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A CENTURY LONG DYNAMICS OF SILVER FIR POPULATION IN MIXED SILVER FIR-EUROPEAN BEECH FORESTS

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Abstract

The long-term dynamics of silver fir in mixed silver fir-European beech forests in Slovenia was studied in three geographically dislocated study areas, i.e. Leskova dolina, Trnovo and Jelovica. In the study, archival data on forest stands for the past century were used to create the GIS database, which included data for the periods 1912-2004 for the Leskova dolina study area, 1897-2003 for the Trnovo study area, and 1899-2002 for the Jelovica study area. In the observed period, substantial changes in diameter structure of silver fir and its proportion in stand volume were recognized. In Leskova dolina and Trnovo, the silver fir population was ageing, while in Jelovica it rejuvenated. In Leskova dolina and Trnovo, the silver fir proportion in stand volume decreased in the observed period, indicating its reciprocal replacement with European beech. The analyses of regeneration and recruitment designated different future potential of silver fir in the study areas. The found dynamics of silver fir is underpinned by a complex array of influential factors, notably past forest use, the impact of large ungulates, and site conditions.

Key words: *Abies alba*, forest management plans, diameter structure, tree species composition, recruitment, regeneration, forest management, large ungulates

STOLETNA DINAMIKA JELKE V JELOVO-BUKOVIH GOZDOVIH

Izvleček

Dolgoročno dinamiko jelke v jelovo-bukovih gozdovih v Sloveniji v treh prostorsko ločenih objektih (Leskova dolina, Trnovo in Jelovica) smo preučevali z arhivskimi podatki o gozdnih sestojih. GIS podatkovna zbirka je obsegala podatke za obdobje 1912-2004 za Leskovo dolino, 1897-2003 za Trnovo in 1899-2002 za Jelovico. V analiziranem obdobju smo ugotovili znatne spremembe debelinske strukture jelke in njenega deleža v lesni zalogi. Populacija jelke se je v Leskovi dolini in na Trnovem starala, na Jelovici pa se je pomladila. Delež jelke se je v Dinaridih zmanjšal, nakazuje se izmenjava jelke z bukvijo. Pomlajevanje in vrast jelke nakazujeta njen različni potencial v raziskovalnih objektih. Na dinamiko vrste vpliva kompleks dejavnikov, še posebno pretekla raba gozdov, vpliv velikih rastlinojedov in rastiščne razmere.

Ključne besede: Abies alba, gozdnogospodarski načrti, debelinska struktura, drevesna sestava, vrast, pomlajevanje, gospodarjenje z gozdovi, veliki rastlinojedi

INTRODUCTION
UVOD

Silver fir (*Abies alba* Mill.) is the third most abundant tree species in Slovenia. It is currently present in 30% of forests, but it occurs abundantly only in 8% of forest cover (Poljanec et al., 2009). Silver fir (hereinafter fir) is naturally admixed to forest stands on approximately one third of forest sites in Slovenia (Dakskobler and Marinšek, 2009) from the colline to the subalpine altitudinal belts, but it finds its optimum in the montane and altimontane altitudinal belts (Ficko and Bončina, 2006). It most often forms mixed stands with European beech (*Fagus sylvatica* L.) or Norway spruce (*Picea abies* Karst.), sometimes also with other species like sycamore maple (*Acer pseudoplatanus* L.), larch (*Larix decidua* Mill.), wych elm (*Ulmus glabra* Huds.), common hornbeam (*Carpinus betulus* L.) or hop hornbeam (*Ostrya carpinifolia* Scop.); pure fir stands are rare. It is a typical shade-tolerant species, enduring frequent and long-lasting canopy shading, but on the other hand it is one of the most demanding and sensitive species in terms of other ecological demands (Prpić, 2001).

In the past, fir was given particular attention in research and forest management (e.g. Brinar, 1964; Levanič, 1997; Diaci, 2009; Ficko et al., 2011). Its proportion in stand volume decreased noticeably after the first national forest inventory in 1947, but the decrease was even more pronounced after 1970. During this period, its proportion more than halved, fir population became older, which was indicated by a strong increase in large-sized trees' proportion and a concurrent decrease of small-sized trees' proportion (Poljanec et al., 2009). In 1970-2008, the area of

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forest stands with more than 25% of fir in stand volume diminished from 18.9% to 9.5% of forest cover in Slovenia (Ficko et al, 2011). These facts indicate that fir is in regression in Slovenia, which is, however, a common feature of central-European forests (e.g. Eckstein et al., 1983, Senn and Suter, 2003). Some analyses showed that the dynamics of fir population may differ at the regional spatial level, but also between different forest types (Poljanec et al., 2009); on certain sites, even its progression was documented (Simončič and Bončina, 2010). In the past, climate and pollution were exposed as the most important factors of fir regression (Brinar, 1964; Levanič, 1997; Prpić, 2001; Elling et al., 2009, Diaci et al., 2010), but the impact of large ungulates, in particular red deer (*Cervus elaphus* L.), needs to be highlighted as well, since fir was often recognized as one of the most palatable and exposed tree species (Motta, 1996; Senn and Suter, 2003; Jarni et al., 2004).

In the last decades, a particularly pronounced fir regression was identified in the Dinaric fir-beech forests (Levanič, 1997; Poljanec et al., 2009; Ficko et al., 2011), where fir is among the main tree species (Kordiš, 1993). Fir-beech forests were recognized as a late-successional forest type, in which fir and beech have been continuously present for the last seven thousand years (Šercelj, 1996; Wick and Möhl; 2006). Fir is an important ingredient of these forests, since its proportion in their »natural« tree species composition would range from 20% to 40% of stand volume (Veselič and Robič, 2001).

In Slovenia, long-term dynamics of fir has not been very thoroughly studied so far (e.g. Gašperšič, 1967; Bončina et al., 2003; Firm et al., 2009; Diaci et al., 2010) and there is no study that would comparatively investigate long-term dynamics of fir on a regional spatial scale within the same forest type. The presented study was part of doctoral dissertation of the first author (Klopčič, 2011). The main aims of this study were 1) to explore long-term dynamics of fir in spatially dislocated study objects of fir-beech forest type, and 2) to evaluate its potential in study objects. We additionally analysed the impact of large ungulates on regeneration of fir and other tree species in Dinaric fir-beech forests in the Leskova dolina study area.

