

Drivers of silver fir regeneration success: Interactions between site conditions, game browsing and close-to-nature forest management

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Abstract: Silver fir (*Abies alba* Mill.) is an ecologically and silviculturally important tree species in Central European forests due to its high production potential and increasing relevance under ongoing climate change. Therefore, its regeneration and promotion are of key importance for both ecosystem functioning and sustainable forest management. This study evaluates the potential of natural (four localities) and artificial (ten localities) regeneration of silver fir under close-to-nature silviculture across two natural forest areas (Křivoklátsko and Český kras; Brdská vrchovina) at altitudes of 362–570 m a.s.l. in Czechia. The objective was to assess the growth potential of fir regeneration across six contrasting site type categories on 62 research plots: acidic (3K, 4K), nutrient-rich (3B), loamy (3H), nutrient-medium (3S), gleyed nutrient-medium (4O) and gleyed acidic (4P) categories; and to quantify game browsing damage. The highest natural regeneration density was recorded on 4O sites, reaching on average 182 800 pcs·ha⁻¹, while the lowest density was observed on 4P (25 600 pcs·ha⁻¹). Compared to the overstorey composition, regeneration layers showed a marked increase in the proportion of silver fir. In contrast, the highest annual height increment of natural regeneration was found on 4P (10.6 cm), significantly exceeding that on 3S (2.1 cm). Browsing damage ranged from 11.0% (3S) to 19.2% (4O). In terms of artificial regeneration, the highest annual height increment was recorded at site type 3H (38.4 cm), whereas the lowest was observed at site type 3B (15.2 cm). Our results show that fir regeneration is mainly driven by site conditions and ungulate browsing, providing a basis for targeted silvicultural and game management to support its long-term persistence.

Keywords: *Abies alba* Mill.; forest vegetation zones 3–4; natural regeneration; site typology; ungulate pressure

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Silver fir (*Abies alba* Mill.) is among the most valuable tree species of Central and Southern European forests (Gazol et al. 2015), owing to its combined economic and ecological importance. These attributes are gaining increasing relevance under the conditions of global climate change (GCC) (Dinca et al. 2022; Frei et al. 2025). In this context, its growth is strongly controlled by climatic variability, particularly seasonal temperature and precipitation patterns, with summer drought acting as a key limiting factor (Šimůnek et al. 2023). As a climax species, silver fir requires shaded conditions during its early developmental stages (Bledý et al. 2024). It also plays a key role in maintaining forest stability and biodiversity, particularly on gleyed and waterlogged sites (Vacek et al. 2015; Bledý et al. 2024). Strategies aimed at enhancing forest resilience and mitigating climate-induced stress increasingly emphasise promoting tree species diversity and using climate-adapted species (Mikulenka et al. 2020; Bottero et al. 2021; Vacek et al. 2023). In this context, silver fir shows strong potential, especially at higher elevations, where it can locally replace Norway spruce [*Picea abies* (L.) Karst.] following disturbance events (Vacek et al. 2015; Hlásny et al. 2021).

Compared to Norway spruce, silver fir exhibits several advantageous traits, including better adaptation to higher air temperatures, greater drought tolerance (Vitali et al. 2017; Vitasse et al. 2019a; Walder et al. 2021), and strong protective functions (Vitasse et al. 2019b). As such, it can significantly help reduce natural risks while simultaneously supporting timber production, biodiversity conservation, and the overall resilience of mountain forests on suitable sites (Dobrowolska et al. 2017; Mikulenka et al. 2020; Bledý et al. 2026). Silver fir also provides important soil-improving (ameliorative) functions, as it contributes to humus formation, enhances nutrient cycling, and supports long-term soil stability in forest ecosystems (Třeštík, Podrázský 2017; Podrázský et al. 2018, 2022). Despite these benefits, silver fir is still viewed unfavourably by some forest managers. The primary constraint limiting its wider use is the difficulty of regeneration, particularly due to its high palatability to ungulate game (Vacek et al. 2014; Klopčič et al. 2017; Brabec et al. 2024). Excessive browsing pressure threatens both planned and target species composition, with cascading effects on forest resilience and the provision of ecosystem services (Poleno et al. 2009; Mori et al. 2017; Cukor et al. 2023).

