https://doi.org/10.17221/76/2023-JFS

Potential of mixed *Picea abies* (L.) Karst. and *Pinus sylvestris* L. forests in lowland areas of Central Bohemia

Pavel Brabec, Jakub Brichta, Zdeněk Vacek, Stanislav Vacek, Václav Šimůnek, Vojtěch Hájek*

Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

**Corresponding author: vacekz@fld.czu.cz*

Citation: Brabec P., Brichta J., Vacek Z., Vacek S., Šimůnek V., Hájek V. (2023): Potential of mixed *Picea abies* (L.) Karst. and *Pinus sylvestris* L. forests in lowland areas of Central Bohemia. J. For. Sci., 69: 470–484.

Abstract: Mixed forests play a key role in terms of stability, production potential, and adaptation to climate change. In addition, the studied Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) belong to the most economically important tree species in Europe. The objectives were to determine the effect of the species composition of these two tree genera on the production, structure, diversity, and growth of mixed stands at lower elevations in the Czech Republic. Based on dendroecological samples, research was also carried out on the influence of climatic factors and climate change on the radial growth of these trees of interest. Mixed forests showed higher timber production by 29.8% compared to spruce and pine monocultures. The production of mature stands ranged from 328 to 479 $m^3 \cdot ha^{-1}$. Spruce achieved higher radial growth, but its growth variability was higher than that of pine. Compared to precipitation, temperatures had a greater influence on the radial growth of both tree species, especially in the growing season. In terms of diversity, mixed stands achieved significantly higher structural differentiation and overall diversity compared to monospecific variants. Mixed stands can achieve higher production potential, diversity, and especially resistance to climatic extremes in the lowland regions of the Czech Republic. The differences between mixed stands and monocultures, i.e. the effect of tree species mixing, depend on the appropriate proportions of tree species and their spatial pattern.

Keywords: climate change; dendrochronology; Norway spruce; productivity; Scots pine

Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) are the most economically important tree species in Europe (Eckenwalder 2009; Krakau et al. 2013; O'Reilly-Wapstra et al. 2014; Sevik, Topacoglu 2015; Caudullo et al. 2016; Brichta et al. 2023). From the point of view of their prosperity in the conditions of global climate change (Vacek et al. 2016, 2023; Usoltsev et al. 2022), their origin (Taeger et al. 2013; Leštianska et al. 2023), the habitat, and stand conditions are important (Mikulenka et al. 2020; Gallo et al. 2021; Kovalevskii et al. 2022). Due to their high production, Norway spruce and Scots pine were planted in different habitat conditions, including outside their natural distribution (Mikeska et al. 2008; Poleno et al. 2009; Caudullo et al. 2016; Durant et al. 2016) where they are often affected by various disturbances (Caudullo et al. 2016; Hlásny et al. 2019, 2021; Šimůnek et al. 2020; Sydorenko et al. 2021). It is primarily true of richer habitats of Scots pine (Mikeska et al. 2008; Brichta et al. 2023), and in the case of Norway spruce, not lower than in the 5th forest vegetation zone unless the habitats are affected by water (Vacek et al. 2007; Poleno et al. 2009).

Supported by the Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, and the Ministry of Agriculture of the Czech Republic (No. QK21010198).

Currently, as a result of global climate change, the main threat to spruce and pine stands is primarily drought and, in connection with that, attacks by insect pests (especially bark beetles *Ips typographus*, *Ips acuminatus*, *Ips sexdentatus*, *Pityogenes chalcographus*), and fungal pathogens such as *Heterobasidion* spp., *Fomes* spp., and *Armillaria* spp., etc. (Komonen et al. 2011; Gao et al. 2017; Buras et al. 2018; Barta et al. 2019; Čermák et al. 2019; Holuša et al. 2019; Knížek et al. 2021). It is precisely periods of climatic stress that negatively affect the photosynthetic activity of Norway spruce and Scots pine, and there is an increase in defoliation and a decrease in radial growth (Flexas, Medrano 2002; Reddy et al. 2004; Vacek et al. 2023). Rising air temperatures, together with low water availability, are responsible for several other diseases and also for the reduced defense capacity of trees against insect pests (Allen et al. 2015; Hlásny et al. 2019, 2021; Knížek et al. 2021; Haberstroh et al. 2022).

