir and beech was also recorded in the Carpathians (Vrska *et al*., 2009). The Carpathian study especially emphasized the interaction of forest grazing, reduction of game and litter ranking as factors favoring silver fir in the past. For all the mentioned reasons, the alternation of beech and fir should be understood as a complex process affected by several natural and anthropogenic factors, which work at different spatiotemporal scales.

As regards managed forests useful information was provided for Slovenian Dinaric fir-beech managed forests. Namely, in the last 30 years the share of silver fir in Dinaric silver fir-beech managed forests decreased even more intensely if compared with the old-growth forest remnant – from 50 to 32 % of the total growing stock (Poljanec *et al*., 2009). Although the forests seem stable and they would function without silver fir, a further decrease of silver fir should be avoided for a variety of economic, ecological and cultural reasons. To ensure the preservation of silver fir, recent adaptive management should be improved with conservation strategies. The main task is to increase recruitment of silver fir in forest stands. Studies in Slovenia showed that germination of silver fir in the Dinaric region was successful (Rozenbergar *et al*., 2007), but later, it was completely removed from the regeneration (above 0.5 m) due to deer browsing, whereas in fenced areas, it recruits permanently in the stand canopy (Jarni *et al*., 2004). Diaci *et al*. (2010) suggested that in conditions with low light availability over a longer period (more than 30 years) and consequently slow growth in height, silver fir is more competitive than beech. Besides, favoring large diameter silver firs as target trees could be an additional measure to increase the portion of silver fir in forest stands and thus mimicking its natural superiority over beech regarding height and age.

In BiH remarkable scientific attention was given to the ecological studies of virgin forests Lom and Perucica (e.g. Nagel and Svoboda, 2008; Nagel *et al*., 2010; Motta *et al*., 2011). It was found out that in Lom endogenous small-scale disturbances determine dynamics of the forest (Motta *et al*., 2011). So, beside structural features Motta *et al*. (2011) included also some ecological examination of the mixed *Piceo–Abieti–Fagetum* Lom forest reserve in BiH. The authors described the structural characteristics and their range of variability, analyzed gap size and gap fraction, reconstructed age structure and disturbance history. There were large (up to 120 cm diameter at breast height) and very old trees (above 400 years). Number and size of stumps and other dead wood served also as a good indicator of disturbance processes.

While in Perucica intermediate disturbances caused by wind have played significant role in natural development of Perucica forest (Nagel and Svoboda, 2008), the disturbance patterns in Lom have been characterized by single-tree or small group mortality (Motta *et al*., 2011; Garbarino *et al*., 2012). On the other hand, just as disturbance is a source of heterogeneity, endogenous factors may also generate niches within a forest community. An example of this includes the small-scale interactions of canopy trees in forests known as "neighborhood effects". Frelich and Reich (1999) define neighborhood effects as processes regulated by canopy trees that affect the replacement probability by the same or other species at the time of canopy mortality. Neighborhood effects include processes such as the influence of the canopy on light transmission (Canham *et al*., 1994) and soil characteristics and nutrient availability (Mladenoff, 1987). Such processes can lead toward reciprocal, random, or self replacement of different species in the canopy and may also play a role in coexistence (Fox, 1977; Woods, 1984).

How different tree species coexist remains an interesting question in many forest ecosystems, especially because knowledge about tree coexistence is crucial for understanding forest dynamics, as well as for successful forest management. Explaining coexistence is particularly challenging for tree species that have considerable niche overlap. A prime example of such coexistence is found in the forests dominated by silver fir and European beech that cover much of central and southeastern Europe, including BiH. Beech and fir are highly shade tolerant species and have similar life history traits, while spruce has somewhat lower threshold of tolerance and sycamore maple the lowest. Therefore, Bosnian OG and managed forests provide a valuable opportunity to study coexistence of tree species that have different shade-tolerance levels. Both exogenous and endogenous processes provide explanations of tree coexistence, and both processes may operate simultaneously in a forest. In this study neighborhood (endogenous) effects are given advantage over disturbance (exogenous) effects since the latter have been studied more intensively in Bosnian OG forests by several other authors (Nagel *et al*., 2010; Motta *et al*., 2011; Rozenbergar, 2012).

Consequently, it is important to notice that structure of virgin forest stands is not constant, unchanging or in the state of balance. We speak about certain intervals, within which stand structure changes (Boncina, 1999). Data from virgin forest Lom can be effectively used for comparison with virgin forest Janj as ecological characteristics and species composition are very similar. Although they are relatively close to each other, slight difference in climatic conditions may exist as well, but no thorough study on that has been conducted due to lack of meteorological data. The only apparent difference is related to bedrock material since dolomite without rocky outcrops underlies OGF Janj and limestone with abundunt rocky outcrops underlies OGF Lom.

2.2 REGENERATION AND LIGHT CONDITIONS

Significant research results emanate also from virgin forests in Slovenia (Mlinsek *et al*. 1980; Diaci and Boncina, 1998; Boncina, 2000; Nagel and Diaci, 2006; Rozenbergar *et al*., 2007; Diaci *et al*., 2010) and Croatia (Mikac *et al*. 2007; Anic and Mikac, 2008). However, ecological characteristics and abundance of ungulates, especially in Slovenia, do not allow direct transfer of conclusions into management of Bosnian forests. Nevertheless, results from different Dinaric virgin forests are highly useful for comparison in order to identify similarities and differences, as well as obstacles and opportunities in their natural development. In the 1970's a net of forest reserves was established in Slovenia (Mlinsek *et al*. 1980), and methodologies for monitoring forest development in strict forest reserves concerning modern demands towards forestry were proposed by Diaci *et al.* (2006). Diaci and Boncina (1998) presented the basic features of stand gaps and regeneration of natural stands of Dinaric fir-beech primeval forests. Boncina (2000) carried out comparative research between Dinaric fir-beech virgin forest Rajhenavski Rog and managed forests in the close vicinity. The author compared the structure of forest stands, and the diversity of plant and bird species.

Storm wind damage in fir-beech remnants of primeval forests was studied by Nagel and Diaci (2006). Diaci and Kozjek (2005) examined the effect of canopy shading on beech sapling architecture in the OG silver fir-beech forests of Pecka and Rajhenavski Rog and the results showed a negative effect of high canopy shading (estimated relative light intensity was below 5 %) on the architectural quality of saplings. In most cases under the shade the most important factor for survival is light, so the species that can tolerate lack of light for prolonged period of time are called shade-tolerant species. However, increase of beech photosynthesis intensity is explainable only to a certain extent by the increase of light (Barnes *et al*., 1998).

Light is not the only factor that affects the survival of trees in the understory. Some studies have shown that only 2 % of relative light is sufficient for early growth of beech under canopy (Madsen, 1994; Rozenbergar, 2007). For example, Madsen and Hahn (2008) indicate that light was significant for height growth of sycamore maple seedlings, while beech was even negatively influenced by increased light. Carbohydrates produced in the process of photosynthesis trees use by priority. In the first place trees use carbohydrates for oxidation which is essential process for tree survival. The second is the restoration of roots and leaf area, then height growth, all of which enable smooth photosynthesis. Production of phloem and xylem is only on the fourth place because it depends on many factors, and thus it may be bolstered with varied silvicultural measures (Smith *et al*., 1997). Height growth at high light is much less intensive at low than at high water availability (Wagner *et al*., 2011) and growth responses after changes in light availability also depend on water availability (Madsen, 1994). Therefore, probably in most cases of importance is combination of factors, including also soil moisture, the presence of nutrients, temperature, humidity, the presence of CO_2, especially when plants are approaching minimum values of each factor that is necessary for their survival (Barnes *et al*., 1998).

The proportion of live crown of the tree is the ratio between photosynthetic and non-photosynthetic area of trees, usually regardless of age. Smith *et al*. (1997) indicate that live crown ratio that is less than 30 %, and especially when less than 20 % leads to decreased production of dendromass, which consequently afflicts height and dbh diameter increment. In cases when live crown ratio is even smaller, trees react with delay to increased light radiation or don't react at all (Rozenbergar, 2007). In determining how much growth space has a tree, it is helpful to assess light that is available to understory trees as it is often a limiting factor for their development, and also to determine basal area of surrounding trees (Lieffers *et al*., 1999). Crown length is generally small in low light conditions for shade-tolerant species, but should be in the same situation even smaller in shade-intolerant species whose lower branches are not viable. Accordingly, Norway spruce should have smaller live crown ratio than silver fir and European beech when light conditions are very low, however, this was not confirmed in the study performed by Stancioiu and O'Hara (2006b).

In the mountain fir-beech-spruce forests that have basal area around 30 m^2/ha and where transmitted scattered light ranges between 20–35 %, regeneration density and competition is high. In these types of situations shade-tolerant species have advantage. If young beech and fir make their way to the upper layer, then spruce remains sub-dominant. Spruce is able to sustain low light conditions for a while, however, it is not able to react fast enough to introduced higher level of solar radiation if too long remained in heavy shade. In better light conditions with light values in the interval 35–70 % and basal area 15–35 m^2/ha silver fir has the most intense height and volume growth. Where light reaches values 80–90 % and where basal area is smaller, all three species exhibit similar growth intensity. Fir shows slow growth at the maximum light values. Even when previously shaded regeneration is released from canopy trees, significant differences regarding growth were not determined between shade-tolerant fir, beech and spruce (Stancioiu and O'Hara, 2006c).

Shade-tolerant species pass during their development through different light conditions. Periods of crown cover and released growth over the life of the tree changes several times. The different physiological mechanisms of tree species minimize consumption and optimize production in poor growing conditions. Research in the northeastern U.S. have confirmed that with increasing shade-tolerance in species the growth of trees is slower in good light conditions, while increasing the probability of survival in low light conditions (Kobe *et al*., 1995). Similar results were observed by researchers in Germany, where the analysis of the effects of shading on the growth of beech, ash and sycamore maple showed that beech has the highest probability of survival in low light conditions, however, it has slowest height growth in good light conditions. At 15 % of relative diffused light, the probability of dying of all observed species was close to 0 (Petritan *et al*., 2007).

In the forests of the eastern part of the United States it was found that 80 % of beech trees survived growth period in understory before they established themselves in the upper layer, while the proportion of maple was only 20 % (Canham, 1985, 1990). For example, Cao and Ohkubo (1999) found that for beech the longest duration of crown cover was 90 years and for maple 55 years, hence beech proved to survive longer periods of shady conditions than maple.

When comparing managed and OG forests, the average light availability at the forest floor does not seem to differ between OG and secondary growth forests (Messier *et al*., 2009), and although unmanaged forests sustain natural processes, biodiversity – expressed as species richness – is not necessarily higher in unmanaged compared to managed forests. This, however, may be a matter of scale (Schulze *et al*., 2009). Diaci *et al*. (2005) carried out a survey in which they established links between the light conditions in gaps and regeneration, and compared these correlations between the managed and unmanaged forests. Research shows the differences in light conditions between gaps in managed and unmanaged forests (higher values in managed forests), despite the fact that the gaps were similar in size.

Rozenbergar *et al*. (2007) examined the growth of young beech and fir trees depending on light conditions in Rajhenavski Rog and Corkova uvala. While there was more woody regeneration and an almost fivefold higher average total regeneration density in Rajhenavski Rog, mainly due to a high density of beech, there was more ground vegetation and a higher density of silver fir seedlings in Corkova Uvala. There was no significant difference in density of large-beech seedlings among the microsites within gaps, yet height and height increment were higher on microsites receiving the highest levels of direct and diffuse radiation. The authors attribute the dominance of beech to browsing damage on silver fir. However, this might not be the only reason as the results from virgin forest Perucica indicate beech dominance in understory (Nagel *et al*., 2010), and ungulates do not make significant browsing damage in this virgin forest.

Understanding the coexistence of silver fir and European beech is rather challenging given that both species have similar life history attributes. During early life stages, both are highly shade tolerant (Ellenberg, 1988), and seedlings of both species establish on a variety of microsite conditions (Szewczyk and Szwagrzyk, 1996). Interspecific differences in shade tolerance may be more pronounced at the pole-sized tree stage, because the ratio of photosynthetic to non-photosynthetic biomass decreases with increasing plant size (Givnish, 1988). Therefore, it is likely that pole-sized trees are only able to recruit to larger stages if sufficient light is available, which is not only dependent on gap size, but also the spatial and temporal pattern of gap formation (Canham, 1989).

Nagel *et al*. (2010) obtained results which indicate that the gap-filling process in Perucica is mainly controlled by advance regeneration rather than post-treefall establishment of seedlings. They also found that the density of the dominant species remained similar between gaps and the forest as a whole across the seedling, sapling, and pole tree life stages, although authors expected higher densities at larger life stages in gaps because of the prediction that growth into larger life stages requires more light (Givnish, 1988). In that study of Perucica, gap size had little influence on the occurrence of shade tolerant beech and fir because they were already established prior to gap formation. Seedlings, saplings, and pole-sized trees of both species occurred across the entire size range of gaps encountered in the study.

However, Nagel *et al*. (2010) did find that the density of pole-sized beech gapfillers increased with gap size, indicating that recruitment to larger life stages is more successful in larger gaps. Of the dominant species, only sycamore maple showed compelling evidence of gap-size partitioning. The density of maple regeneration increased with gap size for all three life stages, and recruitment into pole-sized trees only occurred in gaps > 440 m^2. These results also provide insight into the different life history strategies of the studied tree species. For example, the increased gap capture by fir at larger life stages may reflect its ability to survive longer periods of suppression than beech, resulting in a pool of pole-sized fir to capture gaps after they form. An alternative explanation is that the present pool of pole-sized fir in the study area is a legacy of past conditions when regeneration opportunities were favorable. When transition probabilities were calculated by gap-size class, the only notable trend was that pole-sized beech showed increased gap capture in large gaps, while the opposite trend was found for silver fir. These results again suggest that beech recruits to the pole stage more successfully in large gaps, while fir is better equipped to tolerate the lower light levels at this stage in small gaps.

Nevertheless, there was evidence that the predominance of beech and lack of fir in the regeneration layer is not a recent, temporary pattern. Old inventories from Perucica also documented a general pattern of abundant beech and scarce fir regeneration (Fukarek, 1970; Pintaric, 1978). According to older studies in Janj (Drinic, 1956) and sequential management documents, similar pattern of beech dominance in understory was found in OGF Janj as well. A lack of fir regeneration reported in other beech-fir forests in the northern Dinaric mountains was primarily attributed to high browsing pressure by large herbivores, particularly red deer (*Cervus elaphus* L.) (Klopcic *et al*., 2010; Rozenbergar *et al*., 2007).

Although few studies have examined growth rates of fir and beech in different light conditions during early life stages, there is evidence that beech has faster growth rates than fir over a range of light conditions, particularly at higher light levels (see Stancioiu and O'Hara, 2006b). Furthermore, saplings and pole-sized trees of silver fir can survive in a suppressed conditions under the canopy and slowly increase in height over very long periods (Mayer, 1984). The replacement probability analyses by Nagel *et al*. (2010) indirectly suggested that beech survives for a shorter period under the canopy during the pole stage, which could be due to a decrease in shade tolerance with increasing plant size.

Thus, it is possible that differences in tradeoffs between survival and growth over different light conditions, particularly for pole-sized trees, may promote coexistence of both species (Kobe *et al*., 1995). Variation in the frequency and severity of gap disturbances could then promote coexistence. For example, during periods of infrequent, low intensity disturbances, fir would benefit because of its ability to tolerate long periods of suppression, while periods with higher rates of disturbance would favor beech because of its ability to outperform fir in more lit conditions (Nagel *et al*., 2010).

By looking at older studies, domination of *Fagus sylvatica* in forest understory was also reported by several authors (Safar, 1953, 1965; Mlinsek, 1967a). In Slovenian virgin forests beech appears abundantly in groups, while silver fir occurs individually or in smaller groups (Mlinsek, 1967a). Some authors indicate that fir and beech tend to replace each other in OG forests of the Dinaric mountains (Pintaric, 1978; Prpic *et al*., 2001; Govedar, 2005), but some older data from Perucica and Janj also indicate dominance of beech in the understory over fir regeneration (Fukarek, 1970; Drinic, 1956). Nagel *et al.* (2010) did not determine strong trend toward self- or reciprocal replacement for beech and fir at the seedling and sapling stages. For pole-sized trees and definitive gapfillers, authors found higher probabilities of reciprocal replacement, although self-replacement was also relatively common. Diaci *et al*. (2010) observed that alternation of fir and beech in

Rajhenavski Rog often developed asynchronously, regardless of ungulate density. After all, it seems that answer to this question requires long-term monitoring including even analysis of climate change in studied areas.

3 THE RESEARCH HYPOTHESES

- Light conditions:
    - in managed forests mean values of direct and diffuse radiation in the ground layer are higher than in OG forests,
    - variability of light conditions is greater in managed forests than in OG forests.
- Regeneration
    - in managed forests the cover of ground vegetation and regeneration density are higher than in OG forests,
    - there are no significant differences in mixture, growth and quality of seedlings between OG forests and managed forests.
- Stand structures and mixtures:
    - in OG forests there are significantly more large trees (>50 cm) in both categories – live and standing dead trees,
    - between OG forests and managed forests there are no significant differences in the amount of small and medium-sized woody debris,
    - managed forests feature less variability and diversity in terms of stand structural characteristics (diameter and tree height, density, species mixture, stratification),
    - distribution of dbh diameters in OG forests and managed forests differ significantly,
    - dbh structure of natural mortality in OG forests is significantly different from dbh structure that is cut in managed forests.
- The texture of the forest
    - OG forests have smaller overall gap fraction than managed forests.

4 STUDY SITE AND METHODOLOGY

4.1 DESCRIPTION OF THE STUDY SITE

The research was conducted in virgin forests Janj and Lom, and ten managed forest stands (Table 1). Among those managed stands five of them (31a, 50d, 56, 57/1b, 58a) were chosen on the comparable basis in the close proximity of virgin forest Janj. Another five managed stands (59a, 67a, 68a, 76a, 79a) were surveyed on comparable basis as well in the close proximity of virgin forest Lom which has been intensively investigated in the past few years (Govedar 2005; Lingua *et al.*, 2010; Motta *et al*., 2011; Garbarino *et al*., 2012). Data for OGF Lom were gathered and analyzed in cooperation with prof. dr. Renzo Motta. All research sites were classified as forest association *Piceo-Abieti-Fagetum illyricum* (*dinaricum*), whereas noble broadleaves and other species make only small share. The criterions for choosing managed stands were: the environmental characteristics (site conditions, aspect, etc.) of managed stands had to be similar to that of virgin forests, the cutting intensity of latest cut was typical for selection system (it did not generally exceed 20 % of the growing stock), and last cut was carried out at least four years before field work.

Virgin forest Janj was protected since 1954 by the decision of the State Institute for protection of cultural monuments and natural rarities in BiH. It is believed that even before the official protection of OGF Janj, this forest had not been exposed to logging activities. Unlike most of European OG forests, OGF Janj is a unique site for studying natural regeneration processes since the impact of ungulates has not been reported very significant in previous studies.

Original purpose of the reserve is to serve primarily as an object for scientific research. Due to its inaccessibility forest reserve Janj has also remained undisturbed by human activities. However, the same reason along with some adverse circumstances (economic crisis, war, etc.) yielded only few scientific studies from OGF Janj. In this old-growth forest there is distinguished core area (57.2 ha) which has been strictly protected. The core area is surrounded with buffer zone that has total area of 237.8 ha. In buffer zone only low-intensity cuttings have been performed, mostly in the form of salvage cuttings. Geographic position of this old-growth forest is 44°08’ N, 17°17’ E. Mean annual precipitation is about 1200 mm, while mean annual temperature amounts to 5 °C.

Table 1. Study site characteristics of OG forests Janj and Lom and neighboring managed stands.

Research objects	Altitude (m a.s.l.)	Inclination (°)	Exposure	Bedrock	Soil type	Rocky outcrops (%)	Soil humidity
OGF Janj	1240-1400	0-10	north-western	dolomite	brown soil and rendzina	0	medium
Janj stand 31a	1300-1400	5-10	north-eastern	dolomite and limestone	deep brown soil	0-5	medium
Janj stand 50d	1250-1365	10	north-western	dolomite and limestone	deep brown soil	0-5	medium
Janj stand 56	1250-1372	5	virtually even terrain	dolomite and limestone	deep brown soil and rendzina	0-10	dry-medium humid
Janj stand 57/1b	1250-1380	5-10	north-eastern	dolomite and limestone	deep brown soil and rendzina	0-10	dry-medium humid
Janj stand 58a	1250-1376	5-10	north-eastern	dolomite and limestone	deep brown soil	0-5	dry-medium humid
OGF Lom	1250-1522	5-10	northern	limestone	deep and shallow brown soils	15	medium
Lom stand 59a	1000	4-7	north-western	mostly limestone	deep brown soil	0-5	medium
Lom stand 67a	1000	5-10	north-eastern	limestone and dolomite	deep brown soil	0	medium
Lom stand 68a	1040	5-10	north-eastern	limestone and dolomite	deep brown soil	0	medium
Lom stand 76a	1100-1350	5-7	north-eastern	limestone and dolomite	deep and shallow brown soils	5-10	medium
Lom stand 79a	1100-1450	15	north-western	limestone and dolomite	deep and shallow brown soils	0-5	medium

OGF Lom was established as protected reserve in 1956. This reserve belongs to management area Lom-Klekovaca, near to Drinic. Its geographic position is 44°27’ N, 16°27’ E. Mean annual precipitation in Lom amounts to 1600 mm, while mean annual temperature is approximately 3.5 °C (Maunaga *et al.*, 2005). Smaller intrusions and illegal loggings of individual trees here and there were noticed, however, this did not make significant change in the nature of this old-growth forest.

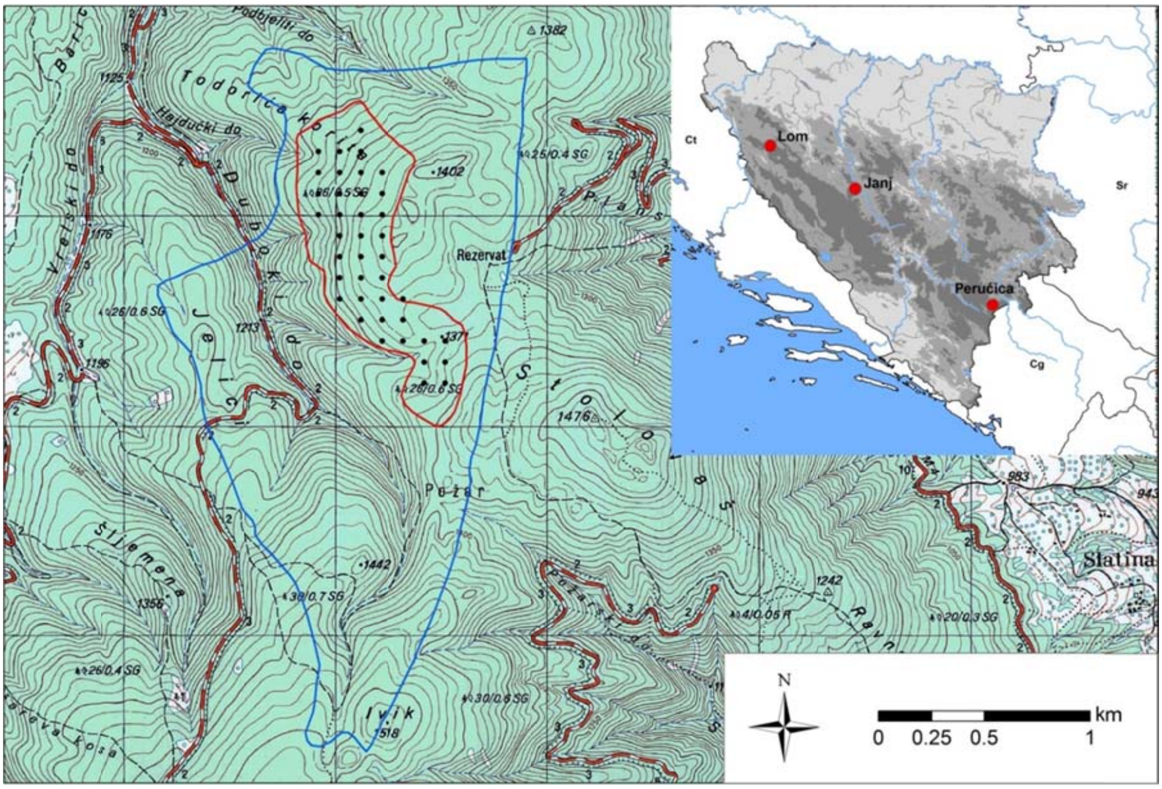


Figure 2. Buffer zone and core area with the research plot network in OGF Janj. Insertion at the upper right-hand side of the picture represents geographic locations of OG forests Lom, Janj and Perucica in BiH.

4.2 SAMPLING AND MEASUREMENTS

Regular 100 m grids in the core areas of OG forests Janj and Lom were superimposed resulting in 40 sampling plots in each of them (Figure 2). In five managed stands that are located close to virgin forest Janj we laid 60 sampling plots over the area (12 in each stand). The same number of sampling plots was laid over in five managed stands in close proximity of virgin forest Lom, so the total in managed forests was 120 sampling plots. Centers of plots in managed forests were at least 25 m away from nearest tractor road. The measurements regarding dbh, tree heights, regeneration characteristics, CWD, and phyto-sociological records, were carried out in the same way in managed and unmanaged forests. Field work was carried out in years 2011 and 2012.

4.2.1 Diameter inventory and height curves

For the purpose of defining stand structure in this study the inventory threshold of 7.5 cm dbh was used meaning that on each sampling plot following inventories were carried out: in a 452 m^2 circular plot (radius = 12 m) species dbh (to the nearest 1.00 cm) for all living trees above 7.5 cm were measured. For evaluation of site quality of multi-layered forest stands many authors find correlation between age and height of no great importance (Flury, 1929; Miletic, 1950; Matic, 1980). Therefore, correlation of dbh and height was taken as more reliable indicator in such stands (Bankovic and Pantic, 2006). Height of trees expressed by functional connections with diameter at breast height is nowadays in BiH considered best indicator of productivity in multi-layered forests. All diameter classes are not equally suitable for determination of site quality (Miletic, 1950; Bankovic and Pantic, 2006). The trees in thinner diameter classes are not favorable indicators of site conditions since in selection forest trees which belong to the lower story of the stand are overshadowed, and thus among them there is no significant difference in heights. It is therefore more appropriate to use higher and thicker trees in order to determine site quality and stand productivity. For site quality evaluation trees that belong to dbh classes above 37.5 cm are considered as relevant (Miletic, 1950). In this study heights of living trees were measured with Vertex IV to the nearest 0.5 m for a sample of 100 trees for each species (spruce, fir, and beech). These data were used for evaluation of site quality as described in Matic (1980).

4.2.2 Measurements of regeneration, transmitted light and phyto-sociological records

Regeneration individuals were tallied in a 78.5 m^2 round plots (radius = 5 m) whereas species were distinguished and separated in different columns. The size of tallied regeneration ranged from height > 10 cm up to dbh < 7.5 cm. Within each large plot on two subplots of 2.25 m^2 (1.5 x 1.5 m) hemispherical photographs were taken and all seedlings smaller than 10 cm in height were counted. The two subplots were set exactly where smaller plot with r = 5 m intercepts the transect within large r = 12 m plots (Figures 3 and 4).

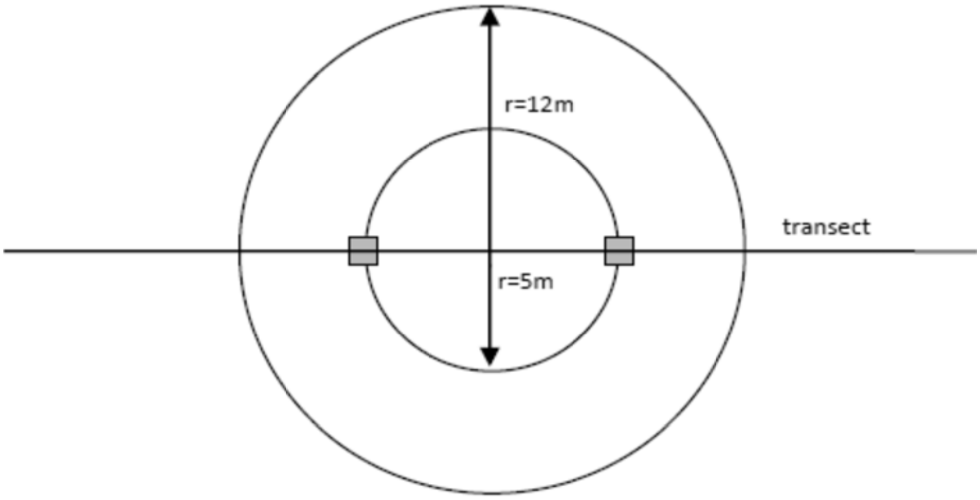


Figure 3. Outline of sample plot and subplots.

At first it was intended to register browsing damage, but field reconnaissance showed no need for it as regeneration was very rarely browsed. The large majority of measured individuals were vital and had mostly straight growth form of terminal shoots. For these sub-plots phyto-sociological records were made, and following characteristics of three most dominant regeneration individuals were determined: height; the length of the stem to the crown (the first living branch); the total length in beech; the length of the last three height increments; average length of lateral shoots below apical shoot in conifers. The most dominant regeneration individuals were considered those with highest probability of survival on the given subplot (in most cases the highest individuals). They had to be higher than 10 cm, but not higher than 130 cm due to position of a fish-eye lens. Measurements pertained to beech, fir and spruce regeneration. Although it was planned to measure three dominant individuals of each species, somewhere we encountered plots with rare or absent regeneration. For this reason, initial subplots in some cases had to be extended to the 3 x 3 m subplots. These added or extended subplots were only used for the purpose of examining regression between light regime and regeneration characteristics. Where two or three individuals of the same species were found the average values of measured characteristics were taken into account. However, due to rare density of regeneration in studied forests even after extension, many subplots had only one dominant individual per species. On some subplots regeneration that could be categorized as dominant was completely absent.

Figure 4. One sub-plot 1.5 x 1.5 m marked with wooden frames set in OGF Janj.

4.2.3 Coarse woody debris

Regarding CWD following measurements were carried out: on two 50 m line intersect oriented northward (the first) and eastward (the second) from the centre of the sampling plot, the logs crossing the line were measured (see Van Vagner, 1968); in two 50 x 4 m rectangular plots centered on the previous line stumps (diameter at the ground and at the top) and snags (dbh) were measured. For each element of CWD species (when possible) and decay class (Nagel and Svoboda, 2008) were recorded (class 1 fresh, class 5 very old); coarse woody debris (CWD) was grouped into snags (standing dead trees, dbh ≥ 7.5 cm and height ≥ 1.3 m), downed logs (fallen stems or branches ≥ 7.5 cm diameter and length > 1 m), and stumps (short, vertical remains from cutting or windthrow, top diameter ≥ 7.5 cm and height < 1.30 m). The separation of snags from logs was established at a 45° leaning angle.

4.2.4 Procedure for light intensity assessment

Hemispherical photography method consisted of four stages: taking photographs (field work), followed by image registration and classification, and at the end calculation of results. Registration, classification and calculation were obtained by using designed software GLA 2.0 (Gap Light Analyzer) to process hemispherical photographs. For this study we used Nikon COOLPIX 5000 digital camera equipped with a Nikon FC-E8 fisheye lens (Figure 5). At each plot required recording device was properly positioned in the horizontal and vertical planes at 1.30 m height above the ground. Also, fisheye lens was positioned towards geographic north which comes at the top of the circular image.

Figure 5. Nikon coolpix 5000 digital camera with fisheye lens.

The goal was to obtain high quality hemispherical photograph. Most photographs were taken when the sky was clouded, and less number of photographs were taken shortly after sunset. The original hemispherical images were entered directly from a digital camera to GLA software application. Prior to image registration data on magnetic deviation from the geographical north, the distortion of the data projection (polar projection), latitude, longitude and altitude, were entered into GLA application. The orientation was horizontal. Network sky region was defined with 36 azimuth and 9 zenith regions, while the position of the sun was measured every two minutes through the growing season. Following meteorological data growing season for study area was estimated to last between 1st May to 1st September. For this work solar constant was 1370 W/m^2. Value of Kt (Cloudiness index) was 0.5; and spectral fraction 0.45. Beam fraction was defined as the ratio of direct (beam) to total (global) spectral radiation incident on a horizontal surface at the ground over a specified period. For study area beam fraction was set at 0.6 for the growing season period. The share of diffuse light in total (global) radiation was set at 0.15 for days when sky is clear.

Classification of images included separation of image plane pixels on white (sky) and black pixels (above-ground parts of trees) using appropriate threshold values. Classification of images was relatively simple when the original image had a normal degree of color contrast between the sky and the canopy. Calculation processes provided the results for transmitted direct radiation (DIR), transmitted diffuse light (DIF), total transmitted light, leaf area index (LAI), and percentage of canopy openness. Overall gap fraction was represented as percentage of canopy openness after gap fractions were corrected for area distortions. Since both the gap fraction (ratio of sky pixels to total pixels per sky-region segment) and canopy openness are expressed as fractions, they both can be plotted on the same graph. Canopy openness, however, is most often expressed as a percentage (Frazer *et al*., 1999).

4.2.5 Determination of developmental phases

Six development phases were distinguished: pole phase, optimal early -, optimal middle -, optimal late phase, selection phase, and terminal phase. Early, middle, and late optimal phases are identical to those described in the article by Boncina (2000). Pole phase was broadly characterized by even-aged structure and dominance of young trees with dbh from 7.5 cm to 27.5 cm. Although developmental phases were visually assessed during data collection, subsequent quantification was applied in order to make distinction of phases more palpable. For distinguishing selection phase slightly modified Mitscherlich approach (1952) was used. This approach gave a rough estimate of selection phase, however, it proved to be suitable for small plots as we gained an insight in diameter distribution of each plot. Accordingly, plots on which the number of small trees (7.5–27.5 cm) ranged from 100 to 700, medium trees (27.5–47.5 cm) from 50 to 300, and number of large trees (>47.5 cm) was less than 70, all expressed per hectare, were grouped into selection phase category. Eventually, terminal phase was characterized with large amounts of standing and/or downed CWD.

4.3 DATA ANALYSIS

To determine site quality by tree species we used standardized height curve lines for spruce, fir and beech, which are currently valid in BiH. The standardized height curves were made for five height classes based on extensive research and data collection on temporary experimental plots for major tree species and different site conditions in BiH (Matic, 1980). For the purpose of analyzing height curves and site suitability for each species, Prodan's function was used as it adequately expresses the correlation between dbh and corresponding heights of measured trees. For determining average height of dominant trees, we used heights of 30 tallest trees for each species.

In ground vegetation analysis, species biospectrum and geospectrum were determined sensu Tomic and Sillic (2004). Species biospectrum showes percentage shares of individual life forms (phanerophytes, hemicrypthophytes, etc.) in the composition of plant association, while geospectrum shows percentage shares of vegetationaly and geographicaly related plant groups within given plant association. Further, Landolt phytoindication values for eight factors (Landolt *et al.*, 2010) were assigned to recorded species. In the relevés we determined average conditions in terms of temperature (T), continentality (K), light conditions (L), moisture (M), soil reaction (R), nutrients (N), humus content (H) and aeration (A). In our calculations we used square root of plant coverage proportion (1–100 %) as weight that was reduced by half in phytoindication values with a higher degree of variation (Landolt *et al.*, 2010). Additionally, we calculated the weighted average of the species on the subplots in order to obtain the estimates for plots.

$$WA_{pop} = \frac{\sum_{i=1}^{s}(FV_i \times Abund_i \times VR_i)}{\sum_{i=1}^{s}(Abund_i \times VR_i)} \quad \dots (1)$$

where WA_{pop} is the weighted average of indication values of plant species for an ecological factor on a relevé, FV_i is the phytoindication value of the [i] row factor, $Abund_i$ is cover value of i-th species, VR_i is range of variation of phytoindication value (I = 1, II = 0.5) and S the number of species in a relevé.

In principal coordinates analysis (PCoA) out of 115 registered species only those which were occurring at least on five (sub)plots were selected; as a result, 65 species were used in calculation process. Plots without plant species were excluded from analysis. Bray-Curtis distance measure was used for differentiation among studied forests; thereby, cover of species (%) was reduced with square root. On the first and second axes various parameters were fitted: woody regeneration, ecological variables (direct and diffuse light), Landolt phytoindication values and cover of 65 species.

In order to determine if a species was associated with a site group, it was necessary to conduct a statistical test of the null hypothesis that there was no such relationship. Under this null hypothesis, the fact that the species was observed at a site belonging to the target site group is due to chance only. A permutation test is a procedure that involves comparing an observed test statistic with a distribution obtained by randomly reordering (i.e., permuting) the data. If the null hypothesis of no association is true, the association value computed after randomly reassigning species occurrence or abundance values to sites will be similar or very close to that observed for unpermuted data. The *p*-value of the permutation test of positive (negative) species preference is the proportion of permutations that yielded the same or higher (lower) association values than that observed for the unpermuted data (De Caceres and Legendre, 2009).

For assessing species predictive values like site determination of community types, we computed indicator values as suggested by McGeoch and Chown (1998). The indicator value approach is well suited for analyzing species-habitat associations based on large biological record databases because it provides potentially unique values (De Caceres *et al*., 2008). Therefore, the IndVal index (Dufrene and Legendre, 1997) for determination of indicator species was used in a permutation test.

In order to distinguish between pure (monospecific) and mixed stands there are various definitions of what mixed and pure stands are, and therefore this topic is triggering a lot of discussion on what is the most appropriate definition. In most cases different countries apply different definitions. After studying the literature and searching through forestry dictionaries the most universal seems to be the definition given in The Dictionary of Forestry (1998). The definition says that pure forest stand is principally composed of one species, conventionally at least 80 % based on tree number, basal area, or volume. Therefore, mixed stand is composed of two or more species so that no species has share above 80 %. Consequently, if number of trees or basal area of one species on our plots exceeded 80 % of total tree number or total basal area of the plot, then such plot would be classified as pure plot. On the contrary, if the share of some other species (beside dominant species) was ≥ 20 % then such plot was classified as mixed plot. Those criteria were applied to distinguish between mixed and monospecific sample plots in studied forests whereas sample plots were treated as micro-stands. Since plots were not very large (452 m^2), the information obtained provided an insight into tendency of tree species to blend with each other on relatively small area, or to build monospecific cohorts on the other hand. Differences in tree species composition at different developmental stages were tested with nonparametric two-variable Chi-square test. In this test there were usually three degrees of freedom and alpha level was always set at $\alpha = 0.05$ as it was done for parametric tests.