Even well-designed silvicultural measures often prove ineffective when ungulate populations are not adequately regulated (Ficko et al. 2016; Cukor et al. 2023).

In addition to herbivory pressure, the success of silver fir regeneration is strongly influenced by stand structure, microclimatic and site conditions, competitive interactions within the regeneration layer, and the applied silvicultural system (Senn, Suter 2003; Vacek et al. 2015; Vitasse et al. 2019a). Close-to-nature and selection silviculture systems appear particularly suitable due to their higher structural complexity (Dobrowolska et al. 2017; Larsen et al. 2022). However, these approaches require advanced silvicultural expertise and careful, adaptive application (Poleno et al. 2009; Vacek et al. 2007, 2015, 2020). Small-scale interventions are essential, as they maintain more stable stand microclimates and create favourable conditions for the regeneration of shade-tolerant climax tree species (Korpel, Vinš 1965; Vacek et al. 2015).

These relationships are particularly pronounced within the 2nd to 4th forest vegetation zones (FVZ), where air temperature and soil moisture regimes, competitive environments, and the ecological niche of silver fir vary considerably (Vitasse et al. 2019a). Regeneration success is generally lowest in the 2nd FVZ due to warmer and drier conditions, whereas the 3rd FVZ has more balanced conditions that support long-term survival under canopy cover. In the 4th FVZ, conditions remain favourable, although regeneration may be limited by strong competition from European beech (*Fagus sylvatica* L.). The most optimal conditions, particularly in terms of soil moisture, are typically found in the 5th zone (Schwarz, Bauhus 2019; Paluch, Jastrzębski 2023; Bledý et al. 2024). Consequently, silver fir performs best on sites with balanced moisture regimes, moderate microclimatic conditions, and stable stand structures, which explains its association with well-structured, multi-layered forests of mid to higher elevations and its weaker presence on extreme or disturbed sites (Dobrowolska et al. 2017; Mikulenka et al. 2020). Given its currently low representation in the Czech Republic (1.3%; MoA 2025) and its fragmented distribution, artificial regeneration will remain an essential tool in the coming decades to supplement insufficient seed sources and support its reintroduction where natural regeneration alone is inadequate (Bezděčková et al. 2024).

The aim of this study is to compare the growth of silver fir under contrasting site conditions (acidic, nutrient-rich, nutrient-medium, loamy, gleyed nutrient-medium and gleyed acidic) in mid-elevation areas of the Plzeň Region. Specifically, the study (i) quantified the growth potential of artificial regeneration across different site conditions, (ii) assessed the density and growth performance of natural regeneration across site types, (iii) evaluated browsing damage in natural regeneration caused by ungulates, and (iv) analysed the relationships between regeneration parameters and browsing intensity. Partial objectives include evaluating the growth potential and structure of natural and artificial regeneration in stands containing silver fir within the 3rd and 4th FVZ.

MATERIAL AND METHODS

Study site. The study plots are located at the boundary of the Plzeň Region and are part of the Collredo-Mannsfeld estate forest property (Forest District Zbiroh). The elevation of the measured stands ranges from 362 m a. s. l. to 570 m a. s. l. The mean annual precipitation in the study area is 583–686 mm (1990–2020), with the highest monthly precipitation occurring in June (79 mm). The mean annual air temperature ranges from 7.0 °C to 7.5 °C, with

the highest monthly mean temperatures in July (17.6 °C). The number of days with snow cover averages 51 days per year, the number of ice days ($T_{\max} < 0$ °C) is approximately 19, and the number of tropical days ($T_{\max} \geq 30$ °C) is about 6. According to the Köppen climate classification, the lower elevations belong to the Cfb category (oceanic climate), while the upper parts of the gradient fall into the Dfb category (warm-summer humid continental climate) (Peel et al. 2007). The slope of the study sites ranges from 2.1° to 13.5°. The parent bedrock of the sites consists of Proterozoic shales, lydite, spilite, and other metamorphic rocks (including slate formations). Soil types of individual stands are presented in Table 1.

