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ORIGINAL PAPER

Effect of vegetation on natural regeneration of mixed silver fir forests in lowlands: a case study from the Rogów region in Poland

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ABSTRACT

Silver fir *Abies alba* Mill. represented a historically high proportion of the natural species composition in Central Europe, but at present, due to forest management, game damage, climate change, and human activities, its share is extremely low. This paper aims to determine the abundance, species diversity, height structure, and especially the effect of competition level (1-4) and vegetation cover (mosses, herbs, ferns, grasses, *Vaccinium*, *Rubus*, tree litter) on the natural regeneration in a fenced forest stand with dominant fir in the tree layer. Research was conducted on 27 research plots in a lowland mixed forest (194 m a.s.l.) in the Rogów region of eastern Poland. Stand volume of the studied stand was 301 m^3/ha at the age of 60 years, with a fir share of 75%. The abundance of natural regeneration reached 52,667 recruits/ha, 63% of which was fir. Fir represented 74% in the initial (height ≤0.5 m) regeneration, while it only composed 8% of the advanced regeneration (height >0.5 m). Comparing tree layers, a decrease in the share of fir and European beech *Fagus sylvatica* L. and an increase of European larch *Larix decidua* Mill. and Scots pine *Pinus sylvestris* L. was observed in natural regeneration. Fir measured the lowest average height (24 cm) of all 15 occurring tree species (average height 43 cm). The mean height of natural regeneration was significantly positively correlated with vertical diversity. The tallest regeneration individuals were observed in the *Rubus* cover. The number of regenerations significantly ($p<0.05$) increased with vegetation cover and species richness. The highest density of fir was observed in the moss cover. The competition level had a significant ($p<0.05$) positive effect on the vertical and species diversity of natural regeneration, while its effect was negative on the proportion of fir. In terms of vegetation species, grasses had the largest effect on natural regeneration, while mosses had the lowest. Silver fir is very sensitive to silvicultural interventions, and it is necessary to support it with effective silviculture approaches during the ongoing climate change.

KEY WORDS

Abies alba, regeneration structure, tree species composition, competition level, Central Europe

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Introduction

Silver fir *Abies alba* Mill. is one of the most important commercial and ecological coniferous tree species in Europe (Poleno *et al.*, 2009; Dobrowolska *et al.*, 2017; Vitasse *et al.*, 2019). It grows in enclaves across Europe, stretching from the south – from the Iberian Peninsula to the Balkan Peninsula – as well as from northwestern Germany through Central Europe to the Carpathian Mountains (Jaworski and Zarzycki, 1983; Westergren *et al.*, 2010; Gazol *et al.*, 2015). Silver fir is distributed on elevated areas with an altitude range of 500-2000 m a.s.l. (Diaci *et al.*, 2011; Mauri *et al.*, 2016). This ecologically valuable tree species, especially in moist and gleyed habitats, increases the static stability, biodiversity, soil quality conditions and forest recreational value of the landscape (Poleno *et al.*, 2009; Mauri *et al.*, 2016; Podrázský *et al.*, 2018). Similar to Norway spruce *Picea abies* (L.) Karst., significant mortality has been observed in fir, with signs of dieback recorded in the previous two centuries (Málek, 1981; Dobrowolska *et al.*, 2017). Initially, fir dieback was more prevalent in the northern part of its natural range, while later, dieback was observed throughout its entire range (Bergmann *et al.*, 1990). However, the potential adaptability of fir to the ever-changing climatic conditions has become increasingly predictable (Vitasse *et al.*, 2019; Mikulenka *et al.*, 2020).

The decline and dieback of fir are the results of several factors, but clear-cutting management of this tree species has probably reduced its ability to adapt to changing environmental conditions. High levels of air pollution in the 1980s equally contributed to this damage in synergism with an overabundance of silver fir woolly adelgid *Dreyfusia nordmannianae* Eckstein (Zakopal 1978; Mrkva 1994; Vacek *et al.*, 2007, 2015; Mikulenka *et al.*, 2020). In this regard, climate-smart silviculture or fertilization may be one solution to promote fir health (Vacek *et al.*, 2020a; Gallo *et al.*, 2021). Hoofed game-induced damage, which in some cases can cause mortality (Ammer, 1996; Heuzea *et al.*, 2005; Vacek *et al.*, 2014), is also a significant limitation to the natural regeneration and the successful growth of fir (Jaworski and Zarzycki, 1983; Gill, 1992; Motta, 1996; Dobrowolska, 2008; Klopcic *et al.*, 2010; Kupferschmid *et al.*, 2013, 2018; Huth *et al.*, 2017). Small-pole and pole-stage stands are also heavily damaged through bark browsing and stripping by deer (Pach, 2005, 2008; Metzler *et al.*, 2012; Vacek *et al.*, 2020b). Regeneration is also negatively affected by frost, especially the increased frequency of late frost events, and can be a significant threat in the future (Maxime and Hendrik, 2011; Gallo *et al.*, 2017; Kupferschmid and Heiri, 2019).