For each studied stand the results for density of trees (n/ha), basal area (m^2/ha) and growing stock (m^3/ha) are presented in tabular and graphical form. Total volume of living trees (comprising whole stem with branches and twigs) and volume of snags were calculated by using the local volume tables for beech, fir and spruce forests in BiH (Drinic *et al*., 1980).

Statistical analyses of data were conducted in Microsoft Excel Version 2007 and SPSS Statistics Version 17.0. All groups before being tested for differences upon certain characteristics had been first tested for normality of distribution and for homogeneity of variances. Normality of distributions was tested using Shapiro-Wilk test and homogeneity of variances was tested using Levene's test.

For testing of differences between OG forests and whole managed forests independent t-test was applied as sample size was large enough to follow the central limit theorem and consequently apply parametric statistics. On the other hand, if criteria for parametric tests were not fulfilled in terms of distribution normality then Mann-Whitney U test and Kruskal-Wallis tests were applied as proxies for independent t-test and ANOVA respectively. When tested groups (stands) had normal distribution but unequal variances (heteroscedasticity), then robust Welch test was applied instead of ANOVA. In all tests $\alpha = 0.05$ level was used. Tukey HSD post hoc test was used after significant ANOVA results, Games-Howell test after significant Welch results, and multiple pairwise Mann-Whitney U as a post-hoc test after results of Kruskal-Wallis test were significant. The latter results were used for differentiation among single stands and compared to OG forests.

The shape of diameter distributions was analyzed using the methodology presented in Leak (1996) and Janowiak *et al*. (2008). For cumulative dbh frequency distribution and for each tree species a series of multiple regressions between the base 10 logarithm of trees per hectare (dependent variable) and all possible combinations of the dbh class midpoint, the midpoint squared or the midpoint cubed (independent variables) were calculated. The highest adjusted R^2 and lowest root mean square error values were used as a basis for selection of the best-fitting model from all significant models ($p < 0.05$). Based on the sign of the coefficient dbh distribution shapes could be classified into: rotated sigmoid (RS), unimodal (UNI), negative exponential (NE), increasing-*q* (IQ) and concave (CO). If shapes were inconsistent or variable, the second best-fitting model was selected.

Neighborhood effects were analyzed using transition probabilities between distinctive stories within studied forests. Preliminary analysis showed that dividing OGF Janj into understory and upper-story solely, would lead to over-simplification of forest structure, especially in regard to beech dominance in upper-story. Therefore, we compared relative tree species abundance in each sampling plot in four distinctive layers: (1) small seedlings ≤ 10 cm height; (2) regeneration from 10 cm in height to 7.5 cm dbh (understory), (3) small trees with dbh from 7.5 cm to 27.5 cm (middle-story), and (4) canopy trees with dbh over 27.5 cm (upper-story). These results take into account dominance in terms of number of each species individuals on sample plot, whereas different results would probably occur if basal area (BA) or growing stock (GS) would be used as a criterion.

Finally, we created four transition matrices to avoid possible oversimplification of data as advised by White *et al*. (1985). In order to examine patterns of tree species replacement, matrices of transition probabilities were constructed based on the: a) proportions of small seedlings (up to 10 cm high) to regeneration, middlestory and upperstory trees; b) proportions of regeneration to middlestory and upperstory trees; and, c) proportions of middlestory to upperstory trees on each sample plot. Those relative frequencies (proportions) were then averaged across all plots so that eventually average transition probabilities of small seedlings, regeneration and midllestory (small trees) were presented for each studied forest. For OG forests we additionally calculated relative abundances of tree species after 20 generations, after species composition was stabilized, using present abundances and transition probabilities (Stevens, 2009). In these calculations maple was not considered, since it was not present in the middle or upper-story. Due to many assumptions of these models, which were difficult to verify and since we didn't sample regeneration below each tree on sampling plots, we focused only on the most obvious relationships.

Differences in presence of CWD were tested with mentioned parametric and/or non-parametric tests. Distributions of CWD amounts were presented across diameter classes since certain species find their habitat in dead wood of different size, not only the total or average amounts are important but also the information on presence of different size of dead wood. Volumes for logs, stumps and broken snags was calculated according to methods described in Motta *et al*. (2006). In this study we did not investigate the diversity of species which depend on dead wood. The analysis of stumps was difficult because stumps, both in managed and OG forests, were at different stage of decomposition, so very often the yearly rings were not recognizable. Besides, even when there were newer stumps in OG forests their cross-sections were irregular in shape making it impossible to determine the exact time of previous disturbance. Therefore, disturbance intensities were based on ratios between number and BA of all stumps present against number and BA of all living trees present on each plot.

All CWD was grouped into three categories: logs, snags and stumps, and their frequencies are presented graphically across diameter classes in order to compare managed and OG forests. Additionally, CWD amounts in studied OG forests were compared to European average for the same forest type (Christensen *et al*., 2005). In this case we used one-sample t-test since standard error of the mean was not available for European mountain mixed forests of the same type.

Slenderness degree (H/D ratio) which provides insight in stability of a forest was based on measured heights and diameters of trees. Slenderness of trees in studied forests was displayed across diameter classes for all studied objects.

The data for comparison of changes in tree species composition of extended dbh size classes was taken from the study of Drinic (1956), state forest inventory in 1965 (Matic *et al*., 1971), Maunaga *et al*. (2005) and our measurements. In 1952/53 Drinic (1956) set four approximately one-hectare large plots across OGF Janj. Since ecological and terrain characteristics are similar across the core area, we decided to take into account results from this study. Next two inventories were made following standard official procedures meaning that concentric circle plots were superimposed in regular grid 100 x 100 m, so those inventories were rather similar to our approach. Individual inventories were not carried out on the same plots and the inventory thresholds slightly differed, however, due to large size of the inventory plots and similar forest structure in the core area, we assume that comparisons were eligible.

Data for comparison with other two OG forests was also taken from Drinic (1956), who in 1952/53 installed additional six plots across reserve in Perucica and four plots in Lom. Data for the recent inventory of OGF Lom originates from Motta *et al*. (2011) and of OGF Perucica from Lucic (2012). Perucica is located cca. 150 km in the south-eastern direction from Janj, while Lom is located about 80 km in the North-West direction from Janj. All three OG forests are located about 90 km from the Adriatic coastline. Lom is on prevalent limestone bedrock with numerous karst phenomena such as sinkholes and rocky outcrops. In Perucica lower parts are characterized by silicate parent material, while in the higher parts limestone is frequent (Drinic, 1956; Fukarek, 1970). As regards climatic influence it is important to notice that from the forest Lom in North-West, through Janj, and to Perucica in East of BiH there is a distinct decline in yearly rainfall (Popovic, 1931).

5 RESULTS

5.1 HEIGHT CURVES AND SITE QUALITY ESTIMATION

The regression between dbh and tree height showed that conifers in OGF Janj grew on site whose class is transitional (between first and second class), whereas beech here grows clearly on first site class. In MF Janj, however, this relationship indicated that site for all three species can be estimated as third site class (Figure 6).

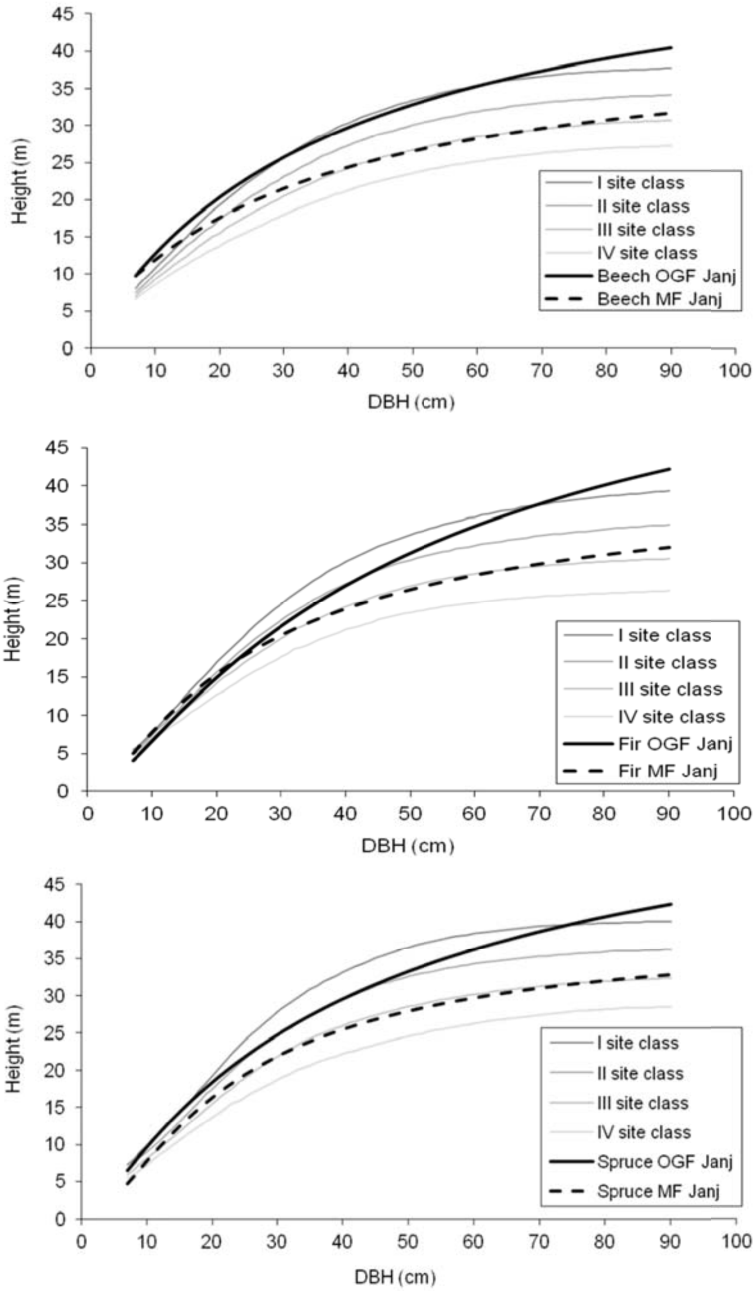


Figure 6. DBH and tree height regressions for beech, fir and spruce in Janj area.

In both MF Lom and OGF Lom spruce trees had equal conditions for its development as they grew on second site class; similarly, conditions for beech in MF Lom and OGF Lom were the same (transitional site class II/III). Only slight difference was found for silver fir since in MF Lom it grew on second site class, while in OGF Lom dbh-tree height regression indicated transitional site class I/II (Figure 7).

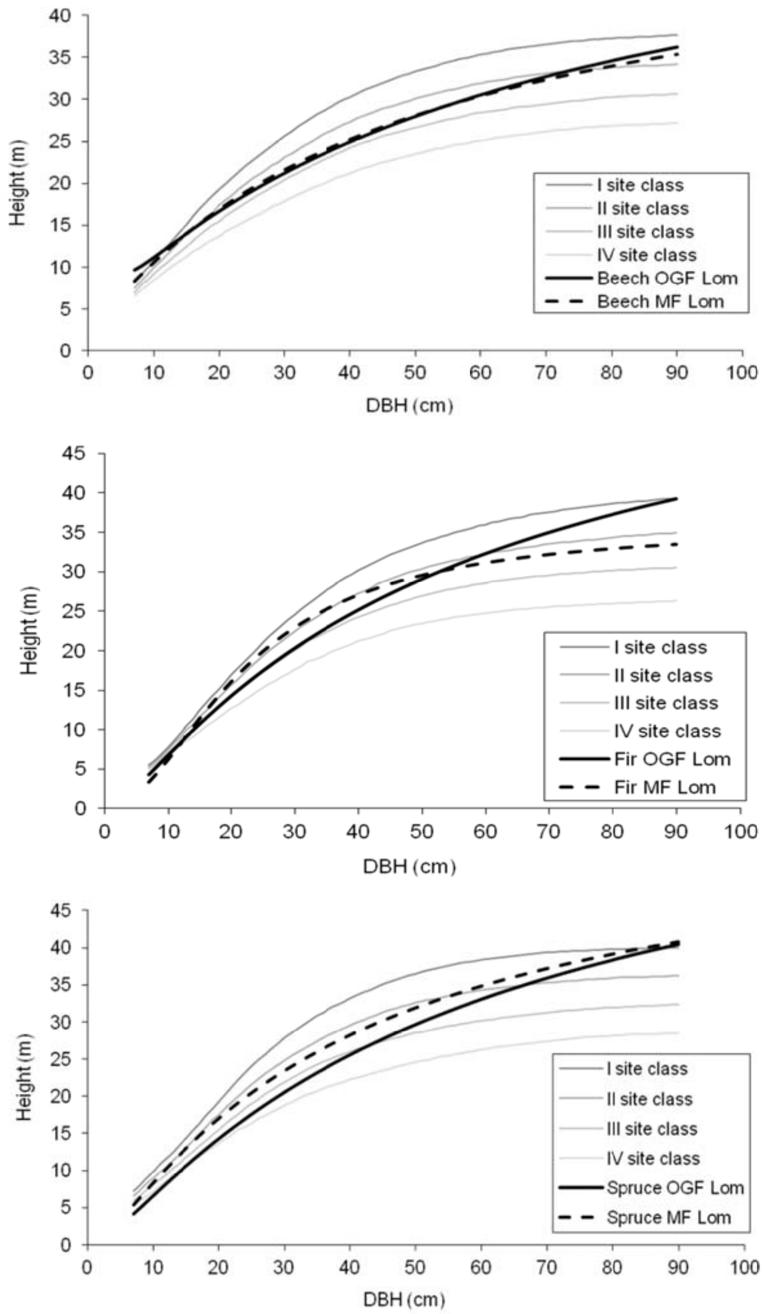


Figure 7. DBH and tree height regressions for beech, fir and spruce in Lom area.

Table 2. Basic statistics for height curves in studied forests.

Study objects	Species	Statistics a	b	c	R^2	St. error (m)	F	Estimated site class
OGF Janj	Fir	5.9821	0.7434	0.0147	0.9017	5.98	263.40	I/II
	Spruce	2.1855	0.6557	0.0161	0.7878	4.96	206.61	I/II
	Beech	-0.4445	0.6590	0.0174	0.8986	1.58	222.80	I
MF Janj	Fir	4.3808	0.5980	0.0240	0.8528	2.96	313.32	III
	Spruce	6.3932	0.3992	0.0252	0.8703	3.30	153.23	III
	Beech	-1.2509	0.7269	0.0236	0.7455	1.88	321.34	III
OGF Lom	Fir	2.4472	0.9727	0.0142	0.8995	1.84	354.30	I/II
	Spruce	5.0208	0.8528	0.0145	0.9405	1.93	207.78	II
	Beech	-2.7426	0.9998	0.0168	0.7256	0.76	403.44	II/III
MF Lom	Fir	12.7084	0.0512	0.0277	0.8208	3.63	344.35	II
	Spruce	3.8347	0.6491	0.0168	0.8594	2.96	360.78	II
	Beech	-1.0230	0.8521	0.0189	0.7908	1.70	190.01	II/III

Statistics shown in the Table 2 indicate relatively small standard error and high coefficient of determination (R^2) for the most cases. Somewhat greater standard error was obtained for fir and spruce in OGF Janj, which was probably caused due to somewhat smaller number of measured trees compared to other study objects. However, since calculated F values were always higher from pertinent table values for the same number of data pairs and level of α = 0.05, correlation between measured heights and dbh values was positively significant for all species and consequently reliable for all studied forests.

5.1.1 Tallest trees in the upperstory

The thickest and tallest individuals that actually were found in OGF Janj were fir trees with 124 cm dbh and 50.5 m height. Thickest and tallest spruce trees had 110 cm dbh and 47.5 m height, and beech with the largest diameter reached 92 cm dbh and 44.7 m height.

In OGF Janj and OGF Lom it did not occur for any of the species that thickest tree was concurrently the tallest whatsoever. The same applies to the managed forests. Such results indicate variability in taper of thicker trees in these uneven-aged forests, which is usually negatively reflected on tree quality, nevertheless, such trees may contribute to overall stability of a forest stand against snow and strong wind (further explained in the Chapter on Slenderness ratio).

Differences in height of 30 tallest trees for single species occurring in different forests were tested with Welch test which indicated that there were differences among tallest fir trees growing in different studied forests (F = 108.6; p = 0.0000). Similar results were obtained for spruce (F = 141.1; p = 0.0000) and beech (F = 47.3; p = 0.0000) as well.

Subsequently, results of post hoc Games-Howell test showed no significant difference for tallest trees of any species between OG forests. However, tallest fir and beech trees in OGF Janj and OGF Lom were significantly higher compared to MF Janj and MF Lom, while tallest spruce trees in OG forests were significantly higher only compared to MF Janj. In all cases where difference was found the level of *p* amounted to 0.0000.

In OGF Janj mean height of 30 highest fir trees was 40.3 m, of spruce 39.8, and of beech 33.5 m. One-way ANOVA yielded significant results (F = 19.71; p = 0.0000) and Tukey HSD test clarified that no signficant differences exist between highest fir and spruce trees, however, those two species were significantly taller from tallest beech trees. In MF Janj mean height of tallest fir trees was 27.8 m, of spruce 25.0, and of beech 25.9 m. One-way ANOVA produced significant results (F = 7.26; p = 0.0010). Unlike in OGF Janj, in MF Janj Tukey HSD test showed that no signficant differences exist between highest spruce and beech trees, while those two species significantly differed from tallest fir trees.

In OGF Lom mean height of largest fir trees was 41.4 m, of spruce 38.8, and of beech 32.3 m. One-way ANOVA yielded significant results (F = 93.84; p = 0.0000) and contrasting to other studied forests Tukey HSD test showed that in OGF Lom signficant differences exist between all three species when it comes to tallest upperstorey trees. In MF Lom tallest spruce trees had greatest mean height reaching 37.5 m, fir trees 35.1 m, and beech 28.2 m. Analysis of variances for this forest also indicated significant results (F = 120.28; p = 0.0000). Akin to OGF Lom, Tukey HSD test showed that in MF Lom signficant differences exist between all three species as regards tallest upperstorey trees.

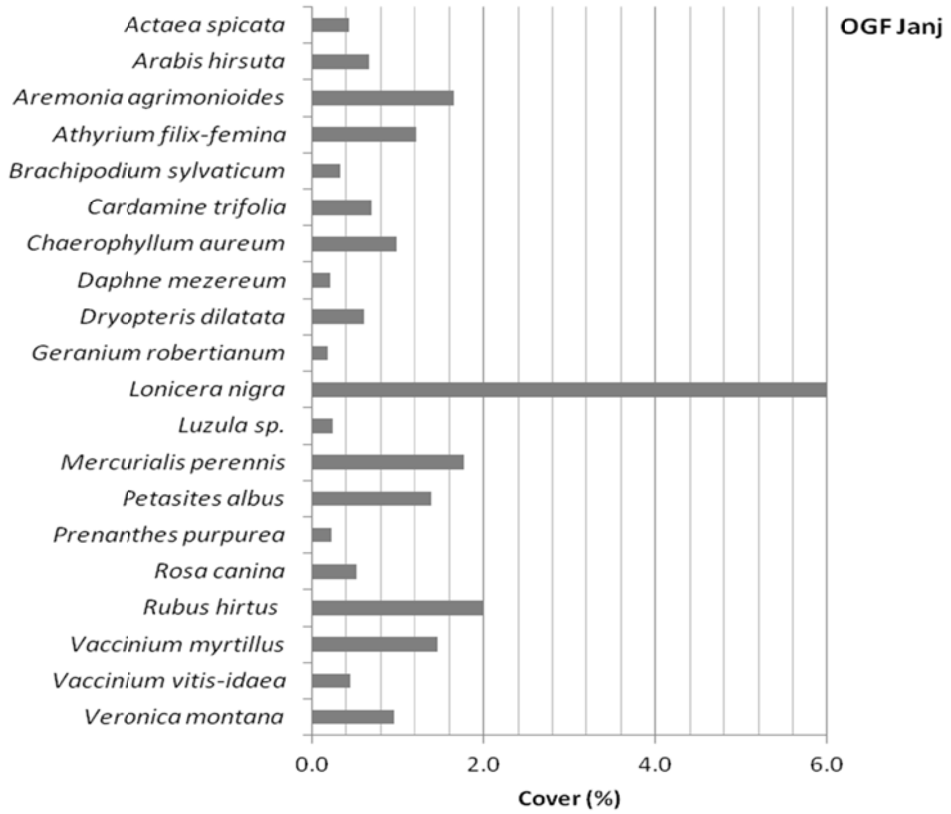
5.2 GROUND VEGETATION

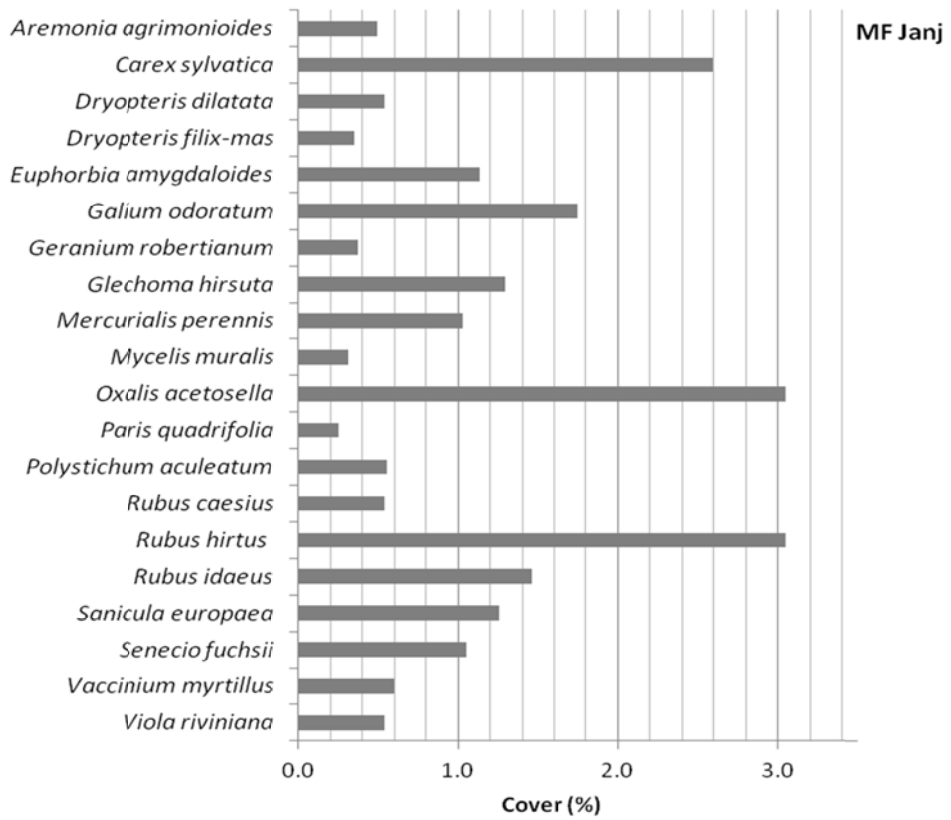
Cover of ground vegetation (without tree species) was greater in managed forests than in OG forests. Average coverage of ground by non-tree vegetation was: in OGF Janj 22.9 %, MF Janj 23.9 %, OGF Lom 9.8 % and MF Lom 27.4 %. When tree species (up to 1.3 m height) were combined with herbaceous species and shrubs, the cover of ground vegetation still remained greater in managed than in OG forests, but the percentages changed and following results were obtained: in OGF Janj 37.7 %, MF Janj 40.8 %, OGF Lom 17.1 % and MF Lom 36.9 %. Cover of ground by tree species is shown in Table 3, while cover of twenty most abundunt non-tree species was shown in Figure 8.

Table 3. Cover of ground (%) by tree species up to 1.3 m in height.

Species	OGF Janj	MF Janj	OGF Lom	MF Lom
Fagus sylvatica	9.73	3.89	2.78	3.11
Abies alba	3.13	7.28	2.81	5.05
Picea abies	0.94	4.49	1.68	0.71
Acer pseudplatanus	0.99	1.34	0.02	0.67
Total	14.80	17.00	7.28	9.54

Species biospectrum showed that coverage of ground by tree species (up to 1.3 m height) was considerably greater in Janj area compared to Lom area. Generally, it was slightly greater in managed than in adjacent OG forests. The share of shrubby species was generally around 20 %, only in OGF Lom around 10 %. The share of phanerophytes ranged between 22 % to 30 % and it was greater in managed forests. The share of chamaephytes revolved between 10 to 14 %, except in OGF Janj where they participated with 25 %. Average for geophytes was around 20 % with the exception of MF Janj with only 11 %. Hemicryptophytes generally ranged between 32–36 %, only OGF Lom deviated in this aspect with 52 %. Geophytes were occurring only in OGF Janj and MF Lom, but their share was negligible. Analysis of geospectrum indicated that species from colder regions were most present in OGF Lom, while Mediterranean geoelements were most present in OGF Janj. Considering coenospectrum it was noticed that species which originally inhabit wet forests (*Carex pendula, Carex remota*) were sporadically occurring in OGF Lom. On the other hand, presence of *Arabis hirsuta* in OGF Janj was unexpected since this species originates from relatively dry and warm meadows. Only one ruderal species was found, and this was *Chaerophyllum aureum* in OGF Janj. Moeso-neutrophilic species were dominant ranging between 36 % (OGF Lom) to 65 % (MF Janj), whereas species characteristic for acidophilic forests were subdominant having cover between 23 % (OGF Lom) to 38 % (MF Lom). *Veronica officinalis* was the only species originating from acidophilic meadows, and it occurred only in MF Lom.


OGF Janj
Actaea spicata
Arabis hirsuta
Aremonia agrimonioides
Athyrium filix-femina
Brachipodium sylvaticum
Cardamine trifolia
Chaerophyllum aureum
Daphne mezereum
Dryopteris dilatata
Geranium robertianum
Lonicera nigra
Luzula sp.
Mercurialis perennis
Petasites albus
Prenanthes purpurea
Rosa canina
Rubus hirtus
Vaccinium myrtillus
Vaccinium vitis-idaea
Veronica montana
0.0
2.0
4.0
6.0
Cover (%)


MF Janj
Aremonia agrimonioides
Carex sylvatica
Dryopteris dilatata
Dryopteris filix-mas
Euphorbia amygdaloides
Galium odoratum
Geranium robertianum
Glechoma hirsuta
Mercurialis perennis
Mycelis muralis
Oxalis acetosella
Paris quadrifolia
Polystichum aculeatum
Rubus caesius
Rubus hirtus
Rubus idaeus
Sanicula europaea
Senecio fuchsii
Vaccinium myrtillus
Viola riviniana
0.0
1.0
2.0
3.0
Cover (%)

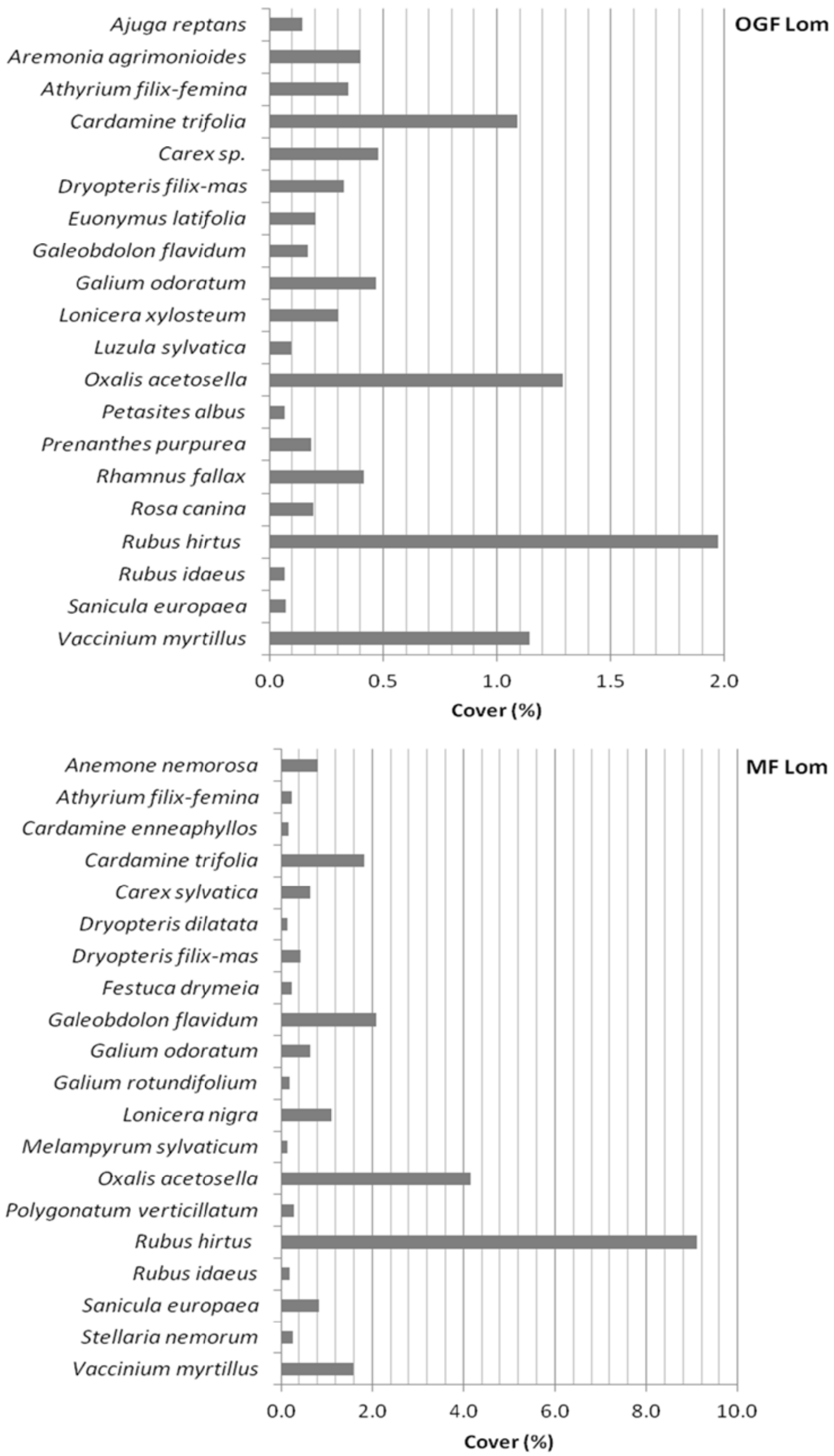


Figure 8. Cover of twenty most abundant herbaceous and shrubby species in studied forests.

Table 4. Indicator species with IndVal index values based on permutation test.

OGF Janj	stat.	*p*-value		OGF Lom	stat.	*p*-value	
Mercurialis perennis	0.729	0.001	***	*Carex sp.*	0.308	0.001	***
Lonicera nigra	0.685	0.001	***	*Lonicera xylosteum*	0.281	0.001	***
Arabis hirsuta	0.622	0.001	***	*Rhamnus fallax*	0.207	0.011	*
Chaerophyllum aureum	0.548	0.001	***	*Luzula sylvatica*	0.184	0.016	*
Veronica montana	0.493	0.001	***	MF Lom	stat.	*p*-value	
Petasites albus	0.431	0.001	***	*Galeobdolon flavidum*	0.833	0.001	***
Vaccinium vitis.idaea	0.335	0.001	***	*Anemone nemorosa*	0.577	0.001	***
Luzula sp.	0.329	0.001	***	*Asarum europaeum*	0.524	0.001	***
Brachipodium sylvaticum	0.284	0.001	***	*Cardamine enneaphyllos*	0.524	0.001	***
Rosa canina	0.270	0.001	***	*Viola reichenbachiana*	0.465	0.001	***
Actaea spicata	0.204	0.018	*	*Sorbus acuparia*	0.445	0.001	***
MF Janj	stat.	*p*-value		*Polygonatum verticillatum*	0.423	0.001	***
Glechoma hirsuta	0.629	0.001	***	*Galium rotundifolium*	0.365	0.001	***
Euphorbia amygdaloides	0.476	0.001	***	*Symphytum tuberosum*	0.342	0.001	***
Viola riviniana	0.401	0.001	***	*Luzula luzulina*	0.274	0.001	***
Rubus caesius	0.286	0.001	***	*Maianthemum bifolium*	0.242	0.002	**
Geranium robertianum	0.269	0.005	**	*Euphorbia carniolica*	0.224	0.003	**
Polystichum aculeatum	0.185	0.044	*	*Lonicera alpigena*	0.224	0.001	***
				Stellaria nemorum	0.224	0.003	**
				Gentiana asclepiadea	0.204	0.005	**

The table 4 presents information on indicator species for all four studied forests. However, to achieve certain level of generalization flora of both managed forests was combined and compared against flora of both OG forests. Therefore, additional permutation was performed which extracted six significant indicator species in managed forests (*Sanicula europea, Carex sylvatica, Mycelis muralis, Senecio fuchsii, Rubus idaeus,* and *Fragaria vesca*) and two significant indicator species in OG forests (*Aremonia agrimonoides* and *Euonymus latifolia*).

From ordination plot we see that MF Janj is least "differentiated", whereas the other three forest study areas differed significantly among each other. First axis (PCO 1) differentiated Lom and Janj areas (Figure 9), while second axis (PCO 2) differentiated between managed and OG forests. Aeration, which indirectly explains soil texture, was closest to the first axis and greatest in OGF Lom, while light regime, nitrogen, soil reaction and temperature were better explained by the second axis. Lowest soil reaction was indicated in MF Lom and greatest in OGF Lom and, although the overall span of soil reaction was rather small (probably between 6.0 to 7.0 pH), indicating small difference in soil reaction between studied forests.

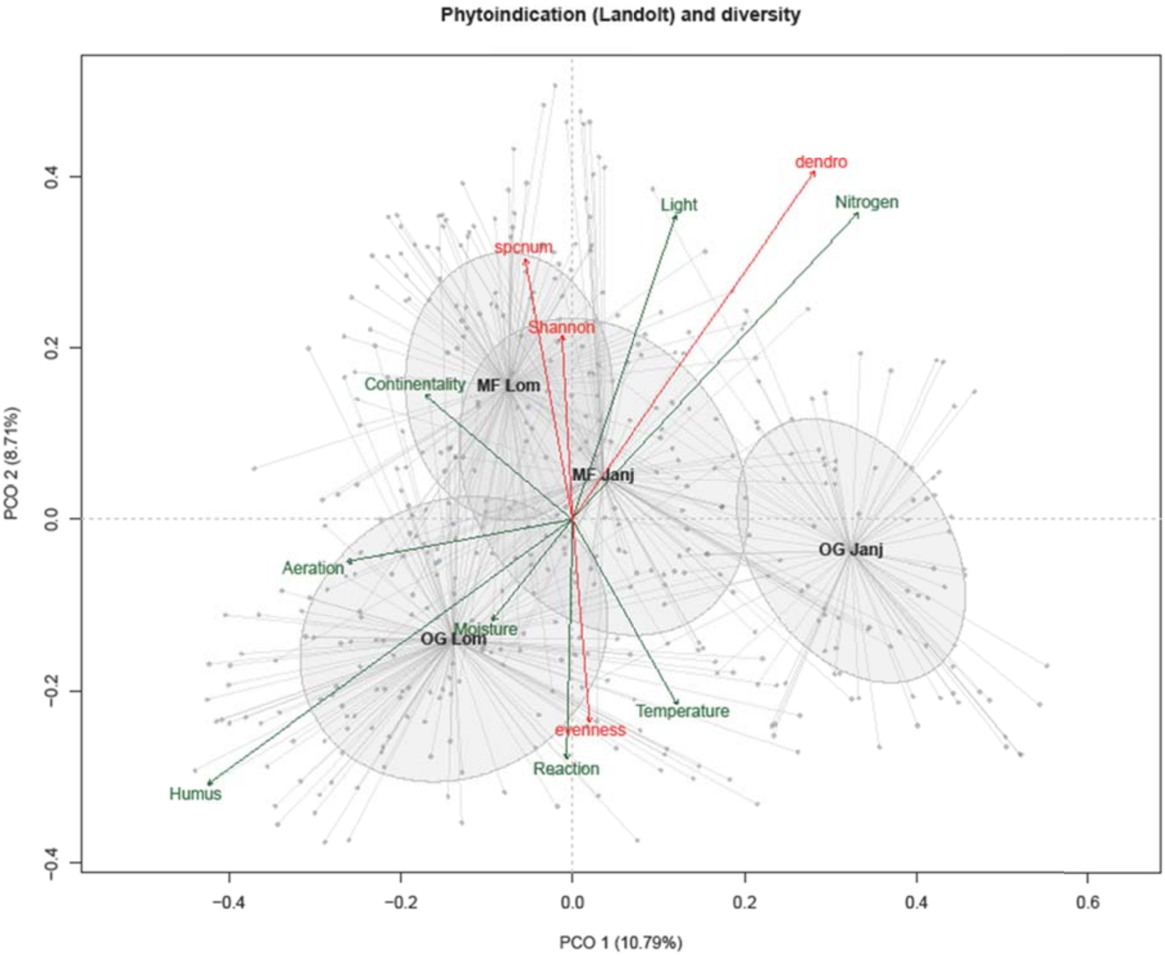


Figure 9. Ordination plot of a Principle coordinate analysis (PCoA) for vascular plant cover in the herb layer (Bray-Curtis distance measure) within OG forests Janj and Lom and surrounding managed forests. Green arrows represent Landolt's phytoindication, while red arrows represent species diversity indicators.