In areas of artificial regeneration, ten stands used as regeneration units (0.07–0.16 ha) are predominantly Norway spruce [*Picea abies* (L.) Karst.] monocultures or mixed spruce stands with admixture of Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Mill.), Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], silver birch (*Betula pendula* Roth), and European beech (*Fagus sylvatica* L.). The planted seedlings were established as bare-rooted stock with an initial height of 26–35 cm at the time of planting; at present, the individuals are five years old. In the study of natural regeneration, four study mature stands are aged 88–147 years with

Table 1. Basic site characteristics of the studied stands differentiated by natural and artificial regeneration of silver fir (*Abies alba* Mill.)

Stand	Site type	Altitude (m a.s.l.)	Slope (°)	Exposure	Soil type	GPS coordinates
Artificial regeneration						
1B11	3B	375	13.0	SE	Haplic Cambisol	49°53'20"N, 13°54'31"E
1B11	3B	387	13.5	SE	Haplic Cambisol	49°53'19"N, 13°54'33"E
13A08	3H	376	2.3	E	Haplic Cambisol	49°55'8"N, 13°52'37"E
13B09	3H	362	4.4	E	Haplic Cambisol	49°55'5"N, 13°52'50"E
36D09	4P	543	4.8	NE	Haplic Gleysol	49°55'16"N, 13°47'50"E
221A08	4P	524	2.9	NE	Haplic Stagnosol	49°45'46"N, 13°46'57"E
44B06	4O	543	2.1	N	Gleyic Cambisol	49°54'38"N, 13°48'29"E
125H09b	4O	548	4.6	SE	Gleyic Luvisol	49°48'56"N, 13°41'32"E
57E11	3K	477	6.8	SE	Dystric Cambisol	49°53'29"N, 13°45'17"E
140B09	3K	518	9.9	NW	Dystric Cambisol	49°49'10"N, 13°37'45"E
Natural regeneration						
227B15b	4O	452	2.6	S	Gleyic Cambisol	49°47'48"N, 13°46'35"E
227D09	4P	570	5.0	NW	Stagnic Cambisol	49°45'43"N, 13°45'49"E
57E11	3K	484	4.3	S	Dystric Cambisol	49°53'30"N, 13°45'15"E
89C09	3S	493	7.2	SW	Haplic Cambisol	49°51'31"N, 13°44'39"E

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a stocking level of 6–8. The dominant species is silver fir (*Abies alba* Mill.), Norway spruce, with admixture of European larch, sycamore maple (*Acer pseudoplatanus* L.), sessile oak [*Quercus petraea* (Matt.) Liebl.], Scots pine, European hornbeam (*Carpinus betulus* L.), silver birch, and European beech. From a forest typological perspective, the following site types were investigated: 3B – nutrient-rich oak-beech (*Querceto-Fagetum mesotrophicum*), 3H – loamy oak-beech (*Querceto-Fagetum illimerosum mesotrophicum*), 4P – gleyed acidic oak-fir (*Querceto-Abietum variohumidum acidophilum*), 4O – gleyed nutrient-medium oak-fir (*Querceto-Abietum variohumidum mesotrophicum*), 3K – acidic oak-beech (*Querceto-Fagetum acidophilum*), and 3S – nutrient-medium oak-beech (*Querceto-Fagetum oligo-mesotrophicum*) site type category (Viewegh et al. 2003).

Data collection. For the assessment of growth potential in artificial regeneration, stands established with comparable bare-root planting stock and of the same age were selected. The selection of artificial regeneration units was based on patch size to ensure objectivity. In total, ten sites were chosen (two sites per typological unit: 3B, 3H, 4P, 4O, and 3K), and within each site, three 10 × 10 m sample plots were systematically established and evenly distributed within the stand (a total of 30 plots). The potential influence of adjacent stand edges on height growth was also taken into account. Within each sample plot, 100–145 individuals of artificial regeneration were measured.