Drought is, therefore, a significant and frequent predisposing factor for forest decline and disturbances (Hlásný et al. 2021; Knížek et al. 2021). The resistance of the forest to drought depends primarily on the intensity of the drought but also on specific functional properties (Greenwood et al. 2017) and can also vary among individuals of the same species (Gazol et al. 2017; Camarero et al. 2018). Compared to Scots pine, Norway spruce is one of the most drought-sensitive European trees (van der Maaten-Theunissen et al. 2013; Hartl-Meier et al. 2014; Leuschner, Ellenberg 2017; Čermák et al. 2019), because it is a species demanding on rainwater or soil moisture and has a shallow root system (Horgan et al. 2003; Johnson, More 2006; OECD 2006; Farjon 2010). In contrast, Scots pine has a deep root system and can obtain water from significantly greater depths than Norway spruce (Praciak et al. 2013). For these reasons, it is advisable to grow spruce and pine in a two-story high forest (Poleno et al. 2009).

In connection with global climate change, the distribution areas of these tree species are also changing. Both Norway spruce and Scots pine are significantly retreating in the more southerly areas of their ranges and at lower altitudes, and, on the contrary, increasing their range at higher altitudes and in their northern locations (Benito Garzón et al. 2008; Reich, Oleksyn 2008; Matìas, Jump 2012; Hanewinkel 2013; Vacek et al. 2023). The management strategy of these stands is consequently changing in an attempt to increase their adaptability to climate change (Vacek et al. 2022). In spruce stands at lower elevations, their transformation into mixed stands corresponds in composition to stands close to nature (Hanewinkel, Pretzsch 2000; Spiecker et al. 2004; Teuffel et al. 2005; Souček, Tesař 2008; Poleno et al. 2009; Švec et al. 2015). In Scots pine stands, existing clearings and clearings created during stand regeneration are shrinking, and natural regeneration methods are increasingly applied as part of shelterwood methods of management (Bielak et al. 2014; Spathelf et al. 2015; Bílek et al. 2016; Drössler et al. 2018; Aleksandrowicz-Trzcińska et al. 2017, 2018; Brichta et al. 2020). The shelterwood method of natural regeneration is more favourable concerning the nature of microhabitats during the ongoing global climate change (Matías, Jump 2012; Aleksandrowicz-Trzcińska et al. 2014, 2017, 2018; Vítámvás et al. 2019; Brichta et al. 2020). In Scots pine stands in richer habitats, rebuilding is also occurring, from both economic and ecological points of view (Čížek et al. 1959; Souček et al. 2018). Considerable areas of these stands are potentially threatened by widespread damage of both abiotic and biotic nature, so it is imperative to look for suitable management alternatives using methods of close-to-nature silviculture (Plíva 2000; Průša 2001). Therefore, it is necessary to implement changes in the species composition aimed at structuring mixed stands with Scots pine, which will better fulfil all the required functions of the forest (Andrzejczyk 2006; Bielak et al. 2014). Mixed stands with varying degrees of structuring ensure higher stability and diversity (Bauhus et al. 2017; Vacek et al. 2021b). The replacement of existing monocultures with mixed stands fulfils the goals of the current forestry policy (Poleno et al. 2009; Novák et al. 2017). In addition, mixed stands, in comparison to monocultures, can achieve higher production potential and carbon sequestration in the context of climate change mitigation (del Río et al. 2016; Pretzsch, Schutze 2016; Vacek et al. 2023). Modifying the species composition towards species mixtures with a higher potential to mitigate the negative effect of climate change is one of the basic silvicultural measures (Fürst et al. 2007; Podrázský, Remeš 2010; Remeš et al. 2020).

This research aims to evaluate the degree of stability and the possibility of adaptability of stands of Norway spruce and Scots pine in the lower areas of Central Bohemia. The specific objectives are to determine (*i*) the production potential of mixed spruce stands, (*ii*) the structure and diversity of the studied stands, and (*iii*) the effect of precipitation, temperature, and climate change on the radial growth of Scots pine and Norway spruce.