Despite the increased management of silver fir stands, the density of its natural regeneration is often very low (Dobrowolska, 2000, 2008; Filipiak, 2002; Filipiak and Barzdajn, 2004; Szymura *et al.*, 2007; Vacek *et al.*, 2014, 2015; Vacek, 2017). One of the reasons for the generally uncommon regeneration of silver fir is the low share of parent trees in forest stands, which are often arranged in tight clusters (Filipiak and Barzdajn, 2004; Hofmeister *et al.*, 2008; Vacek *et al.*, 2015). Within the stands, new individuals are distributed over an area of several square meters close to mature trees (Filipiak, 2002). Here, the quantity and quality of fertility matter (Soulčres, 1962; Paluch, 2005). High-quality seeds are found only in sparse fir stands with well-developed crowns, a prerequisite for a successful natural regeneration (Korpeľ and Vinš, 1965; Skrzyszewska and Chłanda, 2009). Locally, the application of new ecological findings on silver fir silviculture has led to the successful regeneration of fir stands or mixed stands containing fir (Dobrowolska, 2000; Filipiak, 2002; Robakowski and Wyka, 2003; Hofmeister *et al.*, 2008; Mikulenka *et al.*, 2020). Less information is, however, available on the spatial distribution of seedlings in various microhabitats, as well as the effect of ground vegetation on the natural regeneration of fir (Szymura *et al.*, 2007). For example, Paluch (2005) states that *Oxalis acetosella* L. and *Vaccinium myrtillus* L.

indicate trophic and favourably moist soil profiles and conditions for the successful establishment and survival of silver fir seedlings. Conversely, typically unsuitable conditions for the natural regeneration of fir are created by dense ferns such as *Dryopteris filix-mas* (L.) Schott and *Pteridium aquilinum* (L.) Kuhn (Jaworski and Zarzycki, 1983). Therefore, some vegetation creates explicitly suitable conditions for fir regeneration, but others suppress it through space and resource competition (Jaworski, 1973; Pyšek, 1993; Paluch, 2005). High competition of ground vegetation can thus have a negative effect on the availability of resources for fir regeneration. In some cases, it can completely suppress fir recovery (Engeßer *et al.*, 2011).

The prediction of the health and production capacity of silver fir in the context of global climate change is currently an important topic. There are numerous discussions on this issue (Vitasse *et al.*, 2019). For example, some studies (Maiorano *et al.*, 2013; Zimmermann *et al.*, 2014) suggest that silver fir will not be able to withstand the climatic conditions expected to prevail in most regions of Western and Central Europe towards the end of this century. Other studies, however, predict healthy fir stands under climate change in most regions of Central and Eastern Europe (Tinner *et al.*, 2013; Bugmann *et al.*, 2015; Henne *et al.*, 2015; Ruosch *et al.*, 2016; Dyderski *et al.*, 2018b). Bosela *et al.* (2018) add that this will not be the case in the driest and warmest regions of Europe. It should be mentioned that the area of interest for this study in the Rogów region (PL) is located in lowlands, where precipitation is one of the limiting factors.

Numerous studies have been published focusing on the influence of habitat and vegetation on the natural regeneration of major commercial tree species such as Norway spruce *Picea abies* (Štícha *et al.*, 2010; Dyderski *et al.*, 2018a), European beech *Fagus sylvatica* L. (Bílek *et al.*, 2014; Vacek *et al.*, 2015, 2017) and Scots pine *Pinus sylvestris* L. (González-Martínez and Bravo, 2001; Bílek *et al.*, 2018). However, insufficient information is available on silver fir regeneration, especially in lowland areas compared to mountains (Hunziker and Brang, 2005; Paluch, 2005; Szymura *et al.*, 2007). It was this fact that prompted the writing of this manuscript. The main objectives of this work were (i) to assess the structure, density, and species composition of natural regeneration in mixed fir stands, and (ii) to determine the influence of ground vegetation and competition level on the abundance and establishment of natural regeneration of silver fir in the lowland forests in the Rogów area.

Material and Methods

STUDY AREA. The study was carried out in a mixed forest with predominant silver fir in the eastern outskirts of Łódzkie Hills in the central part of Poland. The experimental plot was located close to the town of Rogów in the Strzelna Forest at an altitude of 194 m a.s.l. (GPS coordinates 19°54'41"E, 51°48'55"N). Other admixed and interspersed tree species occurring in the study stand include European larch *Larix decidua* Mill., European beech, sessile oak *Quercus petraea* (Matt.) Liebl., Scots pine *Pinus sylvestris*, European hornbeam *Carpinus betulus* L., and European aspen *Populus tremula* L. The standing volume at the age of 60 years was 301 m^3/ha with 378 trees/ha. The average diameter at breast height was 33.1 cm, with an average height of 22.2 m. In 2017 thinning was performed aiming to remove pioneer tree species like silver birch *Betula pendula* Roth and aspen, as well as to irregularly reduce the density of fir. The same year, to avoid any influence of wild game disturbances, the experimental site was fenced.

The bedrock consists mostly of glacial formations made of clays and sands (Konecka--Betley *et al.*, 1993), with the predominant soil type being Luvisol according to World Reference Base (Zádorová and Penížek, 2011). The forest site is eutrophic. The groundwater level is very low, often too low for trees roots. The vegetation period lasts 211 days on average. The average annual precipitation is 583 mm, of which less than 65% falls during the vegetation period. The average annual temperature is 7.6°C. January is the coldest month with an average monthly temperature of –2.9°C, while July is the warmest month averaging 17.9°C (Ożga, 2002). According to Köppen's (1936) climatic classification, the site falls within the Cfb subtype (oceanic climate) characterized by mild summers and cool but not cold winters, with a relatively narrow annual temperature range, and few thermal extremes.