For natural regeneration, four stands (4O, 4P, 3K, 3S) were selected, and within each stand, eight plots of 5 × 5 m were systematically established (a total of 32 plots). Site conditions were determined in accordance with the typological map of the valid forest management plan for the Zbiroh Forest District. Height measurements were taken with a measuring rod with an accuracy of 1 cm. The recorded variables included individual tree height (cm) and annual apical increment (cm). In each plot, regeneration density (individuals per hectare) was assessed. In natural regeneration, species composition was also evaluated, along with browsing damage, including terminal shoot browsing, lateral shoot browsing, and the occurrence of two or more terminal shoots resulting from previous damage to the main leader.

Data analyses. For statistical analyses, the research plots were classified by forest site type. Differences among site types in regeneration density,

height, height increment, and browsing damage were tested using one-way analysis of variance (ANOVA) followed by Tukey's HSD post hoc test in STATISTICA (Version 14.4, 2026). Prior to ANOVA, the assumptions of normality and homogeneity of variances were verified using the Shapiro–Wilk test and Bartlett's test, respectively. When these assumptions were not met, the non-parametric Kruskal–Wallis test was applied with subsequent multiple comparisons (Siegel, Castellan Jr. 1988). Principal component analysis (PCA) was performed in CANOCO 5 (Šmilauer, Lepš 2014) to evaluate relationships among growth parameters, regeneration density, and browsing damage across the studied site types. Prior to analysis, the data were log-transformed and standardised. The results of the multivariate analysis were visualised using an ordination diagram.

RESULTS

Growth potential of artificial regeneration across site conditions. In terms of both mean height and annual height increment of artificial regeneration, significant differences were detected among the studied site types ($P < 0.0001$; Figure 1). Significantly ($P < 0.05$) lower mean heights were recorded for site types 3K (89.3 ± 2.3 cm) and 3B (90.6 ± 1.8 cm) compared to 3H (133.1 ± 5.1 cm), 4P (122.1 ± 2.7 cm), and 4O (120.9 ± 2.1 cm). Regarding growth performance, the lowest annual height increment in artificial regeneration was found for 3B (15.2 ± 0.8 cm), followed by 3K (18.8 ± 0.7 cm). In contrast, the largest increments were observed for 3H (38.4 ± 1.8 cm) and subsequently for 4P (33.1 ± 0.9 cm), with differences being statistically significant ($P < 0.05$).

Density and growth of natural regeneration across site conditions. In terms of density, height, and annual height increment, significant differences were detected among site type categories ($P < 0.0001$; Table 2). In natural regeneration, significantly ($P < 0.05$) the lowest densities were recorded at 4P ($25\,600$ pcs·ha⁻¹) and 3K ($41\,400$ pcs·ha⁻¹), whereas the highest density was observed at 4O ($182\,800$ pcs·ha⁻¹). The highest mean height on the sample plots was found at 3K (49.2 cm), while the lowest was recorded at 3S (15.3 cm). Similarly, site type 3S showed the lowest annual height increment (2.1 cm). In contrast, the highest annual height increment (10.6 cm) was measured at 4P.