MATERIAL AND METHODS

Study area and natural conditions. The area of interest is managed by the Forests of the Czech Republic, a state enterprise (Lesy ČR, s.p.), and is part of the Konopiště forest enterprise and the Říčany forest district. The forest block has a size of 3.2 km^2 (GPS: 49°58'29'N, 14°43'05'E). The altitude of the studied area ranged from 430 m a.s.l. to 480 m a.s.l. with a characteristic flat relief in the 3rd and 4th forest vegetation zone (Remeš, Kozel 2006). From a typological point of view, these are mainly groups of forest types 3K – *Querceto-Fagetum acidophilum* and 4P – *Querceto-Abietum variohumidum acidophilum* (Viewegh et al. 2003). The predominant soil types are cambisol, pseudogley, and luvisol, with long-term considerable soil acidification (Podrázský et al. 2005; Podrázský, Remeš 2007). The average temperature of the area of interest is 7.5 °C, the total annual precipitation is 600 mm, less than 400 mm in the growing season, and the length of the growing season is about 150 days (Švec et al. 2015). According to the Forest Management Plan, the age of the upper tree layer of the investigated forest stands is in the range of 87–117 years. The investigated mature stands are mixed and made up of two main tree species – Norway spruce and Scots pine. Other admixed tree species are silver fir (*Abies alba* Mill.) and Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco].

Forest management. These are close-to-nature forest stands during the conversion to the shelterwood system, with the application of selection principles, which has been continuous since 1993. The reason for the change in forest management was mainly due to frequent wind damage to spruce or breakage of pine caused by wet snow, under the former clear-cut regimen. The spruce and pine stands that had been destroyed in the past were not reconstructed but were left to develop spontaneously, which allowed natural regeneration to occur, creating large differences in height and thickness between the surviving trees. These sites are now managed according to selection principles, making maximum use of natural regeneration. Artificial regeneration is used only to introduce native tree species that almost disappeared from the area under the previous management. The main criterion for harvesting specific trees is their target diameter (diameter at breast height – *DBH*), not the age of the stand (Remeš, Kozel 2006).

Data collection. The study area was conducted on five rectangular plots of 25 m × 50 m (the size of one plot was 1 250 m^2) in 2022. The permanent research plots (PRPs) were divided into five variants by species composition: (*i*) 92.5–100% pine (pine 100%), (*ii*) 75 ± 7.5% pine and 25 ± 7.5% spruce (pine 75%), (*iii*) 50 ± 7.5% pine and 50 ± 7.5% spruce (pine 50%), (*iv*) 25 ± 7.5% pine and 75 ± 7.5% spruce (pine 25%), and (*v*) 92.5–100% spruce (spruce 100%), see Vacek et al. (2021b). FieldMap technology (EMU; IFER, Czech Republic) recorded the positions of individual trees with $DBH \geq 7$ cm, and their crown projection was measured in four directions. Boundary trees with more than half of their *DBH* lying inside a PRP were counted in. The *DBH* was measured with a Mantax Blue caliper (Haglöf, Sweden) with an accuracy of 1 mm, and the height of the individual trees and the height of the live crown with a Vertex laser hypsometer (Haglöf, Sweden) with an accuracy of 0.1 m.

For the analysis of radial growth, core samples were obtained from the trees with a Pressler auger (Haglöf, Sweden) at the height of 1.3 m in the direction north/south. From each tree species, 30 samples of Norway spruce and 30 of Scots pine from the dominant and co-dominant trees according to the Kraft classification (Kraft 1884) were randomly [RNG function, MS Excel (Version 365, 2023)] taken as the significant growth response (compared to subdominant and suppressed trees; Remeš et al. 2015). All these selected trees only come from the upper tree story with a registration value of *DBH* over 30 cm. The annual increments of the tree rings were then measured with an accuracy of 0.01 mm using an Olympus binocular microscope (SZ51; Olympus, Japan) on a LINTAB measuring table (6d; Rinntech, Germany) and recorded in TsapWin software (Version Professional 4.82b2, 2022). Climate data were taken from the nearest Czech Hydrometeorological Institute (CHMI) station, Ondřejov (49°54'36'N, 14°46'48'E) for the period 1962–2021.