STUDY AREA AND METHODS
OBJEKT IN METODE DELA

Fir dynamics was explored in three study areas of fir-beech forests: Leskova dolina in the Notranjski Snežnik region, Trnovo on the Trnovski gozd plateau, and Jelovica in the Ju-

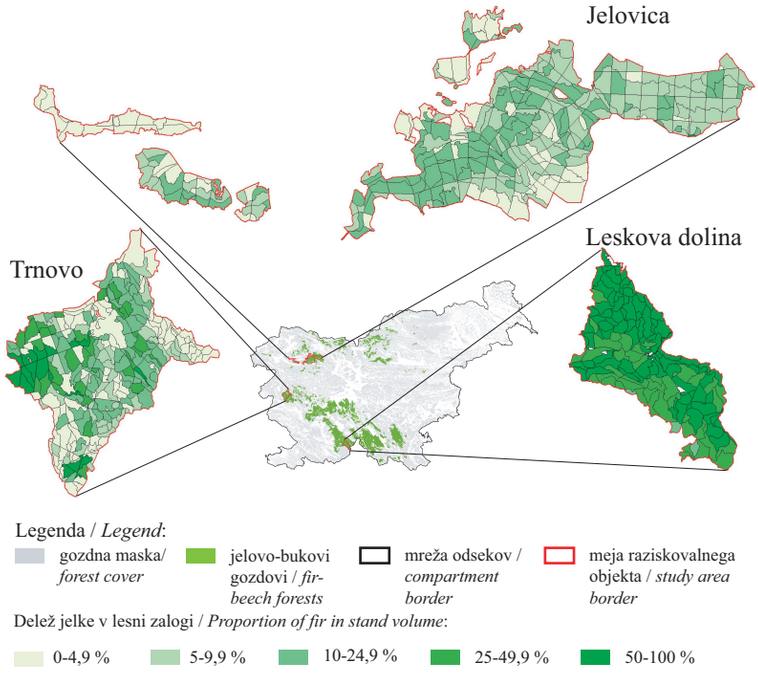

Fig. 1: The locations of study areas, the spread of silver fir-European beech forests in Slovenia, and silver fir proportion in stand volume in compartments within study areas (data source: ZGS, 2010).

Slika 1: Lokacija raziskovalnih objektov, razširjenost jelovo-bukovih gozdov v Sloveniji in delež jelke v lesni zalogi v raziskovalnih objektih (vir podatkov: ZGS, 2010).

lian Alps (Figure 1). The first two objects comprise the majority of homonymous forest management units, while the later comprises the greater part of two forest management units Jelovica and Notranji Bohinj.

Study objects differentiate in site, stand, and floristic characteristics (detailed descriptions of study objects can be found in Klopčič and Bončina, 2012: Table 1). The Leskova dolina forests are a typical representative of Dinaric fir-beech forests with *Omphalodo-Fagetum* (Tregubov 1957 corr. Puncer 1980) Marinček et al., 1993) being the prevailing phyto-sociological community. In these forests, the potential proportion of fir in "natural" tree species composition should be 30-40% of stand volume (Veselič and Robič, 2001). Fir-beech forests in Trnovo were characterized as forest with floristic elements of Dinaric, alpine and Submediterranean vegetation (Surina, 2002) with *Omphalodo-Fagetum* (Tregubov 1957 corr. Puncer 1980) Marinček et al., 1993 var.geogr. *Saxifraga cuneifolia* Surina 2002 being the prevailing phyto-sociological community. The potential proportion of fir in "natural" tree species composition of this forest community is somewhat lower than in Leskova dolina (≈ 20%). The Jelovica forests are characterized as *Homogyno sylvestris-Fagetum* Marinček et al., 1993. The potential proportion of fir in "natural" tree species composition of this forest community is around 20% (Veselič and Robič, 2001), but tree species composition in the majority of these forests is currently dominated by Norway spruce.

Several archival data sources were used in the study: old forest management plans and maps, Josephinian land register, raw data from forest inventories (permanent sampling plots, full callipering). The majority of archival data was acquired from databases (ZGS, 2010) and archives of the Slovenia Forest Service, while Josephinian land register was found in the Archives of the Republic of Slovenia. Nine old forest management plans for Leskova dolina, nine for Trnovo, and ten for Jelovica were used to build the final database (Klopčič and Bončina, 2011; 2012).

A GIS database was developed with a basic spatial unit being forest sub-compartment. Beside old forest management plans to provide the data, archival forest management maps were used for its construction (Klopčič and Bončina, 2011). The database covered the time periods 1912-2004 for the Leskova dolina, 1897-2003 for Trnovo and 1899-2002 for Jelovica.

The long-term dynamics of fir in fir-beech forests was examined by evaluation of changes in its diameter structure and its proportion in stand volume, while its future potential was investigated with the analyses of its regeneration and recruitment in the last inventory period. Obtained results were compared with the values of the same parameters for beech and spruce (regeneration also with sycamore). Diameter structures of the main tree species were calculated from basic data gathered in full callipering or on permanent sampling plots, and presented in 10 cm diameter classes to unify the data in different inventories. Stand volume and volume of a particular tree species were calculated from diameter structure and standard Biolley's tariffs. Recruitment (i.e. the ingrowth of trees above the measurement threshold of 10 cm in dbh) was calculated from the data on the last two measurements on permanent sampling plots (sampling grid 250×500 m: $N_{Leskova\ dolina}$=488, N_{Trnovo}=543; sampling grid 200×200 m: $N_{Jelovica}$=1654). Additionally, recruitment rate index RRI (Yoshida et al., 2006) was calculated for each main tree species (Equation 1):

$$RRI_i = \left(\frac{\left(N_{yold} + Nrec_{i,y}\right)}{N_{yold}} \right)^{0.1} - 1 \qquad [1],$$