Higher temperature and higher soil reaction was indicated for both OG forests. For OGF Lom this was expected due to substantial presence of rocky outcrops in this forest. Between OGF Janj and MF Janj no significant difference occurred in terms of temperature. Presence of tree species was mostly influenced by light regime and nitrogen richness, while diversity of herbaceous and shrubby species was best explained by light regime and continentality of site, although the lines were not very close to each other, and consequently regression between them was not very strong. Moisture was greatest in OGF Lom, while in OGF Janj "trace" of maritime climate was indirectly implied since the line for continentality hits the opposite side. Lowest presence of nitrogen and highest layering of raw humus was indicated in OGF Lom, managed forests were inbetween, while in OGF Janj nitrogene presence was highest and deposit of raw humus was smallest (Figure 10).

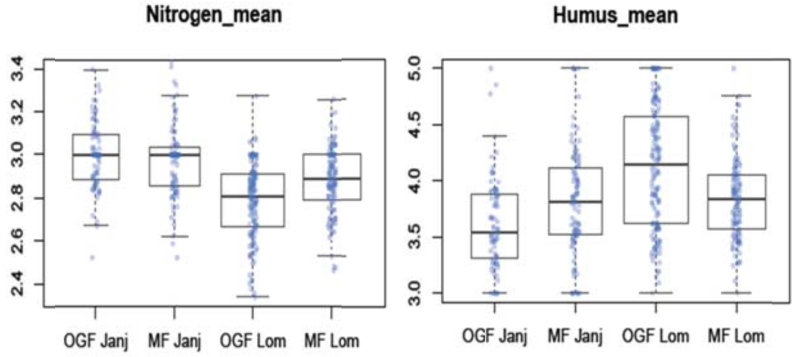


Figure 10. Presence of nitrogen and humus in studied forests according to Landolt's phytoindications.

Species number on single plots varied most in MF Lom and second was MF Janj. Considering Shannon indexes we were not so interested in the average index for one site, but rather in the range of index values within the forest site since the index was calculated for each plot (each plot was treated as a site). For instance, MF Janj had lower median and mean than OGF Janj, however, species diversity and site conditions were more heterogeneous in MF Janj due to largest range (2.57) of Shannon index values on sample plots. Plots in OGF Janj had range of Shannon indexes 1.65, which made this forest more homogeneous than others in terms of species diversity and site conditions. In this sense, range in MF Lom was greater (2.07) compared to OGF Lom (1.76) (Figure 11).

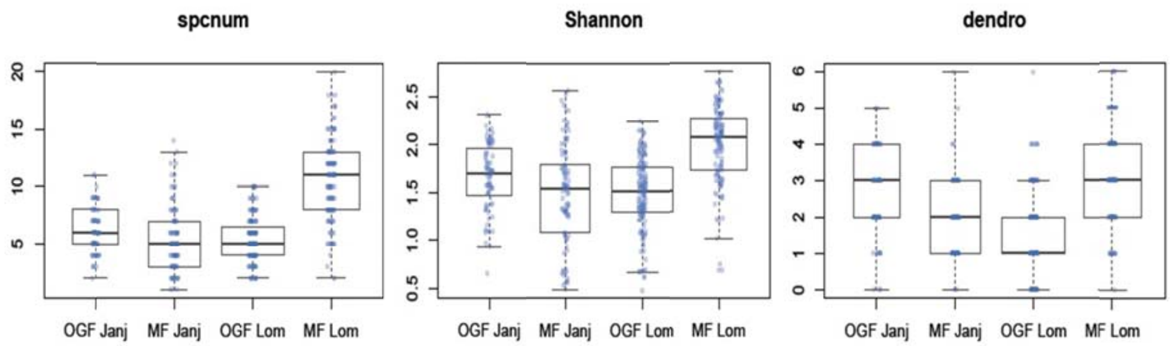


Figure 11. Herbaceous and shrub species number (spcnum) on plots (left), Shannon indexes (in the midlle) and number of tree species (right) on plots in studied forests.

No much difference was found in regeneration density of tree species between managed and OG forests in the height category from 10 cm up to 2 m, except that beech was most abundunt in OGF Janj. Density of beech regeneration from 2 m to 7.5 cm dbh was higher in both OG forests compared to managed forests, however, silver fir dominated managed forests in this category (Figure 12).

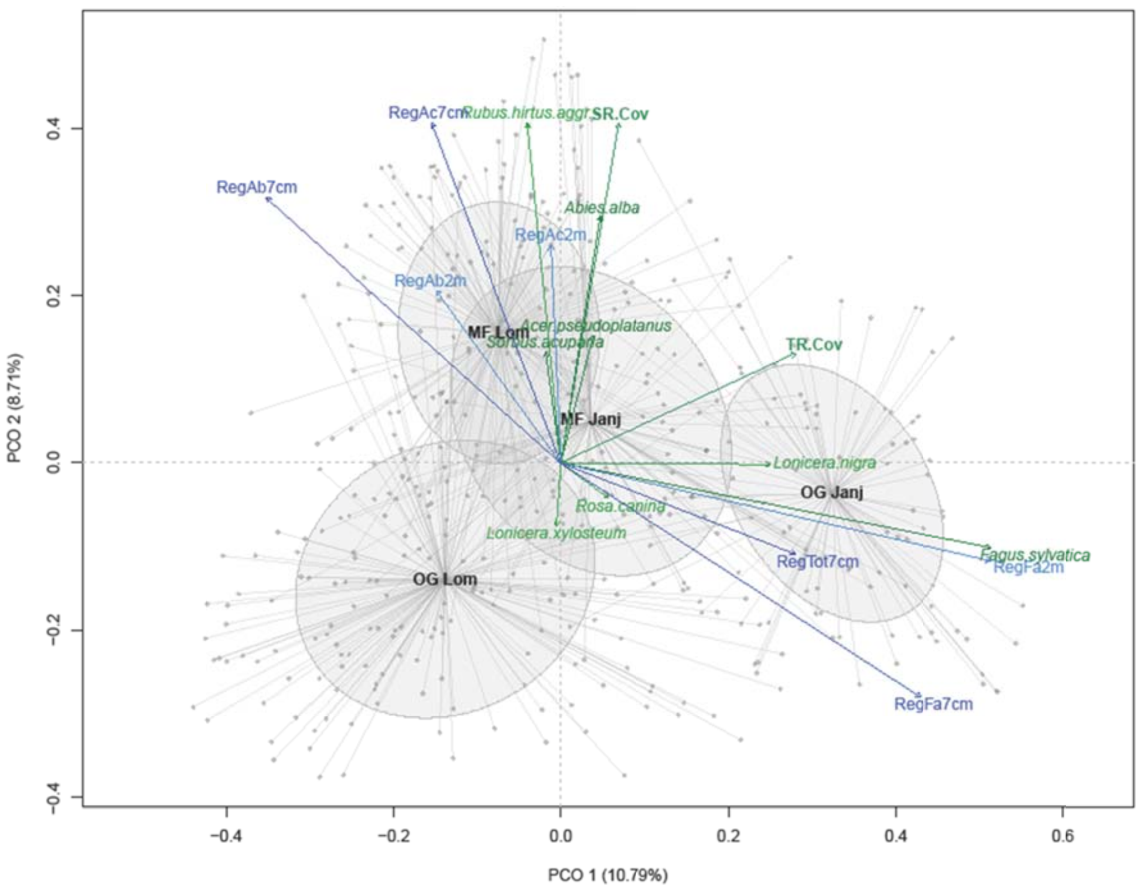


Figure 12. Ordination-biplot of a Principle coordinate analysis (PCoA) for vascular plant cover in the herb layer (Bray-Curtis distance measure) and cover of tree regeneration and shrubs below 1.3 m (green arrows). Blue arrows represent regeneration densities of: a) first height category 10 cm to 2 m for beech (RegFa2m), fir (RegAb2m), maple (RegAc2m), and b) second height category from 2 m to 7.5 cm dbh for beech (RegFa7cm), fir (RegAb7cm), maple (RegAc7cm) and total regeneration density (RegTot7cm).

Species accumulation curve also indicated greater species diversity in managed forests since in both OG forests curves became flat after the number of sample plots was around 50 (Figure 13).

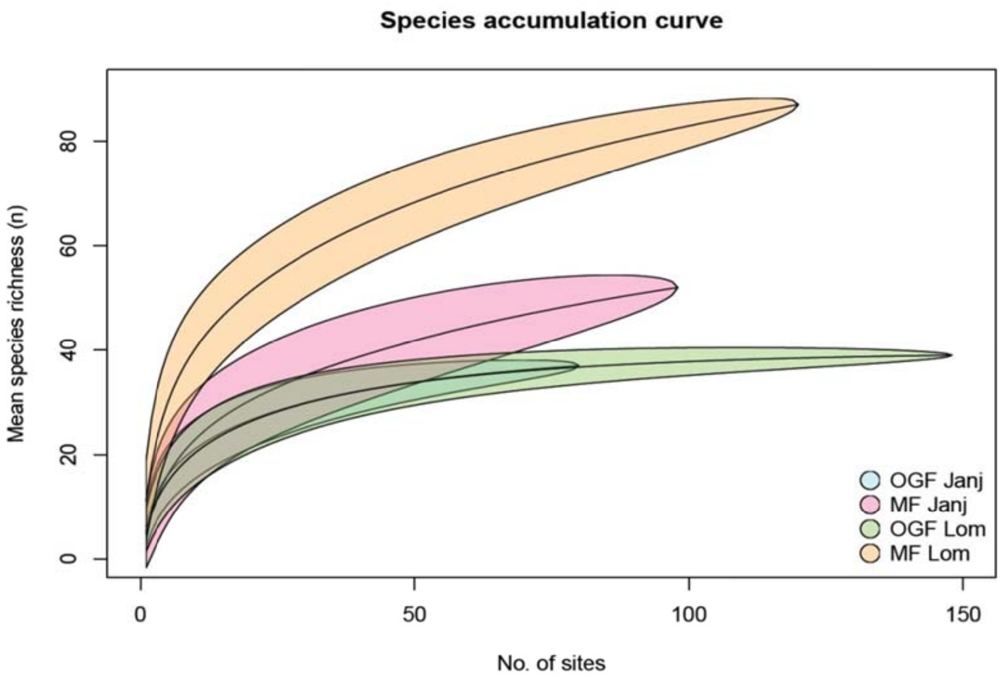


Figure 13. Species accumulation curve representing the increase in mean species richness (n) with the increase in number of sites (plots).

5.3 LIGHT CONDITIONS AND CANOPY OPENNESS

Mean values of transmitted direct light were greater in managed forests Janj (11.9 %) and Lom (7.6 %) than in OG forests Janj (5.8 %) and Lom (5.5 %). Similar outcomes were obtained for diffuse component of solar radiation (Table 5). Standard deviation and variance of both direct and diffuse radiation components showed higher variability of light conditions in managed than in OG forests. Furthermore, frequency distributions of totally transmitted solar radiation also manifested higher variability of light conditions in MF Janj compared to OGF Janj, while difference between MF Lom and OGF Lom was not so apparent (Figure 14).

Table 5. Descriptives for direct (DIR) and diffuse (DIF) components of transmitted solar radiation.

Statistics	DIR (%)				DIF (%)			
	OGF Janj	MF Janj	OGF Lom	MF Lom	OGF Janj	MF Janj	OGF Lom	MF Lom
Mean	5.79	11.89	5.51	7.59	4.99	9.67	5.45	7.57
Std. deviation	3.40	7.63	3.68	4.65	0.91	4.44	2.18	2.96
CV*	58.64	64.15	66.77	61.20	18.31	45.95	40.02	39.14
N (plots)	80	104	150	120	80	104	150	120

*Coefficient of variation

OG forests exhibited similarity in terms of transmitted direct component of solar radiation, however, significant difference was perceived regarding diffuse light (higher values in OGF Lom). MF Janj was characterized with highest percentages of transmitted solar radiation, so it differed significantly even from MF Lom upon both light components (Tables 6 and 7).

Table 6. Results of Mann-Whitney U test for transmitted direct light (DIR).

		N (plots)	Mean ranks	Mann-Whitney U	Z statistic	*p*-value
Pair 1	OGF Janj	80	63.73	1854.5	- 6.437	0.0000
	MF Janj	106	114.71			
Pair 2	OGF Janj	80	119.62	5670.5	- 0.686	0.4930
	OGF Lom	150	113.30			
Pair 3	OGF Lom	150	119.0	6520.5	- 3.889	0.0000
	MF Lom	120	156.16			
Pair 4	MF Janj	106	133.16	4091.0	- 4.443	0.0000
	MF Lom	120	94.59			

Table 7. Results of Mann-Whitney U test for transmitted diffuse light (DIF).

		N (plots)	Mean ranks	Mann-Whitney U	Z statistic	*p*-value
Pair 1	OGF Janj	80	50.31	785.0	- 9.424	0.0000
	MF Janj	106	124.95			
Pair 2	OGF Janj	80	97.94	4595.0	- 2.923	0.0030
	OGF Lom	150	124.87			
Pair 3	OGF Lom	150	109.85	5152.5	- 6.035	0.0000
	MF Lom	120	167.56			
Pair 4	MF Janj	106	131.29	4286.0	- 4.039	0.0000
	MF Lom	120	96.22			

Frequency distributions of totally transmitted solar radiation in studied forests exhibited slightly right-scewed to regular Gaussian bell-shaped curve. Highest percentages in OGF Janj were ranging from 4–6 %, in MF Janj 6–10 %, OGF Lom 4–8 %, and in MF Lom highest peak was between 8–10 %, however, with numerous plots having lower values as well.

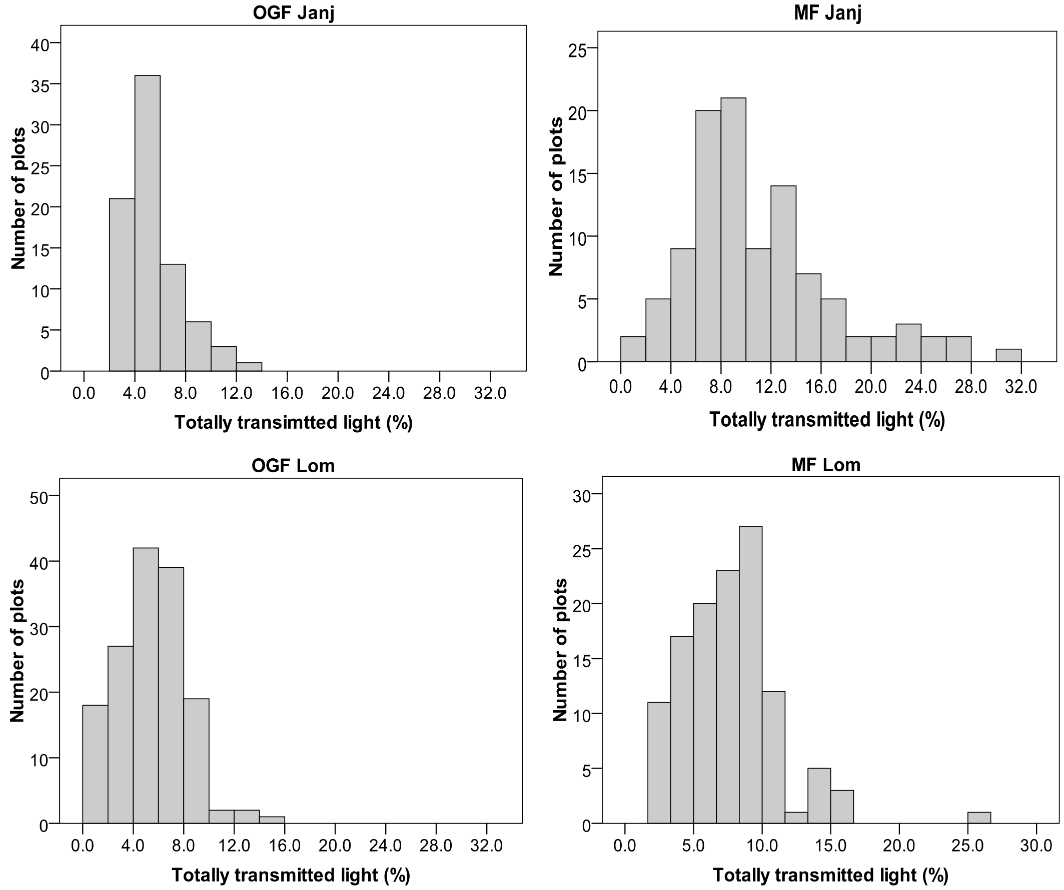


Figure 14. Frequency distributions of totally transmitted solar radiation (direct and diffuse components combined) at 1.3 m above ground on sample plots in studied forests.

In addition, the influence of overall BA on direct (R^2 = 0.12) and diffuse (R^2 = 0.18) transmitted light to the understory was low to moderate.

Box-plots best displayed visually the medians of transmitted direct and diffuse solar radiation. Not only means and medians, but also the overall span of transmitted light percentages was clearly greater in managed forests (Figure 15).

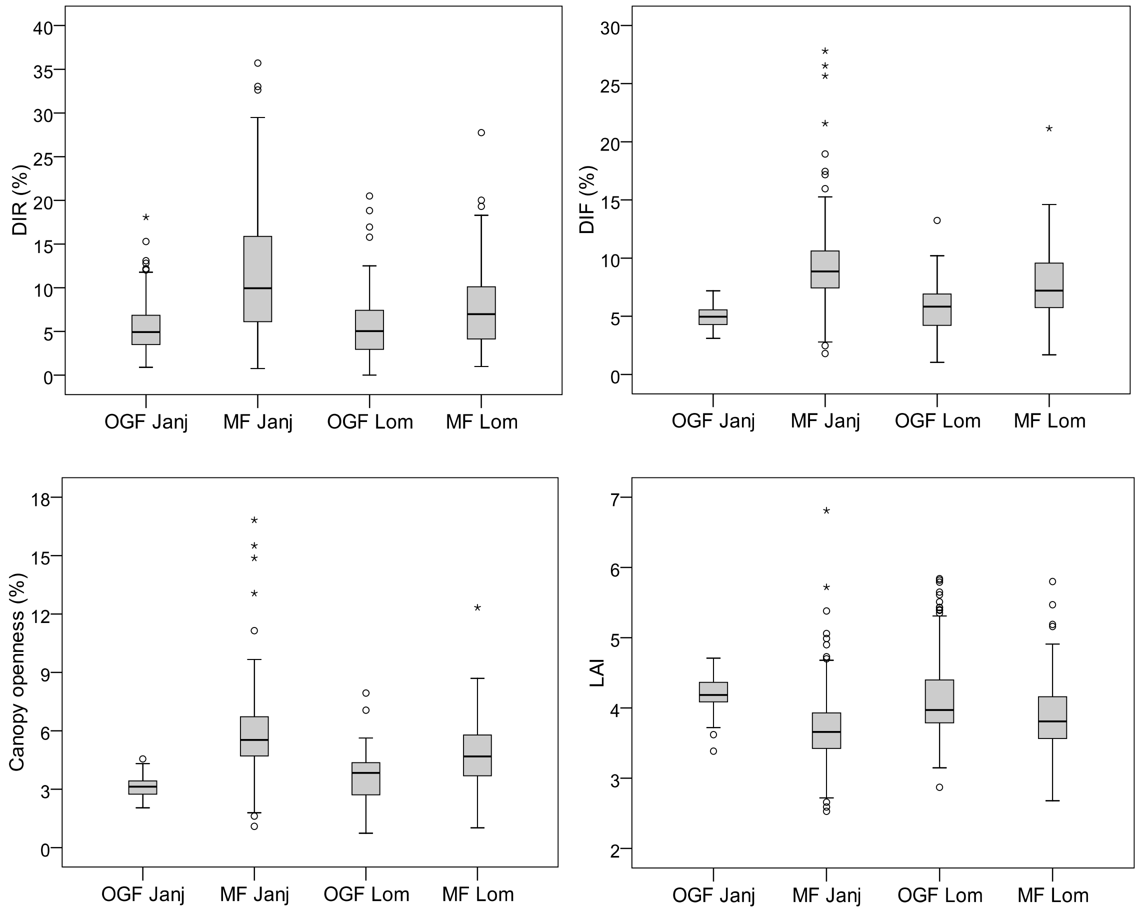


Figure 15. Boxplots of direct (DIR) and diffuse (DIF) light, canopy openness and leaf area index (LAI = leaf area/ground area, m^2/m^2). The box represents the interquartile range, and the horizontal line inside the box shows the median. The whiskers extend to the lowest and highest values below and above the first and third quartile, respectively excluding outliers. Circles and asterisks represent outliers that are more than 1.5 and 3 times the interquartile range, respectively.

Managed forests had greater overall gap fraction compared to OG forests since mean canopy openness in managed forests Janj and Lom amounted to 5.5 % and 4.7 %, while in OG forests Janj and Lom these values were 3.1 % and 3.8 %, respectively. Coefficient of variation of canopy openness was clearly greater in MF Janj (42.98) than in OGF Janj (17.39), while in MF Lom and OGF Lom they were virtually equal (ca 36.90). On the other hand, standard deviation in MF Lom (1.72 %) was greater than in OGF Lom (1.30 %). Frequency distributions indicated greater variation in canopy openness on sampled plots in managed forests compared to OG forests, althought difference between MF Lom and OGF Lom was not so explicit as between MF Janj and OGF Janj (Figure 16).

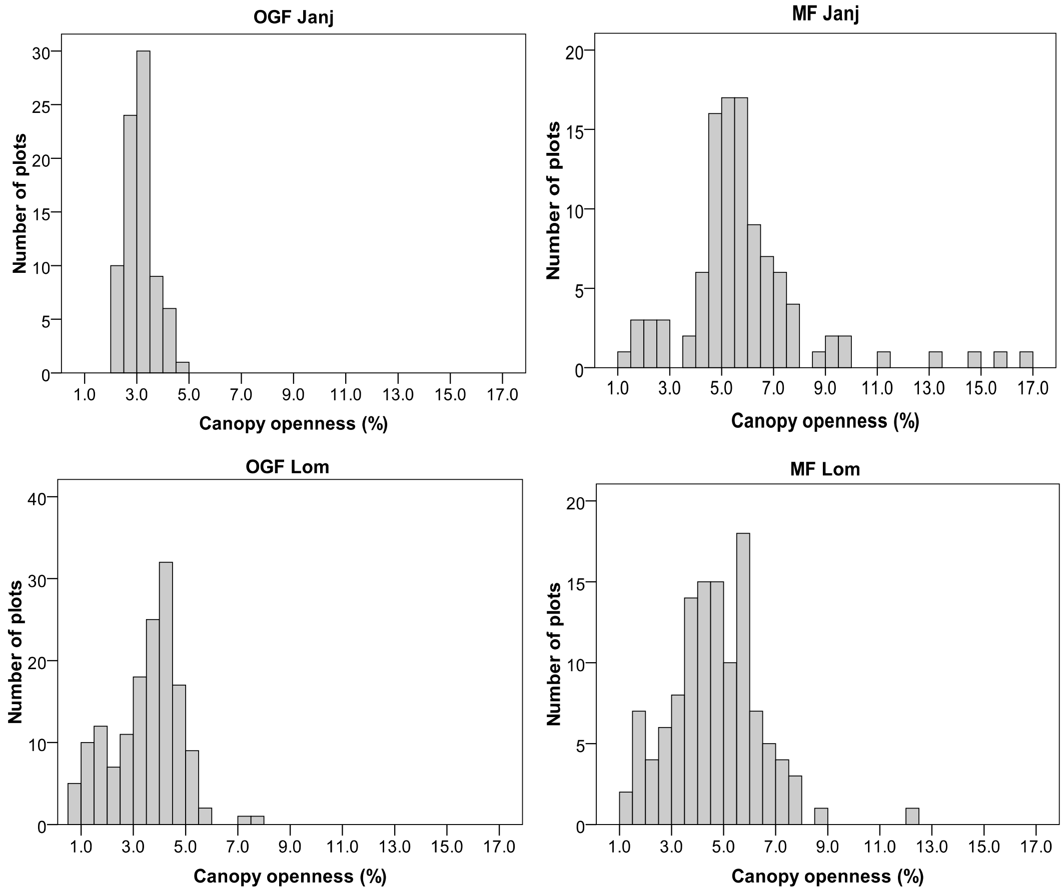


Figure 16. Frequency distributions of canopy openness (%) in studied forests.

Mann-Whitney U test indicated very slight similarity in canopy openness between two OG forests; nevertheless, for all tested pairs significant differences were obtained (Table 8).

Table 8. The results of Mann-Whitney U test for canopy openness.

		N (plots)	Mean ranks	Mann-Whitney U	Z statistic	*p*-value
Pair 1	OGF Janj	80	50.16	773.0	- 9.457	0.0000
	MF Janj	104	125.07			
Pair 2	OGF Janj	80	92.78	4182.0	- 3.783	0.0100
	OGF Lom	150	127.62			
Pair 3	OGF Lom	150	110.55	5257.0	- 5.871	0.0000
	MF Lom	120	166.69			
Pair 4	MF Janj	106	132.08	4203.5	- 4.210	0.0000
	MF Lom	120	95.53			

5.4 DEVELOPMENTAL PHASES

In OGF Janj optimal late phase was predominant on 42.5 % of the area, in OGF Lom however selection phase was dominant on 37.5 % and terminal phase on 20 % of the area. Plots in MF Lom had selection features in 50 % of cases, while in MF Janj plots were most often characterized with optimal early (45 %) and selection phase (33 %). The absolute number of plots with different developmental phases is given in Table 9.

Table 9. Number of plots with different development phases.

Developmental phases	OGF Janj	MF Janj	OGF Lom	MF Lom
Pole	-	5	-	3
Selection	6	20	15	30
Optimal early	2	27	5	13
Optimal middle	6	8	5	14
Optimal late	17	-	7	-
Terminal	9	-	8	-
Total	40	60	40	60

5.5 NATURAL REGENERATION

In OGF Janj regeneration density on sample plots varied from 382 per hectare to 20892 per hectare. Average regeneration density was 4685 per ha, more than in MF Janj where regeneration density on average was 1660 individuals per ha. In MF Lom regeneration density was higher than in OGF Lom.

Table 10. Descriptives for regeneration (from 10 cm height to 7.5 cm dbh).

Statistics	OGF Janj	MF Janj	OGF Lom	MF Lom
Mean	4685	1660	4772	5299
Std. error	740	200	633	327
Median	2675	1019	3501	4968
Range	20510	6242	17793	11720
N (plots)	40	60	40	60

Range of regeneration density was the greatest in OGF Janj. MF Janj and OGF Janj had similar regeneration densities on the lower edge of regeneration range, however, no adjacent managed stand reached the upper edge of the regeneration range in OGF Janj. On the other hand, four out of five managed stands in Lom area had higher lower edge of the regeneration range, but all managed stands had smaller upper edge of the range compared to OGF Lom.

In composition of regeneration in OGF Janj beech made 68.9 %, fir 15.0 %, maple 10.9 %, and spruce only 5.2 %. In MF Janj the share of conifers was noticeably higher, so fir made 50.2 %, beech 33.4 %, spruce 11.4 %, and maple 5.0 %. In OGF Lom difference in regeneration density between beech and fir was not so large like in OGF Janj, whereas the share of spruce was greater for more than 10 %. Beech in OGF Lom made 44.5 %, fir 37.2 %, spruce 16.4 %, and maple only 1.8 %. In MF Lom, like in MF Janj, conifers were also more present than broadleaved species; accordingly, fir constituted 47.5 %, beech 24.4 %, while the share of spruce was rather low with 8.9 %, and the share of maple rather high as this species made 19.9 % of total regeneration in MF Lom (Figure 17). Absolute regeneration densities are given in Table 11.

Table 11. Species mixture in regeneration stage.

Stands	Beech n/ha	Fir n/ha	Spruce n/ha	Maple n/ha	Total n/ha
OGF Janj	3229	701	242	513	4685
Janj 31	297	870	32	255	1454
Janj 50d	637	446	96	64	1243
Janj 56	616	1380	276	42	2314
Janj 57/1b	849	775	403	11	2038
Janj 58a	340	722	191	0	1253
Average for MF Janj	548	839	200	74	1660
OGF Lom*	2101	1756	774	85	4717
Lom 59a	467	2293	449	531	3740
Lom 67a	2261	3907	594	1401	8163
Lom 68a	1019	1964	318	499	3800
Lom 76a	1656	2420	499	1582	6157
Lom 79a	1369	1847	265	1433	4914
Average for MF Lom	1354	2486	425	1089	5355

* In OGF Lom average overall density of regeneration, including species like Sorbus aucuparia and Ulmus spp. was 4772 individuals per hectare.

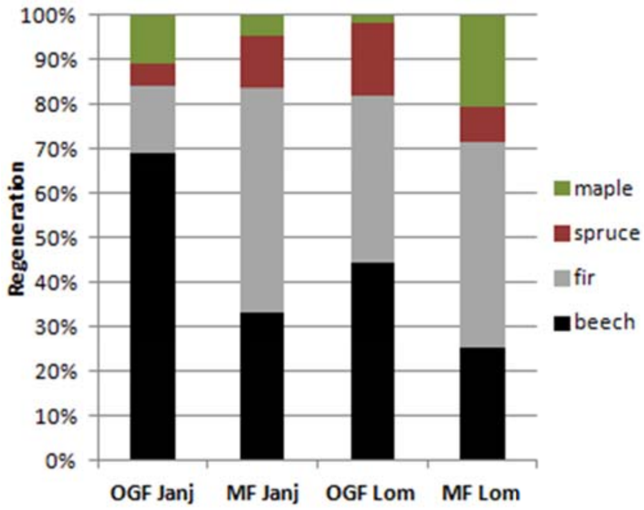


Figure 17. Species composition (%) at regeneration stage (10 cm height to 7.5 cm dbh).

Differences in tree species composition in the regeneration stage were determined for three tested pairs of studied forests, while similarity was expressed only between OGF Lom and MF Lom. Two-variable Chi-square test with three degrees of freedom did not find significant differences between OGF Lom and MF Lom, however, it reported significant differences between following pairs ($p \leq 0.05$):

- OGF Janj vs. MF Janj $\chi^2 = 77.05$
- OGF Janj vs. OGF Lom $\chi^2 = 28.35$
- MF Janj vs. MF Lom $\chi^2 = - 13.73$

Results of t-test indicated significant differences in regeneration mean densities between OGF Janj and MF Janj, but also between MF Janj and MF Lom. On the other hand, no significance was found between OGF Janj and OGF Lom, nor between OGF Lom and MF Lom (Table 12).

Table 12. Results of t-tests for regeneration density means.

Tested pairs	t	df	*p*-value	Mean difference	Std. error difference	95% Confidence interval lower	95% Confidence interval upper
OGF Janj - MF Janj	3.84	78	**0.0000**	2993.60	778.40	1443.91	4543.28
OGF Janj - OGF Lom	- 0.09	78	**0.9290**	- 87.47	974.13	- 2026.83	1851.88
OGF Lom - MF Lom	- 0.54	78	**0.5880**	- 406.17	745.85	- 1891.05	1078.70
MF Janj - MF Lom	- 9.46	118	**0.0000**	- 3639.06	384.42	- 4400.33	- 2877.80

Kruskal-Wallis test was conducted to test for differences in regeneration density means among single stands in Janj and Lom area. In these analyses OGF Janj and OGF Lom were appropriately compared to singular adjacent managed stands. For Janj area the test yielded $\chi^2 = 29.07$ for five degrees of freedom and difference was found at $p = 0.0000$. Similarly, for Lom area Kruskal-Wallis test in SPSS provided $\chi^2 = 25.67$ for five degrees of freedom and significant difference was also determined at $p = 0.0000$. Subsequently, by applying multiple post hoc pairwise Mann-Whitney analyses, it was found that regeneration density in OGF Janj significantly differed from all adjacent managed stands, while OGF Lom was similar with stands 59a, 68a and 79a, and different from stands 67a and 76a.

As regards seedlings smaller than 10 cm the greatest density was recorded in OGF Lom with total of 30163 seedlings per hectare. OGF Janj and MF Janj followed with 14333 and 5302 seedlings per hectare, respectively. In this stage fir was dominant in number in OGF Janj, OGF Lom, and MF Janj. In these forests beech took second place regarding seedlings density. Spruce was slightly less present than maple in OGF Janj, and slightly more present in OGF Lom and MF Janj (Tables 13 and 14).

Table 13. Descriptive statistics for small seedlings ≤ 10 cm.

Statistics	OGF Janj	MF Janj	OGF Lom
Mean	14333	5283	30163
Std. error	1630	959	2264
Median	8889	0	22222
Range	62222	44444	146667
N (plots)	80	120	150

Table 14. Species composition at germination stage (small seedlings ≤ 10 cm).

Stands	Beech		Fir		Spruce		Maple		Total
	n/ha	%	n/ha	%	n/ha	%	n/ha	%	n/ha
OGF Janj	3722	26.0	8500	59.3	1000	7.0	1111	7.7	14333
Janj 31	1482	89.0	0	0	185	11.0	0	0	1667
Janj 50d	1905	25.0	3809	50.0	1270	17.0	635	8.0	7619
Janj 56	185	16.7	555	50.0	185	16.7	185	16.7	1111
Janj 57/1b	1852	62.5	555	18.7	185	6.2	370	12.5	2963
Janj 58a	2778	21.1	7963	60.6	1111	8.4	1296	9.9	13148
Average for MF Janj	1641	30.9	2576	48.6	588	11.1	497	9.4	5302
OGF Lom	2963	9.8	26637	88.3	415	1.4	148	0.5	30163
MF Lom *									

* not available

Similarity in tree species composition in the seedlings stage was indicated between OGF Janj and OGF Lom (χ^2 = - 0.71, $p \leq 0.05$), whereas significant difference was found between OGF Janj and MF Janj (χ^2 = 34.56, $p \leq 0.05$). Note that two-variable Chi-square test that was applied in this analysis had only two degrees of freedom due to unavailability of data from MF Lom.

Significant difference in seedlings density was found only for two pairs: OGF Janj - MF Janj (pair 1) and OGF Janj - OGF Lom (pair 2). The results are shown in the following table.

Table 15. Significant results of Mann-Whitney U test for seedlings density.

Pair 1	N (plots)	Mean ranks	Mann-Whitney U	Z statistic	*p*-value
OGF Janj	80	116.58	2324.5	- 5.474	0.0000
MF Janj	106	75.43			
Pair 2	N (plots)	Mean ranks	Mann-Whitney U	Z statistic	*p*-value
OGF Janj	80	87.91	3785.0	- 4.510	0.0000
OGF Lom	150	129.27			

5.5.1 Height increment of regeneration

In both height categories of regeneration, from 10-50 cm and 50-130 cm, average yearly height increment of beech, fir and spruce was greater in managed forests Janj and Lom compared to adjacent OG forests (Table 16). This was expected since values of direct and diffuse solar radiation were higher in managed than in OG forests, and these two variables were well correlated.

Table 16. Yearly height increment (cm) of beech, fir and spruce regeneration.

		Mean	Median	Min.	Max.	Std. error	N (plots)
Beech seedlings 10-50 cm	OGF Janj	1.9	1.8	0.7	4.5	0.3	18
	MF Janj	4.3	3.8	0.7	8.5	0.6	13
	OGF Lom	1.9	1.5	0.2	5.3	0.4	13
	MF Lom	3.3	2.8	0.8	7.7	0.3	39
Beech seedlings 50-130 cm	OGF Janj	2.8	2.2	0.5	11.0	1.1	9
	MF Janj	11.0	9.8	0.5	24.0	1.6	18
	OGF Lom	3.4	3.2	0.4	9.7	0.8	12
	MF Lom	13.7	13.8	5.3	20.3	0.9	18
Fir seedlings 10-50 cm	OGF Janj	1.8	1.8	1.3	2.2	0.1	6
	MF Janj	1.9	2.1	0.7	4.2	0.3	13
	OGF Lom	1.5	1.3	0.5	3.2	0.1	39
	MF Lom	2.3	1.8	0.4	8.4	0.2	59
Fir seedlings 50-130 cm	OGF Janj	3.8	3.3	2.2	7.3	0.9	5
	MF Janj	6.3	4.3	0.9	16.0	0.9	23
	OGF Lom	4.8	3.3	0.7	16.2	1.0	17
	MF Lom	7.4	6.9	2.7	16.2	0.7	23
Spruce seedlings 10-50 cm	OGF Janj	-	-	-	-	-	0
	MF Janj	1.5	1.2	0.6	3.3	0.4	6
	OGF Lom	1.1	0.9	0.5	1.7	0.2	8
	MF Lom	1.5	1.2	0.7	2.6	0.2	17
Spruce seedlings 50-130 cm	OGF Janj	1.7	1.2	0.5	3.8	0.8	4
	MF Janj	3.3	2.4	0.7	11.0	0.6	20
	OGF Lom	2.1	1.9	0.5	4.0	0.4	9
	MF Lom	5.5	5.6	3.2	8.5	0.9	5

Live crown ratio (LCR) was not well correlated with current light conditions, and therefore this correlation was not presented graphically. LCR was more important to mirror vitality of regeneration as well as development conditions over lifetime up to now rather than reaction of crowns to current light conditions which were recorded as a one-time snapshot. Unlike in case of yearly height increment, results on LCR were variable when single tree species was observed in managed and OG forests. Sometimes higher values of LCR were recorded in OG than in managed forests, indicating in this way that overall vitality of regeneration in OG forests did not fall behind regeneration in managed forests.

The results in this study indicated that conifers had LCR below 0.6 in all studied forests. Only fir in OGF Janj had LCR around 0.6, but the number of sampled individuals was rather small. Beech generally exhibited higher values of LCR than conifers, except its seedlings (category 50-130 cm) in OGF Lom which had low 0.27 LCR (Table 17).

Table 17. Descriptives for live crown ratio (LCR) of two regeneration categories.