Data analyses. The basic structure, diversity, and production characteristics of the tree layer were calculated by the SIBYLA Triquetra software (Version 10.0 alpha, 2015) using a tree-level and spatially explicit data set (Fabrika, Ďurský 2005) based on our measurements. All collected dendrometric parameters of individual trees (see the Data collection section) were used as input data (tree species, coordinates, height, *DBH*, crown width, live crown base, and age). The crown width was derived from the measured area of the crown projection. The PointPro program (Version 2.2, 2010) (Zahradník, Puš, ČZU) was used to calculate the characteristics of the horizontal layout of the trees on PRPs using the Clark and Evans (1954) aggregation index. The tree volume was calculated by the volume equations published in Petráš and Pajtík (1991). Crown closure (Crookston, Stage 1999) and the relative stand density index (Reineke 1933) were then calculated from the measured stand density indicators. The relative *SDI* (stand density index) was calculated as the ratio of the actual value of the stand density index to its maximum value. The stand density index represents the theoretical number of trees per ha if the mean quadratic diameter of the stand component is equal to 25 cm (Reineke 1933). The maximum *SDI* value was derived from the model of yield tables (Halaj 1987). Standard deviations (SD) were calculated for the mean quadratic *DBH* and mean height. Tree biomass was derived according to Petráš et al. (1985), Petráš and Pajtík (1991), and Ledermann and Neumann (2005). The biomass of the roots was calculated using a model by Drexhage and Colin (2001). The content in trees was determined following the research of Bublinec (1994) using the unit content of elements in 10 $mg \cdot kg^{-1}$ of dry matter.

Structural diversity was evaluated based on the horizontal structure (Clark, Evans 1954), the vertical structure using the Arten-profile index (Pretzsch 2006) and vertical diversity index (Jaehne, Dohrenbusch 1997), the structural differentiation of the stand using the indices of diameter and height differentiation (Füldner 1995), and crown differentiation (Jaehne, Dohrenbusch 1997). The Arten-profile index was calculated using the basal area of tree species in individual stand layers. Diameter and height differentiations are related to the ratio between the larger and the smaller diameter/height of all nearest neighboring trees. Finally, the stand diversity index was calculated in connection with complex biodiversity (Jaehne, Dohrenbusch 1997). Total diversity is composed of the following components: tree species diversity, diversity of vertical structure, diversity of tree spatial distribution, and diversity of crown differentiation. The input variables are the number of tree species, maximum and minimum tree species proportion, maximum and minimum tree height, maximum and minimum tree spacing, minimum height to crown base, and minimum and maximum crown diameter (Table 1). Detailed information about the calculation of the used indices can be found in Vorčák et al. (2006) and Vacek et al. (2020).

Tree-ring increment series were individually crossdated (to remove errors caused by missing tree rings) using statistical tests in the PAST application (Version 4.5, 2008) (Knibbe 2007) and subsequently subjected to a visual inspection according to Yamaguchi (1991). If a missing tree ring was revealed,

Table 1. Overview of indices describing the stand diversity and their common interpretation

Criterion	Quantifiers	Label	Reference	Evaluation
Horizontal structure	aggregation index	R (C&Ei)	Clark, Evans (1954)	mean value $R = 1$, aggregation $R < 1$, regularity $R > 1$
Vertical structure	Arten-profile index	A (Pri)	Pretzsch (2006)	range 0–1, balanced vertical structure $A < 0.3$, selection forest $A > 0.9$
	vertical diversity	S (J&Di)	Jaehne, Dohrenbusch (1997)	low $S < 0.3$, medium $S = 0.3–0.5$, high $S = 0.5–0.7$, very high diversity $S > 0.7$
Structure differentiation	diameter differentiation	TM_d (Fi)	Füldner (1995)	range 0–1, low $TM < 0.3$, very high differentiation $TM > 0.7$
	height differentiation	TM_h (Fi)		
	crown differentiation	K (J&Di)	Jaehne, Dohrenbusch (1997)	low $K < 1.0$, medium $K = 1.0–1.5$, high $K = 1.5–2.0$, very high differentiation $K > 2.0$
Complex diversity	stand diversity	B (J&Di)	Jaehne, Dohrenbusch (1997)	monotonous structure $B < 4$, uneven structure $B = 6–8$, very diverse structure $B > 9$