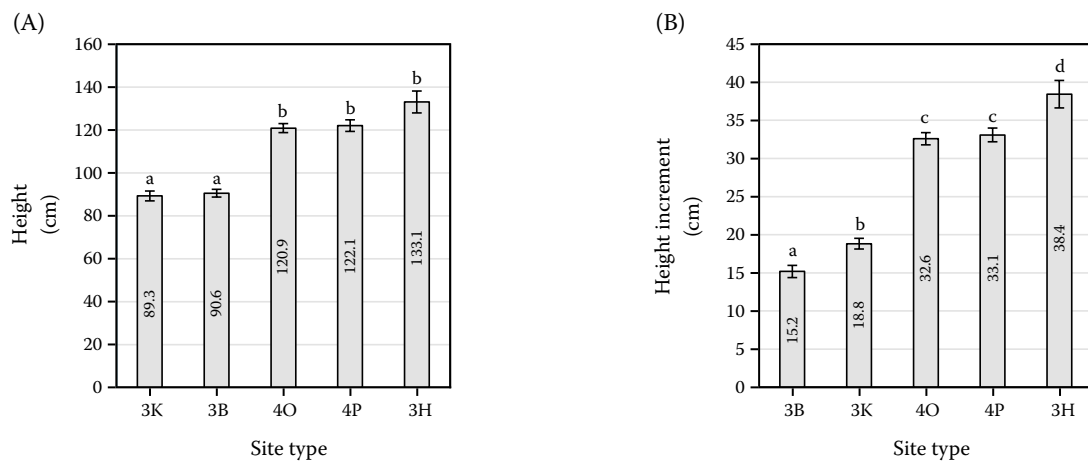


Figure 1. (A) Mean height and (B) mean annual height increment of five-year-old silver fir (*Abies alba* Mill.) artificial regeneration by site type (3K – acidic, 3B – nutrient-rich, 3H – loamy, 3S – nutrient-medium, 4O – gleyed nutrient-medium and 4P – gleyed acidic category) in 2025

Significant differences are indicated by different letters

It should be noted that the compared increment cannot be interpreted as an actual fact, since the natural regeneration age is not the same. The proportion of silver fir in natural regeneration ranged from 89.7% (4P) to 98.3% (4O) with no significant differences, indicating a substantial increase compared to the overstory (on average by 62.8%).

Browsing damage in natural regeneration.

No significant differences in browsing damage were detected among site types in the case of natural regeneration ($P > 0.05$; Table 2). The lowest browsing damage was recorded at 3S (11.0%) and 3K (11.7%), whereas the highest game damage occurred on gleyic sites, specifically at 4O (19.2%) and 4P (18.6%). Browsing damage was markedly more serious in silver fir compared to Norway spruce. In terms of height classes, the highest

browsing damage was observed in the 60–80 cm category, followed by the 40–60 cm class, both exceeding 25%. In contrast, the lowest damage occurred in individuals up to 20 cm in height. A significant negative effect on height increment was detected, particularly in taller height classes. For instance, undamaged silver fir individuals with a mean height of 80–100 cm exhibited an average annual height increment of 13.3 cm, whereas individuals affected by terminal browsing reached only 6.0 cm, representing a 54.8% reduction in growth.

Interactions between natural regeneration parameters and browsing damage. The results of the PCA expressing relationships among growth parameters, regeneration density, and browsing damage across 32 sample plots are presented in the ordination diagram (Figure 2). The first ordina-

Table 2. Basic characteristics of natural regeneration of fir by site type in 2025; significant differences are indicated by different letters

Site type	Number of plots (pcs)	Density (pcs·ha ⁻¹)	Height (cm)	Height increment (cm)	Browsing damage (%)	Share (%)
4P	8	25 600 ^a	46.8 ^b	10.6^b	18.6 ^a	89.7 ^a
4O	8	182 800^c	28.8 ^{ab}	3.3 ^a	19.2 ^a	98.3 ^a
3K	8	41 400 ^a	49.2^b	9.4 ^b	11.7 ^a	90.8 ^a
3S	8	109 400 ^b	15.3 ^a	2.1 ^a	11.0 ^a	96.5 ^a
Test		K-W	ANOVA	ANOVA	ANOVA	K-W
<i>P</i> -value		<u><0.0001</u>	<u><0.001</u>	<u><0.0001</u>	0.1193	0.1966

Bold – significantly highest value; underlined – significant difference; KW – Kruskal-Wallis test; ANOVA – one-way analysis of variance; 3K – acidic; 3S – nutrient-medium; 4O – gleyed nutrient-medium; 4P – gleyed acidic category