where i means tree species, N_{yold} number of trees on a plot at the first inventory, and $Nrec_{i,y}$ number of recruited trees on a plot at the second inventory. RRI index designates the proportion of recruited trees in total number of trees at the first inventory (or how much a total number of trees increased due to recruitment with the presumption that there was no mortality). Regeneration was analysed using the regeneration inventory data (ZGS, 2004). Inventory plots were 5 m × 5 m large and distributed on a 2 km × 2 km grid. On each plot, seedlings and saplings 15-150 cm tall were tallied by tree species and by damage classes. Our sample contained 43 plots, 10 of them being in Leskova dolina, 8 in Trnovo, and 25 in Jelovica. In Leskova dolina (sub-compartments 38A and 39C), browsing on regeneration was additionally examined in 2008. On 33 plots sized 4 m × 4 m placed in fenced areas and on 33 plots of the same size placed in non-fenced areas, regeneration was surveyed by tree species, by height classes and by damage classes (Klopčič et al., 2010).

Statistical differences in diameter distributions of tree species between study areas in observation periods were examined using χ^2-tests. Additionally, differences between study areas in means of tree species proportions, recruitment, RRI, abundance and proportion of tree species in regeneration were analysed by the non-parametric Kruskal-Wallis test, while differences in the number of seedlings and saplings in fenced and non-fenced areas were analysed by the non-parametric Mann-Whitney U test (Zar, 2010).

RESULTS
REZULTATI

During the last century, the diameter structure of fir has changed noticeably in all study areas, but the dynamics differed between them (Figure 2). In Leskova dolina and Trnovo, stand density significantly decreased. In Leskova dolina, the total number of fir decreased for 68/ha in 1912-2004, while in Trnovo the reduction was even larger, amounting to 217/ha in 1897-2003. In Trnovo, the number of fir decreased in all diameter classes, but the proportion of large trees (dbh≥50 cm) in stand volume increased noticeably. Similarly, in Leskova dolina the number of fir in diameter classes of up to 50 cm decreased, while the number of large fir (and its proportion in stand volume) increased. In both study areas, the processes in the fir diameter structure may be described as "population ageing", since the absolute number and proportion of large fir were obviously higher at the end of observation period than at its beginning. On the contrary, in Jelovica the total number of fir noticeably increased in the last century (from 42/ha in 1899 to 58/ha in 2002). In 1899-1973, the number of thin fir (dbh=10-19 cm) increased from 8/ha to 34/ha, while after 1973 this number fluctuated within the 26-32/ha interval. The number of large fir remained practically at the same level. In comparison to fir population, the populations of beech and spruce were noticeably "younger", which is indicated by a larger proportion of thin trees in the total number of beech or spruce in forest stands.

The dynamics of diameter structure was followed by the changes in tree species composition. After 1960, the propor-

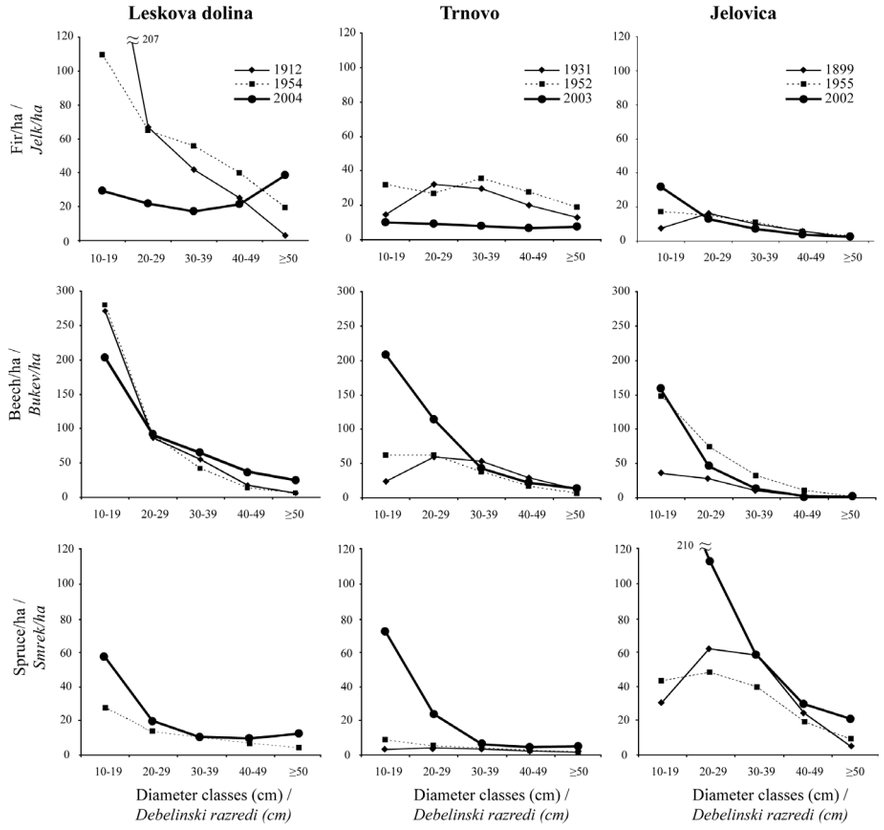

Fig. 2: Diameter structure of silver fir (upper row), European beech (middle row), and Norway spruce (bottom row) in the Leskova dolina, Trnovo and Jelovica study areas (columns).

Slika 2: Debelinska struktura jelke (zgornja vrsta), bukve (srednja vrsta) in smreke (spodnja vrsta) v objektih Leskova dolina, Trnovo in Jelovica (stolpci).

tion of fir in stand volume started to decrease in all study areas (Figure 3). The highest decrease of fir proportion was observed in Trnovo; in 1963-2003, it decreased from 54% to 18%. In the same time period, a fluctuation in dominance between fir and beech was noticed. According to Josephinian land register, the proportion of fir in Leskova dolina in the mid-18th century was noticeably lower (24%) than its current proportion, the dominant species at that time was beech. Until the mid-19th century, the proportion of fir rose to around a half of stand volume, while in 1912 its proportion already reached 68%. During the past century, fir was the dominant tree species at any given time, but in its second half, a decrease in its proportion, similar to that in Trnovo, was detected (from 69% in 1964 to 53% in 2004). By contrast, the proportion of fir in Jelovica was significantly lower than in the other study areas throughout the entire observation period. However, even there a decrease in fir proportion has been registered during the past century (from 16% to 9% in 1899-2002).