Data collection. Data were collected in two steps on a permanent research area of 0.36 ha. First, the position, species, DBH, and height of all individuals in the tree layer (parent stand) were recorded using FieldMap technology (IFER 2007). Second, natural regeneration individuals were measured in a total of 27 circular subplots of 5 m^2 for individuals ≤0.5 m (including) and 10 m^2 for individuals >0.5 m. For all natural regeneration individuals, the species and their height classes were recorded (1: <25 cm; 2: 25-50 cm; 3: 50-100 cm; 4: 100-150 cm; 5: 150-200 cm; 6: >200 cm). In addition to the number of regeneration individuals, the type of vegetation (mosses, herbs, ferns, grasses, *Vaccinium*, *Rubus*, and no vegetation/tree litter) and its share in the total ground vegetation, as well as the competition level of ground vegetation cover, was determined in each subplot. Competition level 1-4 represents the level of ground vegetation that affects the growth of individual tree regeneration (1 – low, 0-25% coverage; 2 – medium, 25-50% coverage; 3 – high, 50-75% coverage; 4 – very high, 75-100% coverage).

Data analysis. In terms of species diversity, indices of species richness (Margalef, 1958; Menhinick, 1964), species heterogeneity (Shannon, 1948; Simpson, 1949), and species evenness (Hill, 1973; Pielou, 1975) were calculated for individual plots (Table 1). The vertical structure was evaluated according to the Gini index (Gini, 1921). Relevant equations of diversity indices are given in Vacek *et al.*, (2020c).

Microsoft Excel was used for basic data analysis and the creation of graphs, specifically species composition and height distribution. Natural regeneration was divided into initial (height ≤0.5 m) and advanced (height >0.5 m) recruits. Statistica 13 (TIBCO, 2017) was used for the following statistical analyses. Data were first tested with the Shapiro-Wilk normality test, and then with the Bartlett variance test. When both requirements were met, the differences between the examined parameters were tested by an analysis of variance (ANOVA) followed by the Tukey HSD test. If normality and variance were not met, the investigated characteristics were tested by the nonparametric Kruskal-Wallis test. The relationship between natural regeneration height, vegetation cover, and competition level was evaluated using Spearman correlation. In the graphical outputs, error bars indicate confidence intervals. Confidence intervals were computed at the 95% confidence level (CI_{95}).

Table 1.

Overview of indices describing regeneration diversity and their common interpretation

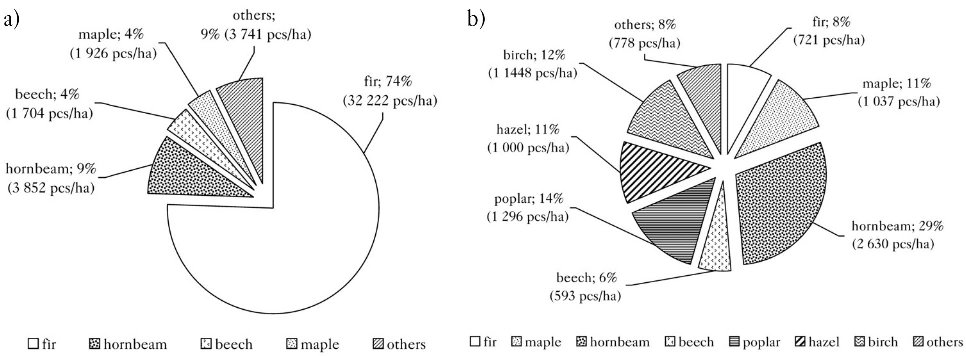
Criterion	Label	Reference	Evaluation
Species richness	D_1 (Mai) D_2 (Mei)	Margalef, 1958 Menhinick, 1964	minimum D=0, higher D= higher values
Species heterogeneity	λ (Sii) H´ (Shi)	Simpson, 1949 Shannon, 1948	range 0-1; minimum λ=0, maximum λ=1 minimum H´=0, higher H´= higher values
Species evenness	E_1 (Pii) E_2 (Hii)	Pielou, 1975 Hill, 1973	range 0-1; minimum E=0, maximum E=1
Vertical diversity	G_h (Gii)	Gini, 1921	range 0-1; low G<0.3, very high differentiation G>0.7

Principal component analysis (PCA) was performed in CANOCO 5 (Microcomputer Power, USA) to evaluate the relationships between the structure of natural regeneration (height, height of fir, density, share of fir), diversity of natural regeneration (see Table 1), competition level, and vegetation cover (vegetation cover total, grasses, herbs, mosses, *Rubus*, *Vaccinium*, tree litter). Data were logarithmized and standardized prior to analysis. The results of the multidimensional PCA analysis were visualized in the form of an ordination diagram.

Results

Regeneration density and tree species diversity. The total number of natural regeneration individuals was 52,667 pcs/ha, with silver fir comprising 62.6% of the species composition. For the abundance of individuals of the initial natural regeneration (height=0.5 m), fir was the most abundant tree species with 74% (32,222 pcs/ha; Fig. 1a), while the total regeneration in this height category reached 43,444 pcs/ha. Hornbeam was also abundant (9%; 3,852 pcs/ha), followed by maple (4%; 1,926 pcs/ha) and beech (4%; 1,704 pcs/ha). Other ligneous species – oak, common hazel *Corylus avellana* L., pine, larch, and small-leaved linden *Tilia cordata* (Mill.) – represented a total proportion of 9% (3,741 pcs/ha).

The values in Fig. 1b reveal a trend of decreasing abundance of fir individuals with their increasing height, the proportion for mature individuals (height >0.5 m initial regeneration) being only 8% (721 pcs/ha). The most abundant tree species in this group is hornbeam (29%; 2,630 pcs/ha). In the case of taller individuals, however, there is a higher diversity of other tree species, as well as a greater species balance (poplar – 14%; silver birch *Betula pendula* – 12%; hazel – 11%; Norway maple *Acer platanoides* L. – 11%; beech – 6%; others – 8%). The total number of mature individuals (height >0.5 m for advanced regeneration) was 9,222 pcs/ha, representing 17.5% of the total regeneration (82.5% initial regeneration).