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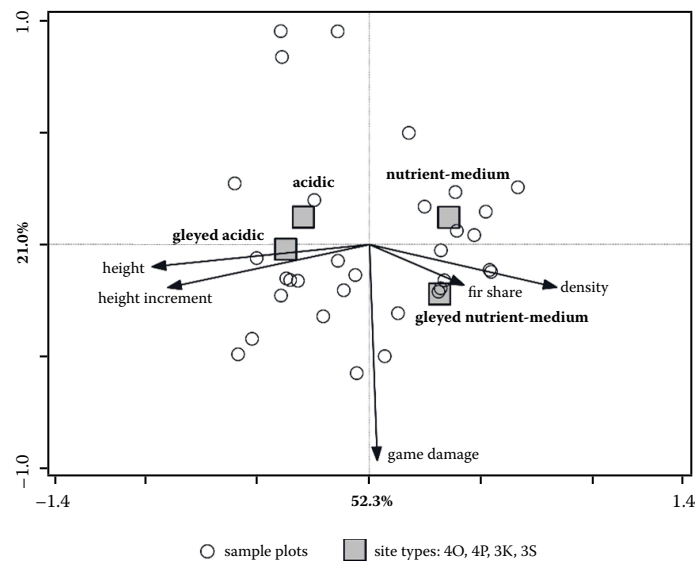


Figure 2. Ordination diagram showing the results of the PCA of relationships among browsing damage, silver fir proportion, and natural regeneration parameters (height, height increment, and density) across 32 sample plots in 2025

tion axis explains 52.3% of the variability, the first two axes together explain 73.3%, and the first four axes account for 99.6% of the total data variability. The y -axis represents browsing damage, while the x -axis reflects height and regeneration density. Regeneration height is positively correlated with height increment, whereas both parameters are negatively correlated with regeneration density for a fir share. In contrast, the proportion of fir shows the lowest explanatory power in the ordination space. No correlation of regeneration density, individual height, or species composition with the proportion of browsing damage was detected across the studied plots. From a typological perspective, site types 4P and 3K exhibit similar characteristics, particularly higher mean regeneration height and height increment. In contrast, the site types 4O and 3S are characterised by high regeneration density. The greatest variability among sample plots was observed in 4P, whereas plots on 3S showed relatively homogeneous regeneration parameters.

DISCUSSION

Our results confirm that silver fir exhibits strong potential for natural regeneration across the studied research plots in the 3rd and 4th FVZ of the Křivoklátsko and Brdy regions. Differences in regeneration density are primarily attributable to variability in seed production under specific site and stand conditions. Fir typically produces

substantial seed crops at 2–3-year intervals, with June precipitation playing a key role in reproductive output (Wohlgenuth et al. 2016; Šimůnek et al. 2026). Another factor that plays a role here is the herbaceous vegetation. In areas with *Vaccinium myrtillus* cover, the density of natural regeneration was lowest; however, its vitality was high because it was protected from browsing damage by the herbaceous vegetation. Similarly, a study from lowland fir forests in Poland demonstrated that vegetation cover significantly influences the density, height growth dynamics, and proportion of fir (Prokúpková et al. 2021).

Silver fir strongly dominated natural regeneration across all study plots. The highest density was recorded on site type 4O, reaching 182 800 pcs·ha⁻¹ with a proportion of 98.3%, whereas the lowest density was observed on site type 4P, with 25 600 pcs·ha⁻¹ and a proportion of 89.7%. The average density of fir regeneration across plots was approximately 89 800 pcs·ha⁻¹. The reduced density on 4P sites is likely related to a lower availability of seed trees compared to 4O stands. At the same time, due to the dense herbaceous vegetation, which not only exhibits a higher proportion of fir but also provides more favourable microsite conditions for germination and early seedling development. As shown by Paluch (2005), higher numbers of fir seedlings are associated with stands containing a greater proportion of old trees, likely due to increased seed input. Maintaining a suffi-