		Mean	Median	Min.	Max.	Std. error	N (plots)
Beech seedlings 10-50 cm	OGF Janj	0.58	0.60	0.25	0.93	0.05	18
	MF Janj	0.69	0.71	0.50	0.80	0.03	13
	OGF Lom	0.65	0.69	0.21	0.93	0.06	13
	MF Lom	0.71	0.78	0.36	0.95	0.03	39
Beech seedlings 50-130 cm	OGF Janj	0.83	0.84	0.68	0.95	0.03	9
	MF Janj	0.79	0.81	0.71	1.00	0.02	18
	OGF Lom	0.27	0.20	0.06	0.56	0.05	12
	MF Lom	0.81	0.85	0.37	0.94	0.03	18
Fir seedlings 10-50 cm	OGF Janj	0.58	0.57	0.46	0.70	0.04	6
	MF Janj	0.49	0.47	0.29	0.74	0.05	13
	OGF Lom	0.53	0.52	0.27	0.73	0.02	39
	MF Lom	0.43	0.44	0.1	0.8	0.02	59
Fir seedlings 50-130 cm	OGF Janj	0.65	0.65	0.61	0.69	0.01	5
	MF Janj	0.55	0.57	0.22	0.93	0.04	23
	OGF Lom	0.49	0.40	0.25	0.78	0.05	17
	MF Lom	0.58	0.60	0.16	0.84	0.03	23
Spruce seedlings 10-50 cm	OGF Janj	-	-	-	-	-	0
	MF Janj	0.56	0.60	0.26	0.75	0.08	6
	OGF Lom	0.58	0.58	0.40	0.80	0.05	8
	MF Lom	0.43	0.42	0.15	0.71	0.04	17
Spruce seedlings 50-130 cm	OGF Janj	0.40	0.42	0.27	0.48	0.05	4
	MF Janj	0.55	0.51	0.26	0.91	0.04	20
	OGF Lom	0.43	0.42	0.30	0.60	0.04	9
	MF Lom	0.54	0.55	0.30	0.65	0.06	5

We can notice that apical dominance ratio for conifers in Janj and Lom areas was far below threshold ratio of 1.0 (Table 18), and according to this indicator regeneration of fir and spruce in both managed and OG forests grew in low light environments.

Table 18. Apical versus lateral shoot in conifers.

		Mean	Median	Min.	Max.	Std. error	N (plots)
Fir seedlings 10-50 cm	OGF Janj	0.31	0.28	0.27	0.43	0.03	6
	MF Janj	0.39	0.40	0.13	0.67	0.05	13
	OGF Lom	0.26	0.25	0.10	0.45	0.01	39
	MF Lom	0.44	0.29	0.07	4.00	0.08	59
Fir seedlings 50-130 cm	OGF Janj	0.36	0.32	0.26	0.59	0.06	5
	MF Janj	0.66	0.57	0.11	2.44	0.11	23
	OGF Lom	0.46	0.40	0.11	1.05	0.07	17
	MF Lom	0.70	0.62	0.20	1.60	0.07	23
Spruce seedlings 10-50 cm	OGF Janj	-	-	-	-	-	0
	MF Janj	0.62	0.47	0.16	1.33	0.19	6
	OGF Lom	0.48	0.50	0.20	0.67	0.04	8
	MF Lom	0.47	0.36	0.12	1.67	0.09	17
Spruce seedlings 50-130 cm	OGF Janj	0.55	0.52	0.28	0.9	0.13	4
	MF Janj	0.60	0.62	0.17	1.36	0.07	20
	OGF Lom	0.51	0.58	0.10	0.82	0.07	9
	MF Lom	0.71	0.67	0.40	1.05	0.12	5

Plagiotropism in beech regeneration was not strongly expressed despite high values of GS which was generally dominated by conifers. Height/length ratio showed only slight differences between managed and OG forests in terms of "upright" growth of beech seedlings (Table 19).

Table 19. Height/length ratio of beech regeneration.

		Mean	Median	Min.	Max.	Std. error	N (plots)
Beech seedlings 10-50 cm	OGF Janj	0.77	0.77	0.57	0.95	0.02	18
	MF Janj	0.81	0.81	0.63	0.95	0.02	13
	OGF Lom	0.86	0.87	0.75	1.00	0.02	13
	MF Lom	0.79	0.80	0.41	0.96	0.02	39
Beech seedlings 50-130 cm	OGF Janj	0.69	0.70	0.56	0.77	0.02	9
	MF Janj	0.87	0.89	0.71	1.00	0.44	18
	OGF Lom	0.80	0.81	0.64	0.91	0.02	12
	MF Lom	0.85	0.86	0.74	0.98	0.02	18

Significant positive correlation was found between direct light and yearly height increment of beech (R = 0.48, df 81, $p \leq 0.05$) and spruce (R = 0.56, df 30, $p \leq 0.05$) which were 10-50 cm high as well as of silver fir 50-130 cm high (R = 0.47, df 64, $p \leq 0.05$). Diffuse light was stronger predictor of height increment of beech 50-130 cm high (R = 0.69, df 56, $p \leq 0.05$) and spruce 50-130 cm high (R = 0.72, df 36, $p \leq 0.05$), but direct light was also good and significant predictor with just slightly lower values of regression coefficients compared to diffuse light (beech R = 0.65 and spruce R = 0.67). Similarly, diffuse light had significant influence on silver fir height growth, but regression coefficient was somewhat smaller compared to direct light (R = 0.40). No significant correlation was determined for silver fir below 50 cm whatsoever (Figure 18). Regarding LCR, only direct light had significant positive influence on live crown ratio of spruce 50-130 cm high (R = 0.67, df 36, $p \leq 0.05$), wheras no significant influence was manifested on beech and fir as well as smaller spruce regeneration.

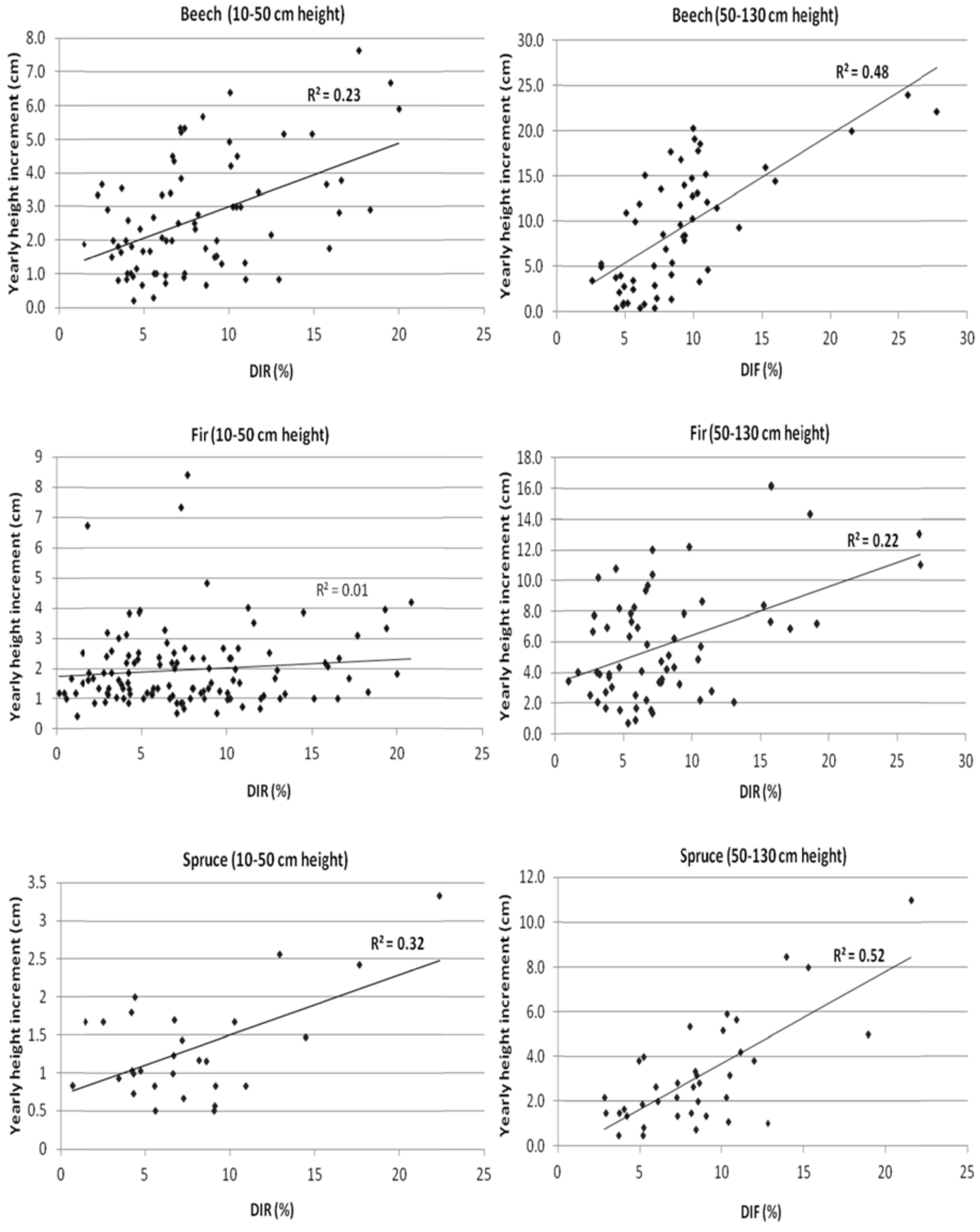


Figure 18. The influence of direct and diffuse light (%) on yearly height increment (cm) in beech, fir and spruce seedlings.

Fir BA proved to be a significant predictor of fir regeneration density. Namely, the density of fir regeneration was decreasing in both categories (up to 2 m height and from 2 m up to

7.5 cm dbh) with the increase of fir BA. On the other hand, beech BA was positively associated with the density of beech and spruce regeneration up to 2 m height, whereas the ingrowth of spruce from 2 m up to 7.5 cm dbh was negatively influenced with the increase of beech BA. These results refer to plots in all four studied forests (Table 20). However, when only plots in OG forests were observed it was found that BA of upperstory beech trees above 27.5 cm dbh had strong negative influence on the number of small middlestory beech trees from 7.5 cm to 27.5 cm dbh, and these two variables were significantly correlated in downward direction (R = 0.53, df = 31, $p \leq 0.05$; Figure 19). Total BA and conifers BA in OG forests did not negatively affect the number of middlestory beech trees. There was even slight positive regression between conifers BA and number of middlestory beech trees, but this was neither strong nor statistically significant regression.

Table 20. Results of the generalized linear multivariate analysis for regeneration from 10 cm up to 2 m height (Fir 2 m, Beech 2 m, Spruce 2 m) and regeneration from 2 m height up to 7.5 cm dbh (Fir 7.5 cm dbh, Beech 7.5 cm dbh, Spruce 7.5 cm dbh, Maple 7.5 cm dbh) predicted by beech BA, fir BA and cover of herbaceous plants.

Variables		Dependent						
Indepen-dent	Stats.	Fir 2 m	Beech 2 m	Spruce 2 m	Fir 7.5 cm dbh	Beech 7.5 cm dbh	Spruce 7.5 cm dbh	Maple 7.5 cm dbh
BA Fir	intercept	- 0.0389			- 0.0532			
	std. error	0.0097	ns	ns	0.0193	ns	ns	ns
	signif.	***			**			
BA Beech	intercept		0.0497	0.0568			- 0.1221	- 0.0437
	std. error	ns	0.0203	0.0258	ns	ns	0.0464	0.0187
	signif.		*	*			**	*
Herb. cover	intercept							0.0224
	std. error	ns	ns	ns	ns	ns	ns	0.0111
	signif.							*

* Significance code: p < 0.001
** Significance code: p < 0.01
*** Significance code: p < 0.05

Simultaneously with independent variables shown in the Table 20, the influence of direct light, diffuse light and spruce BA on density of regeneration below 2 m was observed, but no significant results were obtained for these variables.

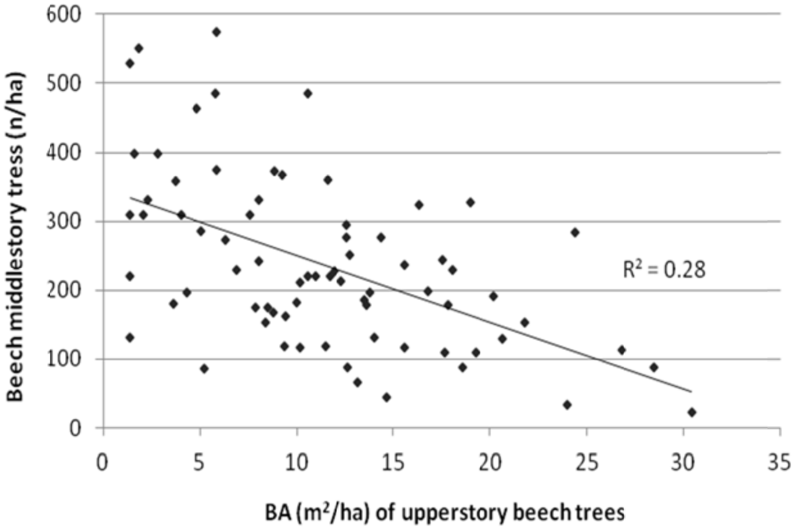


Figure 19. Significantly negative regression of BA of upperstory beech trees above 27.5 cm dbh on the number of small middlestory beech trees (dbh between 7.5 cm and 27.5 cm) in OG forests Janj and Lom.

5.6 TREE SPECIES COMPOSITION

As regards composition by number of trees above 7.5 cm at breast height, OGF Janj was mostly composed of beech (63.4 %), followed by fir and spruce which took part with 22.9 % and 13.9 %, respectively. Similar ratio among tree species was determined in OGF Lom (beech : fir : spruce : maple = 60.5 % : 24.9 % : 14.1 % : 0.4 %, respectively). On the other hand, in MF Janj most present in number were fir trees (48.2%), whereas beech and spruce shares were almost equal (25.8 % and 24.3 %, respectively). Maple in this forests participated with 1.8 %. In MF Lom beech and fir dominated equally with 35.9 % and 35.0 %, while share of spruce in terms of tree number fell behind (26.4 %). In this forest share of maple amounted to only 2.8 %, yet this was the highest share of this species among studied forests (Table 21, Figure 20).

Table 21. Species mixture by number of trees.

Stands	Beech n/ha	Fir n/ha	Spruce n/ha	Maple n/ha	Total n/ha
OGF Janj	328	117	72	0	516
Janj 31a	227	475	57	39	798
Janj 50d	177	252	186	2	617
Janj 56a	53	573	168	9	804
Janj 57/1b	212	205	195	6	617
Janj 58a	210	136	221	4	571
Average for MF Janj	176	328	165	11	681
OGF Lom	296	122	69	2	489
Lom 59a	76	245	129	26	475
Lom 67a	171	310	166	15	662
Lom 68a	286	184	109	28	607
Lom 76a	358	177	135	7	677
Lom 79a	175	123	245.1	7	551
Average for MF Lom	213	208	157	17	594

Differences among studied forests in terms of species composition by tree number were tested with two-variable Chi-square test with three degrees of freedom which yielded non-significant results for pairs OGF Janj *vs*. OGF Lom and MF Janj *vs*. MF Lom, while significant difference at $p \leq 0.05$ was indicated for two pairs:

- OGF Janj *vs*. MF Janj $\chi^2 = 26.77$
- OGF Lom *vs*. MF Lom $\chi^2 = 16.81$

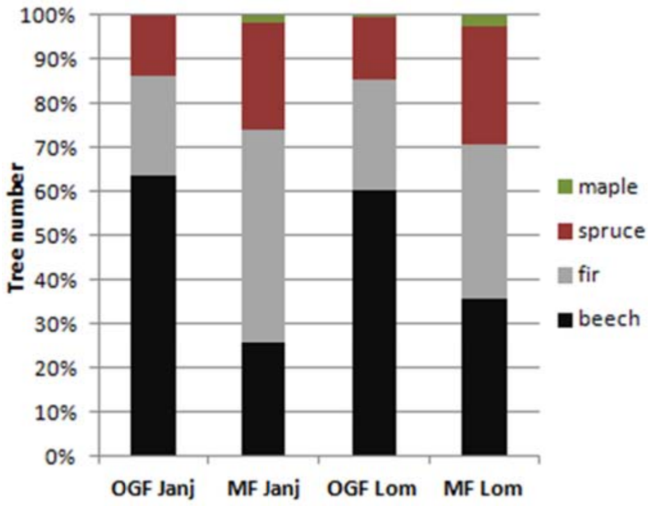


Figure 20. Composition of studied forests by number of trees.

Considering BA, in composition of OGF Janj silver fir made 52.0 %. Norway spruce and European beech contributed with 30 % and 18 %, respectively. These three species combined made 66.7 m^2/ha, and no surprise that sycamore maple was not present in the upper canopy, though site conditions suit this species well. Somewhat lower percentual share of fir was found in MF Janj which contained 49.5 %. Norway spruce share in BA was slightly greater than that of European beech, while sycamore maple was also present in BA of MF Janj, however, its share was only 0.8 % (Table 22, Figure 21).

Table 22. Species composition by basal area (BA).

Stands	Beech m^2/ha	Fir m^2/ha	Spruce m^2/ha	Maple m^2/ha	Total m^2/ha
OGF Janj	11.8	34.7	20.2	0	66.7
Janj 31a	15.1	17.5	2.3	0.6	35.5
Janj 50d	7.3	15.1	10.7	0.0	33.1
Janj 56	2.9	24.0	9.1	0.6	36.5
Janj 57/1b	8.1	17.0	14.9	0.1	40.1
Janj 58	7.4	14.4	10.6	0.1	32.5
Average for MF Janj	8.2	17.6	9.5	0.3	35.5
OGF Lom	14.3	22.2	10.4	0.3	47.1
Lom 59a	4.1	16.4	27.6	1.2	49.2
Lom 67	4.4	19.5	16.0	0.6	40.5
Lom 68	8.9	14.9	15.6	1.8	41.3
Lom 76	13.0	9.5	12.5	0.5	35.5
Lom 79	4.0	5.7	30.5	0.5	40.7
Average for MF Lom	6.9	13.2	20.4	0.9	41.4

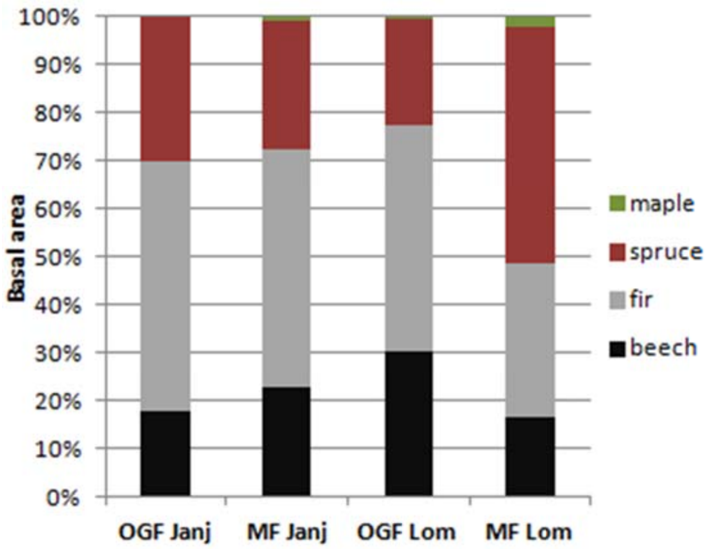


Figure 21. Composition of studied forests by basal area.

BA of OGF Lom was mainly composed of fir and beech (47.1 % and 30.3 %, respectively). Spruce made up to 22.0 % and maple was hardly present with 0.7 %. In MF Lom spruce was prevailing with 48.7 %, fir attributed with 31.7 %, and beech had share of 17.4 %. In this forest maple was slightly more perceptible than in other studied forests since its share in BA amounted to 2.2 %.

Similar outcomes of testing differences in species composition concerning BA were obtained like in case of species composition by tree number since OG forests significantly differed from managed forests; however, no difference was found when two OG forests were compared or when two managed forests were compared to each other. Consequently, significant results of two-variable Chi-square tests at $p \leq 0.05$ for species composition pertaining to BA refer to the remaining two pairs:

- OGF Janj *vs*. MF Janj $\chi^2 = 11.19$
- OGF Lom *vs*. MF Lom $\chi^2 = 18.02$

In the composition of GS in OGF Janj fir took part with 53.3 %, spruce followed with 30.9 %, and beech had its share of only 15.8 %. As we can notice, significant discrepancy in tree species ratio occurred when different criteria for species composition were applied, so that beech was most dominant in tree number, however, it was less present in BA and GS compared to fir and spruce. Details on GS composition in studied forests are given in Table 23.

Table 23. Species mixture by growing stock (GS).

	Beech		Fir		Spruce		Maple		Total
Stands	m^3/ha	%	m^3/ha	%	m^3/ha	%	m^3/ha	%	m^3/ha
OGF Janj	191.6	15.8	647.6	53.3	376.0	30.9	0	0	1215.1
Janj 31	228.8	48.2	210.4	44.4	30.0	6.3	5.1	1.1	474.2
Janj 50d	103.5	22.0	210.0	44.6	157.0	33.3	0.3	0.1	470.7
Janj 56	46.0	9.4	304.0	62.0	129.1	26.3	11.0	2.2	490.0
Janj 57/1b	109.5	18.5	252.5	42.6	228.5	38.6	1.6	0.3	592.1
Janj 58a	99.9	21.4	214.4	45.9	151.3	32.4	2.0	0.4	467.6
Average for MF Janj	117.5	23.9	238.2	47.9	139.2	27.4	4.0	0.8	498.9
OGF Lom	213.0	27.9	366.1	48.0	178.3	23.4	5.7	0.8	763.1
Lom 59a	69.7	8.3	260.1	31.1	488.7	58.4	18.7	2.2	837.2
Lom 67a	62.3	10.1	293.2	47.7	251.7	40.9	7.4	1.2	614.6
Lom 68a	125.9	19.0	239.0	36.2	266.7	40.4	29.3	4.4	660.9
Lom 76a	202.9	36.6	142.6	25.7	201.4	36.3	7.3	1.3	554.3
Lom 79a	62.8	9.6	83.5	12.8	499.7	76.4	8.0	1.2	654.1
Average for MF Lom	104.7	16.7	203.7	30.7	341.6	50.5	14.1	2.1	664.2

5.6.1 Mixed vs. monospecific plots

When considering stem number criteria, 15 % of all plots in OGF Janj and 5 % in OGF Lom were monospecific plots, whereas beech was the only species that tended toward creation of pure cohorts. On the other hand, in 11.7 % of monospecific plots in MF Janj only fir exhibited such tendency. MF Lom had 6.7 % of monospecific plots whereas 3.3 % were pure fir plots, 1.7 % pure beech plots and 1.7 % pure spruce plots. The absolute numbers of mixed and monospecific plots based on stem number are shown in Figure 22.

On the other hand, when considering BA criteria in OGF Janj there were 17.5 % of pure fir plots and 5 % of pure spruce plots, while in OGF Lom there was 5 % of pure fir plots. In MF Janj the number of pure plots for fir, beech and spruce was 15 %, 1.7 %, and 6.7 %, respectively. In MF Lom there was 11.7 % of pure spruce plots, while beech and fir created only 1.7 % of pure plots each. The absolute number of mixed and monospecific plots based on BA are shown in Figure 23.

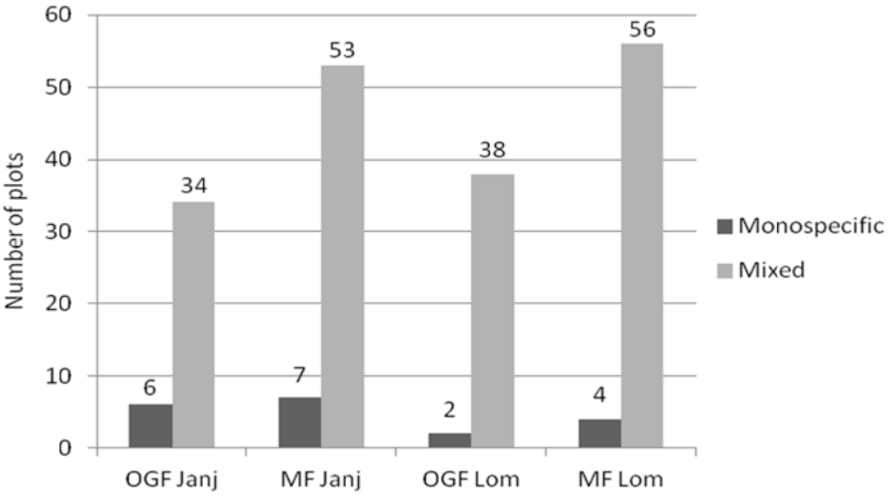


Figure 22. The number of mixed and monospecific plots based on stem number.

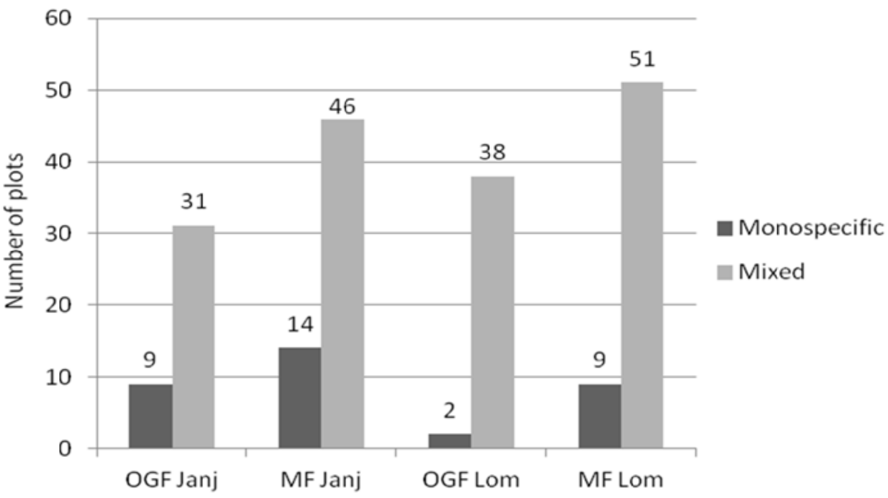


Figure 23. The number of mixed and monospecific plots based on BA.

5.7 REPLACEMENT PATTERNS AND NEIGHBORHOOD EFFECTS

In understory of OGF Janj beech regeneration (10 cm height up to 7.5 cm dbh) was prevailing in density on 77.5 % of the area (of the measured plots), fir dominated on 10 %, sycamore maple 7.5 %, and Norway spruce was least present dominating only on 5 % of all plots in the core area. In next stage (middlestory) beech was omnipresent dominating on 39 plots or 97.5 % of the area, while Norway spruce was found to be dominant only on one plot. In the upper canopy of OGF Janj most numerous were silver fir trees which were dominant on 25 plots, while Norway spruce and European beech dominated in this stage on 8 and 7 plots, respectively.

Figure 24. Dense beech regeneration in OGF Janj.

On plots where beech was found as dominant species in the upperstory mostly the same species dominated the understory (5 out of 7 plots), while fir and maple grew under beech only on one plot each. In the middlestory only fir was found on one plot under beech mature trees. Therefore, beech replaces itself thoroughly (dominates all three layers) on 4 plots out of 7. On the other hand, when fir was dominant in upperstory beech in understory was dominant on 21 out of 25 plots, while spruce and maple dominated two plots each. Unlike beech, silver fir hence didn’t exhibit self-replacement pattern in OGF Janj. Under mature fir trees, beech regeneration was found to be dominant in 84 % of cases, while spruce and maple regeneration under the same conditions were dominant in 8 % of cases each. Fir regeneration was not dominant under mature fir trees whatsoever. Middlestory under mature fir trees was completely occupied by beech allowing thus no ingrowth of other species.

On plots where Norway spruce was dominant species in the canopy layer, in 62.5 % cases beech was dominant in understory and fir in 37.5 % cases. Middlestory under mature spruce trees is also completely occupied by beech. Therefore, fir and spruce did not exibit self-replacement patterns in OGF Janj. Most of the core area in OGF Janj was characterized by replacement of two tree species through mentioned three layers. However, on several plots there were three species each occurring in different layer (story). Such arrangement was found on 17.5 % of the area. In 12.5 % cases beech, fir and spruce replace each other through layers in various ways, while in 5 % cases maple was in understory being overtopped by beech in middlestory and fir in canopy layer. Table 24 shows absolute number of plots in OGF Janj with dominant species in different stories.

Table 24. Number of plots in OGF Janj with dominant species in different stories.

		Dominant species in upperstory		
		Spruce	Fir	Beech
Dominant species in understory	Fir	3	0	1
	Beech	5	21	5
	Spruce	0	2	0
	Maple	0	2	1
Dominant species in middlestory	Fir	0	0	1
	Beech	8	24	6
	Spruce	0	0	1
	Maple	0	0	0

In MF Janj we see different replacement pattern since fir regeneration and small trees seem to grow well under mature fir trees, as well as under spruce and beech mature trees (Table 25). Beech regeneration and small trees also here were more often dominant under mature fir than mature spruce and beech trees, however, difference in MF Janj was not so distinctive as in OGF Janj. In regeneration stage spruce most effectively occupied forest floor under mature fir trees. Interestingly, spruce small trees mostly dominated plots under mature spruce trees. These are useful information on tree species “cooperation”, nevertheless, the results from managed forests need to be treated with caution since management regime has significant influence on structure and composition of forest stands.

Table 25. Number of plots in MF Janj with dominant species in different stories.

		Dominant species in upperstory		
		Spruce	Fir	Beech
Dominant species in understory	Fir	13	13	8
	Beech	6	9	3
	Spruce	1	3	1
	Maple	0	2	0
Dominant species in middlestory	Fir	7	16	5
	Beech	4	6	5
	Spruce	9	5	1
	Maple	0	0	1

In the understory of OGF Lom fir was dominant species in number on 17 plots or 42.5 % of the area, beech regeneration on 15 plots or 37.5 %, and spruce regeneration on 8 plots or 20 % of the area. In the middlestory of this forest beech small trees were clearly dominant on 38 plots, that is, in 95 % of all plots, while fir and spruce small trees dominated only on 2.5 % of the area each. In the upperstory of OGF Lom beech was also numerously the most dominant species on 21 plot or 52.5 % of cases, fir dominated on 12 plots or 30 %, and spruce on 7 plots or 17.5 % of the core area. On five plots in OGF Lom two species were equally numerous in the upperstory creating hence unclear picture of stand layering; consequently, for those five plots replacement pattern was not determined. In MF Janj one plot and in MF Lom six plots had unclear replacement pattern.

In OGF Lom we see that fir and spruce regeneration most often dominate in the understory of those plots in which beech dominates in the upperstory. Contrary to OGF Janj, in this old-growth forest fir regeneration dominated in understory of five plots where mature fir trees were also dominant in the upperstory. Beech regeneration was more-less equally dominant on plots under different tree species. Regarding middlestory, beech small trees were predominant throughout the whole area of OGF Lom. They exhibited best ingrowth under mature beech trees, but were also most dominant on plots where fir and spruce dominated the upperstory (Table 26).

Table 26. Number of plots in OGF Lom with dominant species in different stories.

		Dominant species in upperstory		
		Spruce	Fir	Beech
Dominant species in understory	Fir	3	5	8
	Beech	3	5	5
	Spruce	0	0	6
	Maple	0	0	0
Dominant species in middlestory	Fir	0	0	0
	Beech	6	10	19
	Spruce	0	0	0
	Maple	0	0	0

Figure 25. In OGF Lom fir and spruce regeneration often occupy downed logs.

In understory of MF Lom fir regeneration was prevailing in 65 % of cases, while beech and maple dominated on 16.7 % of the area each, and spruce regeneration only on 1.7 % of the area. In middlestory of this forest domination of fir small trees was determined on 45 % of the area, beech small trees dominated 43.3 % and spruce small trees 11.7 % of the area. Finally, upperstory of MF Lom was dominated by spruce trees on 48.3 % of the area, fir trees were dominant on 30 %, beech trees on 18.3 % and maple trees dominated only on 2 plots or 1.7 % of the area in MF Lom.

Regeneration pattern in this managed forest indicated that fir regeneration and small trees successfully grow on those microlocations (plots) where spruce or fir dominate the upperstory. Somewhat lower dominance of fir regeneration was noticed when mature beech trees were dominant on plots. On the other hand, beech small trees were most dominant on plots where mature spruce trees dominated the upperstory (Table 27).

Table 27. Number of plots in MF Lom with dominant species in different stories.

		Dominant species in upperstory		
		Spruce	Fir	Beech
Dominant species in understory	Fir	19	9	6
	Beech	4	4	1
	Spruce	0	1	0
	Maple	5	3	2
Dominant species in middlestory	Fir	11	11	1
	Beech	15	6	5
	Spruce	2	0	3
	Maple	0	0	0

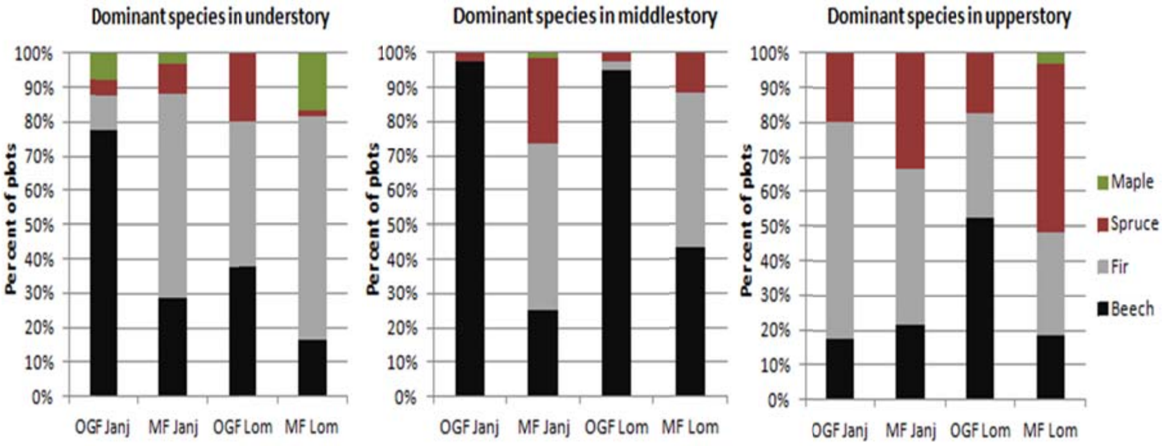


Figure 26. Dominant species in understory, middlestory and upperstory on plots in studied forests.

5.7.1 Transition probabilities

For category of seedlings ≤ 10 cm in OGF Janj transition matrix indicated that beech seedlings had highest probabilities to potentially replace mature beech, fir and spruce trees. Fir seedlings followed with noticeably lower probability values, while seedlings of spruce and maple had the lowest chances to occur and replace mature trees in current climatic and structural conditions of OGF Janj. Beech from regeneration stage had also highest chances to replace mature trees of all three species, whereas ratios for fir regeneration were lower and for spruce and maple virtually the same compared to seedlings phase (Table 28). Within next upper developmental phase, chances of beech to replace mature trees were growing across matrices, so the highest probabilities were obtained for beech small middlestory trees. In the Table 28 we see that beech regeneration has the highest ratios of occurrence even under small trees indicating therefore high level of durability in suppressed conditions.

Table 28. Transition matrices for OGF Janj.

		Small seedlings ≤ 10 cm			
		Beech	Fir	Spruce	Maple
Upperstory Trees	Beech	0.57	0.29	0.08	0.06
	Fir	0.59	0.25	0.08	0.07
	Spruce	0.65	0.23	0.07	0.05
		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory Trees	Beech	0.73	0.14	0.07	0.06
	Fir	0.69	0.11	0.09	0.11
	Spruce	0.68	0.20	0.05	0.06
		Small trees (7.5–27.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory Trees	Beech	0.74	0.15	0.10	0.00
	Fir	0.83	0.10	0.07	0.00
	Spruce	0.83	0.09	0.08	0.00
		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Small Trees	Beech	0.63	0.16	0.10	0.11
	Fir	0.75	0.13	0.04	0.08
	Spruce	0.68	0.16	0.09	0.07

In MF Janj fir seedlings exhibited highest transition probabilities for replacement of mature beech and spruce trees. Beech seedlings were falling behind fir seedlings having just slightly higher chances to replace mature fir trees. Spruce and maple also in this forest exhibited low ratios, still somewhat higher than in OGF Janj. On the other hand, beech regeneration had highest probabilities to replace canopy trees. In next, middlestory level, again fir takes over with highest probabilities for canopy replacement, whereas chances of spruce in this phase noticeably increased compared to earlier phases. We may, however, not forget that trees at middlestory level are partly subject to marking and cutting in managed forests which may lead to underestimation of beech middlestory trees capability to occupy upperstory of a stand (Table 29).

Table 29. Transition matrices for MF Janj.

		Small seedlings ≤ 10 cm			
		Beech	Fir	Spruce	Maple
Upperstory trees	Beech	0.25	0.53	0.14	0.09
	Fir	0.42	0.35	0.07	0.16
	Spruce	0.38	0.45	0.10	0.07
		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory trees	Beech	0.53	0.23	0.11	0.13
	Fir	0.47	0.33	0.14	0.05
	Spruce	0.50	0.31	0.15	0.05
		Small trees (7.5–27.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory trees	Beech	0.28	0.51	0.20	0.00
	Fir	0.24	0.53	0.23	0.00
	Spruce	0.28	0.34	0.38	0.00
		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Small trees	Beech	0.48	0.29	0.16	0.06
	Fir	0.50	0.33	0.08	0.09
	Spruce	0.44	0.32	0.21	0.03

In OGF Lom transition odds differ from those in OGF Janj in a way that beech regeneration in OGF Lom has lower probabilities, while fir and spruce have higher probabilities for canopy replacement than in OGF Janj. In fact, fir regeneration had the best outlooks from regeneration to replace middlestory trees as well as mature canopy trees. What was very interesting here is that fir regeneration exhibited high tendency to replace not only mature beech and spruce trees, but fir trees as well. In middlestorey of OGF Lom yet, beech played the most significant role and had by far highest odds to enter upperstorey from middlestory level (Table 30). Please note that transition (occurrence) matrices for small seedlings in OGF Lom and MF Lom were not calculated, and consequently not compared due to unavailability of data for small seedlings in MF Lom.

Table 30. Transition matrices for OGF Lom.