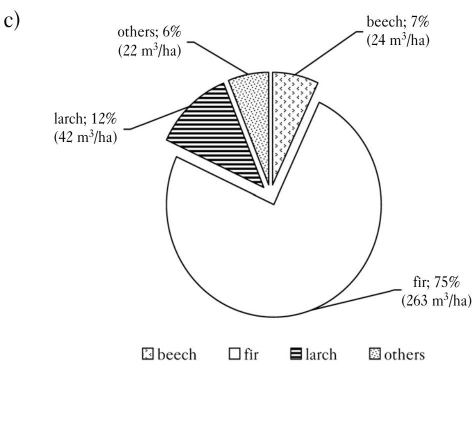


Fig. 1.

Summary of tree species composition for all research plots in 2021 for the a) initial (height ≤0.5 m) natural regeneration (according to numbers), b) advanced (height >0.5 m) natural regeneration, and c) mature stand (according to the stand volume)

The description of the tree layer (Fig. 1c) is also essential, where fir was the main tree species (75%; 263 m^3/ha). Concerning the total standing volume (351 m^3/ha), larch comprised a significant proportion (12%; 42 m^3/ha). Beech (7%; 24 m^3/ha) and pine (2%; 6 m^3/ha) also contributes to the structure of the tree layer. The remaining tree species make up 4% (16 m^3/ha).

In terms of species diversity of natural regeneration, species richness reached a low (D_1=0.469) to medium (D_2=0.089) diversity, species heterogeneity ranged within the medium values (λ=0.481, H´=0.479), and species evenness was high (E_1=0.640, E_2=0.621).

Height structure of regeneration. The abundance of fir individuals shows a decreasing trend as tree height increases, with the highest number of fir regeneration in the lowest height class (individuals <0.25 m) – 24,568 pcs/ha (Fig. 2). Firs are also abundant in the second height class (0.25-0.5 m) – 7,622 pcs/ha, but are rarely found in the 0.5 m range, with none present in the 2.0 m height limit. The highest numbers of other tree species are found in the second height class (0.25-0.5 m) – 16,132 pcs/ha. In this height category, the numbers of individuals of other tree species also exceed those of fir. Other tree species individuals are present in all height classes of interest. Overall, the highest numbers of natural regeneration individuals are found in the first age class <0.25 m, and their numbers decrease steadily as the regeneration height increases.

In terms of the average height of natural regeneration of individual species, fir had the lowest average height (19 cm), followed by oak (27 cm), larch (34 cm) and pine (36 cm; Fig. 3). On the other hand, hazel (122 cm), birch (119 cm) and goat willow *Salix caprea* L. (94 cm) were the tallest. The tree species with similar average height were hornbeam (72 cm), rowan (73 cm), hawthorn (75 cm), linden (75 cm), and cherry (75 cm). The overall average height of all regeneration individuals was 43 cm. Vertical diversity according to the Gini index was medium (G_h=0.408) for all tree species or low (G_h=0.176) in the case of the fir regeneration.

Interaction between vegetation cover, competition level, and regeneration. Competition level had no significant (Kruskal-Wallis test: $H_{(3, N=27)}$=2.74, p=0.43) effect on the height of natural regeneration of fir, while it had a significant (Kruskal-Wallis test: $H_{(3, N=27)}$=10.72, $p<0.05$) effect on the height of all recruits (Fig. 4). The significantly ($p<0.05$) highest mean height of all recruits was on competition level 4 (86.4 cm ±32.1 CI_{95}) compared to the lowest on level 1 (25.3 cm ±6.3 CI_{95}). The competition level also had a significant (Kruskal-Wallis test: $H_{(3, N=27)}$=7.27, $p<0.05$) effect on the share of fir in natural regeneration, while the significantly ($p<0.05$) lowest

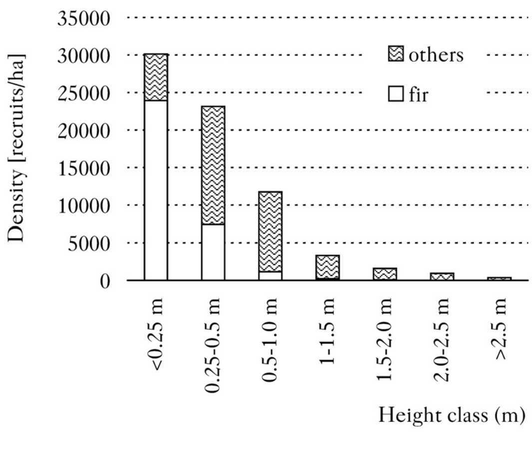


Fig. 2.

Height structure of natural regeneration on research plots differentiated by the tree species composition of silver fir and other tree species in 2021

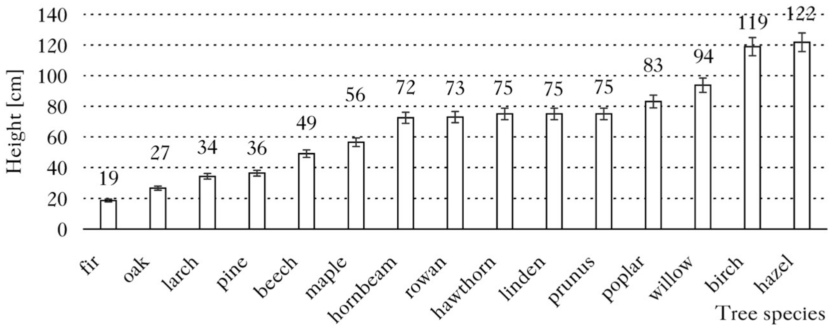


Fig. 3.