C&Ei – Clark and Evans index; Fi – Füldner index; J&Di – Jaehne and Dohrenbusch index; Pri – Pretzsch index a tree ring of 0.01 mm in width was inserted in its place. Residual chronologies and detrended average tree ring series were calculated in the ARSTAN program (Version 49v1a, 2017) (Cook, Holmes 1984). Firstly, negative exponential spline and subsequently, 0.67n spline were used for age detrending (Grissino-Mayer et al. 1992). The analysis of negative pointer years was carried out, as shown in Schweingruber (1996) and Desplanque et al. (1999). For each tree, the pointer year was tested as an extremely narrow tree ring that does not reach 40% of the increment average from the four preceding years. The occurrence of the negative year was proved if such a strong reduction in increment occurred in at least 20% of trees on the plot. To express the relationship between climate characteristics (monthly average temperatures and the sum of precipitation in particular years) and radial growth, the DendroClim software (Version 1.0, 2002) was used (Biondi, Waikul 2004).

The dendrochronological indicators were calculated in R software (Version 4.2.1, 2022) with the dplR package instructions (Bunn, Mikko 2018). The expressed population signal (*EPS*) was calculated to indicate the reliability of the chronology (Fritts 1976). The *EPS* dendrochronological data set results for every research plot were *EPS* > 0.85 to preserve a strong climatic signal in the used chronology. The signal-to-noise ratio (*SNR*) indicator was calculated, representing the strength of the chronology. Finally, the *R-bar* (inter-series correlations) and *ar*1 (first-order autocorrelation) was computed (Fritts 1976) for pine and spruce. The differences between individual tree species in terms of radial growth were tested in STATISTICA 13 (Version 13.4.0, 2018) using analysis of variance (ANOVA) and Tukey's HSD (honestly significant difference) test. The variability of radial growth was indicated by the standard deviation.

RESULTS

Production potential. Production characteristics of forest stands on permanent research plots differentiated by the species composition are shown in Table 2. The number of trees ranged from 256 trees·ha^{-1} in spruce monoculture to 512 trees·ha^{-1} in a stand with an equal proportion of spruce and pine (in this variant, the highest basal area was also reached – 39.0 m^2·ha^{-1}). Similarly, the stand density index of monospecific stands reached values 0.44–0.54 compared to higher numbers (0.60–0.71) in the case of mixed forests. Stand volume was in the range of 351–479 m^3·ha^{-1}, while mixed stands reached up to 29.8% higher production compared to monocultures. The mean annual increment ranged from 3.35 to 5.04 m^3·ha^{-1}·y^{-1}. Likewise, tree biomass and carbon sequestration were more advantageous in mixed stands.

Structure and diversity. No differences were found in the horizontal structure between the individual plots, while the spatial pattern was random in all cases (Table 3). All other variants show considerable differences in structural indices favoring mixed stands over monocultures. The highest rich vertical structure was observed in the case of variant spruce 75 : 25 pine compared to the lowest for pure spruce stands. Height, diameter, and crown structural differentiation were low in monocultures and moderate in mixed forest stands, especially in variants with a 50% representation of spruce and pine. Regarding overall diversity, monocultures reached a complex *B* index in the range of 2.573–3.329 and mixed forests 4.661–5.960.

Table 2. Production characteristics of the stand on permanent research plots differentiated by the species composition (variants) in 2022

Variant	*DBH* (cm)	*h* (m)	*v* (m^3)	*N* (trees·ha^{-1})	*G* (m^2·ha^{-1})	*V* (m^3·ha^{-1})	*HDR* –	*SDI* –	*CC* (%)	*MAI* (m^3·ha^{-1}·y^{-1})	*BIO* (t·ha^{-1})	C_{BIO} (t·ha^{-1})
Pine 100%	38.7	25.09	1.369	256	30.0	351	64.8	0.54	74.9	3.73	262	137
Pine 75%	34.6	24.82	1.150	416	38.9	479	71.7	0.71	81.6	5.04	356	187
Pine 50%	31.2	21.87	0.859	512	39.0	440	70.1	0.68	67.6	4.58	315	165
Pine 25%	34.5	22.10	1.002	400	37.1	401	64.1	0.60	61.7	4.18	276	144
Spruce 100%	34.1	28.48	1.077	304	27.7	328	83.5	0.44	75.7	3.35	211	110