		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory trees	Beech	0.36	0.39	0.24	0.02
	Fir	0.38	0.41	0.20	0.02
	Spruce	0.29	0.54	0.16	0.01
		Small trees (7.5–27.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory trees	Beech	0.70	0.19	0.10	0.01
	Fir	0.72	0.19	0.09	0.00
	Spruce	0.68	0.20	0.12	0.00
		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Small trees	Beech	0.38	0.41	0.19	0.02
	Fir	0.29	0.46	0.23	0.01
	Spruce	0.26	0.47	0.27	0.01

In neighboring MF Lom we see that management activities favored regeneration and small trees of beech against fir and spruce compared to OGF Lom. Besides, spruce regeneration in OGF Lom had higher odds, while in MF Lom spruce small trees had higher possibility to replace canopy trees. Similarly, fir regeneration in OGF Lom had higher ratios, on the other hand, in MF Lom fir small trees had higher odds to occupy upperstorey (Table 31) than in OGF Lom.

Table 31. Transition matrices for MF Lom.

		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory trees	Beech	0.50	0.26	0.07	0.17
	Fir	0.47	0.25	0.09	0.20
	Spruce	0.48	0.23	0.06	0.24
		Small trees (7.5–27.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Upperstory trees	Beech	0.49	0.33	0.19	0.00
	Fir	0.41	0.45	0.14	0.00
	Spruce	0.47	0.36	0.17	0.00
		Regeneration (10 cm height–7.5 cm dbh)			
		Beech	Fir	Spruce	Maple
Small trees	Beech	0.50	0.24	0.07	0.18
	Fir	0.48	0.23	0.09	0.19
	Spruce	0.49	0.24	0.06	0.21

5.8 DIAMETER STRUCTURE

Tree density was the greatest in MF Janj with 682 trees/ha. In MF Lom stocking density was characterized with 596 trees/ha, while OGF Janj and OGF Lom followed with 516 and 489 trees per hectare, respectively. In OGF Janj variation of number of trees on sample plots ranged from 243 to 995 trees/ha. More descriptive statistics are given in Table 32.

Table 32. Descriptives for tree density (trees/ha).

Statistics	OGF Janj	MF Janj	OGF Lom	MF Lom
Mean	516.4	681.5	489.4	595.6
Std. Error	24.5	27.5	18.9	23.2
Median	487.0	663.0	498.0	553.0
Range	752.0	774.0	669.0	730.0
N (plots)	40	60	40	60

Independent t-test involving total means (total for all tree species) of number of trees on sampled plots indicated significant differences between pairs OGF Janj - MF Janj and OGF Lom - MF Lom, but also between MF Janj and MF Lom (Table 33, Figure 27).

Table 33. Results of t-tests for equality of tree density means in studied forests.

Tested pairs	t	df	*p*-value	Mean difference	Std. error difference	95% Confidence interval lower	upper
OGF Janj - MF Janj	- 4.20	78	**0.0000**	- 165.02	39.25	- 242.93	- 87.11
OGF Janj - OGF Lom	0.87	78	**0.3870**	27.02	31.03	- 34.75	88.81
OGF Lom - MF Lom	- 3.28	78	**0.0010**	- 106.18	32.34	- 170.37	- 41.99
MF Janj - MF Lom	2.38	118	**0.0190**	85.86	35.98	14.61	157.12

While differences old-growth vs. managed forest are conceivable and to certain extent acceptable, it was surprising that two managed forests differed significantly in stand density. Therefore, closer look was taken into individual managed stands.

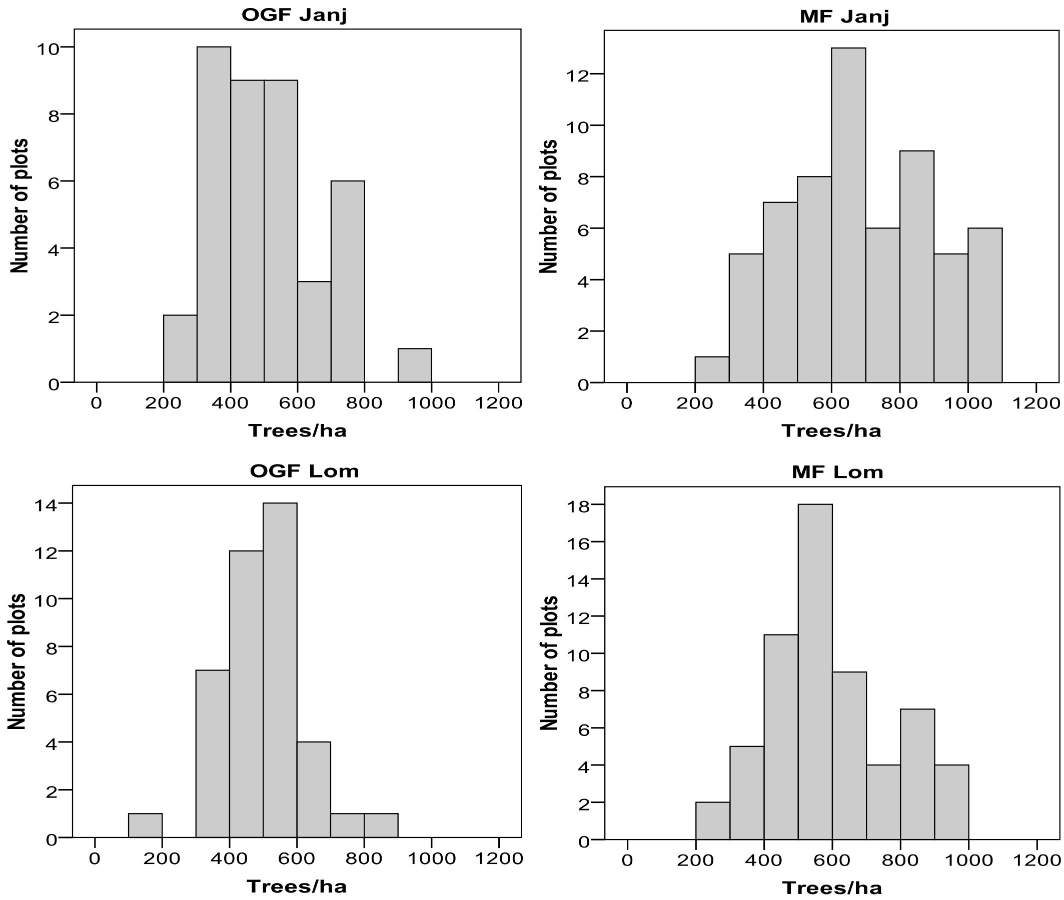


Figure 27. Tree density frequencies in studied forests.

Analysis of variance yielded significant results and post hoc Tukey HSD test provided two subsets of similar stands in Janj area (F = 5.23; p = 0.0000). Managed stands 50d, 57/1b, 58a, and OGF Janj, belong to the first subset of similar stands, while managed stands 31a, 50d, 56a and 57/1b belong to the second subset of similar stands. However, all individual managed stands had higher absolute tree densities compared to adjacent OG forests.

Alike for Janj area, ANOVA indicated significant differences between individual managed stands in Lom and OGF Lom (F = 3.54; p = 0.0070). In this case post hoc Tukey HSD test also differentiated two subsets of similar stands in terms of stand density. First subset comprised OGF Lom and managed stands 59a, 68a and 79a, while second subset of similar stands comprised OGF Lom and managed stands 67a, 68a, 76a and 79a. Such result for Lom area implies that greater differences occur among particular managed stands than between OGF Lom and managed stands.

5.8.1 Diameter distributions in single stands

In four managed stands in Janj area dbh distribution for all species included was NE and only one stand had IQ distribution. Fir, beech and spruce exhibited NE shape in three stands and IQ shape in one stand each. RS pattern had only fir in one managed stand in Janj. In one stand regression for beech was not significant at $p = 0.05$ for any of seven combinations of dbh, dbh^2 and dbh^3 (Table 34).

Table 34. Distribution shapes in single managed Janj stands when the span of dbh classes was 10 cm.

	Managed stand 31a				Managed stand 50d			
	Fir	Spruce	Beech	Total	Fir	Spruce	Beech	Total
RMSE	0.10	0.27	0.15	0.07	0.18	0.20	0.13	0.10
Adj. R^2	0.98	0.68	0.71	0.99	0.91	0.90	0.95	0.98
N (dbh class)	6	5	5	6	8	7	6	8
Shape	NE	NE	IQ	NE	NE	NE	NE	NE
	Managed stand 56a				Managed stand 57/1b			
RMSE	0.11	0.04	Nonsig.	0.05	0.09	0.09	0.06	0.04
Adj. R^2	0.96	0.99	Nonsig.	0.99	0.97	0.97	0.99	0.99
N (dbh class)	6	6	6	6	8	7	5	8
Shape	NE	IQ	Nonsig.	NE	RS	IQ	NE	NE
	Managed stand 58a							
RMSE	0.13	0.20	0.04	0.13				
Adj. R^2	0.93	0.89	0.99	0.97				
N (dbh class)	8	6	5	8				
Shape	IQ	NE	NE	IQ				

Table 35. Distribution shapes in single managed Lom stands when the span of dbh classes was 10 cm.

	Managed stand 59a				Managed stand 67a			
	Fir	Spruce	Beech	Total	Fir	Spruce	Beech	Total
RMSE	0.24	0.29	0.11	0.29	0.32	0.20	0.28	0.17
Adj. R^2	0.75	0.61	0.90	0.82	0.75	0.87	0.85	0.92
N (dbh class)	7	9	5	9	7	7	6	7
Shape	IQ	IQ	IQ	IQ	NE	IQ	NE	NE
	Managed stand 68a				Managed stand 76a			
RMSE	0.32	0.13	0.17	0.19	0.17	0.23	0.22	0.11
Adj. R^2	0.72	0.88	0.95	0.92	0.91	0.67	0.91	0.98
N (dbh class)	9	8	6	9	7	7	8	8
Shape	NE	RS	NE	NE	NE	IQ	NE	NE
	Managed stand 79a							
RMSE	0.22	0.09	0.28	0.45				
Adj. R^2	0.84	0.87	0.86	0.70				
N (dbh class)	6	6	8	8				
Shape	NE	UNI	CO	IQ				

In managed Lom area three stands had NE and two stands IQ distribution for total trees. Fir had NE shape in four and beech in three stands. Spruce in managed Lom area did not exhibit NE shape at all; it had IQ shape in three stands, RS in one stand and UNI distribution in one stand as well. Fir and beech had IQ shape in one stand each. CO dbh distribution was found only for beech in one managed stand in Lom (Table 35). Please note that slight differences may occur between results presented above and results for distribution shapes when the span of dbh classes equals 5 cm.

5.8.2 Comparison of dbh distributions in OG forests and managed forests

The frequency distribution of diameters in OGF Janj was dominated by beech within small diameter classes, but its share sharply declined towards medium and large diameter classes. Large diameter classes were dominated by fir and spruce (Figures 28, 29). The best-fitting multiple regression model for dbh frequency distribution for fir and spruce indicated UNI shape, while for beech and cumulative distribution RS shape was indicated (Table 36). Only for OGF Janj results were the same, if tested for 5 or 10 cm dbh classes. Interestingly, MF Janj (average of five managed stands in Janj) also exhibited RS pattern for overall trees. In this forest fir and beech had the same form, only spruce had IQ shape. However, when dbh class span of 5 cm was applied the shape of overall trees was IQ, as for beech and fir. In this analysis spruce kept IQ shape.

On the other hand, in OGF Lom overall distribution was NE, whereas fir and spruce had IQ and beech RS distribution. In MF Lom overall dbh distribution was IQ, fir had NE, spruce UNI and beech CO distribution (Table 36, Figure 30). However, when dbh class span of 5 cm was applied the shape of overall trees was NE in MF Lom. Results for fir, spruce and beech in MF Lom did not change regardless of dbh class span. Analysis with dbh class span of 5 cm for OGF Lom yielded different distribution shapes of singular species, so fir had RS, spruce NE, and beech also NE distribution; nevertheless, distribution of overall trees in OGF Lom remained NE regardless of dbh class span.

Table 36. Parameters of the best-fitting model for multiple regressions between the base 10 logarithm of trees per hectare and all possible combinations of dbh, dbh^2 and dbh^3 (dbh class span was 10 cm) for OG forests Janj and Lom and adjacent managed forests.

	MF Janj				OGF Janj			
	Fir	Spruce	Beech	Total	Fir	Spruce	Beech	Total
RMSE	0.03	0.04	0.01	0.03	0.18	0.14	0.07	0.11
Adj. R^2	0.99	0.99	1.00	0.99	0.86	0.85	0.99	0.97
N (dbh class)	8	7	6	8	12	11	7	12
Shape	RS	IQ	RS	RS	UNI	UNI	RS	RS
	MF Lom				OGF Lom			
RMSE	0.18	0.18	0.15	0.16	0.33	0.22	0.04	0.21
Adj. R^2	0.92	0.94	0.96	0.96	0.74	0.85	0.99	0.94
N (dbh class)	9	9	8	9	12	11	7	12
Shape	NE	UNI	CO	IQ	IQ	IQ	RS	NE

RMSE - root mean square error, UNI – convex or unimodal shape, RS - rotated sigmoid shape,
IQ – increasing-*q*, CO – concave (sensu Janowiak *et al*., 2008)

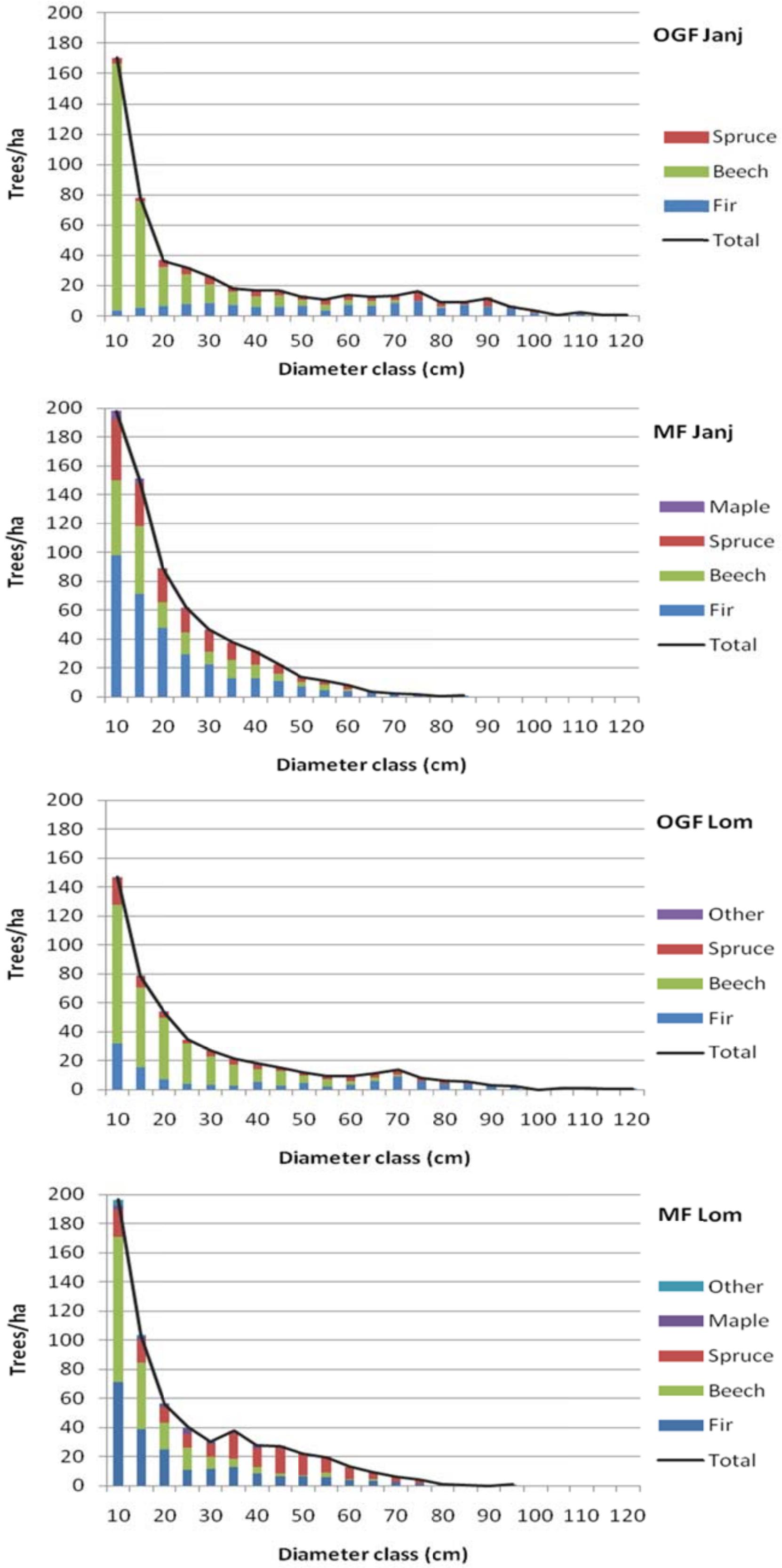


Figure 28. Diameter distributions of living trees in studied forests.

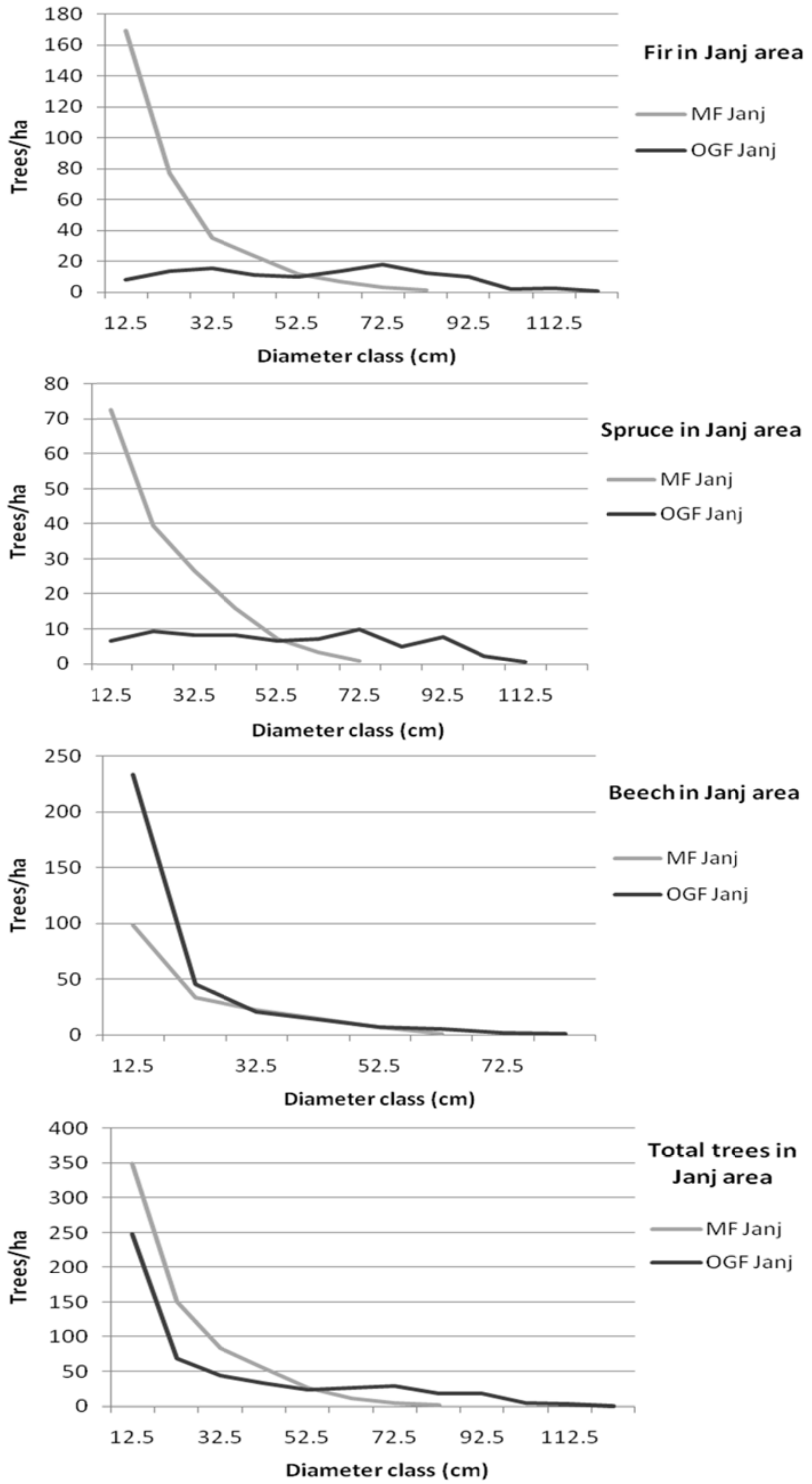


Figure 29. Distributions of fir, spruce, beech, and overall trees in MF Janj and OGF Janj.

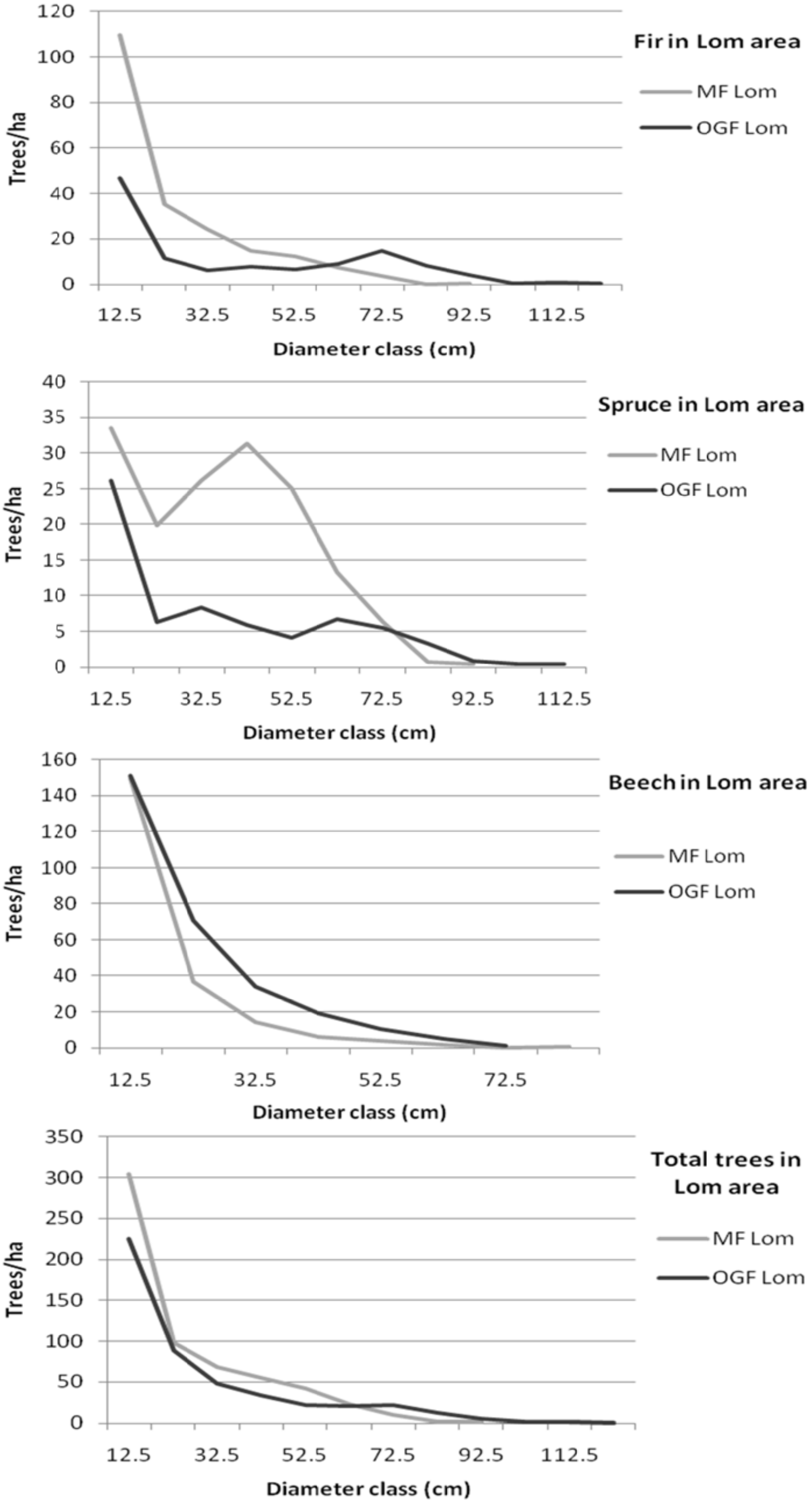


Figure 30. Distributions of fir, spruce, beech, and overall trees in MF Lom and OGF Lom.

Considering only managed single stands, NE distribution was prevailing (Table 37).

Table 37. Distribution shapes for all ten managed forests.

Shape	Beech	Fir	Spruce	Total (all species)
NE	6	7	3	7
IQ	2	2	5	3
RS		1	1	
UNI			1	
CO	1			
nonsign. model	1			

Regarding total number of large trees with dbh over 50 cm in OGF Janj amounted to 115 per ha (fir 64 trees/ha, spruce 37 trees/ha, beech 14 trees/ha), in OGF Lom 73 per ha, while in managed forests Lom and Janj there numbers were 62 and 37 per hectare, respectively. In the latter trees with dbh above 80 cm were almost absent, while in OGF Janj there was 39, and in OGF Lom 13 such trees per hectare (Table 38).

Table 38. Frequency of large trees (n/ha) in studied forests.

DBH class	OGF Janj	MF Janj	OGF Lom	MF Lom
50	13	14	12	22
55	11	11	10	20
60	14	8	9	13
65	13	3	12	10
70	13	3	13	6
75	16	1	8	4
80	9	0	6	1
85	9	1	5	0
90	12		3	0
95	6		2	1
100	3		0	
105	1		1	
110	2		1	
115	1			
120	1			
Total	122	42	81	76

5.8.3 Mean diameters

The greatest mean diameter was determined in OGF Janj (41.3 cm), on second place was OGF Lom with 35.4 cm, while mean diameters of managed forests Lom and Janj were 30.4 cm and 26.5 cm, respectively.

Table 39. Descriptive statistics for total mean diameters (cm).

Statistics	OGF Janj	MF Janj	OGF Lom	MF Lom
Mean	41.3	26.5	35.4	30.4
Std. Error	1.1	0.6	0.8	0.8
Median	41.0	25.9	35.1	29.5
Range	32.4	21.5	26.0	28.9
N (plots)	40	60	40	60

Table 40. Mean diameters (cm) for tree species in studied forests.

	OGF Janj	MF Janj	OGF Lom	MF Lom
European beech	22.2	25.7	25.2	20.4
Silver fir	60.6	28.7	49.2	27.6
Norway spruce	58.2	24.6	43.3	39.9
Sycamore maple	-	18.8	-	26.0

We see that measures of variability for mean diameters of all species combined were greater in OGF Janj than for MF Janj, however, they were greater in MF Lom than in OGF Lom. Interquartile range of mean diameters also indicated such relationship between OG and managed forests (Figure 31).

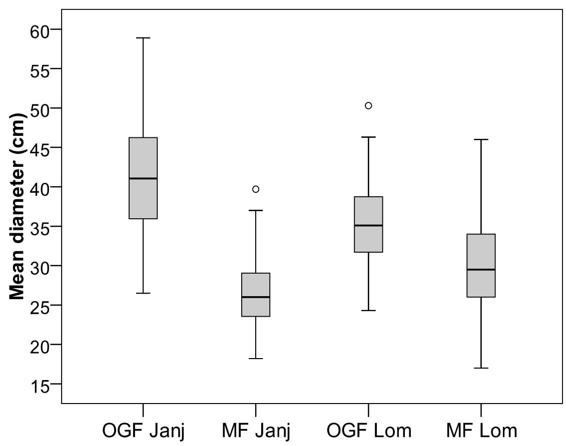


Figure 31. Boxplot of total mean diameters (all species combined).

In Figure 32 we see that most plots in OGF Janj had mean diameter between 35 and 40 cm dbh, and second peak occurred between 46 and 50 cm dbh. In MF Janj most plots had mean diameter between 23 and 25 cm dbh. In OGF Lom most plots had mean diameter between 30 and 37 cm dbh, and in MF Lom between 25 and 30 cm dbh.

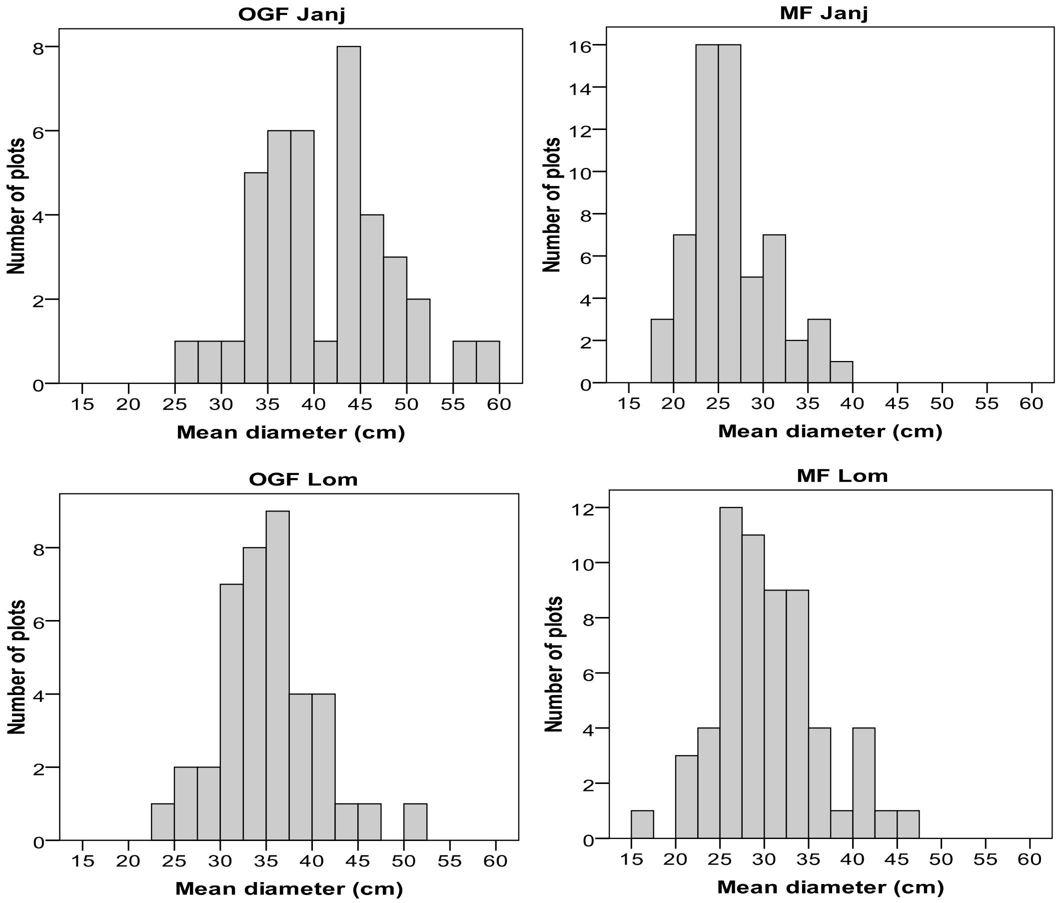


Figure 32. Mean diameter frequencies in studied forests

Results of t-test regarding mean diameters indicated significant differences among all pairs of studied objects (Table 41).

Table 41. Results of t-tests for equality of mean diameters.

Tested pairs	t	df	*p*-value	Mean difference	Std. error difference	95% Confidence interval lower	95% Confidence interval upper
OGF Janj - MF Janj	11.03	78	**0.0000**	14.85	1.34	12.17	17.54
OGF Janj - OGF Lom	4.17	78	**0.0000**	5.84	1.39	3.05	8.62
OGF Lom - MF Lom	4.20	78	**0.0000**	5.18	1.2339	2.73	7.64
MF Janj - MF Lom	-4.08	118	**0.0000**	-3.90	0.95	-5.79	-2.00

Due to non-normal distribution of mean diameters and heteroscedasticity in some managed stands in Janj area, Kruskal-Wallis test was applied to test for differences. The results indicated significant differences among mean stand diameters. SPSS provided Chi-square statistic 36.73 for five degrees of freedom (p = 0.0000). Therefore multiple pairwise Mann-Whitney U test was run as post-hoc test. It was found that OGF Janj significantly differs from all managed stands in Janj in terms of mean diameters. Besides, post-hoc Mann-Whitney U test revealed significant differences between managed stands 31a and 57/1b, and between stands 56a and 57/1b.

In Lom area mean diameters distribution exhibited homogeneity of variances (homoscedasticity), however, non-normal distribution in some managed stands was found, so Kruskal-Wallis test applied for Lom area as well. Calculated Chi-square statistic was 28.40 for five degrees of freedom (p = 0.0000). Since this test also found significant differences among stand mean diameters, multiple post-hoc Man-Whitney U tests was used to detect among which stands these differences occurred. Subsequently, four managed stands in Lom area (67a, 68a, 76a, 79a) had similar mean diameter distributions. It was determined that stand 59a differed from those four managed stands, however, it was similar to OGF Lom. On the other hand, mean diameters in OGF Lom significantly differed from stands 67a, 68a, and 76a.

5.9 BASAL AREA

OGF Janj had superior BA with 66.7 m^2/ha. Second most stocked was OGF Lom with 47.1 m^2/ha, while MF Lom and Janj followed with 41.5 m^2/ha and 35.5 m^2/ha, respectively. Range of BA was greatest in OGF Janj (Table 42). Some plots in this OGF had certain similarity regarding minimal values of BA with some plots in MF Janj, however, no adjacent managed stand had similar values of BA at the upper edge of the range.

Table 42. Descriptive statistics for BA (m^2/ha) in studied forests.

Statistics	OGF Janj	MF Janj	OGF Lom	MF Lom
Mean	66.7	35.5	47.1	41.5
Std. error	2.8	1.0	1.8	1.5
Median	65.8	36.6	47.0	39.8
Range	76.5	35.8	48.7	52.9
N (plots)	40	60	40	60

On the contrary, OGF Lom had most similar range with managed stand 68a, and somewhat less similarity with stand 59a, although this stand had even greater mean BA area than OGF Lom.

Naturally, highest concentration of total BA in OGF Janj was on those plots which had large trees with dbh over 50 cm. Most plots were characterized with BA around 55 m^2/ha and 85 m^2/ha. In MF Janj most plots had BA between 38 and 40 m^2/ha, and secondary peaks were reserved for plots with BA 25 to 30 m^2/ha. In OGF Lom most plots had BA in range between 45 and 50 m^2/ha, while in MF Lom most present were plots with BA 35 to 40 m^2/ha (Figure 33).

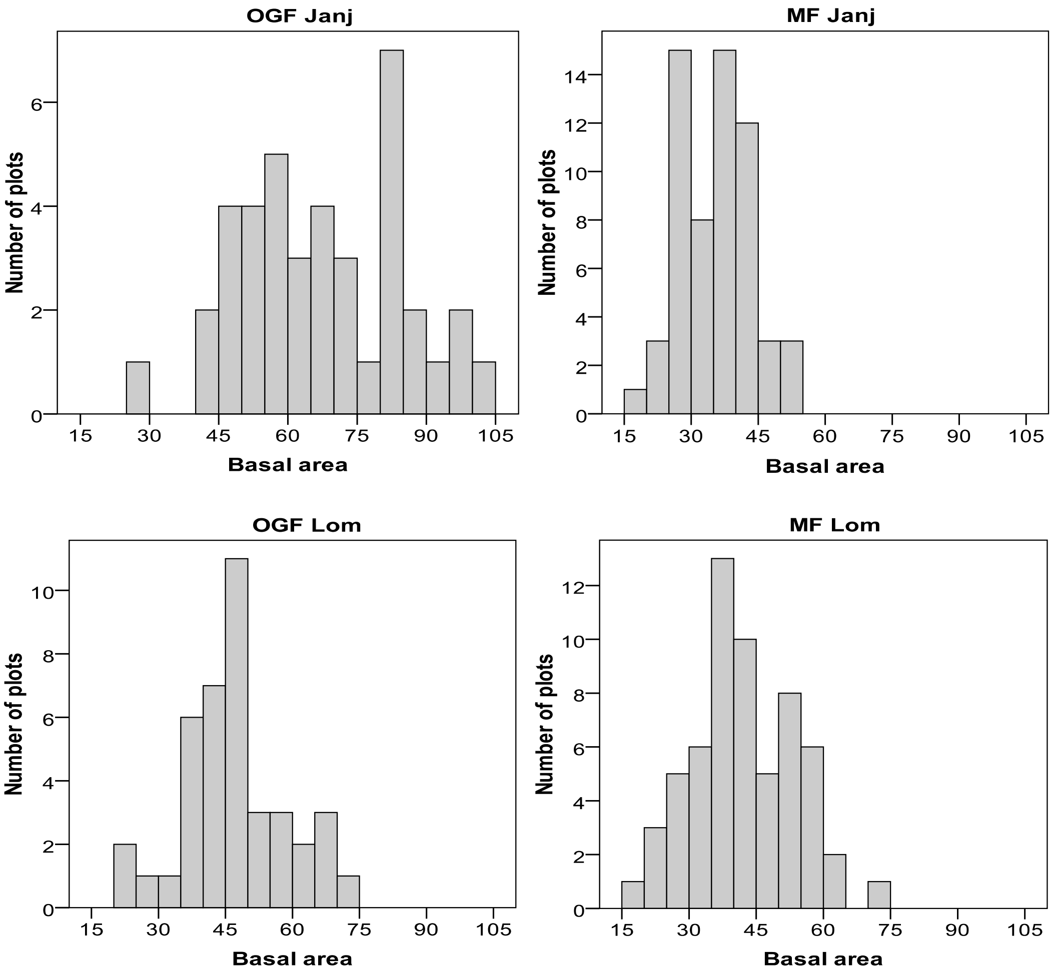


Figure 33. Basal area (m^2/ha) on plots in studied forest.

According to t-test there was no significant difference in BA between MF Lom and OGF Lom, while between other pairs difference was statistically significant (Table 43).

Table 43. Results of independent t-tests for BA values in studied forests.