Mean height of natural regeneration on research plots differentiated by tree species in 2021; error bars indicate standard error

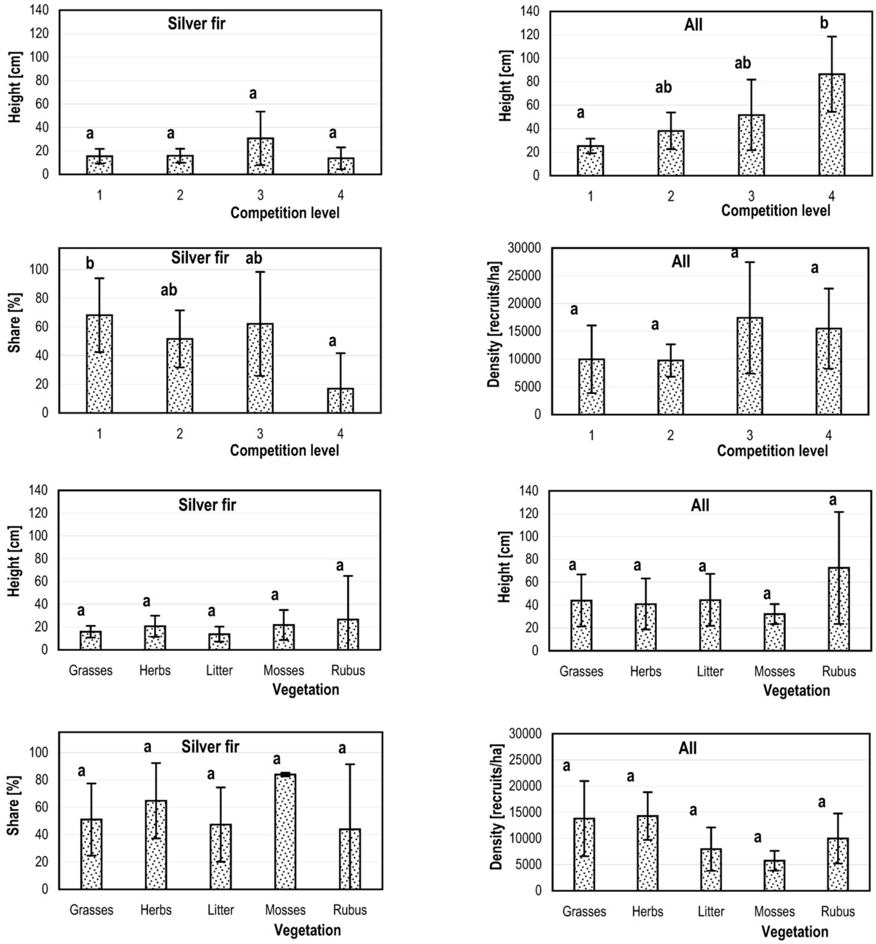


Fig. 4.

Effect of competition level (upper graphs) and vegetation cover (lower graphs) on mean height and number of natural regenerations on research plots differentiated by silver fir (left), and for all natural regeneration (right) in 2021; error bars indicate confidence intervals at the 95% confidence level; significantly (Kruskal-Wallis test or ANOVA, p<0.05) different values are marked by different letters share was observed on level 4 (16.9% ±24.7 CI_{95}) compared to the highest on level 1 (68.2% ±25.7 CI_{95}). No significant (ANOVA: $F_{(3, 23)}$=1.66, p=0.20) effect of the competition level was observed for the density of all regeneration, including fir.

The type of vegetation cover had no significant (Kruskal-Wallis test: $H_{(4, N=26)}$=1.88, p=0.75) effect on the mean height of fir, however, maximum fir height was observed in *Rubus* (26.6 cm ±38.2 CI_{95}) and the lowest in tree litter (13.7 cm ±6.6 CI_{95}; Fig. 4). Similarly, no significant effect on height was observed in the case of all recruits (Kruskal-Wallis test: $H_{(4, N=26)}$=2.99, p=0.56), whereas the highest natural regeneration (72.5 cm ±49.0 CI_{95}) was observed in *Rubus* compared to mosses (32.2 cm ±8.8 CI_{95}). Mosses also had a negative effect on the density of all recruits on the research plots. On the other hand, a positive effect of mosses on the share of fir was observed. However, differences in the type of vegetation cover on both the regeneration density (ANOVA: $F_{(4, 21)}$=1.27, p=0.31) and the share of fir (Kruskal-Wallis test: $H_{(4, N=26)}$=3.00, p=0.56) were not significant.