Simultaneously with changes in fir proportion, changes in proportion of beech occurred in Leskova dolina and Trnovo. The observed increase in fir proportion was mainly due to a reduced proportion of beech. When fir proportion culminated in the mid-20th century and then began to drop, it resulted in increased proportion of beech, but also spruce, which has been replacing fir on some sites. In Jelovica, on the contrary, spruce was the dominant species in the entire observation period, while proportions of fir and beech fluctuated between 8% and 17% of stand volume.

Recruitment of fir was generally low in the last inventory period (on the average 13.5 recruited fir/ha/10 years) and significantly lower than recruitment of beech (37.3 recruited beech/ha/10 years) and spruce (87.2 recruited spruce/ha/10 years). Total recruitment and recruitment per tree species (absolute values and RRI values) significantly differed between study areas (all $p<0.000$; Figure 4). Recruitment was the highest in Jelovica (190.2/ha/10 years), followed by Trnovo (94.2/ha/10 years), and Leskova dolina (61.3/ha/10 years). Recruitment of fir reached the highest value in Jelovica; on the average, there were 21.8 recruited fir/ha/10 years in 1992-2002, representing 11.5% of total recruitment. In Leskova dolina, recruitment of fir averaged 3.1/ha/10 years in 1994-2004 (5.1% of total recruitment), while in Trnovo only 0.7 fir/ha/10

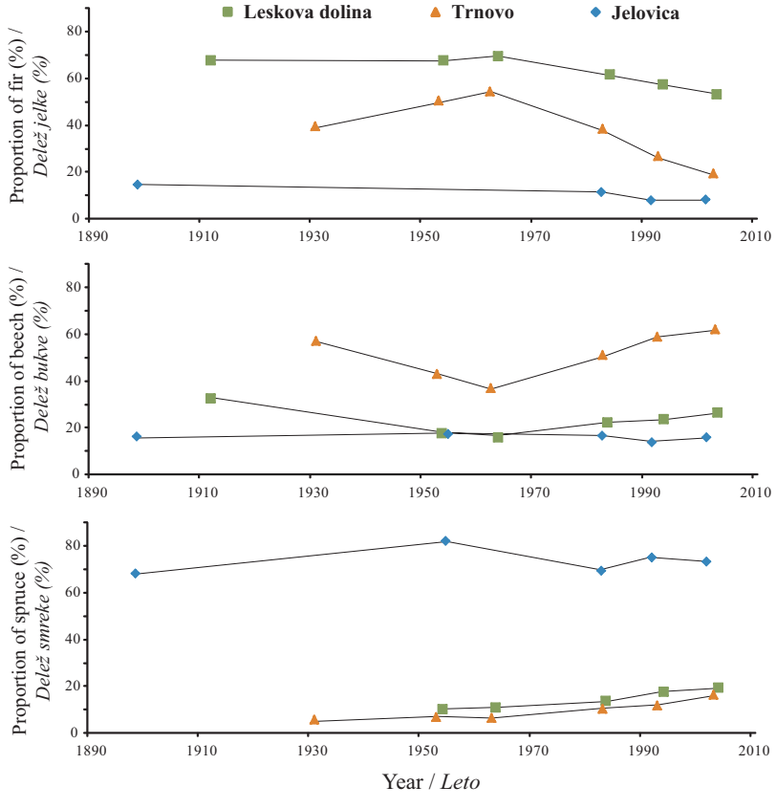

Fig. 3: The dynamics of silver fir, European beech and Norway spruce proportions in total stand volume in the observation period.

Slika 3: Dinamika deležev jelke, bukve in smreke v skupni lesni zalogi v preučevanem obdobju.

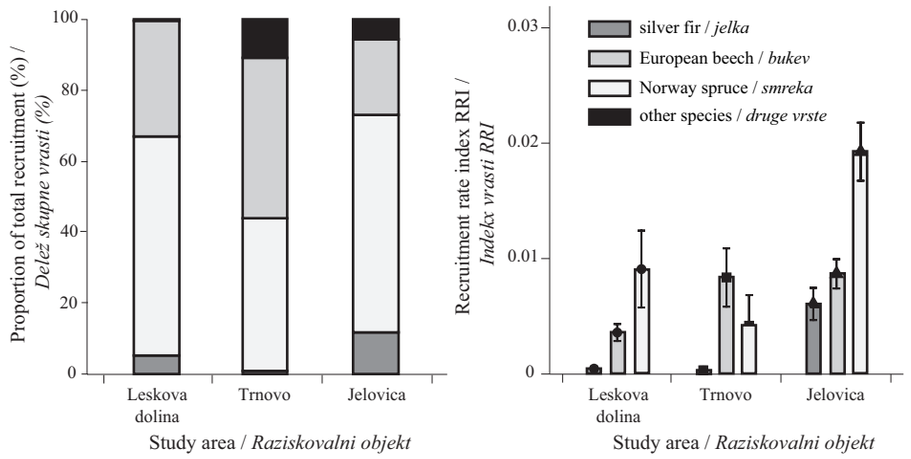

Fig. 4: Recruitment of silver fir, European beech, Norway spruce, and other species in the study areas.

Slika 4: Vrast jelke, bukve, smreke in drugih vrst v raziskovalnih objektih.

years was recruited in 1993-2003 (0.8% of total recruitment). If compared, beech and spruce represented significantly higher proportions in total recruitment in all study areas (Leskova dolina 32.8% and 61.7%, Trnovo 45.4% and 43.0%, Jelovica 21.3% and 61.5%, respectively).