BIO – tree biomass; C_{BIO} – carbon sequestration in tree biomass; *CC* – canopy closure; *DBH* – mean quadratic diameter at breast height; *G* – basal area; *h* – mean height; *HDR* – slenderness coefficient; *MAI* – mean annual increment; *N* – number of trees per hectare; *SDI* – relative stand density index (stocking); *v* – mean tree volume; *V* – stand volume

https://doi.org/10.17221/76/2023-JFS

Table 3. Indicators of stand biodiversity on permanent research plots by species composition (variants) in 2022

Variant	*R* (C&Ei)	*A* (Pri)	*S* (J&Di)	TM_d (Fi)	TM_h (Fi)	*K* (J&Di)	*B* (J&Di)
Pine 100%	0.907	0.537	0.364	0.256	0.125	0.744	3.329
Pine 75%	0.948	0.404	0.732	0.280	0.287	1.358	5.631
Pine 50%	0.964	0.682	0.676	0.417	0.322	1.387	5.960
Pine 25%	0.989	0.706	0.749	0.393	0.308	1.051	4.661
Spruce 100%	1.021	0.244	0.266	0.270	0.103	0.495	2.573

A (Pri) – Arten-profile index (Pretzsch); *B* (J&Di) – stand diversity index (Jaehne and Dohrenbusch); *K* (J&Di) – crown differentiation (Jaehne and Dohrenbusch); *R* (C&Ei) – aggregation index (Clark and Evans); *S* (J&Di) – vertical diversity (Jaehne and Dohrenbusch); TM_d (Fi) – index of diameter differentiation (Füldner); TM_h (Fi) – index of height differentiation (Füldner)

Table 4. Characteristics of tree-ring chronologies for Scots pine and Norway spruce

Tree species	No. trees	Mean *RW* (mm)	Mean min–max (mm)	Age min–max	*ar*1	*R-bar*	*EPS*	*SNR*
Scots pine	30	2.06 ± 1.08	1.09–3.32	77–92	0.69	0.83	0.90	9.38
Norway spruce	30	3.34 ± 1.45	1.36–4.08	73–104	0.63	0.85	0.92	11.02

Age min–max – age range of youngest and oldest sample tree; *ar*1 – first-order autocorrelation; *EPS* – expressed population signal; mean min–max – mean ring-width range in mm from smallest to biggest tree; mean *RW* – mean ring width in mm; No. trees – number of trees; *R-bar* – inter-series correlation; *SNR* – signal-to-noise ratio

Radial growth and climate. Characteristics of tree-ring chronologies for Scots pine and Norway spruce in Table 4 showed that spruce revealed a significantly ($P < 0.05$) higher radial increment compared to pine (by 38.3%). Scores of *EPS* and *SNR* were also higher for spruce in both cases. On the other hand, pine showed lower radial growth variability. Higher variability of growth, including its dynamics in spruce is shown in Figure 1. This figure also demonstrates that the only negative