The results of the PCA showing the interactions between the structure and diversity of natural regeneration, vegetation cover, and competition level on 27 plots in the Rogów area are presented in the ordination diagram in Fig. 5. The first ordination axis explains 39.9% of data variability, the first two axes explain 54.3%, and the first four axes together explain 72.2% of data variability. The *x*-axis represents the species richness of natural regeneration, while the *y*-axis represents the share of fir in the regeneration as well as the *Vaccinium* cover. The mean height of natural regeneration showed a significantly positive correlation with vertical diversity

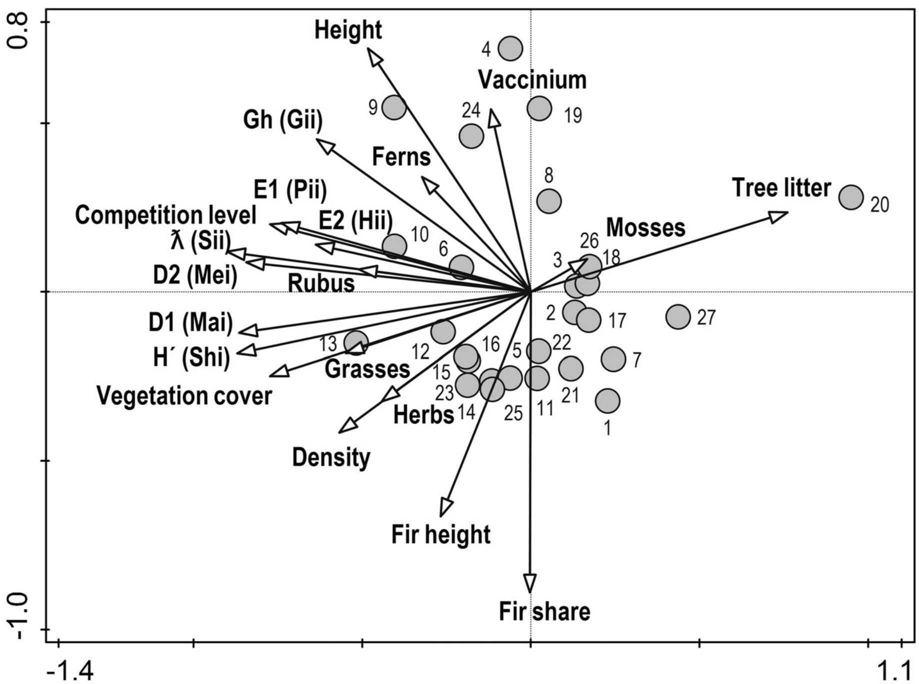


Fig. 5.

Ordination diagram of PCA results depicting relationships between the structure of natural regeneration (height, height of fir, density, share of fir), diversity of natural regeneration (see Table 1), competition level, and vegetation cover (vegetation cover total, grasses, herbs, mosses, *Rubus*, *Vaccinium*, tree litter); ○ symbols indicate research plots (1-27)

(r_s=0.95, p<0.001), competition level (r_s=0.56, p<0.01), and species evenness (r_s=0.51-0.52, p<0.05), and a significant (r_s=–0.73, p<0.01) negative correlation with the share of fir in natural regeneration. The abundance of regeneration significantly increased with the vegetation cover (r_s=0.50, p<0.05) and species richness *D1* (r_s=0.53, p<0.01), while it decreased significantly (r_s=–0.49, p<0.05) with tree litter cover. The competition level had a significantly (r_s=0.46-0.70, p<0.05) positive effect on all structural and species indices of natural regeneration. Specifically, in terms of vegetation cover, grasses had the highest effect on natural regeneration. On the other hand, the lowest explanatory parameter in the ordination diagram was moss cover.

Discussion

The study's results demonstrate significant relationships between the habitat and stand conditions and the stand regeneration in mixed stands of silver fir on eutrophic sites at lower altitudes. The number of regeneration individuals was 52,667 pcs/ha, of which 63% was represented by silver fir (compared to 75% in the tree layer). In addition to fir, a decrease in the share of beech, and an increase in the share of larch and pine in natural regeneration was also observed compared to tree layer composition. Similar results, in terms of the abundance of natural regeneration of fir stands in Poland, were reported by Jaworski and Fujak (1983) and Paluch and Jastrzębski (2013). In contrast, lower regeneration numbers in Europe are documented, for example, by Dobrowolska (2000), Filipiak (2002), Filipiak and Barzdajn (2004), Szymura *et al.* (2007), Hofmeister *et al.* (2008), Elling *et al.* (2009), and Vacek *et al.* (2015). One of the reasons for the relatively scarce regeneration of silver fir is high levels of browsing damage by deer (Motta, 1996; Senn and Suter, 2003; Vacek *et al.*, 2014). However, tree fructification and habitat also play an important role (Paluch, 2005; Skrzyszewska and Chłanda, 2009). Fir seeds germinate better as the seedlings thrive on the mor-humus horizon rather than on raw humus (Rousseau, 1960; Grunda, 1972). Orman and Szewczyk (2015) documented abundant natural regeneration of fir on heavily decomposed wood in the Western Carpathians and on mineral soil after windthrows (Janík *et al.*, 2014).

In this study, study plots were located in eutrophic habitats where the natural regeneration of fir is worse than in acidic microhabitats because of strong competition (Korpeľ and Vinš, 1965; Jaworski, 1973; Schrempf, 1978; Ellenberg, 1988; Paluch, 2005; Ujházy *et al.*, 2005; Woziwoda, 2008; Paluch and Jastrzębski, 2013; Woziwoda and Kopeć 2015). Due to global climate change, there has been a succession of mixed stands, including silver fir, that shows an increasing proportion of deciduous tree species, especially hornbeam and oak (Zerbe, 2002; Czerepko, 2004; Kopeć *et al.*, 2011; Woziwoda and Kopeć, 2015). Therefore, it is necessary to maintain a sufficient proportion of fir in stands through consistent silvicultural management with an emphasis on shelterwood practices (Vacek *et al.*, 2015). With silvicultural interventions, it should be taken into account that fir is a shade-tolerant tree species, however, it matures (exhibit fluorescence and fructification) only in full sun (Horvat-Marolt, 1985; Dobrowolska *et al.*, 2017).