Similarly as the analysis of recruitment, the analysis of regeneration showed a very low proportion of fir in the total number of seedlings and saplings (Figure 5). The lowest proportion of fir was found in Trnovo (2.3%), while slightly higher proportions were registered in Leskova dolina (4.8%) and Jelovica (7.6%). In Trnovo, beech and sycamore were most abundantly present in the regeneration, with the proportion of spruce reaching only 0.5%. In Leskova dolina, beech and sycamore prevailed in the regeneration, while spruce was present in similar proportion as fir. In contrast, in Jelovica

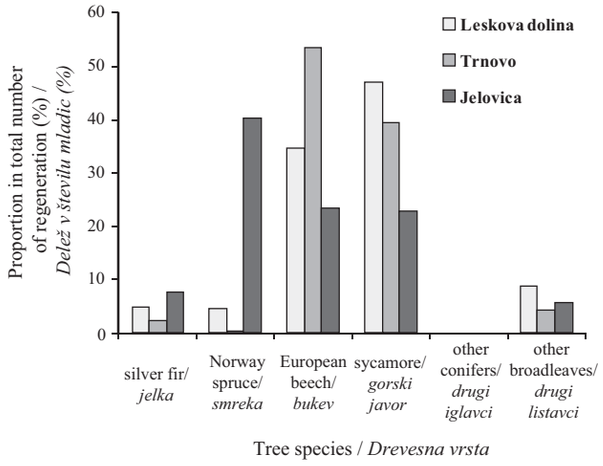

Fig. 5: Regeneration of tree species in the study areas.

Slika 5: Pomlajevanje drevesnih vrst v raziskovalnih objektih.

spruce strongly prevailed in the regeneration, but beech and sycamore were abundantly registered as well.

The regeneration and recruitment success of individual tree species may be importantly influenced by large ungulate impact. The overall browsing rate on regeneration was the highest in Leskova dolina (29%), slightly lower in Trnovo (26%), and the lowest in Jelovica (16%). The data on browsing rate per individual tree species were not available; such data would give a more detailed insight in the potential of fir and other species in the study areas.

The analysis of regeneration in fenced and non-fenced areas in Leskova dolina showed that no statistically significant differences existed in total number of seedlings and saplings between fenced and non-fenced areas (p=0,078), whilst differences in their numbers per height classes and per tree species were statistically significant (Figure 6). In fenced areas, all tree species successfully recruited into higher height classes, even fir recruitment was relatively high (625 fir/ha in the height class above 130 cm). On the contrary, in non-fenced areas fir and sycamore have not succeeded to overgrow the height of 50 and 130 cm, respectively. Fir regenerated successfully (3,352 seedlings/ha in the height class of up to 20 cm), but its recruitment was practically neutralized since only 152 fir/ha were registered in the height class of 20-49 cm. Above the height of 50 cm, no fir was tallied. Similar was found for sycamore, which successfully recruited to the height of 130 cm, but no higher sycamore saplings were surveyed. In contrast, beech successfully regenerated and recruited in fenced and non-fenced areas. Spruce was, however, rare since only 189/ha in fenced areas and 208/ha in non-fenced areas was tallied.

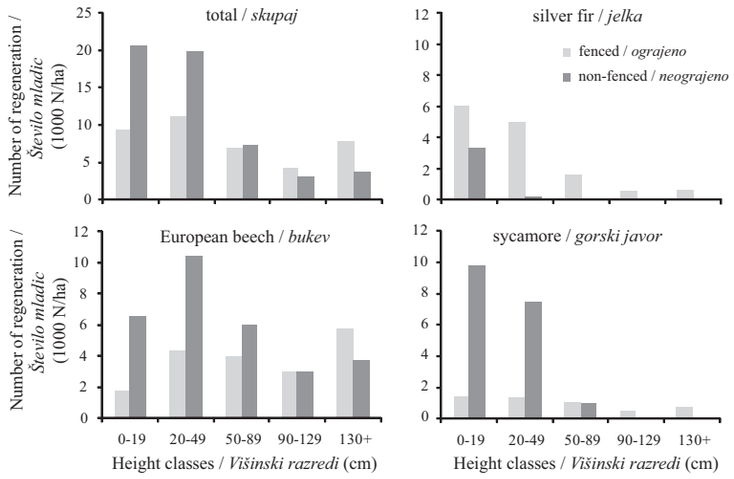

Fig. 6: The impact of large ungulates on the regeneration of Dinaric silver fir-European beech forests in Leskova dolina: the comparison of regeneration between fenced and non-fenced areas.

Slika 6: Vpliv rastlinojedcev na pomlajevanje dinarskih jelovo-bukovih gozdov v Leskovi dolini: primerjava števila mladic na ograjenih in neograjenih površinah.

DISCUSSION
RAZPRAVA

During the past century, fir underwent large changes in mixed fir-beech forests. The analysis of its diameter structure suggested two countervailing courses of its dynamics: "a regeneration" of its population in Jelovica and "an ageing" in Dinaric Mountains (Leskova dolina and Trnovo). In Jelovica, the increase in the number of thin fir was mostly a consequence of the application of close-to-nature, irregular shelterwood silvicultural system with longer regeneration periods (GGN Jelovica, 1973; 1983; GGN Notranji Bohinj, 1973; 1983) and a consequence of lower densities of large ungulates, especially of red deer, before 1990, which both enabled a successful regeneration and recruitment of fir. In Leskova dolina and Trnovo, insufficient recruitment of thin fir – a consequence of past forest management goals and measures (Gašperšič, 1967) and a high impact of large ungulates (Klopčič et al., 2010) – resulted in the fir population's reduced number and ageing process. Similar dynamics of fir was reported from Croatia (Čavlović, 2000), the Italian Alps (Motta and Garbarino, 2003), and the Carpathians (Vrška et al., 2009), while others reported on an ageing process in some other tree species (e.g. of eastern hemlock (*Tsuga canadensis* (L.) Carr.); Frelich and Lorimer, 1985).