cient proportion of mature, seed-producing fir individuals is therefore essential. At the same time, continuous recruitment of trees into higher diameter classes is necessary to prevent stand ageing (Ficko et al. 2011). These factors represent key drivers of natural regeneration density (Dobrowolska 1998; Sagnard et al. 2007; Poleno et al. 2009). The observed regeneration densities were comparable to or higher than those reported elsewhere in Europe (Paluch 2005; Vacek et al. 2015; Frei et al. 2022, 2025) and appear sufficient to ensure the future persistence of fir in the studied stands (Poleno et al. 2009).

Regarding ungulate damage, browsing intensity in the lowest height class (0–20 cm) remained below 10%, indicating relatively low pressure on the youngest individuals, which typically remain below the main browsing level and vegetation cover (Vacek et al. 2014). In intermediate-height classes (20–80 cm), the proportion of damaged individuals ranged from 20% to 30%. Overall, browsing damage of fir across the study plots (11.0–19.2%) was substantially lower than values reported by Vacek et al. (2015), Vacek (2017) or Frei et al. (2025). For comparison, Brabec et al. (2024) reported an average damage rate of 76.3% across 78 research plots in the Czech Republic.

From a typological perspective, site types 4P and 3K showed similar characteristics in natural regeneration, particularly higher mean height and height increment compared to 3S and 4O, which were characterised by higher regeneration densities. The greatest variability among research plots was observed on 4P sites, whereas 3S sites exhibited relatively homogeneous regeneration parameters, likely reflecting both site and stand conditions (Poleno et al. 2009). In artificial regeneration, the lowest annual height increment was recorded for site type 3B (15.2 cm), while the highest was observed for 3H (38.4 cm). As noted by Bledý et al. (2024), appropriate site typology is a key factor for the successful growth of silver fir, which can outperform other major commercial tree species under suitable conditions.

The potential to increase the proportion of silver fir in Central European forests has been emphasised by Kölling (2007), who identified fir as a species capable of partially replacing Norway spruce at warmer and drier sites. Despite this, current stand compositions indicate that fir is rarely dominant, even though it represents a natural component of forest ecosystems. Korpel (1989) concluded

that silver fir can function as a principal codominant species, particularly in the 4th–6th FVZ. However, current and future management must also account for ongoing environmental changes affecting fir growth and vitality (Bledý et al. 2024).

A key limitation of this case study is the relatively limited number of research plots and their uneven spatial distribution, together with differences in species composition of the parent stands (varying proportions of fir), which may reduce the representativeness of environmental gradients and limit the generalizability of the results. In addition, the findings may be influenced by the origin of the silver fir planting material used (Kowalkowski et al. 2025). More broadly, genetic variation and provenance effects can further affect both growth dynamics and subsequent resilience to climatic stress, potentially limiting the transferability of the results, as different provenances may substantially shape growth performance and adaptive capacity (Čáp et al. 2024).

CONCLUSION

The results indicate a high potential for natural regeneration of silver fir under the given site and stand conditions of the studied research plots in the 3rd–4th FVZ within the Plzeň region, particularly under close-to-nature forest management. Successful natural regeneration is contingent upon the effective integration of silvicultural and game management. Another important factor in promoting natural regeneration in this case is the use of deeper ploughing or other methods of disturbing the soil surface to improve seed germination. Under such conditions, abundant natural regeneration can develop successfully, provided that ungulate damage remains within ecologically tolerable limits. From a typological perspective, the most favourable microsite conditions for natural regeneration were associated with site type 4O (gleyed nutrient-medium oak–fir), while the highest height increment was recorded in site type 4P (gleyed acidic oak–fir). In contrast, within artificial regeneration, the greatest growth potential was observed at site type 3H (loamy oak–beech). In the context of ongoing climate change, the conversion of Norway spruce stands to silver fir is likely to become an increasingly important adaptive silvicultural strategy. Therefore, translating these findings into practical forest management is essential.

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