Tested pairs	t	df	*p*-value	Mean difference	Std. error difference	95% Confidence interval lower	95% Confidence interval upper
OGF Janj - MF Janj	9.83	78	**0.0000**	31.15	2.61	25.97	36.34
OGF Janj - OGF Lom	5.88	78	**0.0000**	19.59	3.33	12.96	26.22
OGF Lom - MF Lom	1.78	78	**0.0780**	4.52	2.35	-0.52	9.57
MF Janj - MF Lom	-3.28	118	**0.0010**	-5.89	1.79	-9.45	-2.34

Since Levene test of homogeneity of variances indicated significant difference between variances in Janj area ($p < 0.05$), robust Welch test of equality was applied. The test yielded relevant F statistic 6.75 for five degrees of freedom and $p = 0.0000$. Post hoc Games-Howell test found that BA values were not significantly different among five managed stands in Janj, however, all of them differed significantly from OGF Janj BA.

In managed stands of Lom and OGF Lom variances were homogeneous, so one-way ANOVA was applied to test for differences in BA. The results of ANOVA indicated significant difference in BA values among tested stands ($F = 2.82$; $p = 0.0230$). Post hoc Tukey HSD test revealed that only stand 76a differed significantly from OGF Lom, while other managed stands in Lom were similar to OGF Lom in terms of BA values. Among managed stands in Lom no significant differences were found.

5.10 GROWING STOCK

Akin to BA, mean GS was highest in OGF Janj (1215.1 m^3/ha), and second highest was determined in OGF Lom (763.1 m^3/ha). Managed forests Lom and Janj followed with 664.3 m^3/ha and 498.9 m^3/ha, respectively. Difference between OGF Janj and MF Janj was more noticeable than between OGF Lom and MF Lom (Table 44).

Table 44. Descriptive statistics for GS (m^3/ha) in studied forests.

Statistics	OGF Janj	MF Janj	OGF Lom	MF Lom
Mean	1215.1	498.9	763.1	664.3
Std. Error	54.9	17.03	31.2	26.2
Median	1218.3	495.5	750.8	648.5
Range	1527	609	880	929
N (plots)	40	60	40	60

Most plots in OGF Janj had total GS between 800 m^3/ha and 1000 m^3/ha, and second peak on the histogram was in range 1200–1250 m^3/ha. In MF Janj there were three distinctive peaks regarding distribution of GS on sample plots. First and highest peak comprised plots with GS 350–400 m^3/ha. Second and third peak comprised plots which had GS in range 500–600 m^3/ha.

In OGF Lom two peaks were clearly distinguishable on GS histogram. Their range varied from 600 m^3/ha to 800 m^3/ha. Similarly, in MF Lom two peaks were also more discernible than others, and as a result most plots were characterized with GS between 500 m^3/ha to 700 m^3/ha (Figure 34).

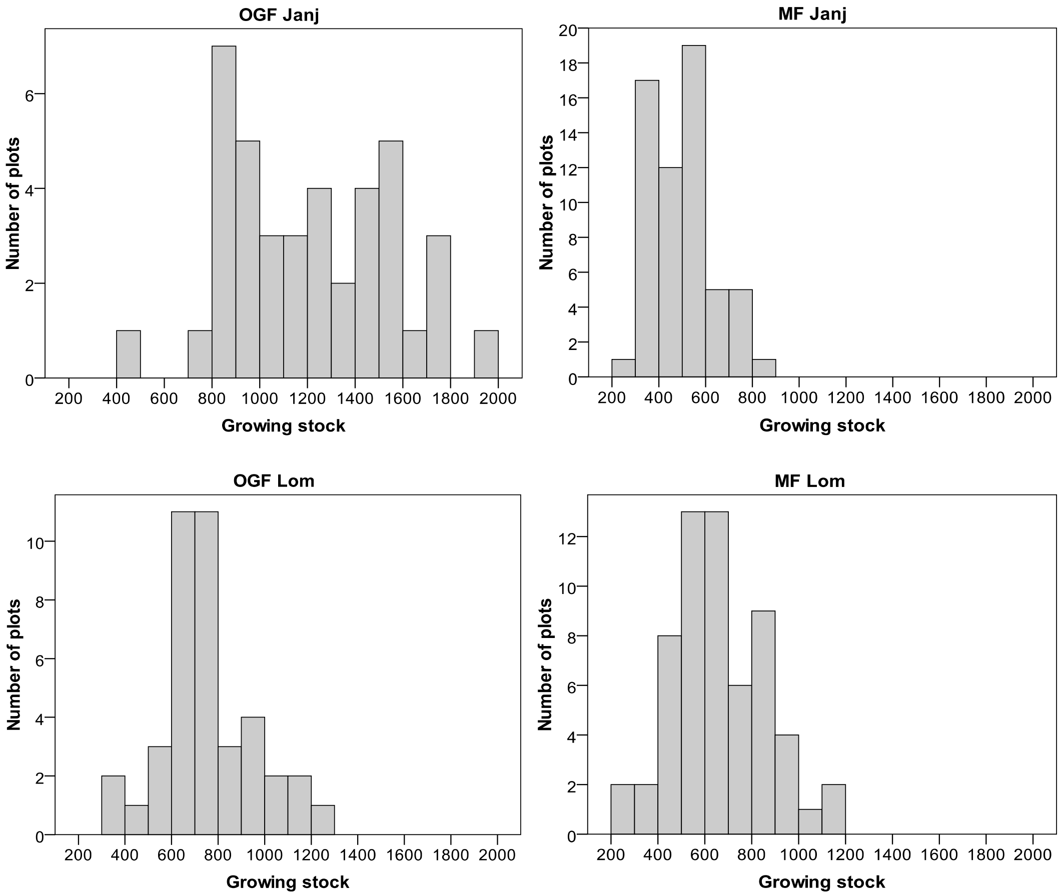


Figure 34. Frequencies of GS (m^3/ha) in studied forests.

Range of GS, as with BA, was the greatest in OGF Janj. However, the gap between this forest and MF Janj was even more pronounced in case of GS. The upper edge of the GS range amounted to 1946.4 m^3/ha on one plot (recalculated on hectare). However, this can be considered rather as an extreme value since next lower value was 1790.3 m^3/ha.

In Lom area OGF Lom had lower edge of the range smaller than even three managed stands and more-less equal to one stand in managed part of Lom. However, only managed stand 59a was close to the maximum of GS in OGF Lom.

In OGF Janj the greatest "carriers" of GS were the trees in diameter classes 75 cm and 90 cm. Beech volume was virtually equally distributed from smallest dbh class up to the class 70 cm. Within dbh class 72.5–77.5 cm beech was not present, and afterwards slightly occurred only in dbh class of 80 cm. On the other hand, fir and spruce were abundant in thicker dbh classes. Most of fir volume was in the range of diameter classes between 70 cm and 95 cm. For spruce wood volume two peaks were distinguishable: first in dbh class of 75 cm, and the second in dbh class of 90 cm. The share of maple is negligible.

In MF Janj there was only one peak for GS which occurred within diameter class 40 cm. Beech volume was mostly distributed within dbh classes 35 cm and 40 cm. Volume of fir trees was almost identical to perfect Gaussian curve having the highest concentration within dbh class of 45 cm. Highest peak for spruce volume occurred within dbh class of 40 cm. Maple was more present in GS of MF Janj than in OGF Janj. Nevertheless, it still had quite small share which varied from 0.3 to 0.6 m^3/ha within lower dbh classes from 10 cm to 30 cm.

Diameter class of 70 cm had clearly highest wood volume in OGF Lom. Beech concentrated its GS within dbh class 45 cm, fir within dbh class 70 cm, and spruce also within dbh class 70. Fir, however, accounted for the largest part of GS in thicker diameter classes. The share of other species was negligible.

Total GS in MF Lom was mostly represented within diameter class 55 cm. Beech accumulated most part of its GS also in the same class. Fir had more-less equally high level of GS in dbh classes ranging from 35 cm to 70 cm with class 55 cm being slightly above the others. Spruce was most represented species in GS of MF Lom concentrating especially in diameter classes between 45 cm and 65 cm with the class 50 cm being slightly above the other diameter classes. The share of maple was distributed in different amounts from 0.2–4.1 m^3/ha among dbh classes 10 cm to 50 cm (Figure 35).

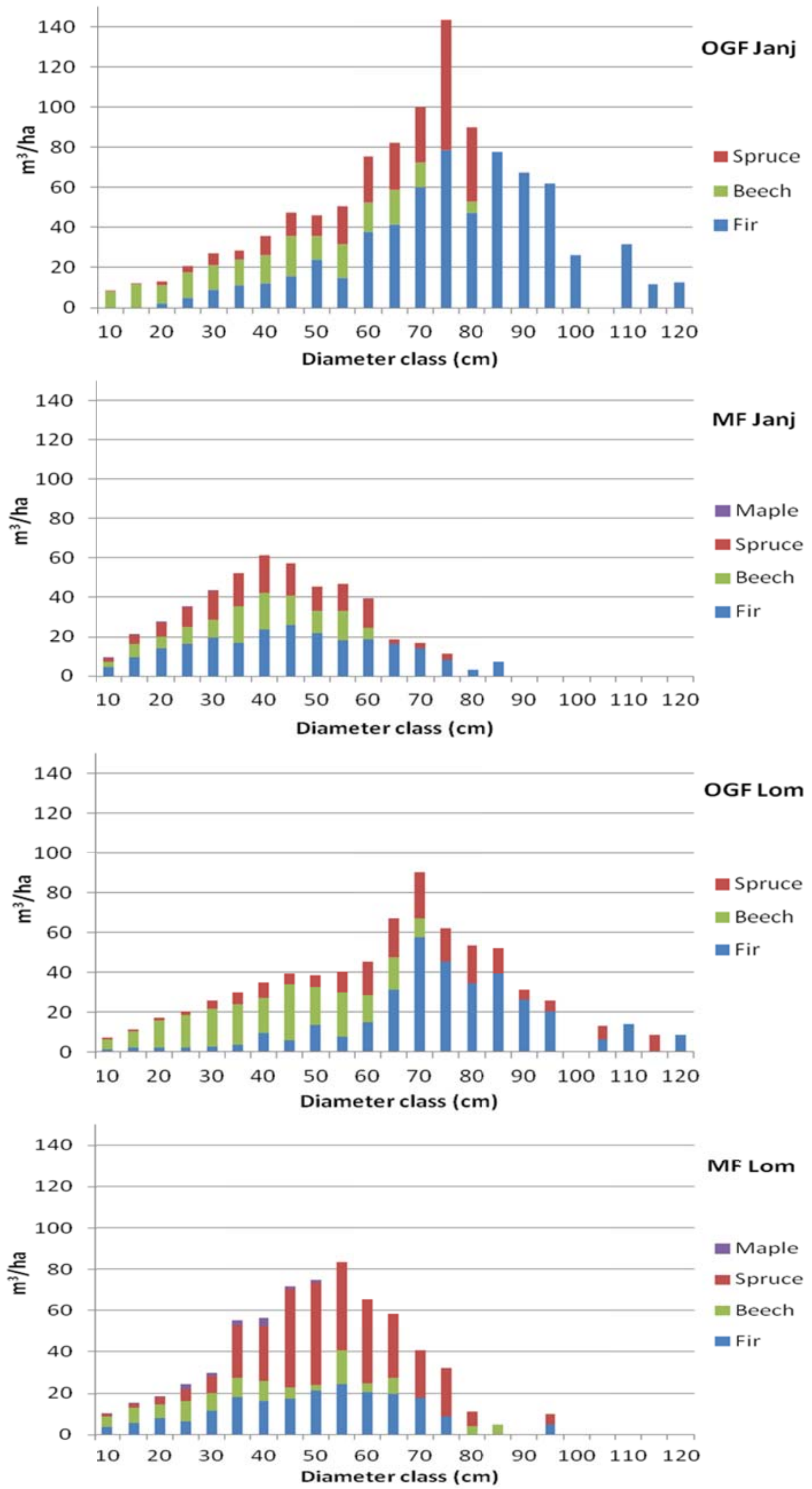


Figure 35. GS (m^3/ha) distribution in managed and OG forests Janj and Lom.

Results of independent t-test showed no difference in GS means among OGF Lom and MF Lom; however, for other compared pairs (OGF Janj - MF Janj, OGF Lom - MF Lom, MF Janj - MF Lom) significant differences were found (Table 45). Unexpectedly, greater difference in absolute values of GS occurred between the two managed forests than between OGF Lom and MF Lom.

Table 45. Results of independent t-tests for GS in studied forests.

Tested pairs	t	df	*p*-value	Mean difference	Std. error difference	95% Confidence interval lower	95% Confidence interval upper
OGF Janj - MF Janj	11.93	78	**0.0000**	714.25	59.87	595.05	833.45
OGF Janj - OGF Lom	7.15	78	**0.0000**	451.97	63.21	326.12	577.81
OGF Lom - MF Lom	1.81	78	**0.0740**	80.99	44.64	-7.90	169.88
MF Janj - MF Lom	-5.28	118	**0.0000**	-165.34	31.27	-227.27	-103.41

Among managed stands in Janj the greatest GS had stand 57/1b that reached 592.0 m^3/ha, and smallest stock was calculated for managed stand 58a which had 467.6 m^3/ha. Afterwards, when comparing individual managed stands with each other and with OG forests, variances of GS in both areas Janj and Lom were not homogeneous. Therefore, in both cases robust Welch test was applied instead of ANOVA.

Initially, robust Welch test of equality of GS means yielded F statistic 8.86 for five degrees of freedom and difference was significant at p = 0.0000. Post hoc Games-Howell test found that GS values were not significantly different among five managed stands in Janj, however, all of them differed significantly from OGF Janj.

In MF Lom average GS values were perceptibly higher than in MF Janj. To illustrate this fact, for instance, stand 59a had 837.0 m^3/ha and this was higher value not only compared to other managed stands but also compared to OGF Lom. The smallest GS within MF Lom had managed stand 76a which amounted to 554.3 m^3/ha.

When individual managed stands were compared among each other and with OGF Lom, Welch test provided F = 4.45 for five degrees of freedom, and difference was significant at p = 0.0040. Subsequently, post hoc Games-Howell test showed that GS values in stand 59a differed significantly from those in stands 67a, 76a and 79a. Interestingly, OGF Lom did not differ significantly from any of surrounding managed stands in terms of GS means.

5.11 COARSE WOODY DEBRIS

The greatest amount of CWD was found in OGF Janj which had 368.5 m^3/ha of dead wood in different forms and decay stages. Second highest mean amount of CWD was determined in OGF Lom (327.3 m^3/ha). Managed forests Lom and Janj followed with 75.4 m^3/ha and 62.6 m^3/ha, respectively (Tables 46, 47). Difference between OGF Janj and MF Janj was slightly more perceptible than between OGF Lom and MF Lom. Furthermore, it is noticeable that in case of OG forests, the higher the GS the higher amount of CWD. However, situation in managed forests was slightly different since MF Janj had smaller amount of GS but greater amount of dead wood compared to MF Lom.

Table 46. Descriptives for CWD (m^3/ha) in studied forests.

Statistics	OGF Janj	MF Janj	OGF Lom	MF Lom
Mean	386.5	75.4	327.3	62.6
Std. Error	26.8	6.8	20.3	4.2
Median	389.0	69.3	316.2	56.2
Range	731	227	490	137
N (plots)	40	60	40	60

Most parts (plots) in OGF Janj had between 400–450 m^3/ha and 200–250 m^3/ha of CWD. Maximum was 893 m^3/ha and minimum 162 m^3/ha. From this we can notice that minimum from OGF Janj was relatively close to the maximum in MF Janj. In MF Janj one peak on histogram was distinguishable (up to 50 m^3/ha) indicating that most plots in this forest had much lower quantity of CWD than OGF Janj. In MF Lom amounts were lower with the peak between 40–60 m^3/ha. Beside mean value, minimum and maximum values in this forest were also conspicuously lower than in OGF Lom. Most plots in OGF Lom were characterized with 300–350 m^3/ha, whereas minimum was 88 m^3/ha and maximum amounted to 578 m^3/ha (Figure 36).

The ratio CWD/GS in OGF Janj amounted to 0.32. Most of CWD volume in this old-growth forest was in logs, followed by snags and stumps with the ratios 0.79, 0.19 and 0.02, respectively. Logs were hence more frequent than snags and stumps together. In MF Janj the ratio CWD/GS was 0.15, in OGF Lom 0.43, and in MF Lom 0.09. In MF Janj the ratio logs : snags : stumps was 0.70 : 0.03 : 0.27; in OGF Lom 0.72 : 0.25 : 0.03; and in MF Lom 0.64 : 0.04 : 0.32, respectively.

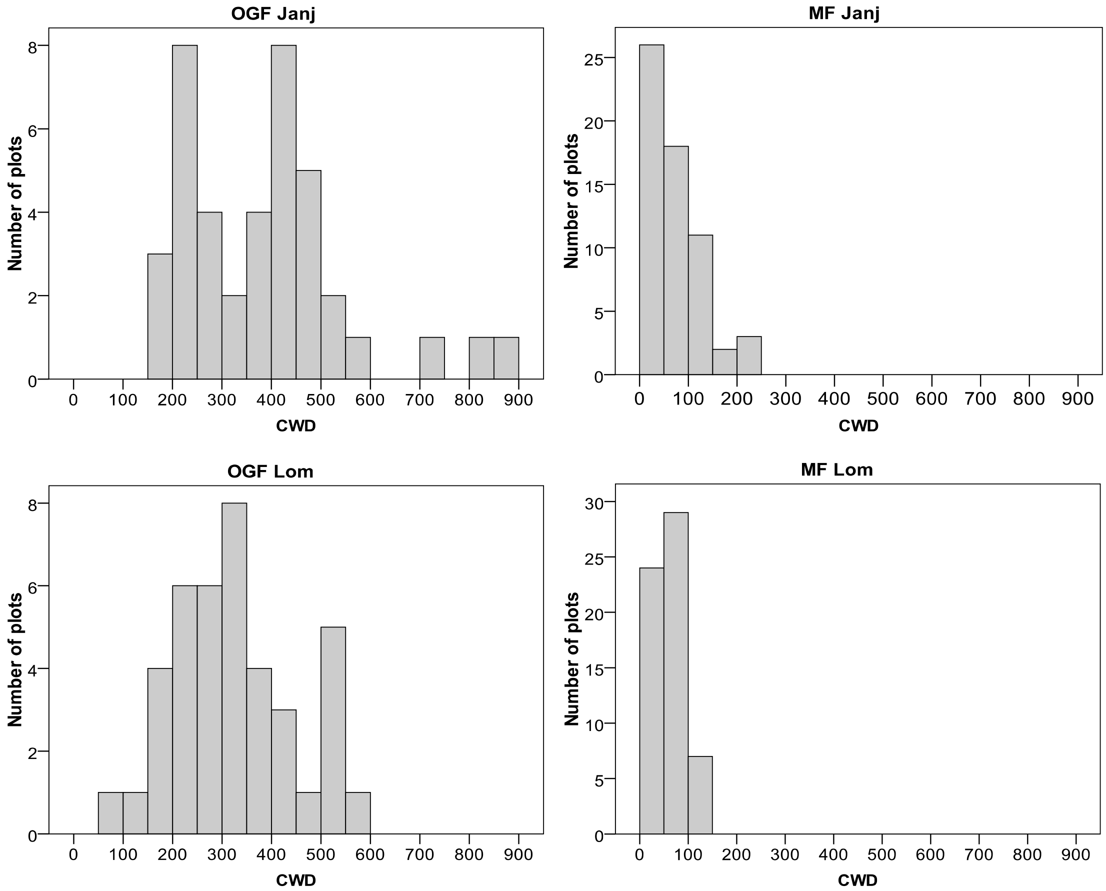


Figure 36. CWD volumes (m^3/ha) on plots in studied forests.

Table 47. Volume of different CWD categories.

		Snags (m^3/ha)	Logs (m^3/ha)	Stumps (m^3/ha)	Total (m^3/ha)
OGF Janj	Mean	70.9	306.7	8.8	386.5
	Range	0–510.2	103.8–582.5	0–26.1	162.1–892.6
	SD*	107.8	125.2	5.5	169.7
MF Janj	Mean	2.0	53.2	20.3	75.4
	Range	0–39.2	0.7–215.1	1.8–50.8	5.9–233.1
	SD	5.4	51.1	9.0	52.4
OGF Lom	Mean	81.4	236.4	9.5	327.3
	Range	0–298.8	49.3–487.2	0–33.4	88.1–578.2
	SD	80.9	109.2	7.5	128.2
MF Lom	Mean	2.6	39.9	20.1	62.7
	Range	0–101.0	1.5–132.1	6.0–41.6	12.8–149.7
	SD	13.1	29.8	8.1	32.9

SD* - standard deviation

In OGF Janj all five CWD decay classes were present only in logs, whereas the fifth decay class was prevalent. Most snags were in first decay class, while fifth class was not present. Most frequent stumps were in fourth decay class (Table 48). On the other hand, large standing snags (>50 cm dbh) were present with 19 trees/ha in OGF Janj and 18 trees/ha in OGF Lom, contributing so to biodiversity and survival of other species, especially nesting birds which depend on them. Interestingly, the number of thinner snags (7.5–50 cm dbh) in OGF Janj was lower amounting to only 16 trees/ha, while in OGF Lom there was 25 snags per hectare in this category.

We tested also for relations between CWD volume and GS, but we didn't find any statistically significant correlations. In MF Janj fourth and fifth class of logs were mostly present. Most stumps occurred in fourth decay class, while snags were generally scarce in this forest. In OGF Lom most logs were found in fifth class, snags in third class, and stumps in fourth class. There was 18 large standing snags per hectare in this old-growth forest (snags >50 cm dbh). In MF Lom most logs were found in fourth and fifth class, stumps in fourth class, while snags were very scarce like in MF Janj.

Table 48. Different decay classes of CWD in studied forests.

	Decay classes	Snags (m^3/ha)	Logs (m^3/ha)	Stumps (m^3/ha)
OGF Janj	1	20.1	2.2	0.0
	2	16.2	30.3	0.5
	3	18.8	64.2	3.0
	4	15.8	88.8	5.3
	5	0	121.2	-
MF Janj	1	0.1	0.5	0.0
	2	0.2	1.0	1.2
	3	0.4	4.9	5.7
	4	1.3	21.8	13.3
	5	0.1	24.9	-
OGF Lom	1	2.3	4.0	0.0
	2	24.2	16.3	1.1
	3	32.5	42.7	2.5
	4	22.4	77.7	5.9
	5	0.0	95.8	-
MF Lom	1	0.0	0.1	0.0
	2	1.8	1.1	2.7
	3	0.5	7.2	4.9
	4	0.3	15.2	12.5
	5	0.0	16.3	-

Figure 37. Snags in OG forests Janj (left) and Lom (right).

Figure 38. Stunning downed log (left) and traces of woodpecker activity (right) in OGF Janj.

Independent t-test indicated that significant differences exist between OGF Janj - MF Janj and OGF Lom - MF Lom, while between OGF Janj - OGF Lom and MF Janj - MF Lom no significant differences were found in terms of CWD means (Table 49).

Table 49. Results of independent t-tests for equality of CWD means.

Tested pairs	t	df	*p*-value	Mean difference	Std. error difference	95% Confidence interval lower	95% Confidence interval upper
OGF Janj - MF Janj	11.04	78	**0.0000**	308.80	27.95	253.15	364.46
OGF Janj - OGF Lom	1.76	78	**0.0820**	59.18	33.62	-7.76	126.11
OGF Lom - MF Lom	12.33	78	**0.0000**	260.46	21.12	218.42	302.51
MF Janj - MF Lom	1.60	118	**0.1120**	12.78	7.99	-3.04	28.61

Some of the individual managed stands exhibited non-normal distributions and for this reason Kruskal-Wallis test was applied to test for differences between individual managed stands and OG forests. The results of the test were significant ($p \leq 0.05$, two-tailed) for both studied areas, Janj and Lom. In Table 50 the results of post-hoc analysis revealed significant statistical differences between all managed stands and OG forests Janj and Lom, respectively.

Table 50. Multiple pairwise Mann-Whitney post-hoc analysis for CWD amounts in Janj and Lom areas.

Pairs in Janj area	*p*-value	Pairs in Lom area	*p*-value
OGF Janj – Stand 31a	0.0000	OGF Lom – Stand 59a	0.0000
OGF Janj – Stand 50d	0.0000	OGF Lom – Stand 67a	0.0000
OGF Janj – Stand 56a	0.0000	OGF Lom – Stand 68a	0.0000
OGF Janj – Stand 57/1b	0.0000	OGF Lom – Stand 76a	0.0000
OGF Janj – Stand 58a	0.0000	OGF Lom – Stand 79a	0.0000

On diameter distributions of different CWD categories or types we see that logs were most present in OGF Janj up to diameter class of 70 cm, and in stronger dbh classes snags and stumps became equal or more present than logs. In MF Janj logs were superior in diameter classes up to 20 cm, and in thicker diameters the percentage of stumps was clearly higher than percentage of logs. Snags in this forest were hardly visible. In OGF Lom domination of logs in dbh classes was noticed up to diameter class of 65 cm, and in the following classes snags and logs equalized or took over logs. In MF Lom up to diameter class 15 cm logs dominated, while the number of stumps and subsequently their percentage in thicker dbh classes was higher. Snags in this managed forest were also very rare (Figure 39).

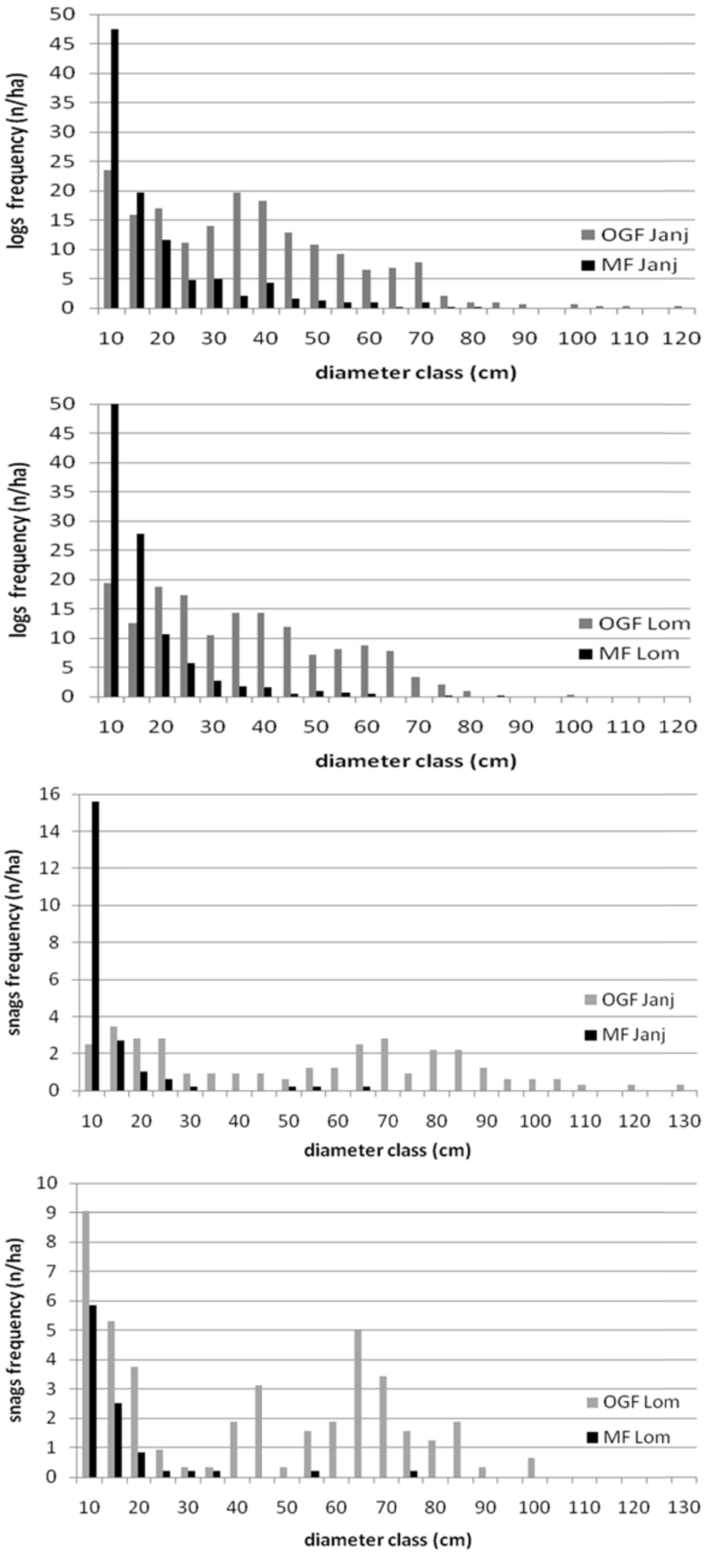


Figure 39. Diameter distributions of logs (above) and snags (below).

Only thin snags in diameter class of 10 cm were more frequent in MF Janj compared to OGF Janj. However, in all other diameter classes snags in OGF Janj were clearly more frequent. Frequency of snags in OGF Lom was higher in all diameter classes compared to MF Lom. The number of stumps was greater in managed forests in all diameter classes compared to OG forests.

When only categories of small and medium-sized CWD were observed, consistent results were obtained. For example, small logs were more present in managed forests, while medium-sized logs were more present in OG forests. Stumps of both categories, small and medium-sized, were clearly more present in managed than in OG forests. Medium-sized snags were clearly more numerous in OG forests, while only results for small snags were variable. Namely, greater number of small snags were found in OGF Lom than in MF Lom, while in MF Janj there were more small snags than in OGF Janj (Table 51). Such outcome came out particularly due to high number of snags in dbh class with the mid-point 10 cm (16 snags/ha) in MF Janj.

Table 51. Presence of small and medium-sized logs, snags and stumps (n/ha).

	logs (n/ha)		snags (n/ha)		stumps (n/ha)	
	small	medium	small	medium	small	medium
OGF Janj	56	87	9	7	3	21
MF Janj	79	19	19	1	17	72
OGF Lom	51	75	18	7	13	37
MF Lom	101	13	9	1	53	94

5.12 DISTURBANCE INTENSITY BASED ON STUMPS

Mean densities of stumps of all decay classes were greater in managed than in OG forests (Table 52). In OG forests some plots did not have stumps at all, while the maximum number of stumps was registered in MF Lom (550 stumps of all decay classes per hectare).

Table 52. Mean and range values for stumps in studied forests.

	Density mean (n/ha)	Range (n/ha)	Volume mean (m^3/ha)	Range (m^3/ha)
OGF Janj	48	0–100	8.8	0–26.1
MF Janj	161	62–325	20.3	1.8–50.8
OGF Lom	74	0–200	9.5	0–33.4
MF Lom	234	50–550	20.1	6.0–41.6

Mean density considering number of stumps was greatest in MF Lom due to more intense cutting of small-diameter trees, however, when we observe the ratio of stumps BA and BA of living trees, we can see that disturbance intensities in MF Lom and MF Janj were the same. The ratios in OG forests were smaller (Table 53).

Table 53. Disturbance ratios based on number and BA of stumps.

		Mean	Median	Min.	Max.	Std. error
OGF Janj	N stumps/N living trees	0.10	0.09	0.00	0.35	0.01
	BA stumps/BA living trees	0.19	0.15	0.00	1.16	0.03
MF Janj	N stumps/N living trees	0.21	0.21	0.06	0.40	0.01
	BA stumps/BA living trees	1.26	1.15	0.37	3.13	0.07
OGF Lom	N stumps/N living trees	0.15	0.14	0.00	0.45	0.01
	BA stumps/BA living trees	0.31	0.25	0.00	0.76	0.03
MF Lom	N stumps/N living trees	0.40	0.36	0.13	0.83	0.03
	BA stumps/BA living trees	1.26	1.09	0.24	3.68	0.08

The observation of stump distributions in both areas showed unimodal shapes (Figure 40).

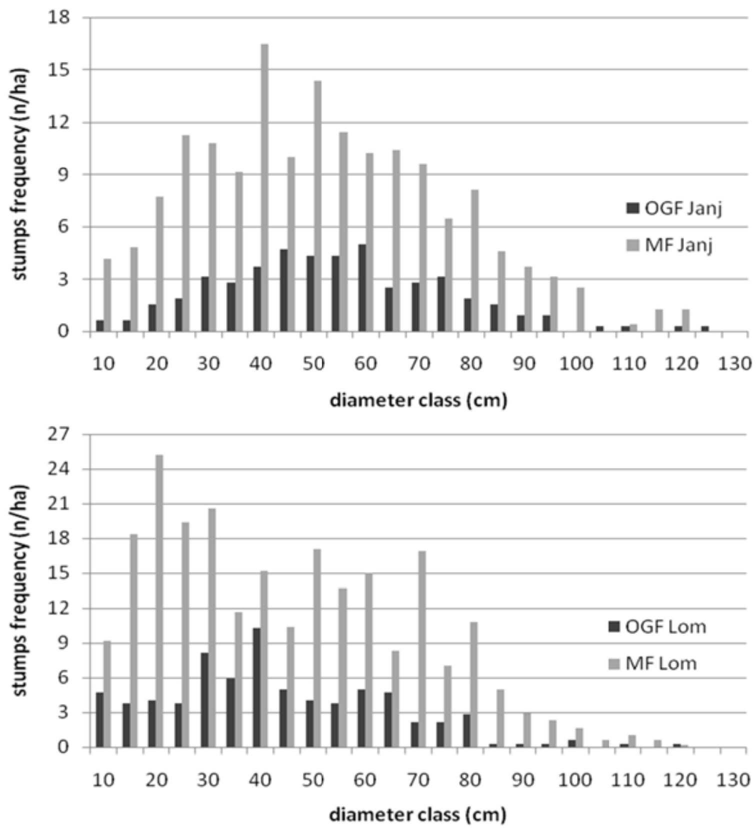


Figure 40. Diameter distributions of stumps.

5.13 SLENDERNESS RATIO

In OG forests slenderness ratios across dbh classes were similar to those in managed forests. Large trees above 50 cm dbh had slenderness ratios in range from below 40 up to 60. H/D ratio above 80 was exceeded only by beech in OGF Janj (7.5–37.5 cm dbh), while in MF Janj, OGF Lom and MF Lom only beech 7.5–17.5 cm dbh had critical ratio above 80. This may indirectly indicate its heavier competition for light compared to conifers during early developmental stages. Spruce in smaller dbh classes was “bordering” or slightly exceeding critical ratio of 80 in OGF Janj, MF Janj and MF Lom, whereas in OGF Lom this species seemed to be more stable. In all studied forests fir had slenderness ratios below 80, even in smallest dbh classes (Figure 41).

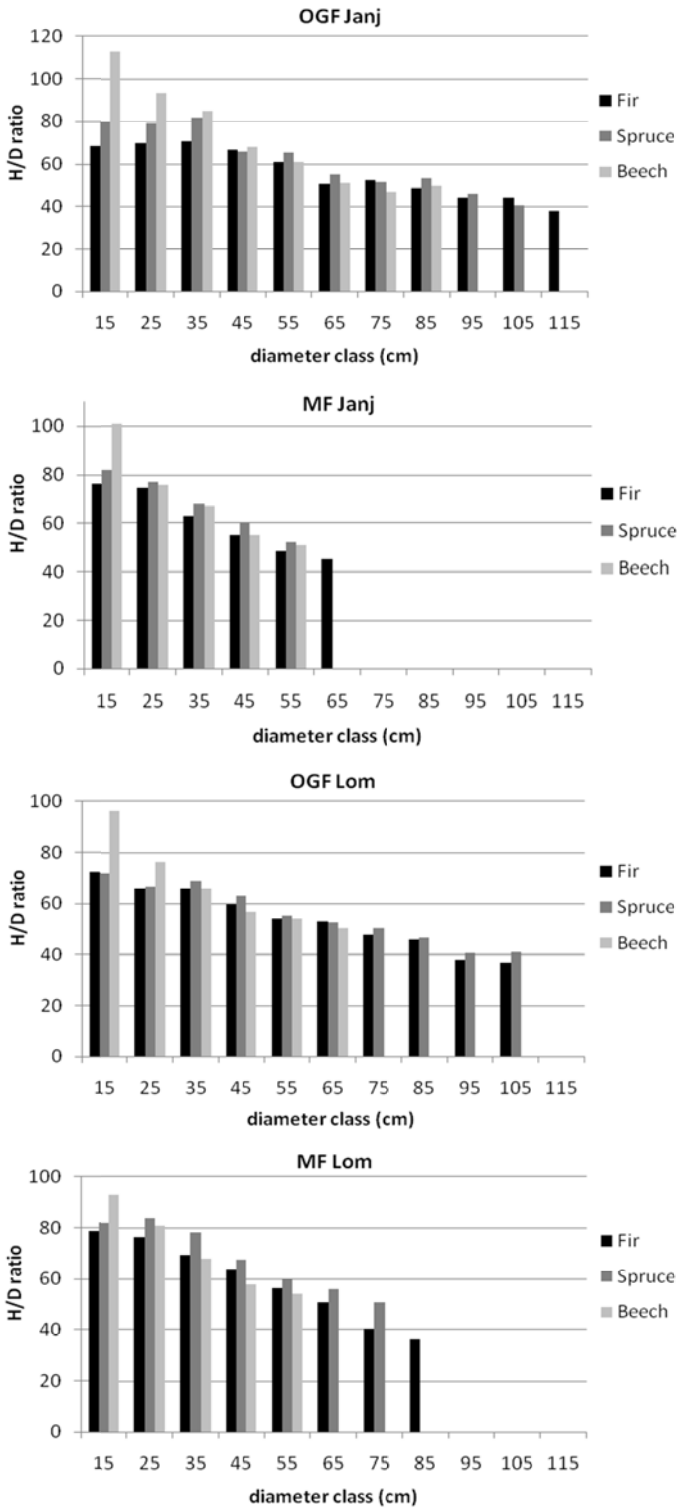


Figure 41. Slenderness of trees in studied forests (10 cm dbh class span).