An excess of fir mortality over its recruitment reduced its proportion in stand volume, obviously in the Dinaric Mountains, but less in the Alps. The observed dynamics of beech (and partly also spruce) was exactly the opposite of the dynamics of fir, indicating the "natural" process of their alternation (Korpel, 1995) or, in our opinion more appropriately, the fluctuations in dominance among these species in fir-beech forests (Wick and Möhl, 2006; Vrška et al., 2009; Diaci et al., 2010). Šercelj (1996) perceived that in these forests fir and beech do not thrive together and at the same time, but that fir encroaches upon beech stands, and *vice versa*. Both species fluctuate in their dominance in stand volume and in mature stands they only give an impression of a united formation. In the last centuries, these fluctuations have not been (only) naturally driven, as was frequently thought in the past (e.g. Korpel, 1995), but have more or less posed (directly and indirectly) as a human-driven process (Vrška et al., 2009; Diaci et al., 2010; Klopčič et al., 2010). In mixed forests, a replacement of fir with beech (e.g. Gašperšič, 1967; Vrška et al., 2009) or spruce (Heuze et al., 2005) has frequently been reported, generated and influenced mainly by past forest use such as litter raking and forest pasture (Vrška et al., 2009), by differences in past forest management, reflected in different distributions of canopy gap size (Nagel et al., 2010), and by the impact of large ungulates (Klopčič et al., 2010). Similar factors influenced fir dynamics as well, with past forest use, large ungulate impact and site conditions standing out. The latter affected mainly the proportion of fir in a "natural" tree species composition. In fir-beech forests, the proportion of fir in the "natural" tree species composition is somewhat lower in the Alps (≈20%) than in the Dinaric

Mountains (≈30-40%), while the proportion of spruce is noticeably higher in the Alps (Veselič and Robič, 2001).

Past use of fir-beech forests substantially altered the "natural" structure and tree species composition of forest stands before the introduction of regular forest management, but even more so after its beginning. Differences among silvicultural systems and the intensities of silvicultural measures were often identified as an important factor influencing stand dynamics (Sendak et al., 2003; Montes et al., 2005; Yoshida et al., 2006). The same was (indirectly) proven also in our study, since past forest management differed between study areas (Klopčič, 2011; Klopčič and Bončina, 2012). In Jelovica, past forest management system followed the classical approach to forestry, which favoured spruce over other tree species (GGN Jelovica, 1899); the proportion of fir consequently decreased. After the 1960s, more close-to-nature oriented forest management system (GGN Jelovica, 1973; 1983; GGN Notranji Bohinj, 1973; 1983) stabilized the proportion of fir at around 10%, while its current diameter structure indicates a possible increase of its proportion in the future. In Trnovo, regular shelterwood silvicultural system (GGN Trnovo, 1897) and, after the 1960s, more large-scale irregular shelterwood system (GGN Trnovo, 1973) were obviously favourable for regeneration of beech, but less so for fir. The latter was recognized as not prosperous when large-scale silvicultural systems are applied (Stancioiu and O'Hara, 2006). In Leskova dolina, fir was exclusively promoted for its economic reasons in the past (Gašperšič, 1967). It was of crucial importance for the selection forest management practiced there from the beginning of the 20th century (Schollmayer, 1906). The prescribed accumulation of volume increment and the subsequent rise of stand volume, together with a high browsing rate of fir regeneration, resulted in an insufficient recruitment of fir and a consecutive ageing of fir population. In the 1970s, the recruitment of fir was still inhibited, in some cases still made impossible, despite the introduction of the small-scale irregular shelterwood silvicultural system in combination with the selection system (GGN Leskova dolina, 1994; 2004), which both should promote shade-tolerant species (Stancioiu and O'Hara, 2006).

Fir dynamics was importantly influenced by large ungulates (i.e. red deer, roe deer (*Capreolus capreolus* L.), chamois (*Rupicapra rupicapra* L.), and mouflon (*Ovis musimon* Pallas)), which selectively browse tree species regeneration and thus codetermine tree species composition and reduce the number of recruited trees, in particular of the most palatable tree species such as fir (Motta, 1996). The impact of large ungulates on fir dynamics is long-lasting. In some areas in Central Europe, fir regeneration is browsed to the extent that it never passes the seedling phase (Ott, 1989; Senn and Suter, 2003; Jarni et al., 2004; Heuze et al., 2005). Moreover, Klopčič, Jerina and Bončina (2010) proved that beside past forest management high red deer densities in Leskova dolina were one of the key reasons for the decrease in the number of thin fir due to its insufficient recruitment in the past century.

Differences in large ungulate densities between study areas have substantially influenced fir dynamics. In the observation period, the highest large ungulate densities were recorded in Leskova dolina, where red deer density reached 5.8 animals/km^2 in the 1980s, but was afterwards reduced to a current density of approximately 3 animals/km^2 (Klopčič et al., 2010). Densities of other large ungulate species were noticeably lower: roe deer 1.3 animals/km^2, chamois 0.04 animals/km^2 (Stergar et al., 2009). In Trnovo, the impact of large ungulates has been significantly lower than in Leskova dolina, since in 2004-2008 the average red deer density was only 0.3 animals/km^2, roe deer density 3.7 animals/km^2, chamois density 2.1 animals/km^2, and mouflon density 0.06 animals/km^2 (Stergar et al., 2009). It would have been expected that lower densities of large ungulates would manifest in a higher share of more palatable tree species (e.g. fir) in regeneration and/or mature stands, but this hypothesis has not been confirmed in Trnovo. Obviously, (past) forest management and site conditions are much more important than the impact of large ungulates in this study area. In Jelovica, large ungulate densities were lower in the past than in the last two decades, which contributed to the enhancement of fir and broadleaves and their higher proportions in regeneration and recruitment. In the last two decades, the red deer density rose substantially and averaged 1.8 animals/km^2 in 2004-2008, while densities of other species were much lower: roe deer 0.6 animals/km^2, chamois 0.5 animals/km^2, and mouflon 0.05 animals/km^2 (Stergar et al., 2009). Due to the increased red deer density, higher browsing damages on regeneration can be expected, in particular on regeneration of more palatable tree species such as fir and some broadleaves.