In the studied eutrophic habitats, the ground vegetation had a significantly higher effect on natural regeneration than in acidic habitats (Beckage *et al.*, 2000; Paluch and Jastrzębski 2013; Woziwoda and Kopeć, 2015; Vacek and Matějka, 2010; Vacek *et al.*, 2010, 2017). Silver fir regenerates well on a cover of *Luzula pilosa* (L.) Willd., *Majanthemum bifolium* (L.) F.W. Schmidt, *Lycopodium annotinum* (L.) A. Haines, or *Rubus fruticosus* L. (Jaworski, 1973). In our case, the abundance of regeneration is positively correlated with vegetation cover (the more vegetation, the greater the regeneration), which is closely related to the canopy cover, and positively correlated with species richness. Similar results were reported both by Hofmeister *et al.* (2008) and Vacek *et al.* (2015).

Ground vegetation on acidic sites not only promote growth in the juvenile stages of regenerating individuals but also protect them against deer browsing (Senn and Suter, 2003; Vacek *et al.*, 2014; Vacek, 2017). In the studied forest stand, grasses had the highest influence on natural regeneration in terms of vegetation type, while mosses had the lowest influence. This is similarly reported, for example, by Korpeľ and Vinš (1965); Jaworski (1973); Korpeľ (1995) and Vacek *et al.* (2017). In terms of height structure, the highest individuals were recorded at sites with the presence of *Rubus* (27 cm), while the smallest individuals were recorded in habitats dominated by tree litter and no ground vegetation (14 cm).

Species diversity of natural regeneration in the study lowland area was low to medium according to species richness (D_1=0.469, D_2=0.089), medium according to species heterogeneity (λ=0.481, H´=0.479), and high according to species evenness (E_1=0.640, E_2=0.621). In comparison, higher species heterogeneity and evenness, but lower species richness was observed in fenced spruce-beech-fir stands on the Orlické hory Mts. (Vacek *et al.*, 2014). However, significantly lower species diversity was seen in this study on unfenced forest stands, similar to a study on the Krkonoše Mts. in Czechia (Prokůpková *et al.*, 2019).

Despite the increased silvicultural management of silver fir stands, natural regeneration is often insufficient, and height is poor compared to other tree species (Dobrowolska, 2000, 2008; Vacek *et al.*, 2015; Mikulenka *et al.*, 2020). Our firs reached the smallest average height (24 cm) of all 15 present tree species, with the average height of all individuals being 43 cm. Specifically, 74% of all fir trees were found in the initial natural regeneration (h≤0.5 m), while in the advanced natural regeneration (h>0.5 m), the representation was only 8%. This is because silver fir is very sensitive to silvicultural interventions (Dobrowolska *et al.*, 2017). Forestry systems used in Europe are among the main reasons for silver fir decline in stands in some areas (Vrška *et al.*, 2009). In the study region, the presence of silver fir reflects the suitability of the forest management regimen applied. Therefore, it is necessary to maintain a sufficient proportion of fir in stands through consistent silvicultural management, with an emphasis on shelterwood management and selection thinning practices (Vacek *et al.*, 2015; Mikulenka *et al.*, 2020). A regeneration period of at least 30-40 years seems appropriate for supporting fir trees (Bernadzki, 1965). As already mentioned, in the context of global climate change, the disappearance of silver fir from warmer and drier areas in Slovenia has been observed primarily in fragmented forests and at the borders of its natural range (Ficko *et al.*, 2011). The negative impact of the warming climate has also been observed in southwestern Europe (Gazol *et al.*, 2015), especially in the Mediterranean, where the fir decline has been linked to increased drought stress (Čavlović *et al.*, 2015).

Finally, the main limitation of the current study is that it was a non-repeated measurement, not a long-term study. Long-term research is very important for studying the dynamics of forest stands, including the changes in species composition (Pretzsch, 2009; Vacek *et al.*, 2017). On the other hand, this dynamic was partially replaced in our study by a comparison of the species composition of different developmental stages of regeneration and subsequently the tree layer. The second limitation of our research is the small area of interest. On the other hand, 27 experimental plots were examined in this forest complex and several case studies dealing with fir also provide important insights into silviculture practice and forest management (Barbu, 2009; Vacek *et al.*, 2014). Furthermore, case studies can guide future studies. The main benefit of this research is the unique and rare altitude position in the lowland. Silver fir is a typical tree species in hill and mountain forests (Konnert and Bergmann, 1995; Diaci *et al.*, 2011; Dobrowolska *et al.*, 2017). Thus, the studied lowland area could model dynamics of fir forests on mountains in relation to climatic changes associated with the lack of precipitation and rising temperatures in the future.

Conclusion

The studied mixed lowland stands in the Rogów area of Poland indicated a high natural regeneration potential (52,667 pcs/ha), with fir comprising 63% of the regeneration species composition, 12% less than in the tree layer. The proportion of fir decreased significantly with increasing height, where fir represented 74% of the initial natural regeneration, but 8% in the advanced regeneration. At the same time, fir showed on average the lowest height values when compared to the average height of the other tree species, while the highest was seen in pioneer tree species (birch and hazel). In terms of the vegetation influence, analyses revealed a significant positive effect of ground vegetation competition on the height of all natural regeneration individuals, which is closely correlated to gaps in the canopy. The vegetation cover type had no demonstrable effect on the height of fir regeneration individuals, but the tallest individuals were recorded at sites with the presence of the tallest vegetation – *Rubus*. In general, however, grasses had the greatest effect on fir regeneration. This can be a major problem in nutrient-rich sites with a loose canopy. We recorded a decreased proportion of fir as the competition level increased. This points to one of the main silvicultural recommendations, which is to promote fir or maximize caution in the release (canopy opening) of this shade-tolerant tree species. Other factors such as the influence of microhabitat, the competition of the parent layer, or the fact that this is a case study from lower altitudes should also be taken into account when interpreting the results.