5.14 STRUCTURAL CHANGES OF OLD-GROWTH FORESTS JANJ, LOM AND PERUCICA DURING SIX DECADES

In OGF Janj the share of beech in tree density was similar in first two inventories of 1952 and 1965, with 38 % and 37 %, respectively. It substantially increased to 54 % and 63 % in last two inventories of 2003 and 2011, respectively. During 1952-2011 spruce decreased from 30 % to 14 %, while fir share decreased less intensively from 32 % to 23 %, respectively. Similar pattern of beech progression and conifer decline was indicated in OG forests Lom and Perucica (Figure 42). This trend was comparable also regarding shares of tree species in relation to BA. Here, the only exception was an increase of the fir share in OGF Janj from 43 % to 52 % from 1952 to 2011, respectively. Increase of beech share in density was statistically significant for all three OG forests, while its increase in BA was only significant for Perucica.

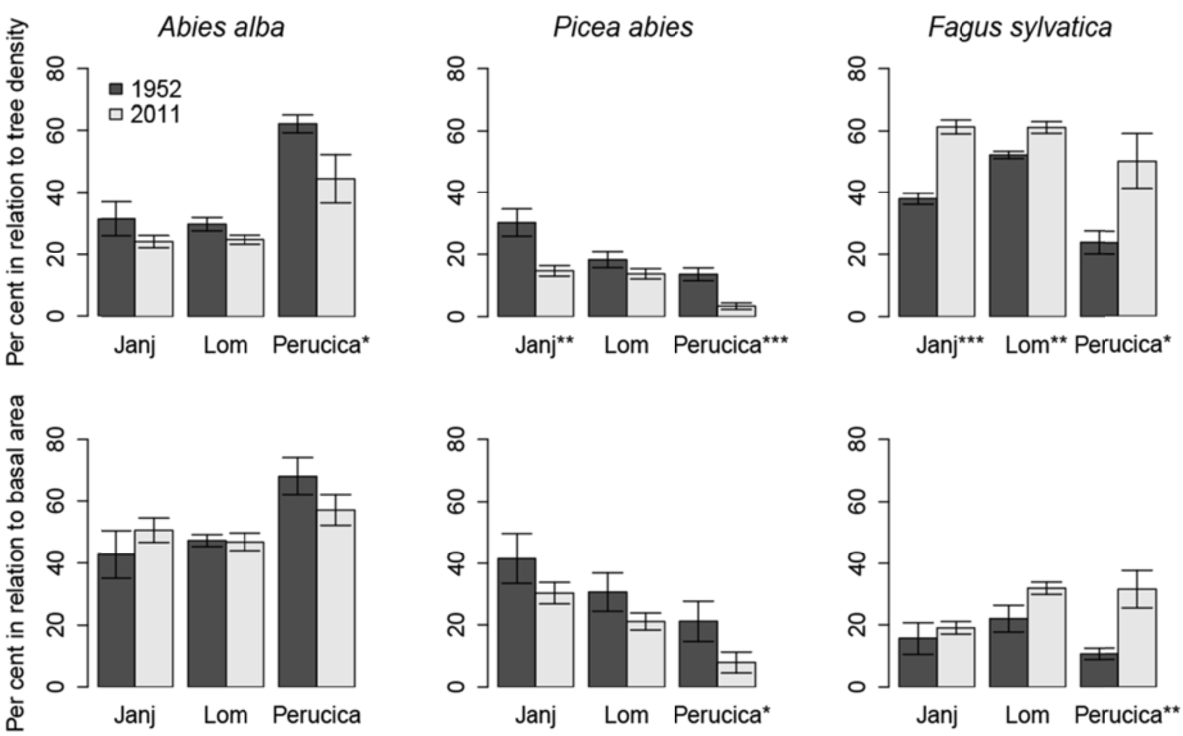


Figure 42. Change in tree species composition according to tree density (above) and BA (below) in last six decades. One, two and three star denote significance code of $p < 0.001$, $p < 0.01$ and $p < 0.05$, respectively.

In all inventories tree species composition in extended dbh size classes in OG forests Janj and Lom according to number of individuals showed similar overall pattern (Figure 43). Beech significantly prevailed in the first extended dbh class, while spruce and fir dominated in the third class. Exception was OGF Perucica in 1952 where silver fir was dominant across all dbh classes, while spruce and beech showed similar pattern according to increasing dbh classes as in other sites, however with a smaller share.

During the last half of the century the proportion of beech in the first extended dbh class of OGF Janj continually increased, from 53 % in 1952 to 88 % in 2011. On the other hand, the share of both spruce and fir in the same size class was on constant decline. In recent decades beech became prevalent in the second extended dbh class. Its share also increased in the third extended dbh class, from modest 5 % in 1952 to 12 % in 2011. Relative abundance of fir in second and third extended diameter class didn’t change much, while that of spruce moderately decreased (Figure 43a,b,c,d). Also in OGF Lom share of beech from 1952 to 2011 increased from 71 % to 74 %, 43 % to 62 % and 9 % to 12 % within first, second and third extended diameter class, respectively. During the same period share of spruce moderately decreased over all classes, while silver fir share decreased only in the mean dbh class (Figure 43e,f). In Perucica increase of beech and decrease of conifers were similar to Janj and Lom, however they were more pronounced (Figure 43g,h).

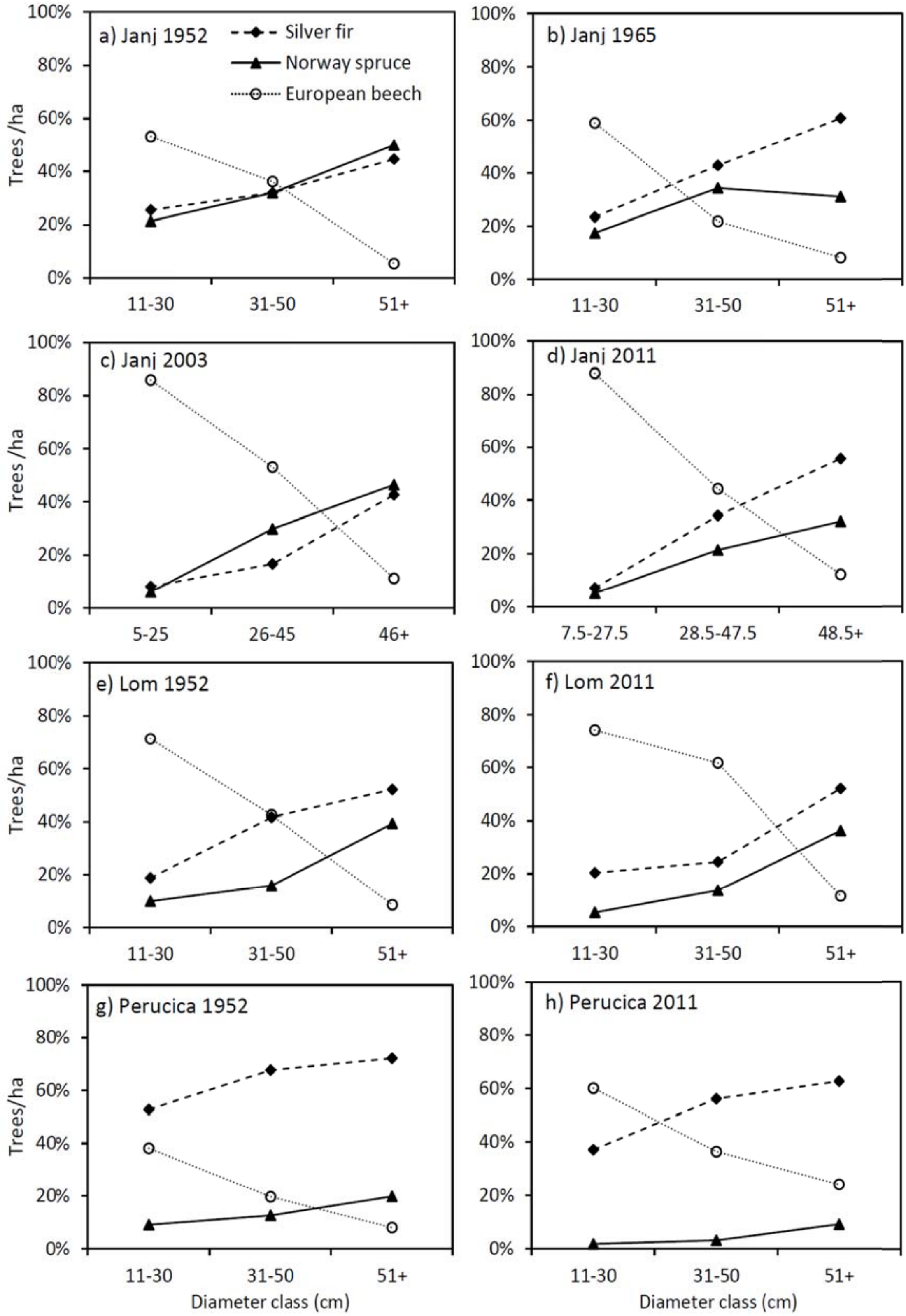


Figure 43. Changes in tree species composition regarding density within extended dbh size classes in OGF Janj at different years of inventory and comparison with OG forests Lom and Perucica (span of dbh classes was 20 cm due to slightly different dbh thresholds in older inventories).

For cumulative tree dbh distributions (20 cm dbh classes) best-fitting multiple regression models changed from IQ to RS in Janj, from NE to RS in Lom, and from VAR to NE in Perucica (Table 54, Figure 44). In all three OG forests the total number of trees in the first diameter class (7.5–17.5 cm) increased, while it decreased through medium diameters. In 1952 the best-fitting model for both conifers in all three OG forests was IQ. This indicates increasing reduction rate in number of trees from one diameter class to the next with increasing tree size and could be indicative of past disturbance within group of large diameter trees. In the following sixty years the fir model changed to UNI in Janj, to RS in Lom and to CO in Perucica. The UNI model may indicate problems with recruitment. Spruce model changed to RS in Lom, and remained of the same IQ shape in Janj and Perucica. Changes from IQ to RS and CO may indicate improved conditions for large diameter trees. During observed period the shape of beech frequency distributions changed from NE, VAR and CO to CO. This indicates shift of beech to larger diameter trees.

Table 54. Parameters of the best-fitting model for multiple regressions between the base 10 logarithm of trees per hectare and all possible combinations of the dbh (span of dbh classes was 20 cm due to slightly different dbh thresholds in older inventories).

	Janj 1952				Janj 2011			
	Fir	Spruce	Beech	Cumulative	Fir	Spruce	Beech	Cumulative
RMSE	0.12	0.11	0.09	0.12	0.12	0.23	0.13	0.06
Adj. R^2	0.92	0.93	0.99	0.95	0.95	0.78	0.99	0.99
N (dbh class)	5	5	4	5	6	6	6	6
Shape	IQ	IQ	NE	IQ	UNI	IQ	CO	RS
	Lom 1952				Lom 2011			
RMSE	0.09	0.09	0.15	0.10	0.08	0.02	0.09	0.04
Adj. R^2	0.97	0.96	0.91	0.98	0.97	0.99	0.99	0.99
N (dbh class)	6	6	5	6	6	6	6	6
Shape	IQ	IQ	VAR*	NE	RS	RS	CO	RS
	Perucica 1952				Perucica 2011			
RMSE	0.18	0.09	0.08	0.14	0.03	0.10	0.08	0.09
Adj. R^2	0.94	0.95	0.99	0.97	0.99	0.86	0.99	0.99
N (dbh class)	7	7	7	7	7	7	7	7
Shape	IQ	IQ	CO	IQ	CO	IQ	CO	NE

VAR* - variable dbh distribution (sensu Janowiak *et al*., 2008)

Graphical comparison of empirical dbh distributions revealed several similarities among OG forests and inventories (Figure 44). Beside empirical dbh distributions also curves of best regression models were inspected. This enabled a direct comparison despite different dbh class thresholds between years of measurements. In all cases beech dbh distribution followed approximate straight line if densities are plotted in logarithmic scale, indicating closest match with NE. In recent inventory beech was more frequent across all dbh classes,

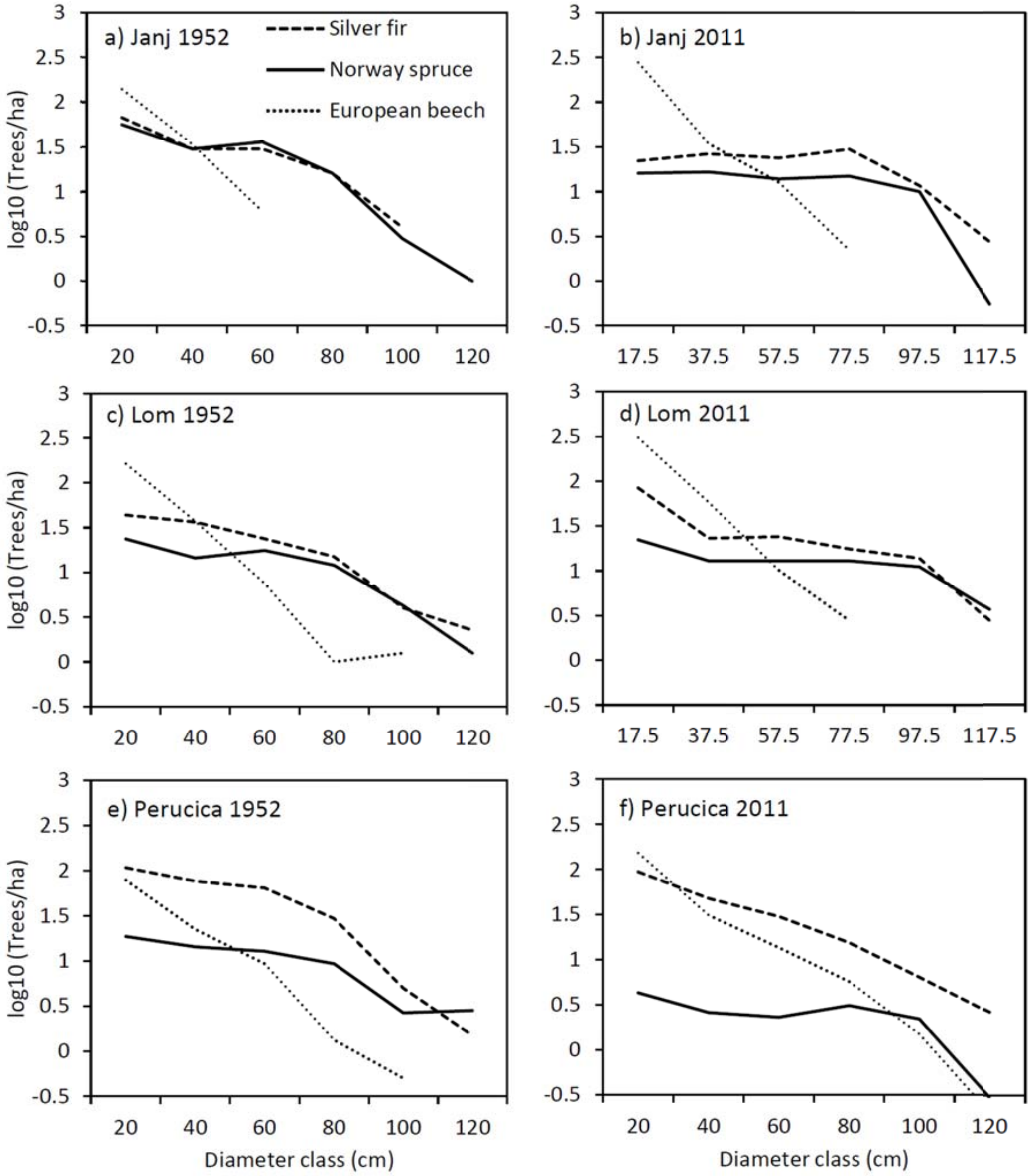


Figure 44. Comparison of diameter distributions for OGF Janj in 1952 (a) and 2011 (b), OGF Lom in 1952 (c) and 2011 (d), and OGF Perucica in 1952 (e) and 2011 (f).

and it shifted also to larger dbh classes. However, the shape remained relatively similar between years and OG forests. Beech distribution had the steepest slope of all tree species, which may be attributed to a higher mortality rate.

Distributions of conifers were more irregular in shape and they indicated for both species a non-constant *q* ratio across dbh classes. In all inventories and OG forests spruce curve was consistently most “flattened” within smaller (lower) dbh classes among all species. Between inventories spruce density decreased over all classes in Janj and Perucica, but this was more pronounced within small dbh classes. In Lom spruce density decreased across medium dbh classes and slightly increased in smaller and larger (Figure 44c, d). The same was true for fir, while in Perucica fir decreased over all classes.

6 DISCUSSION

6.1 OVERVIEW OF TESTED RESEARCH HYPOTHESES

Before going into detailed discussion of most emphasized topics of this dissertation, first an overview of outcomes regarding tested hypotheses is given as follows:

1. Mean values of transmitted direct and diffuse light as well as overall variability of light conditions were greater in the ground (understory) layer of managed forests Janj and Lom than in adjacent OG forests.

2. In managed forests the cover of ground vegetation and seedling density were higher than in OG forests. Mean yearly height growth of beech, fir and spruce seedlings was greater in managed forests, while the quality of seedlings was rather similar. Differences in tree species composition in the regeneration stage were found between OGF Janj and MF Janj, while similarity was indicated between OGF Lom and MF Lom.

3. In OG forests there were incomparably more large living trees and snags with dbh above 50 cm than in managed forests. The difference for living trees was even more pronounced above dbh of 80 cm.

4. Dead wood in the category of small logs was significantly more present in managed forests, while medium-sized logs were more present in OG forests. Stumps of both categories, small and medium-sized, were clearly more present in managed than in OG forests. Medium-sized snags were more numerous in OG forests, while only results for small snags were variable.

5. Canopy beech, fir and spruce trees in OG forests were significantly taller from those in managed forests. The only exception was spruce which was slightly taller in OGF Lom than in MF Lom as well, however, the difference was not statistically significant.

6. Managed and OG forests had rather similar shapes of diameter distributions, however, they universally differed in a way that smallest dbh class contained more trees in managed forests, whereas the presence of trees with dbh above 50 cm was clearly greater in OG forests.

7. Significant differences between OG and managed forests were found in terms of tree densities and mean diameters, however, structural attributes such as BA and GS were rather similar between OGF Lom and MF Lom. Measures of variability for mean diameters

of all species combined were greater in OGF Janj than in MF Janj, nevertheless, they were greater in MF Lom than in OGF Lom.

8. Species diversity in the ground layer (woody and herbaceous plants) and site conditions were more heterogeneous in managed than in OG forests due to larger range of Shannon index values on sample plots. Sycamore maple above dbh 7.5 cm had low but constant share in composition of managed forests, while in OG forests it was virtually absent in the midlle- and upper-story despite its constant presence in regeneration layer.

9. Mean values of total CWD on sample plots in OG forests were significantly higher than in managed forests. This difference occurred in the first place due to large presence of downed logs in OG forests. Diameter distributions of snags and stumps in OG and managed forests were vastly disparate. Presence of stumps was significantly lower in OG forests, which indirectly implied lower disturbance intensities of their canopies compared to managed forests.

10. OG forests had significantly smaller overall gap fraction (canopy openness) compared to managed forests. In addition, in managed forests ground layer species such as *Senecio fuchsii*, *Rubus idaeu*s and *Fragaria vesca* were found as indicator species. These species are known as inhabitants of large openings within forested areas, whereas *Euonimus latifolia*, the species known for its high shade-tolerance, was determined as indicator species in OG forests.

6.2 SITE CHARACTERIZATION BASED ON HEIGHT CURVES

General observation from obtained results was that in all studied forests beech in middle-story had more vigorous growth than conifers, however, sometime afterwards when trees start entering the upper story, fir and spruce take over beech. Similar results were obtained in studies of Drinic (1956) and Govedar (2005). Comparison of tree heights of 30 tallest canopy trees showed that beech, fir and spruce trees in OG forests were significantly taller from those in managed forests. The only exception was spruce which was slightly taller in OGF Lom than in MF Lom, however, the difference was not statistically significant. Very great tree heights were also found by some other authors. For instance, Tschermak (1910) found that beech canopy trees in Bosnian OG forests had average height of 38 m, whilst average height of fir canopy trees was 46 m (max. 58 m) and spruce 54 m (max. 62 m). Tregubov (1941) also reported similar heights for those species in OG forests of Klekovaca (Lom area) at the time. Assman (1970) indicated that trees which grew under crown cover in their early life longer maintained their growth and ultimately reached taller heights than sunlit trees which developed rapidly in the early stages. Therefore, if MF Janj would be taken out from regular management or cutting intensity would be decreased, the increase of tree heights in the upperstory could be expected since environmental conditions are similar to those found in OGF Janj.

6.3 PHYTOINDICATION, SPECIES DIVERSITY AND CANOPY OPENNESS

Landolt's phytoindication showed lowest presence of nitrogen, highest layering of raw humus and highest temperature in OGF Lom, which led to conclusion that this OG forest reflected more extreme site conditions in the layer of ground vegetation; managed forests were altogether inbetween, while OGF Janj reflected best or most favorable site conditions. Eutric cambisols which dominate in OGF Janj, although slightly shallower than calcocambisols in OGF Lom, provide more effective growing space for root system development (especially fine root endings) of middlestory and upperstory trees (Maunaga *et al*., 2005). Moreover, Landolt's phytoindication implied somewhat higher presence of nitrogene and thinner layer of raw humus in OGF Janj. Despite given results and substantial presence of rocky outcrops in OGF Lom, we can not say that this forest represented extreme site taking into account some soil characteristics (moisture, aeration, reaction), amount of precepitation, etc. On the contrary, OGF Lom also provides favorable conditions for development of climax species such as beech, fir and spruce.

Not only soil conditions but also canopy openness influence forest development and species composition (Canham, 1990; Cao and Ohkubo, 1999). OG forests had significantly smaller overall gap fraction (canopy openness) compared to managed forests. Consequently, ground layer species such as *Senecio fuchsii*, *Rubus idaeu*s and *Fragaria vesca* were found as indicator species in managed forests. These species are known as inhabitants of large openings within forested areas, whereas *Euonimus latifolia*, the species known for its high shade-tolerance, was determined as indicator species in OG forests. Sycamore maple above dbh 7.5 cm had low but constant share in composition of managed forests, while in OG forests it was virtually absent in the middle- and upper-story despite its constant presence in regeneration layer.

Shannon indexes and number of species on plots indicated slightly greater diversity of vascular plant species and dendro (woody) species in managed forests than in OG forests. This is in line with some European studies (e.g. Boncina, 2000), however, contrary to some American studies (e.g. Angers *et al*., 2005). This difference is likely due to different natural disturbance and management regime between regions. Species accumulation curve showed that increasing sample size in managed forests would lead to even greater diversity of flora, while such observation was not met for OG forests. Overall biodiversity including mammals, birds, insect species, fungi, etc. may be greater in OG forests, however, these variables were not encompassed in this dissertation.

6.4 THE IMPACT OF CLIMATE AND DEVELOPMENTAL PHASES ON SITE ASSESSMENT

Late optimal phase with conifers being dominant in the upperstory of OGF Janj resulted in very high GS (1215 m^3/ha), which is probably around maximum that this forest can reach. In the future with ageing and dying of trees and progression of terminal phase, significant reduction in GS may be expected, especially if beech replaces conifers in the upperstory to a larger extent. On the other hand, most plots in OGF Lom were characterized with terminal phase, so we don't really know how high volume would this forest yield if late-optimal phase would be present on most plots in this forest. Consequently, our site assessment referred to current site conditions, which are naturally subject to change (Boncina, 1999).

High precipitation and significant amount of dead wood in OGF Lom are certainly main factors contributing to maintenance of this extraordinary forest. Another issue is related to species coexistence and the influence of continental and maritime climates on seedling occurrence (Horvat *et al*., 1974). Overview of vegetation maps for BiH showed that above the belt of mixed beech-fir-(spruce) forests, in the (sub)alpine belt pure spruce forests grow if continental climate prevails, while areas with maritime influence seem to give preference to subalpine pure beech forests. Maritime influence was pronounced in OGF Janj (Milosavljevic, 1973), and this climate extends itself probably to the top of mountain Klekovaca (Lom) where one side of this mountain exhibits maritime climate with beech on top areas and the other side is characterized with continental climate, and as a rule of thumb, is populated with spruce on top areas.

6.5 LIGHT CONDITIONS AND REGENERATION CHARACTERISTICS

Mean values of transmitted direct and diffuse light as well as overall variability of light conditions were greater in the ground (understory) layer of managed forests Janj and Lom than in adjacent OG forests. The understory light level around 5 % in OG forests Janj and Lom was similar to the results from other OG forests (see Messier *et al*. in Wirth *et al*., 2009). Spatially, the frequency distribution of understory light levels in studied OG and managed forests was slightly right-skewed to normal, while some of previous studies indicated markedly right-scewed distribution with most microsites having low light conditions, and a few microsites with higher light levels (Beaudet *et al*. 2007; Bartemucci *et al*. 2006). BA did not serve as a good predictor of transmitted light or regeneration density up to 1.3 m above ground. To the same conclusion came Madsen (1994), Lundqvist and Friedman (1996), Chrimes and Nilson (2005), whereas Brown and Parker (1994) found that simple measures of forest structure such as estimated aboveground biomass and leaf area index (LAI) are not correlated with average light transmittance.

Mean yearly height growth of beech, fir and spruce regeneration was greater in managed forests than in adjacent OG forests, while the quality (vitality) of regeneration was rather similar. However, it was determined that transmitted light had no significant influence on height increment in regeneration category below 50 cm. Significant influence of light, nonetheless, was determined only on height increment of regeneration in the height category 50–130 cm. Statistically significant regressions between transmitted light and densities of regeneration up to 1.3 m in height were not determined whatsoever, neither for single species nor for total density. As performed by Rozenbergar (2012), the results from this study also indicate greater need for measurements of transmitted light at greater heights above ground and tallying higher regeneration individuals among which competition for light is far more intensified.

According to Grassi and Giannini (2005), if length of regeneration crown is below 60 % of total stem length, then light conditions can be considered as unfavorable or limiting for normal development. Conifers had LCR ratio below 0.6 in all studied forests. Only fir in OGF Janj had LCR around 0.6, but the number of sampled individuals was rather small. Beech generally exhibited higher values of LCR than conifers, except its seedlings (category 50–130 cm) in OGF Lom which had low 0.27 LCR. Therefore, we may assume that social positions of beech were more favorable in the regeneration stage, or such differences occurred due to biological and morphological differences between beech on one hand and conifers on the other.

Grassi and Giannini (2005) also stated that seedlings of fir and spruce with apical dominance ratio (ADR) or the ratio between apical and lateral shoot(s) below 1.0 are likely to be considered as light-stressed. We can notice that apical dominance ratios for conifers in Janj and Lom areas were far below threshold ratio of 1.0, and according to this indicator seedlings of fir and spruce in both managed and OG forests grew in low light environments. Total height/length ratio in beech showed only slight differences between managed and OG forests in terms of “upright” growth of beech seedlings. Plagiotropism in beech seedlings was not strongly expressed despite high values of GS which was generally dominated by conifers. Smejkal *et al*. (1995; see in Reiniger, 2000) gave an explanation on fir-beech exchange in the vertical profile of a stand. Namely, they stated that fir absorbs blue component of solar radiation while simultaneously letting red light component pass through its crowns down to the understory where beech takes advantage of it. When beech is in the upperstory and fir in the understory absorption preferances remain the same, only vertical positions of the species change.

6.6 TREE SPECIES COMPOSITION

Regeneration density was greater in MF Lom and smaller in MF Janj compared to densities in OG forests. There was no significant difference in species composition of regeneration between the two OG forests, while significant differences were found between OGF Janj and MF Janj. On the other hand, similarity in regeneration composition was indicated between OGF Lom and MF Lom. Species composition involving trees above inventory threshold (7.5 cm) indicated significant differences between managed and OG forests, whereas no significant difference was found between the two OG forests or between the two managed forests. Such outcome could be ascribed to the influence of forest management since the comparing areas were more-less similar in terms of site conditions.

Observations from relatively small inventory plots (452 m^2/ha) indicated that only 15 % in OGF Janj, 5 % in OGF Lom, 11.7 % in MF Janj and 6.7 % in MF Lom, were monospecific plots or pure cohorts considering number of one species individuals. Even when BA was used as a criterion for distinction, the percentages of pure cohorts was only slightly greater. This indicated high tendency of beech, fir and spruce to mix with each other and one below other on relatively small area. Such pattern is typical of selection forests (Schütz, 2001; Boncina, 2011). However, OG forests which were characterized with lower disturbance intensity and higher BA values, displayed similar pattern as well. Therefore, it is not only disturbance intensity which dictates forest dynamics, but also what understory and middlestory trees of these species are capable of enduring before the release takes place (Canham, 1990).

Knowing the mixture ratio by the number of trees and dbh structure serves as an important indicator for planning silvicultural works, because it indicates the direction of stands development, especially its succession stage. It also reveals eventual natural species shift in forest stands (Safar, 1953, 1965; Fukarek, 1965; Mlinsek *et al*., 1980), which may not be always congruent with production management goals. If trees of all species in a mixed stand have similar dimensions, then their share by number will be similar to their share by BA or GS. However, if dimensions are noticeably differing, that is, if trees of one species are thicker than some other species, then mixture ratio expressed in n/ha of constituent species will conspicuously deviate from ratio expressed in m^2/ha (Stojanovic and Krstic, 2000). For instance, in OGF Janj species composition in regard to number of trees was strongly in favor of beech with 63 %, whereas in regard to BA fir dominated with 52 %. Therefore, we need both ratio types to get thorough insight in composition of forest stands.

6.7 REPLACEMENT PATTERNS

Conditions in the surface soil layer (water content, layer of humus, pH reaction, etc.), frequency and abundance of seed production of different species, current climate conditions (Drobyshev *et al*., 2010) can influence occurrence of seedlings of one species or another. In OGF Lom spruce small seedlings were virtually equally occurring under beech and spruce mature trees, and they had higher transition probabilities and higher overall density compared to Janj area. Despite significant shares of Norway spruce in the upperstory, its regeneration and small trees were generally given low chances to replace mature trees in any of studied forests in the near future. One of the reasons for this could be in high values of GS which are not suitable for spruce regeneration (Stojanovic and Krstic, 2000; Govedar, 2005). In understory and middlestory dominant species on plots in OG forests was beech. Similar results for OG forests were obtained by Rozenbergar *et al.* (2007) and Nagel *et al*. (2010).

In regeneration and pole stage, however, species coexistence largely depends on the level of shade-tolerance of established seedlings (Rozenbergar, 2012). Schütz (1969) found that shade-tolerance of fir and spruce is longer in OGF Janj compared to Swiss plenter forests. This study showed that 26 % of sampled fir trees and 12 % of sampled spruce trees spent in suppressed conditions more than 200 years reaching height of only around 15 m. However, following canopy disturbance these trees were able to occupy the upperstory of this virgin forest.

Similar results for fir and spruce shade-tolerance were obtained by Magin (1959; see Assman, 1970). In his book Assman also gave an example stating that 80–100 years old beech trees in mixed beech-fir-spruce forest stand may be within the same natural growth phase as a 20–30 year old beech natural regeneration which has just been freed from cover. To similar conclusion came Miscevic (1964) while studying pure uneven-aged beech forests in Serbia. However, recent study on beech durability in shaded conditions with precisely measured transmitted light showed that this species cannot revitalize its growth after being hardly suppressed for a longer period of time (Rozenbergar, 2012).

6.8 DIAMETER STRUCTURE, BASAL AREAS AND GROWING STOCKS

Measures of variability for mean diameters of all species combined were greater in OGF Janj than in MF Janj, nevertheless, they were greater in MF Lom than in OGF Lom. As regards diameter distributions managed forests and OG forests had rather similar shapes, however, they universally differed in a way that smallest dbh class contained more trees in managed forests, whereas the presence of trees with dbh above 50 cm was clearly greater in OG forests. Considering several previously mentioned studies which tested and testified capabilities of fir, spruce and beech to endure long periods of time in shaded conditions, it was no surprise that in managed forests Janj and Lom dbh distributions were RS and IQ. Even OG forests Janj and Lom with higher GS values exhibited dbh distribution shapes considered to provide dbh demographic equilibrium (RS and NE shape, respectively). Both conifers in OGF Janj and spruce in MF Lom had UNI dbh distribution without sufficient self-replacement possibility even from the understory. Both conifers in OGF Lom and spruce in MF Janj expressed IQ distribution, while RS shape was characteristic for beech in OG forests and MF Janj whereas in MF Lom this species had CO distribution. However, when single managed stands were observed, fir and beech expressed NE distribution most often, and spruce distribution had IQ shape in most of the stands (Janj and Lom combined). Consequently, in seven managed stands cumulative distribution had NE shape and three managed stands were characterized with IQ diameter distribution.

In several other mixed OG mountain forests in Eastern and South-eastern Europe the most frequent shape of the cumulative dbh distributions was also the RS shape, followed by the IQ, NE and UNI shapes (Diaci *et al*., 2011). RS shape was most often reported in OG forests, but somewhere in managed forests as well (Goff and West, 1975; Janowiak *et al*., 2008). However, IQ shapes are more expected to develop in managed forests since they are usually characterized with the absence of large-diameter trees (Leibundgut, 1982; Leak, 1996; Janowiak *et al*., 2008). In OG forests IQ shape may develop following damage by windthrow (Diaci *et al*., 2011).

BA and GS values also represent important indicators of forest structure. This study revealed significant differences in tree densities and mean diameters between managed and OG forests in both areas, however, considering BA and GS values no significant difference was found between MF Lom and OGF Lom. Optimal GS is supposed to allow satisfactory regeneration and ingrowth of young trees if plenter structure is to be maintained. This issue is somewhat simpler to solve in pure forest stands. Namely, Schütz (1997) and Saniga (1998) implied that in pure managed beech forests total GS shall not exceed 300 m^3/ha if dbh demographic equilibrium is to be secured. This limit is similar to the target GS prescribed for Bosnian pure managed beech forests with selection structure. The difference in site conditions may lead to different productivity even among the same species pure forests. In this sense, for instance, due to favorable site conditions the primeval beech forest in the Bieszczady Mountains (Poland) had volume up to 430 m^3/ha and still kept selection structure (Jaworski, 2000).

The issue of optimal GS in mixed forests becomes far more complex since not only site conditions but also interactions between different tree species in the vertical profile is very important. In our studied forests we witnessed domination of fir and spruce in the upperstory, but there was no hindrance for recruitment of small beech trees up to dbh of 27.5 cm, even when GS was exceeding 1000 m^3/ha as we have seen in OGF Janj. Nevertheless, this study also showed that increase of beech BA and GS in the upperstory led to the decrease of small middlestory beech trees on sample plots. Similar results were obtained by Cavlovic *et al*. (2006).

According to Schütz (1997), the increment maximization and long-term structural stability in mixed spruce-fir-beech forests should be attained at around 350–400 m^3/ha. However, not only OG forests, but also managed forests Janj and Lom had rather high GS values (499 m^3/ha and 664 m^3/ha, respectively). Moreover, these values were significantly higher from officially prescribed target values 362 m^3/ha in Janj area and 530 m^3/ha in Lom area. Obviously, different interests at the local level made significant difference in terms of management goal setting. Our results indicated that official target values could be better adjusted to the natural potential of beech-fir-spruce forests in the study area, and that revision of management goals in some parts of BiH may be necessary. In Switzerland some mixed forests composed mostly of fir and spruce had plenter structure while simultaneously being characterized with high GS such as Neuenburger Jura plenter forest with 611 m^3/ha and Emmental plenter forest with 674 m^3/ha (Schütz, 1969). Additionally, Bachofen (1999) proposed target GS of 563 m^3/ha for Hasliwald plenter forest (also in Switzerland). In Serbia, target values for mixed fir-spruce-beech forests may vary between 500–550 m^3/ha (see Medarevic *et al*., 2008). Furthermore, long-term study by Mitcherlich (1952) in mixed plenter forests showed that amount of GS in range from 200–600 m^3/ha did not have significant influence on ingrowth of young trees, therefore, climate conditions may be stronger predictor of poles recruitment in the middlestory (Bachofen, 1999). The reason that influence of climate variables on forest dynamics was not performed in this study is due to the lack of detailed meteorological data for study areas.

To secure sustainability not only structural attributes (such as dbh structure, GS, etc.) are important, but certain stability indicators as well. In this sense, slenderness degree

(*German* Schlankheitsgrad) or H/D ratio served as a reliable indicator of susceptibility of trees to be broken or outrooted by wind or snow. Critical H/D ratio of 80 for a single tree or at a stand level was indicated by several authors (Chroust, 1980; Johann, 1980; Merkel, 1975; Rottmann, 1983). In OG forests Janj and Lom slenderness ratios across dbh classes were similar to those in managed forests, and generally below the critical ratio. Only beech and spruce exhibited slenderness ratios above critical level in smaller dbh classes, whereas fir in all cases had slenderness ratios below 80, indicating thus higher resistance toward exogenous factors such as wind and snow.

6.9 COARSE WOODY DEBRIS

Within MCPFE which was held in Vienna in April 2003 (MCPFE Work Programme), volume of standing dead wood and of dead wood lying on forest floor was addressed as one of criteria necessary for maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems. Importance of dead wood has not been recognized in BiH until recently. As a result, no data on this parameter were collected in previous studies and inventories.

In this study dead wood in the category of small logs was significantly more present in managed forests, while medium-sized logs were more present in OG forests. The same distribution of logs was presented by Spies and Franklin (1991). Stumps of both categories, small and medium-sized, were clearly more present in managed than in OG forests. Medium-sized snags were clearly more numerous in OG forests, while only results for small snags were variable. Similarly to results by Spies and Franklin (1991), greater number of small snags were found in OGF Lom than in MF Lom; nonetheless, in MF Janj there were more small snags than in OGF Janj. Finally, in OG forests there was incomparably more snags with dbh above 50 cm than in managed forests.

Managed forests and OG forests did not always differ significantly in terms of some structural attributes, such as BA and GS (e.g., in Lom area); however, there seems to be clear-cut difference between managed and OG forests in terms of CWD. Namely, when considering mean values of total CWD significant differences were found whenever managed forests (or even single stands) were compared to OG forests. Since the results indicated similarities between OG forests on one hand, and between managed forests on the other, it seems that CWD is a suitable characteristic to distinguish between managed and unmanaged forests, and could be hence used as a reliable indicator when assessing old-growth characteristics and naturalness of a forest.