Population of current canopy trees, but also of some sub-canopy trees, in Leskova dolina (Gašperšič, 1967;

Klopčič et al., 2010) and Trnovo (GGN Trnovo, 1887) should have germinated in the mid-19th century, when red deer was exterminated after 1848. It can be concluded that one of the possible survival strategies of fir is the so-called "window of opportunity" (Senn and Suter, 2003) – a contemporary occurrence of appropriate environmental (site) and stand conditions, such as low population densities of large ungulates, partial- and full-seed years, an accordant (natural and anthropogenic) disturbance regime, an appropriate structure and composition of mature stands – which enables its abundant regeneration and successful recruitment into the stand canopy. "The window of opportunity" was recognized as a survival strategy of eastern hemlock in mixed stands with broadleaves in North America (Frelich and Lorimer, 1985), which is of similar importance there as fir in mixed fir-beech forests, and Scots pine (*Pinus sylvestris* L.) and spruce in boreal forests in Sweden (Linder, 1998). However, the question that arises is in what spatial and temporal constellation such "window of opportunity" might occur in mixed fir-beech forests. Additional question is as to what densities of large ungulates, especially of red deer, would allow fir to successfully regenerate and recruit into the stand canopy. The relationship between browsing rate of fir and red deer density was found to be explicitly non-linear and weak. Some results indicated that a reduction in the browsing rate of fir should be recorded only for exceptionally low large ungulate densities (Jerina, 2008); the main cause for that is supposed to be its high palatability.

Future potential of fir in mixed fir-beech forests differed significantly between study areas. In Leskova dolina and Trnovo, a further decrease of fir proportion in stand volume may be expected, since its population is relatively old and significantly older than populations of beech and spruce. Additionally, its share in regeneration and recruitment is low. In Jelovica, maintenance or even a small increase of fir proportion in stand volume may be expected due to its relatively young population and significant share in regeneration and recruitment.

Despite a delineated future potential of fir, predicting its future in fir-beech forests and broader is rather unreliable. Most of the research (Eckstein et al., 1983; Senn and Suter, 2003; Vrška et al., 2009; Ficko et al., 2011) demonstrated a decline in fir proportion in the future, in the Dinaric Mountains most likely to the level before the (intensive) forest management began. However, on certain sites in Slovenia (e.g. Bohor region; Simončič and Bončina, 2010) and elsewhere (e.g. Poland; Dobrowolska and Veblen, 2008), observations showed a progression of fir, indicating that fir can be successful even in the current environmental conditions and that "the window of opportunity" may occur even in current conditions. In mixed fir-beech forests or any other mixed forests, a constant proportion of fir should not be accurately determined. Fir (or any other species) proportion is a dynamic parameter, which should be critically judged and determined according to site conditions and (long-term) stand dynamics. In the analysed forests, fir has been an important component for several millennia, as well as large ungulates. Therefore, a compromise solution through a constructive, common work of all interested public, but most of all through an adaptive forest management has to be found to maintain both of them.

POVZETEK
SUMMARY

Jelka (*Abies alba* Mill.) je tretja najpogostejša drevesna vrsta v slovenskih gozdovih. V zadnjih 60-70 letih je njen delež v lesni zalogi stalno upadal, njena razširjenost se je krčila, populacija pa se je starala. Vse našteto nakazuje regresijo jelke, ki je bila najizrazitejša v dinarskih jelovo-bukovih gozdovih. Primerjalna študija dolgoročne dinamike jelke na regionalni prostorski ravni v gozdovih istega gozdnega tipa v Sloveniji in širše še ni bila napravljena, zato smo z raziskavo želeli 1) preučiti dinamiko jelke v preteklem stoletju v treh prostorsko dislociranih raziskovalnih objektih jelovo-bukovih gozdov in 2) ovrednotiti prihodnji potencial jelke v raziskovanih gozdovih.

Raziskavo smo opravili v treh raziskovalnih objektih s prevladujočimi jelovo-bukovimi gozdovi, in sicer v Leskovi dolini na območju Notranjskega Snežnika v Dinaridih, Trnovem v Trnovskem gozdu in na Jelovici v Julijskih Alpah. Objekti se med seboj razlikujejo v rastiščnih značilnostih, pretekli rabi gozdov in trenutni zgradbi gozdnih sestojev. Dinamiko jelke smo analizirali z arhivskimi podatki o gozdnih sestojih, ki smo jih pridobili iz starih gozdnogospodarskih načrtov, gozdnogospodarskih kart, jožefinskega katastra in drugih virov neobdelanih podatkov z gozdnih inventur. Izdelali smo GIS-podatkovno zbirko, katere osnovna prostorska enota je bil odsek. Podatkovna zbirka je za objekt Leskova dolina vsebovala podatke za obdobje 1912-2004, za Trnovo za obdobje 1897-2003 in

za Jelovico za obdobje 1899-2002. Dolgoročno dinamiko jelke smo ovrednotili s spremembami njene debelinske strukture in deleža v skupni lesni zalogi ter z analizama vrasti v zadnjem načrtovalnem obdobju in pomlajevanja. Statistične razlike v izbranih kazalcih med raziskovalnimi objekti in med posameznimi inventurnimi obdobji smo preverjali z neparametričnimi statističnimi testi.

Debelinska struktura jelke se je v zadnjem stoletju značilno spreminjala v vseh raziskovanih objektih, vendar sta se dinamika in velikost sprememb v objektih razlikovala. V Leskovi dolina in na Trnovem se je sestojna gostota v zadnjem stoletju značilno zmanjšala za 68 oziroma 217 jelk/ha. Število debelih jelk (prsni premer ≥ 50 cm) (in njihov delež v lesni zalogi) se je opazno povečal, kar ob hkratnem zmanjšanju števila tankih dreves nakazuje staranje njene populacije. Na Jelovici je v opazovanem obdobju skupno število jelk naraslo, predvsem zaradi povečanja števila tankih dreves (prsni premer < 30 cm). V vseh raziskovalnih objektih je bila populacija jelke razvojno starejša od populacij bukve in smreke.