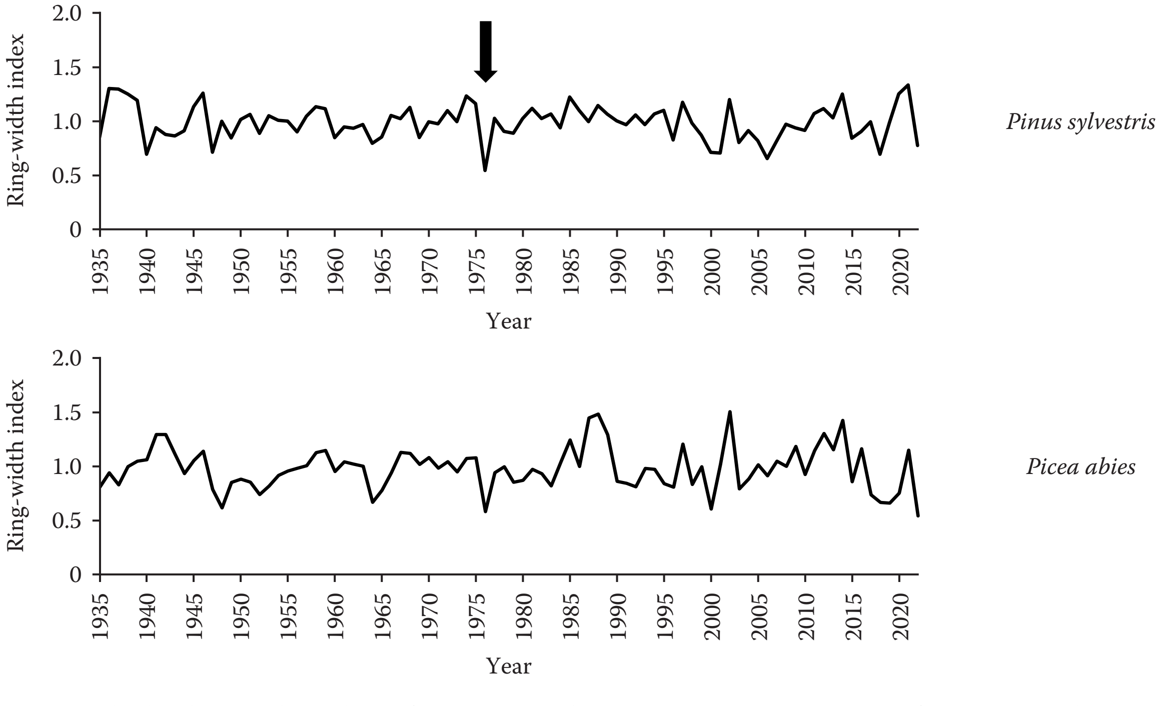

Figure 1. Standardised mean chronology of Scots pine and Norway spruce in 1935–2022 after removing the age trend expressed by the tree-ring index

Negative pointer years are highlighted with a black arrow.