In addition, one sample t-test showed that European average amount of CWD (220 m^3/ha) in beech-fir-spruce OG forests (Christensen *et al*., 2005) was significantly lower than average dead wood volume in OGF Janj (p < 0.05, one-tailed). Abundant dead wood in Janj was expected as this old-growth forest represents long-established mountainous forest reserve; besides, fir and spruce have been dominant in the upper story for at least six decades. Moreover, following disturbance these two species decay more slowly than beech (Harmon *et al*., 1986). Although we often were not able to differentiate tree species when measuring dead wood due to decaying processes, this was probably the main reason along with high productivity which made OGF Janj very copious with CWD. Even higher amount of CWD (420 m^3/ha) was reported for mixed beech-fir-spruce OGF Biogradska gora in Montenegro (Motta *et al*., 2014). Deadwood volumes in managed forests Janj and Lom were incomparably higher than average deadwood volumes in managed forests of several European countries (see Deadwood – living forests. The importance of veteran trees and deadwood to biodiversity: WWF Report, 2004).

Presence of stumps was significantly lower in OG forests compared to managed forests, which indirectly implied lower disturbance intensity of their canopies. This especially referred to OGF Janj. Namely, disturbance ratios showed only one stump on 10 living trees in this OGF, and this pertains to last few decades since the comparison between managed and OG forests involved all stumps (of which some were created decades ago).

6.10 COMPARISON OF OGF JANJ TO SOME OTHER EUROPEAN OLD-GROWTH FORESTS

Tree species composition according to GS in OGF Janj comprised one of the highest shares of conifers (84 %) when compared to other OG forests in the region (Drinic, 1956; Anic and Mikac, 2008; Diaci *et al*., 2011; Motta *et al*., 2011). Similar low percentage of beech (18 %) was found in OGF Igman in BiH, which is located about 92 km in South-East direction. In Janj spruce was present with especially high percentage (30 %), which can be compared with more continental Carpathian or Alpine OG forests, for example Lucka Bela with also 30 % (Firm *et al*., 2008). Very likely continentality and high altitude positively influenced share of spruce in Janj (Horvat *et al*., 1974). However, past natural or anthropogenic disturbance events cannot be excluded. Near Janj's core area is a geographical name "Pozar" in Serbian language which translates to fire in English.

Also in OG forests Lom and Perucica conifers were dominant in BA, with 68 % and 65 %, respectively (Motta *et al*., 2011; Lucic, 2012). Regarding tree density in all three OG forests beech was the dominant species with 63 %, 60 % and 50 % in Janj, Lom and

Perucica, respectively. Average GS of 1215 m^3/ha and BA with 67 m^2/ha in OGF Janj were also among the highest ever measured in Europe over larger areas and not on selected permanent plots (comp. Leibundgut, 1982; Korpel, 1995; Stojanovic *et al*., 2005; Motta *et al*., 2014). Average GS in Lom was with 763 m^3/ha lower, and in Perucica with 937 m^3/ha between these two values.

High GS in Janj is likely a result of high percentage of conifers, good site quality and a relatively long period (up to 60 years) without significant natural disturbances. The latter was indicated also by the forest structure with the absence of large gaps or cohorts of small trees. In Janj the average CWD volume was with 387 m^3/ha above average value in Lom (327 m^3/ha). Motta *et al*. (2014) also found very high values of deadwood in mixed Dinaric OG forests Perucica and Biogradska gora (406 and 420 m^3/ha, respectively).

In Janj the understory and the middle-story were dominated by beech in regard to tree density, while the upper-story was dominated by fir and spruce. In spite of beech dominance in lower stories and frequent replacement patterns by beech, there was some indication of reciprocal replacement between species. Moderate reciprocal replacement was often reported for mixed forests with silver fir (e.g. Tregubov, 1941; Simak, 1951; Safar, 1952). Transition matrices indicated future decrease of beech in the middle- and increase in the upper-story, if the assumptions of the model are to be met (White *et al*., 1985; Stevens, 2009). The probability that a canopy fir and spruce would be replaced by middle story beech doesn't depend solely on its frequency, since both conifers attain higher position within canopy. Thus, the assessment of the future species mixture with transition probabilities is above all an indication of potential beech progression.

6.10.1 Six decades of structural changes in OG forests Janj, Lom and Perucica

Comparison of new inventories (Motta *et al*., 2011; Lucic, 2012 and this study) with studies from Drinic (1956), Matic *et al*. (1971), Maunaga *et al*. (2005) may be biased since data was not collected on the same plots. Therefore, emphasis was on changes that were strongly expressed, preferably synchronous across OG forests and consistent with the data from recent more intensive inventories. During past six decades the average tree density in Janj and Lom increased for 25 % and 10 %, respectively, while in Perucica a decrease was indicated. Density increase in Janj and Lom may be attributed to the recent history of endogenous disturbance, but partially also to the 2.5 cm lower dbh limit at recent inventory. Total BA increased in Janj for 13 %, while it decreased in Lom and Perucica for 6 and 26 %, respectively.

In all reserves the share of spruce and fir in tree density decreased, while the share of beech increased. Also the share of beech in BA increased, while the share of spruce decreased. The share of fir in BA increased in Janj, stayed stable in Lom and decreased in Perucica. It seems that fir better compensated for the decrease in density by diameter growth when compared to spruce. Castagneri *et al*. (2014) drew similar conclusions after studying cores of oldest trees in OGF Lom. Another reason for more stable fir structure might be in less indirect anthropogenic disturbance in Bosnia when compared to Slovenia, Croatia and Slovakia. Namely, lower SO_2 emission (Berge *et al*., 1999) and lower deer densities (Census of game density in hunting area Sipovo, 2013) may have influenced less expressed silver fir dieback in Bosnia. Diaci *et al*. (2011) indicated a synchronous silver fir decline in most studied south-east European mixed mountain OG forests, while Bosnian mixed mountain OG forest Igman and Trstionica increased the share of fir in BA. The data from this study indicated stronger decrease of spruce, when compared to fir, which may be attributed to its greater susceptibility to drought and high temperatures at the limit of its geographic range towards Adriatic Sea (Horvat *et al*., 1974; Castagneri *et al*., 2014) or its successional stage due to past (anthropogenic) disturbance. This is also in line with present spruce decline in National Park Northern Velebit in Croatia, but see Battipaglia *et al*. (2009) for different results.

Comparison of tree species composition showed for all inventories and OG forests beech dominance in the first extended dbh class, its decrease along extended dbh classes and increase of conifers. This may be due to the inferior competing ability of beech in larger dbh classes (see Motta *et al*., 2011), but since the species mixture changed with time in favor of beech, it may also indicate onset of beech progression already before 1950s. Lower density of conifers compared with beech may, to some extent, not be in conflict with the demographic equilibrium due to lower mortality of conifers. This was indicated also by the less steeply sloped curves of their dbh distributions (comp. Shimano, 2000). However, stable dbh frequency shapes in time would be expected, if different natural mortality rate would be the main reason for the dbh distribution shape patterns.

The best fitting curves for dbh frequency of conifers indicated IQ shape in 1952, while in the recent inventory their shapes were more variable. For conifers IQ distributions may indicate, due to increasing Q, a higher mortality rate in large-diameter trees and potentially past disturbance, while UNI shape (Janj) may indicate past heavier disturbance, a succession or insufficient recruitment (Leak, 1996; Janowiak *et al*., 2008). NE and RS shapes are often reported as frequent in OG forests (Leak, 1996; Diaci *et al*., 2011). In OG northern hardwoods Ducey *et al*. (2013) found deviations from a classic “balanced” exponential distribution on plots heavily stocked with beech, however, in our study beech was sub-dominant to conifers and in all inventories exhibited tendency towards NE and CO shapes. CO patterns in beech were often observed due to few widely scattered large trees. It seems that they have filled some of the space made available by the conifer decline.

6.10.2 Historical evidence and possible causes of recent beech progression

Coexistence of spruce, fir and beech is a complex subject (Safar, 1952; Mlinsek, 1967a; Pintaric, 1978; Paluch, 2007; Nagel *et al*., 2010). It is driven by the interaction of many factors, anthropogenic and natural. While small scale endogenous disturbance favors fir, intermediate disturbance promotes beech, spruce and admixed broadleaved species (Leibundgut, 1982; Nagel *et al*., 2010). Regarding site conditions, conifers are for example more susceptible to competition from ground vegetation than broadleaves, therefore they are more successful in regeneration on rockier sites or acidic soils, and on CWD with less abundant ground flora (Ott *et al*., 1997). Beside natural drivers of stand composition in OG forests also influence of indirect anthropogenic factors may be strong (Golubovic, 1963; Peterken, 1996; Vrska *et al*. 2009; Diaci *et al*., 2010). Air pollution, over-browsing and position within agricultural landscape may change natural processes (Nowacki and Abrams, 1994).

Factors influencing coexistence act at different spatial scales from tree neighbourhood effects, through regional impact of diverse deer densities and air pollution, to a larger scale impact of climate change. Moreover, species coexistence in mixed mountain forests should be observed also from the long-term perspective, since all three species are long-lived and reach ages up to five centuries and more. Often dominant trees in OG forests originated two to four centuries ago (Mlinsek, 1967b; Schütz, 1969; Motta *et al*. 2011). At that time the densities of ungulates in Dinaric Mountains were significantly lower with some species even extinct due to poaching (Klopcic *et al*., 2010) and the climate was cooler (little ice age, 16th–mid 19th century period; Sercelj, 1996; Mann *et al*., 1999; Buntgen, *et al*. 2013).

Measuring rings on dominant trees just around what is today the core area of Janj, Schütz (1969) determined that fir establishment took place in the period between 1600 to 1660, and around the year 1740; whereas spruce according to the same source originates mostly from the period 1620 to 1685. Of course there were some other short periods of establishment of these species, however, above-mentioned periods were indicated as periods of massive conifers regeneration. These periods overlap with the Little Ice Age which brought lower temperatures and seemingly triggered waves of fir and spruce regeneration in Janj. Besides, in managed forests conifers were favored and beech treated as a non-commercial species. It was often felled as firewood or for charcoal and potash production (Matic, 1983). This type of forest exploitation didn't require sophisticated logging infrastructure and has affected some remote OG forests (Diaci *et al*., 2011). Before the last century cooler climate, unregulated logging of beech and low densities of ungulates favored regeneration of conifers.

During the last century, new constellation of factors evolved which gave indirect competitive advantage to beech. Already at the beginning of the 20th century warmer climate was reported for south and east Europe when compared to mid-19th century (Brunetti *et al*. 2006; Buntgen *et al*. 2013). Warm spells induced diffuse decline of conifers in mixed mountain forests on extreme sites and at limits of their geographic range (Safar, 1951). After WWII in former Yugoslavia a modern silviculture was introduced taking a full account of beech, while forest grazing was prohibited (Mlinsek, 1996). In 1950s with the onset of accelerated industrialization air pollution started, which negatively affected conifers, especially silver fir (Prpic, 1989; Elling *et al*., 2009). This species was weakened also by increasing densities of ungulates (Klopcic *et al*. 2010). Higher temperatures and longer vegetation periods coupled with nitrogen deposition may have also contributed to more exuberant ground vegetation (Sebesta *et al*., 2011; Kellner and Redbo-Torstensson, 1995), which represents a greater obstacle for the development of conifer than beech seedlings (Ott *et al*., 1997).

In BiH, air pollution was less accentuated compared to other parts of Yugoslavia (Berge *et al*., 1999), beside this game densities were never considered as excessive. Especially red deer was extremely rare, while roe deer and chamois densities even nowadays rarely exceed one animal per square kilometre (Diaci *et al*. 2011; Census of game density in hunting area Sipovo, 2013). On the other hand, the consequences of the climate fluctuations at the beginning of the 20th century in BiH were given a great attention in the scientific literature (comp. Safar, 1951 and references therein). Already in 1923 and 1924 bark beetle calamities on fir and spruce in the Dinaric Mountains were reported (Batic, 1930). The new wave of calamities started after extremely hot and dry summer of 1928, which was followed by a harsh winter (compare to meteorological data in Brunetti *et al*. 2006; Böhm *et al*., 2009; Kress *et al*., 2010). This resulted in patchy and diffuse decline of conifers in south-exposed and shallow soil sites, which was later followed by a large-scale bark beetle calamity on conifers: spruce, fir and Scotch pine (*Pinus sylvestris* L.) with the exception of black pine (*Pinus nigra* J.F.Arnold; see Bambulovic, 1930; Tregubov, 1941). Some authors shared opinion that bark beetle calamities were partially caused by unregulated felling and improper handling of felling residues (Batic, 1930; Omanovic, 1932). According to Popovic (1931) in the year 1928 only individual conifers at most exposed sites were weakened by the drought and consequently infested by bark beetles, while at the beginning of 1929 already groups of 10 to 15 trees were attacked, and by the end of 1929 circular patches of 100 trees and more. In the year 1930 size of patches reached 1000–5000 trees. Also healthy trees were attacked, but not small tress and saplings. At the start of the calamity its upper borderline was at about 1200 m, but by the year 1930 the calamity reached altitude of 1400 m a.s.l. Also Tregubov (1941), an early researcher of OG forests in Lom area mentioned these events.

The next important period of high summer temperatures and drought was in late 1940s and early 1950s (comp. to Brunetti *et al*., 2006; Böhm *et al*., 2009; Kress *et al*., 2010). For these events reports of bark beetle calamities in OGF Perucica are available. According to Eic (1951) and Golubovic (1963) in the fir dominated part of OGF Perucica 20,000 m^3 of infested conifers logs were cut down, which represented about 10 % of exploitable timber. Logs were not properly handled, which even increased the potential for beetle infestations. Eic (1951) further stated that the increased infection was also due to the fires in the neighbouring forests after heavy forest exploitation.

The bark beetle outbreaks in early 1920s, the severe climatic event in 1928, which was followed by droughts of late 1940s and early 1950s in interaction with anthropogenic disturbances (Safar, 1951) had weakened the competitive strength of conifers and probably induced a large-scale synchronous regeneration wave of beech, which was observed already by the early researchers of OG forests (Safar, 1951; Pintaric, 1978).

Beech seed crops are more seldom when compared to conifers (Kantorowicz, 2000), however beech mast years are becoming more frequent in the last century, possibly due to temperature increases, climatic extremes and increased atmospheric nitrogen (Drobyshev *et al*., 2010). Regarding disturbance events in BiH from 1920s to early 1950s it is also important that the early summer drought is a strong masting predictor for beech (Piovesan and Adams, 2001). Large-scale synchronous regeneration of beech has probably delayed regeneration of conifers, which lasted for several decades (Nagel *et al*., 2010). Documented climatic events, likely coupled with anthropogenic disturbances were indicated in this study by: (1) the beech dominance within small trees in all inventories and its increase over all dbh classes in recent inventories, (2) the future decrease of beech middle-story modelled with transition probabilities, (3) the IQ shape of dbh frequency distribution in 1950s for conifers in all OG forests and by (4) the changes in dbh frequency distributions. Also some other recent studies suggested these events, e.g. the disturbance study in Motta *et al*. (2011) and gap age analysis in Bottero *et al*. (2011).

6.11 SYNTHESIS

(a) General findings about the structure based mostly on descriptive analysis; most of them were expected, some may be trivial. There may be importance of these results in addition to the pool of measurements in OG forests: taller and larger trees, higher BA, higher share of senescent phase, more CWD, etc.
(b) General findings about vegetation and regeneration ecology (they are site/disturbance specific (*Piceo-*)*Abieti-Fagetum*):
- less light (and variability of light regimes), less ground vegetation, lower plant diversity in OG forests, negative influence of BA on fir, positive influence of light on height increment (species specific).
(c) Novel findings about regeneration ecology and forest structure
- long-term decline of conifers in OG forests (replacement matrices, distribution shapes, species composition); lower share of conifers in OG forests than in managed forests, and non-sustainable dbh structures (also shares in social positions) in OG forests.

Facit:
The long-term comparison of old-growth forest structure indicated decline of conifers (especially Norway spruce). Although smaller coniferous seedlings (up to 10 cm in height) were present in both types of forests, comparison of recent data in managed and OG forests indicated greater compositional stability of managed forests. Thus, selection management may help to hold back long-term conifer decline, while on the other hand no negative effects regarding diversity of vascular plants were found.

7 CONCLUSIONS

Application of selection (plenter) system in managed beech-fir-spruce forests Janj and Lom led to creation of dbh distribution shapes similar to those found in adjacent OG forests, while simultaneously causing difference in terms of tree species composition. Ground vegetation and light conditions were more diverse in managed forests. On the other hand, OG forests were characterized by greater abundance in CWD. Dbh distributions in managed and OG forests were rather similar since they both exhibited shapes considered to provide certain demographic equilibrium. However, they universally differed in a way that smallest dbh class contained more trees in managed forests, while in OG forests there was more large living trees and snags with dbh above 50 cm. Total tree number was greater in managed forests, while mean diameter, BA and GS values were higher in OG forests; nevertheless, the difference in BA and GS was not significant in Lom area.

Among single managed stands in Janj and Lom areas GS values varied significantly, calling thus for careful planning of management activities on stand level as well as on forest type level. Although site conditions and species composition between MF Lom and MF Janj were rather similar, unexpectedly greater difference in absolute values of GS occurred between them, than for instance between OGF Lom and MF Lom. This indicates that setting management goals and pursuing them, even through the similar cutting pattern but different intensity, leads to significant differences in structural attributes and species composition. It's not only the amount of GS but silvicultural system which influences tree species composition. This study showed that single tree selection cutting does not promote sufficient recruitment of shade intolerant sycamore maple and mid-shade tolerant Norway spruce. This is in line with the findings from other studies (Schwartz *et al*., 2005; Yoshida *et al*., 2006; Boncina *et al*., 2014). Nonetheless, it is important to emphasize that single selection system allowed constantly low presence of maple (1–2 %), while in OG forests this species was practically absent in middle- and upperstory.

Long-term analysis pointed out progression of beech regeneration and small trees in virgin forests Janj, Lom and Perucica in last six decades. However, we need to be cautious with this conclusion because the results of long-term analysis may have been slightly affected by the different sampling methods in previous inventories. Consequently, studies of this kind coupled with more detailed data on climate changes are needed in the future as the inventories in next 10-20 years would have greater certainty of confirming or denying the trend of beech progression indicated in this study. Unlike in OG forests, domination of fir regeneration and small trees was found in managed forests. This was not surprising since within selection system small beech trees were cut for firewood, whereas conifers at the same stage were left uncut. In this way selection management may help to mitigate or hold back long-term conifer decline and increase compositional stability of managed forests.

Replacement patterns indicated strong mutual support among beech, fir, spruce, and maple; however, what species will get the chance to occupy forest upperstory depends largely on the dynamics and intensity of natural disturbances and silvicultural measures. Low intensity of natural disturbances in OG forests and single tree selection cutting in managed forests did not provide sufficient recruitment of spruce in understory and midllestory despite significant presence of this species in the upperstory of all studied forests. Therefore, if the share of spruce, and maple as well, is to be increased in the future, gradual change towards group selection or irregular shelterwood system may be considered by policy makers and forest managers. This may be important from the aspect of tree species adaptation to warming climate in BiH (see also Castagneri *et al*., 2014), especially because long-term analysis in OG forests indicated greater decline of spruce than that of fir.

Finally, preservation of living veteran trees, snags and the species which depend on highly shaded conditions could be balanced partly in managed forests whereas skillfull spatial planning would be necessary, or in bordering forested areas which have no forest roads, so low level of wood exploitation is possible. Such areas are still copious in BiH. Otherwise, they should be deliberately designated.

8 SUMMARY

Managed mixed forests composed of beech, fir and spruce represent ecologically and economically very important forest category in Bosnia and Herzegovina. One of significant aspects of sustainability verification is a comparison of managed forests with unmanaged references. This study involved comparison between Dinaric mixed mountain OG forests Janj and Lom and adjacent managed stands on the same site (*Piceo-Abieti-Fagetum illyricum*), which were managed with a selection (plenter) system for more than a century. The measurements regarding dbh, tree heights, regeneration characteristics, CWD, light regime and phyto-sociological records, were carried out in the same way in managed and unmanaged forests. Consequently, following attributes were compared: tree density, dbh distribution shapes, tree species composition, mean diameter, BA, GS and CWD. Differences between managed and OG forests were found regarding attributes such as tree number, mean diameter, veteran trees and CWD; however, the results for species mixture were variable. BA and GS values were higher in OG than in managed forests, however, the difference was not statistically significant in Lom area. Despite high values of GS, dbh distributions in managed and OG forests were rather similar since they both exhibited shapes considered to provide certain demographic equilibrium. However, they universally differed in a way that smallest dbh class contained more trees in managed forests, whereas in OG forests there were incomparably more large living trees and snags with dbh above 50 cm than in managed forests. The difference for living trees was even more pronounced above dbh of 80 cm. Besides, canopy beech, fir and spruce trees in OG forests were significantly taller from those in managed forests. Mean values of total CWD on sample plots in OG forests were significantly higher than in managed forests. This difference occurred in the first place due to large presence of downed logs in OG forests. Presence of stumps was significantly lower in OG forests compared to managed forests, which indirectly implied lower disturbance intensities of their canopies. Dead wood in the category of small logs was significantly more present in managed forests, while medium-sized logs were more present in OG forests. Stumps of both categories, small and medium-sized, were clearly more present in managed than in OG forests. Medium-sized snags were more numerous in OG forests, while only results for small snags were variable.

Beside structural attributes, understory light regime and canopy openness were determined and correlated with regeneration characteristics. Mean values of transmitted direct and diffuse light as well as overall variability of light conditions were greater in the ground (understory) layer of managed forests Janj and Lom than in adjacent OG forests. OG forests had significantly smaller overall gap fraction (canopy openness) compared to managed forests. In addition, in managed forests ground layer species such as *Senecio fuchsii*, *Rubus idaeus* and *Fragaria vesca* were found as indicator species. These species

are known as inhabitants of large openings within forested areas, while *Euonimus latifolia*, the species known for its high shade-tolerance, was determined as indicator species in OG forests. Species diversity in the ground layer (woody and herbaceous plants) and site conditions were more heterogeneous in managed than in OG forests due to larger range of Shannon index values on sample plots. Sycamore maple above dbh 7.5 cm had low but constant share in composition of managed forests, while in OG forests it was virtually absent in the middle- and upper-story despite its constant presence in regeneration layer. In managed forests the cover of ground vegetation was greater than in OG forests. Mean yearly height growth of beech, fir and spruce seedlings was greater in managed forests, while the quality of seedlings was rather similar. Differences in tree species composition in the regeneration stage were found between OGF Janj and MF Janj, while similarity was indicated between OGF Lom and MF Lom.

Conclusively, this study pointed out progression of beech regeneration and small trees in virgin forests and progression of fir regeneration and small trees in managed forests. Although neighborhood effects indicated strong mutual support among beech, fir, spruce, and maple, what species will get the chance to occupy the upperstory of a managed forest depends largely on the dynamics and intensity of silvicultural measures. In case of high GS values distortion of sustainable dbh distributions does not necessarily takes place, however, the issue of regulating tree species composition comes to surface. Similarly to natural disturbance pattern in OG forests Janj and Lom, single tree selection system in surrounding managed forests did not lead to sufficient recruitment of spruce in understory and midllestory despite its significant presence in the upperstory. Small canopy openings made through single tree selection cutting provided small and constant share of maple in managed forests, however, if the share of spruce and maple is to be increased in the future, slight change in silvicultural approach may be necessary. Simultaneously and on the same managed area, preservation of living veteran trees, snags and the species which depend on highly shaded conditions remains difficult but challenging task for forest managers. Certainly, in order to have such multipurpose goal achieved skillfull spatial planning of silvicultural activities would be necessary on stand level. The other option would be deliberate designation of small protected areas which often adhere to intensively managed areas, but still have no forest roads, which makes them suitable for preservation of old-growth characteristics.

9 POVZETEK

Raznolikost sestojnih struktur v dveh mešanih gorskih pragozdovih in bližnjih gospodarskih gozdovih v Bosni in Hercegovini

Gospodarski mešani gozdovi, ki jih sestavljajo bukev, jelka in smreka predstavljajo ekološko in ekonomsko zelo pomembno skupino gozdov v Bosni in Hercegovini. Primerjava gospodarskih gozdov z referenčnimi pragozdnimi sestoji predstavlja enega izmed pomembnih vidikov preverjanja trajnosti. Pričujoča študija vključuje primerjavo Dinarskih jelovo-bukovih gorskih pragozdov Janj in Lom s sosednjimi gospodarskimi sestoji na primerljivem rastišču (*Piceo-Abieti-Fagetum illyricum*), kjer že več kot stoletje prebiralno gospodarijo (ger. Plenterwald, ang. selection system). Merila za izbir gospodarskih gozdov so bila: okoljske značilnosti gospodarskih gozdov so morale biti primerljive pragozdnim (primerljive rastiščne razmere, lega, itd.), sestoji so bili sredi intervala med dvema sečnjama, oziroma je bila zadnja sečnja izvedena najmanj štiri leta pred izpeljavo terenskih snemanj, jakost sečnje je bila tipična za prebiralno gospodarjenje (npr. ni presegala 20 % lesne zaloge).

Osrednja, strogo varovani dela pragozdov Janj in Lom, pokrivata površini 75,2 in 55,8 ha. Nadmorska višina raziskovalnih objektov je v razponu od 1000 do 1500 m nadmorske višine. Prevladujoča geološka podlaga vseh raziskovalnih objektov so karbonatni sedimenti. Prevladujejo pokarbonatna rjava tla in rendzine, različnih globin. Srednja letna temperatura raziskovalnih objektov je v razponu od 3,5–6.0° C; vsota letnih padavin pa se giblje v razponu od 1200–1600 mm.

V osrednjih območjih pragozdov Janj in Lom smo postavili sistematično mrežo 100 x 100 m ter na presečiščih zakoličili po 40 raziskovalnih ploskev. V petih sestojih v neposredni bližini vsakega izmed pragozdov, smo prav tako postavili sistematično vzorčno mrežo s po 12 vzorčnimi ploskvami na sestoj. Skupaj smo torej postavili 80 ploskev v pragozdovih in 120 v gospodarskih gozdovih. Za proučevanje sestojnih struktur smo uporabili merskih prag 7,5 cm prsnega premera, kar pomeni, da smo na vsaki vzorčni ploskvi izpeljali naslednje meritve: na 452 m^2 veliki krožni ploskvi (radij = 12 m) prsnih premer po vrstah (na 0,01 m natančno) za vsa živa drevesa nad merskim pragom; pomlajevanje po drevesnih vrstah (od 10 cm do 750 cm višine) smo analizirali na manjši, 78,5 m^2 veliki okrogli ploskvi (radij = 5 m). Na vzhodnem in zahodnem robu male krožne ploskve, kjer je le-ta sekala transekt, smo postavili dve kvadratni 2,25 m^2 (1.5 x 1.5 m) veliki raziskovalni pod-ploskvi za analize pomlajevanja. Na njih smo prešteli vse mladje po drevesnih vrstah, izpeljali popis zeliščne plasti in v sredinski legi posneli fotografijo hemisfere. Poleg tega smo določili tri dominantna drevesca vsake drevesne vrste v pomladku in jim izmerili naslednje značilnosti: višina; dolžina debelca do krošnje (do prvega venca živih vej); skupna dolžina debelca pri bukvi; dolžina zadnjih treh višinskih prirastkov; povprečna dolžina stranskih poganjkov pod apikalnim poganjkom pri iglavcih.

Kot dominantna smo upoštevali vsa tista drevesca z najvišjo verjetnostjo preživetja na določeni pod-ploskvi, kar so bili v večini primerov tudi najvišji primerki. Za izbor so morali biti višji od 10 cm in hkrati manjši od 130 cm, zaradi meritev svetlobe z objektivom ribje oko na tej višini. Med dominantne primerke je bilo pretežno uvrščeno mladje bukve, jelke in smreke. Čeprav so bile načrtovane meritve treh dominantnih primerkov posamezne vrste na vseh ploskvicah, smo pogosto naleteli na ploskvice brez mladja ali z redkimi primerki, zato smo meritve dominantnih primerkov po poskusnih snemanjih po potrebi razširili na večje ploskve velikosti 3 x 3 m. Te dodane, oziroma razširjene pod-ploskve smo uporabili le v modelih proučevanja regresijskih odvisnosti med sončnim sevanjem, ekološkimi dejavniki in značilnostmi podmladka. Kjer je bilo na pod-ploskvicah več primerkov določene vrste, smo v izračunih upoštevali srednje vrednosti izmerjenih značilnosti. Zaradi sorazmerno redkega podmladka v proučevanih sestojih je bilo veliko pod-ploskev le z enim primerkom.

Za proučevanje velikih drevesnih ostankov smo izpeljali naslednje meritve: na dveh 50 metrskih transektih, ki sta bila usmerjena proti severu (prvi) in vzhodu (drugi) od središča mesta vzorčenja, smo izmerili podrtice, ki so prečkale transekta (glej Van Vagner, 1968); na dveh pravokotnih ploskvah, velikosti 50 x 4 m, ki sta bili položeni preko sredine prej omenjenih transektov, smo izmerili panje (premer pri tleh in na vrhu panja) ter sušice (prsni premer). Za vsak element velikih drevesnih ostankov (kjer je bilo to mogoče) smo ocenili razred razkroja po metodi Nagel in Svoboda (2008) (razred 1 sveže, razred 5 skoraj popolnoma razkrojeno deblo). Velike drevesne ostanke smo uvrstil: v sušice (stoječa odmrla drevesa, prsni premer ≥ 7,5 cm in višina ≥ 1,3 m), podrtice (padla debla in veje s premerom ≥ 7,5 cm in dolžino ≥ 1 m) in panje (kratki, navpični ostanki debel po sečnji ali vetrolomu s premerom ≥ 7,5 cm in višino < 1,30 m). Za ločevanje podrtic in sušic smo uporabili kot 45°.

Ocenjevanje svetlobnega sevanja z metodo hemisferične fotografije so sestavljale štiri faze dela: fotografiranje (terensko delo), sledili sta registracija in razvrščanje slik ter izračun končnega rezultata. Za fotografiranje smo uporabili Nikon COOLPIX 5000 digitalni fotoaparat, opremljen z Nikon FC-E8 objektivom ribje oko. Na vsaki točki smo snemalno napravo uravnali v vodoravni in navpični ravnini na višini 1,30 m nad tlemi. Fotoaparat smo uravnali v smeri geografskega severa, tako da je bil vrh krožne fotografije vedno usmerjen proti geografskem severu. Registracijo, razvrščanje in izračun smo izpeljali s pomočjo programske opreme GLA 2.0 (Gap Light Analyzer) za obdelavo hemisferičnih fotografij. Terenske meritve smo izpeljali v letih 2011 in 2012.

Za vsak sestoj so rezultati za gostoto dreves (n/ha), temeljnico (m^2/ha) in lesno zalogo (m^3/ha) predstavljeni s preglednicami in grafikoni. Skupen volumen živih (celotno steblo z vejami in vejicami) in odmrlih dreves smo izračunali s pomočjo lokalnih tarif za bukev, jelko in smreko (Drinic et al., 1980). Oblike porazdelitev prsnih premerov dreves smo analizirali z uporabo metodologije iz Leak (1996) in Janowiak s sod. (2008). Sosedske učinke med drevesnimi vrstami smo analizirali s pomočjo verjetnosti prehodov med značilnimi sestojnimi plastmi v proučevanih gozdovih. Verjetnosti prehodov smo izračunali na temelju deležev drevesnih vrst v spodnji in srednji plasti, srednji in zgornji plasti ter spodnji in zgornji plasti. Vse velike drevesne ostanke smo združili v tri skupine: odmrli ležeči ostanki (podrtice), odmrla stoječa drevesa (sušice) in panji.

Statistične analize podatkov smo izpeljali v programu Microsoft Excel različice 2007 in SPSS Statistics različice 17.0. Testirali in primerjali smo naslednje znake: gostoto dreves, debelinsko porazdelitev, sestavo drevesnih vrst, srednji premer, temeljnico, lesno zalogo in volumen velikih drevesnih ostankov. Razlike med pragozdovi in gospodarskimi gozdovi smo ugotovili med naslednjimi znaki: število dreves, povprečni premer, stara drevesa in volumen velikih drevesnih ostankov. Rezultati primerjav pri vrstni sestavi so bili spremenljivi glede na način gospodarjenja. Vrednosti temeljnice in lesne zaloge so bile višje v pragozdu kot v gospodarskem gozdu, vendar pa razlika ni bila statistično značilna v območju pragozda Lom. Kljub visoki lesni zalogi so bile porazdelitve prsnih premerov tako v gospodarskem gozdu kot v pragozdu podobne in so nakazovale določeno demografsko ravnotežje.

Vendar pa bi lahko na splošno ugotovili, da vsebuje najnižji debelinski razred v gospodarskem gozdu več dreves kot v pragozdu. V pragozdu je bilo veliko več debelejših (premer 50 cm in več) tako živih kot odmrlih dreves. Razlika v številu živih dreves je bila še bolj izrazita pri debelinah nad 80 cm. Poleg tega so bile bukve, jelke in smreke v zgornji drevesni plasti pragozdov bistveno višje od tistih iz gospodarskih gozdov. Srednje vrednosti skupnega volumna odmrlih dreves na vzorčnih ploskvah pragozdov so bile bistveno višje kot v gospodarskih gozdovih. Do te razlike je prišlo zaradi velikega števila odmrlih ležečih ostankov v pragozdovih. Panjev je bilo bistveno manj v pragozdu kot v gospodarskem gozdu, kar nakazuje na manjšo prisotnost motenj v izbranih pragozdovih. Odmrlih drevesnih ostankov tanjših dimenzij je bilo precej več v gospodarskem gozdu, medtem ko je bilo v pragozdovih več odmrlega lesa srednjih velikosti. Malih in srednje velikih panjev je bilo značilno več v gospodarskih gozdovih. Odmrla stoječa drevesa srednjega premera so bila številnejša v pragozdovih, medtem ko so bili rezultati primerjave odmrlih stoječih dreves malega premera spremenljivi.

Poleg strukturnih lastnosti, smo izmerili še svetlobne razmere v sestojih in zastiranje z drevesnimi krošnjami ter ju korelirali z značilnostmi mladovja. Srednje vrednosti difuzne in direktne svetlobe pod zastorom so bile višje v gospodarskih gozdovih Janj in Lom, kot pa v bližnjih pragozdovih. Prav tako višja je bila variabilnost svetlobnih razmer. V pragozdovih je bil značilno manjši skupni delež odprtin v sestojnih krošnjah v primerjavi z gospodarskimi gozdovi. Poleg tega, so bile v gospodarskih gozdovih v zeliščni plasti vrste kot so *Senecio fuchsii, Rubus idaeus* in *Fragaria vesca* spoznane kot indikatorske vrste. Te vrste naseljujejo predvsem večje odprtine znotraj gozdnatih območij, medtem ko je bila vrsta *Euonymus latifolia* - znana po sencozdržnosti, ugotovljena kot indikatorska vrsta v pragozdovih. Glede na večji razpon vrednosti Shannonovih indeksov raziskovalnih ploskev, je bila večja heterogenost vrstne raznolikosti vaskularnih rastlin ugotovljena v gospodarskih gozdovih kot pa v pragozdovih. Gorski javor nad prsnim premerom 7,5 cm je zajemal sicer nizek, a stalen delež v sestavi gospodarskih gozdov, medtem ko je bil v pragozdovih, kljub stalni prisotnosti v mladovju, v srednji in zgornji drevesni plasti praktično odstoten. Prav tako je bila pokritost s pritalno vegetacijo višja v gospodarskih gozdovih. Povprečni letni višinski prirastek mladja bukve, jelke in smreke je bil višji v gospodarskih gozdovih, medtem ko v kakovosti mladja ni bilo večjih razlik. V vrstni sestavi mladja so bile ugotovljene razlike med ploskvami v pragozdu Janj in ploskvami v gospodarskem gozdu Janj ter podobnosti med ploskvami v pragozdu Lom in ploskvami v gospodarskem gozdu Lom.

Raziskava je nakazala prevladovanje bukovega mladja in manjših dreves v pragozdu ter uspešnost napredovanja mladja in manjših dreves jelke v gospodarskem gozdu. Čeprav so medsosedski odnosi nakazali močno medsebojno podporo med bukvijo, smreko, jelko in gorskim javorjem, sta predvsem dinamika in intenziteta gozdnogojitvenih ukrepov ključna vplivna dejavnika, ki odločata katera vrsta bo dobila priložnost za prerast v zgornjo drevesno plast. Študija nakazuje, da visoke lesne zaloge ne vplivajo na splošno demografsko ravnotežje v proučevanih sestojih, pojavljajo pa se odstopanja pri posameznih drevesnih vrstah, kar kaže na vprašanje dolgoročne stabilnosti drevesen sestave. Podobno kot pri naravnem vzorcu motenj v pragozdovih Janj in Lom, drevesno prebiralno gojenje gozdov ni bistveno izboljšalo deleža smreke v spodnji in srednji plasti, kljub znatni prisotnosti v zgornji plasti. Odpiranje manjših vrzeli preko prebiralne sečnje posameznih dreves je zagotovilo nizek, vendar stabilen delež gorskega javorja v gospodarskih gozdovih. Če bi v bodočnosti želeli povečanje deleža gorskega javorja in smreke, bi bile potrebne manjše spremembe pri gozdnogojitvenem pristopu v smeri nekoliko večjih koncentracij sečnje (skupinsko prebiranje, skupinsko postopno gospodarjenje). Izsledki nakazujejo, da bo tudi v prihodnje na širšem območju raziskave ohranjanje velikih živih dreves, sušic in podrtic ter sencozdržnih vrst težka in zahtevna naloga gozdarjev. Zagotovo pa je, da bi za uresničevanje takšnega večnamenskega cilja potrebovali podroben prostorski načrt gozdnogojitvenih ukrepov na sestojni ravni. Druga možnost bi lahko bila načrtna določitev manjših zavarovanih območij, ki se pogosto stikajo z intenzivno gospodarskimi območji, a so zaradi pomanjkanja gozdnih cest zelo primerni za ohranjanje pragozdnih značilnosti.

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