Delež jelke v lesni zalogi se je po letu 1960 začel manjšati. Največje spremembe smo ugotovili v objektu Trnovo, kjer se je delež jelke v lesni zalogi v obdobju 1963-2003 zmanjšal s 54 na 18 %. V istem obdobju je prišlo tudi do izmenjave v dominanci v skupni lesni zalogi med jelko in bukvijo. V Leskovi dolini je ob koncu 18. stoletja delež jelke znašal 24 %, vendar se je do leta 1912 povečal na 68 %. V zadnjem stoletju je bila jelka stalno dominantna drevesna vrsta, vendar smo v obdobju 1964-2004 zaznali upad njenega deleža za 16 %. Na Jelovici je bil delež jelke ves čas bistveno manjši kot v drugih dveh objektih, vendar smo tudi tu v obdobju 1899-2002 ugotovili upad deleža jelke iz 16 na 9 %.

Vrast jelke je bila v zadnjem inventurnem obdobju v splošnem majhna in v vseh raziskovalnih objektih značilno manjša od vrasti bukve in smreke. Vrast jelke je dosegla najvišjo vrednost na Jelovici (21,8 jelke/ha/10 let oziroma 11,5 % vseh vraslih dreves), nižjo v Leskovi dolini (3,1 jelke/ha/10 let oziroma 5,1 % vseh vraslih dreves), najnižjo pa na Trnovem (0,7 jelke/ha/10 let oziroma 0,8 % vseh vraslih dreves). Pomlajevanje jelke v izbranih raziskovalnih objektih kaže podobno sliko kot analiza vrasti. Njen delež v skupnem številu mladic je bil majhen, najmanjši na Trnovem (2,3 %), nekoliko večji pa v Leskovi dolini (4,8 %) in na Jelovici (7,6 %). V raziskavi smo ugotovili velik vpliv rastlinojedcev na obilje in preraščanje pomladka jelke.

V zadnjih sto letih je jelka v jelovo-bukovih gozdovih doživela velike spremembe. Analiza njene debelinske strukture kaže dve nasprotni razvojni tendenci: pomladitev populacije na Jelovici in njeno staranje v Leskovi dolini in na Trnovem. Presežek njene mortalitete nad vrastjo v sestoje je pripeljal do njenega manjšega deleža v lesni zalogi jelovo-bukovih sestojev, bistveno v Dinaridih in nekoliko manj v Alpah. V raziskavi smo ugotovili izmenjave v dominanci med jelko in bukvijo, pri čemer najverjetneje ne gre za povsem naraven proces, temveč za posledico posrednih in neposrednih človekovih vplivov. Ključni vplivni dejavniki tega procesa so bili pretekla raba gozdov, način gospodarjenja in gostote velikih rastlinojedov. Podobni dejavniki vplivajo tudi na dinamiko jelke, še posebno pretekla raba gozdov, vpliv velikih rastlinojedov in rastiščne razmere. Slednje vplivajo predvsem na delež jelke v »naravni« drevesni sestavi. Pretekla raba je spremenila naravno zgradbo in drevesno sestavo jelovo-bukovih sestojev že v obdobju pred načrtnim gospodarjenjem z gozdovi, še močneje pa po njegovem začetku. Gozdnogojitveni sistemi so se med raziskovalnimi objekti razlikovali, kar je dodatno povzročilo razlike v dinamiki jelke. Različne gostote velikih rastlinojedov v raziskovalnih objektih so tudi vplivale na dinamiko jelke. Vpliv rastlinojedov je bil največji v Leskovi dolini, kjer so bile gostote jelenjadi opazno večje kot v drugih dveh objektih. Na Jelovici je gostota jelenjadi v zadnjih desetletjih narasla, zato lahko v prihodnosti pričakujemo več poškodb v pomladku občutljivih vrst, kot so jelka in nekateri listavci.

Ker naj bi trenutna populacija vladajočih in sovladajočih pa tudi nekaterih podstojnih jelk v Leskovi dolini in na Trnovem vzklila v dokaj kratkem časovnem obdobju sredi 19. stoletja, lahko zaključimo, da je ena izmed možnih strategij uspeha jelke t.i. »okno priložnosti« (angl.: window of opportunity), sovpadanje ustreznih okoljskih in sestojnih razmer, kot so dovolj nizke gostote rastlinojedcev, obdobja polnih obrodov, ustrezen režim (naravnih in antropogenih) motenj, ugodne zgradbe in drevesne sestave odraslih sestojev, ki v relativno kratkem časovnem obdobju omogočijo njeno obilno pomladitev in uspešno preraščanje ter vraščanje v sestoje. Vendar se poraja vprašanje, v kakšnih časovnih in prostorskih okvirih se v jelovo-bukovih gozdovih pojavlja »okno priložnosti«. Prav tako ni znano, pri katerih gostotah rastlinojedov, predvsem jelenjadi, se jelka še uspešno pomlajuje in vrašča v odrasle sestoje.

Prihodnji potencial jelke v jelovo-bukovih gozdovih se značilno razlikuje med raziskovalnimi objekti. V gozdovih Leskove doline in Trnovega lahko pričakujemo nadaljnje upadanje deleža jelke, na Jelovici pa ohranitev njenega deleža na sedanji ravni ali celo majhno povečanje deleža v lesni zalogi. Delež jelke v mešanih sestojih je treba razumeti kot dinamično kategorijo upravljanja z gozdnim ekosistemom, presojati ga je treba glede na rastiščne razmere in razvojno dinamiko gozdnih sestojev. Jelka je v jelovo-bukovih gozdovih prisotna vsaj zadnjih nekaj tisočletij, prav tako rastlinojedi, kot pomembna komponenta teh gozdov. Poiskati moramo načine za ohranitev obeh naravnih sestavin teh gozdov, kar pa je mogoče le s konstruktivnim delovanjem vseh in adaptivnim upravljanjem gozdnih ekosistemov.

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