Authors' contribution

A.P. – conceptualization, methodology, data collection, manuscript preparation, funding acquisition, manuscript corrections, supervision, project administrator; J.B. – conceptualization, data collection, manuscript preparation, manuscript corrections; Z.V. – data curation, methodology, statistical analysis, visualization, manuscript preparation, funding acquisition, manuscript corrections; K.B. – conceptualization, methodology, manuscript preparation; T.A. – conceptualization, methodology, manuscript preparation; S.V. – manuscript preparation, manuscript corrections; I.Š. – manuscript preparation; L.B. – manuscript preparation; Z.F. – manuscript preparation.

Conflicts of interest

No conflicts of interest.

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STRESZCZENIE

Wpływ runa leśnego na odnowienie naturalne mieszanych lasów jodłowych na nizinach: studium przypadku z Lasów Rogowskich

Jodła pospolita *Abies alba* Mill. jest ważnym gospodarczo gatunkiem drzewa iglastego, którego udział w lasach Europy w ostatnich dziesięcioleciach drastycznie spadł. Celem pracy było zbadanie wpływu typu pokrywy runa (ścioła, mszysta, zielna, borówkowa, zadarniona, paprociowa, jeżynowa) i poziomu konkurencji wyrażonego stopniem pokrycia (1 – mały, 0-25%; 2 – średni, 25-50%; 3 – duży, 50-75%; 4 – bardzo duży, 75-100%) na zagęszczenie, różnorodność gatunkową oraz strukturę wysokościową odnowień naturalnych w drzewostanie z dominacją jodły. Badania przeprowadzono na terenie Leśnego Zakładu Doświadczalnego w Rogowie (centralna Polska, ~194 m n.p.m.), wykorzystując w tym celu 27 kołowych powierzchni badawczych w ogrodzonym 60-letnim drzewostanie rosnącym na siedlisku lasu świeżego.

Łączne zagęszczenie drzew w warstwie odnowienia wyniosło 52 667 szt./ha, z czego 63% stanowiła jodła. W porównaniu z macierzystą warstwą drzew w odnowieniu naturalnym zaobserwowano zmniejszenie udziału procentowego jodły i buka zwyczajnego oraz wzrost udziału modrzewia europejskiego i sosny zwyczajnej (ryc. 1). W warstwie nalotów (wysokość ≤0,5 m; 43 444 szt./ha) najliczniej reprezentowanym gatunkiem była jodła (74%; 32 222 szt./ha). Zagęszczenie jodły malało w kolejnych analizowanych klasach wysokości odnowienia. W warstwie podrostów (wysokość >0,5 m) udział tego gatunku wynosił zaledwie 8% (721 szt./ha) (ryc. 2). Całkowite zagęszczenie podrostów wynosiło 9222 szt./ha (17,5% wszystkich odnowień). Najliczniej reprezentowanym gatunkiem w tej warstwie był grab (29%; 2630 szt./ha). Wyższe klasy wysokościowe odnowienia cechowały się większą różnorodnością gatunkową drzew i większą równomiernością ich występowania. Średnia wysokość osobników wszystkich badanych gatunków drzew wynosiła 43 cm, przy czym jodła była najniższa (19 cm), a brzoza brodawkowata najwyższa (122 cm) (ryc. 3).

Analizy statystyczne wykazały istotny wpływ konkurencji runa leśnego na średnie wysokości ogółem odnowień naturalnych (test Kruskala-Wallisa: $H_{(3,\ N=27)}=10,72$, $p<0,05$), jednak wpływ tego czynnika nie został potwierdzony w przypadku jodły (ryc. 4). Nie potwierdzono też statystycznie istotnego wpływu typu pokrywy runa na średnie wysokości wszystkich odnowień oraz samej jodły, choć najwyższe okazy tego gatunku odnotowano na powierzchniach z obecnością jeżyny (26,6 cm), a najniższe na pokrywie typu ścioła (13,7 cm). Średnia wysokość odnowień naturalnych była dodatnio skorelowana z ich różnorodnością pionową ($r_s=0,95$, $p<0,001$), poziomem konkurencji ($r_s=0,56$, $p<0,01$) i równomiernością gatunkową ($r_s=0,51$-$0,52$, $p<0,05$), natomiast ujemnie skorelowana z udziałem jodły w odnowieniu naturalnym ($r_s=-0,73$, $p<0,01$) (ryc. 5).

Stwierdzony istotny wpływ roślinności runa na zagęszczenie, różnorodność gatunkową oraz strukturę wysokościową odnowień naturalnych ma również implikacje praktyczne. Planując odnowienie naturalne jodły, należy brać pod uwagę konkurencję ze strony roślinności runa oraz samosiewów innych gatunków drzew i krzewów. Szczególną uwagę należy zwrócić na początkowe nasilenie cięć odnowieniowych, które powinno być na tyle niskie, aby zapewnić cienioznośnej i bardzo wolno rosnącej jodle przewagę konkurencyjną nad innymi gatunkami runa leśnego i tym samym umożliwić jej przejście do następnej fazy rozwojowej.