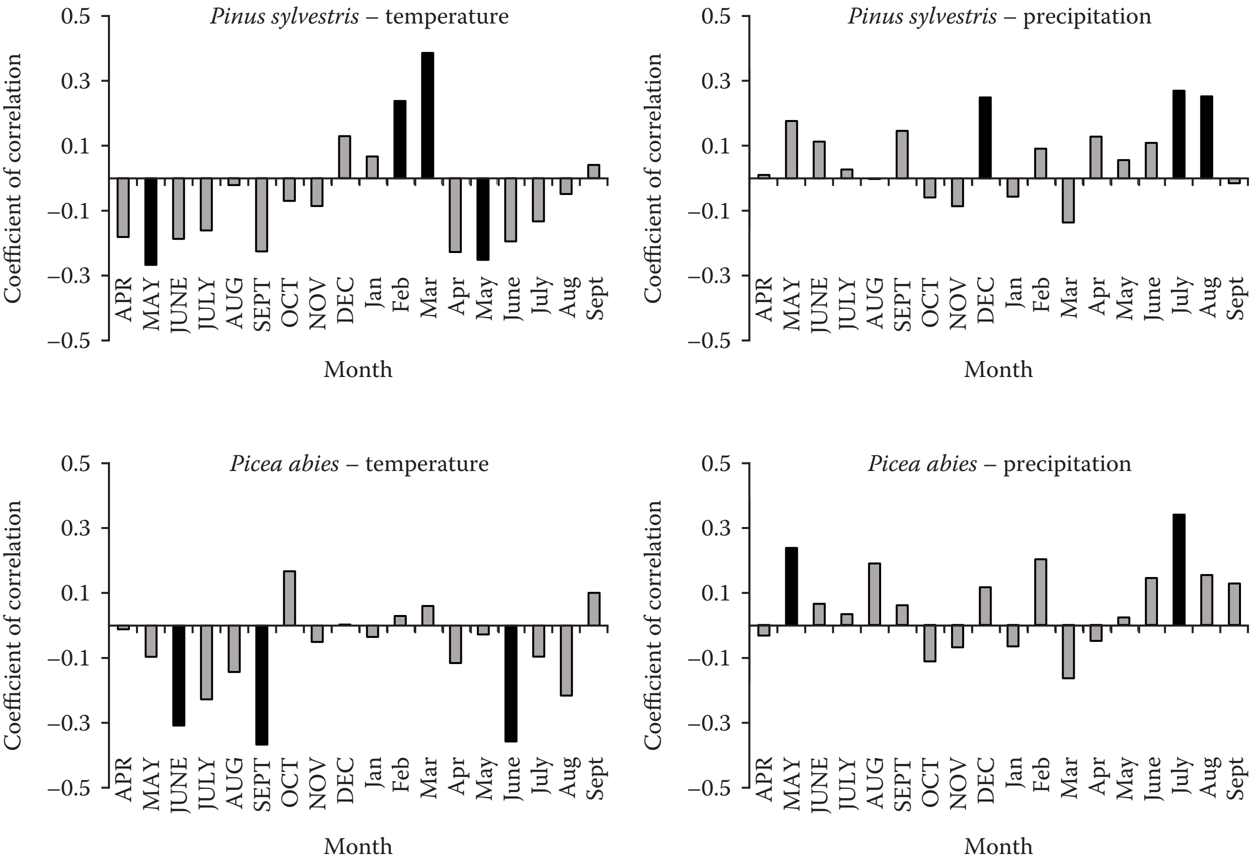

Figure 2. Coefficients of correlation of the regional residual index tree-ring width chronologies of Scots pine and Norway spruce with monthly average air temperature and monthly precipitation differentiated according to tree species

The period from April of the preceding year (capital letters) to September of the current year (lower-case letters) between 1962 and 2021 was used for all correlation analyses presented. Correlation values are highlighted only if a significance level corresponding to $P < 0.05$ was reached.

pointer year characterised by extremely low growth was detected in pine for the year 1976. In that year, the extremely low temperature in March (–0.7 °C, historical mean 2.6 °C) and long-term drought in June (20 mm, mean 84 mm) was measured. The negative pointer year (NPY) was not found in the case of spruce.

Figure 2 illustrates the effect of climate factors on radial growth by coefficients of correlation of the regional residual index tree-ring width chronologies of Scots pine and Norway spruce with monthly average air temperature and monthly precipitation. Generally, pine was more sensitive to climatic factors compared to spruce. Compared to precipitation, temperatures had a greater influence on the radial growth of both tree species, especially in the growing season. The principal month affecting the radial growth was July of the current year for both tree species.

DISCUSSION

Currently, forests are exposed to various disturbances, which are profoundly influenced by climate (Abdullah et al. 2019). Consequently, small- and large-scale natural forest disturbances or, at the least, a significant decline in tree growth is occurring, both at high elevations (Albrich et al. 2020) and at lower elevations (D'Andrea et al. 2019), where, moreover, a recent retreat or gradual mortality of once stable tree species is evident (Tangwa et al. 2022). Climate change is expected to affect the susceptibility of forests to calamities and also to affect the frequency, intensity, duration, and timing of various disturbances, particularly at lower elevations (Stanturf et al. 2014). Lack of precipitation and, as a consequence, more frequent and longer-lasting droughts will be an increasing risk to the growth, ecological stability, and vitality of forest ecosystems under global climate change (Seidl et al. 2011; Dyderski et al. 2018). This may often include the bare forest existence due to a significant increase in disturbances, especially in spruce and pine monocultures (Vacek et al. 2023). According to data from the Forest Protection Service [Lesní ochranná služba (Lubojacký, Knížek 2021)], the total infestation of Norway spruce by bark beetle in the Czech Republic in 2020 was at least 25 million m^3. Hundreds of thousands of cubic meters more are represented by their infestation of Scots pine. In general, coniferous forests in Czech lowlands appear not to be very promising in the context of climate change, precisely due to the extreme damage caused by abiotic and biotic factors, especially in the last decade (Hlásny et al. 2021; Liška et al. 2021). Some sources, however, point to the high adaptability of pine, specifically to climate change, e.g. in relation to the afforestation of agricultural or logging areas (Vacek et al. 2021a). Of course, both of the most economically exploited coniferous tree species in the Czech Republic are demonstrably subject to negative environmental factors, but in order to meet the requirements of the industry, it is necessary to also grow their stands in the lowlands, using pine with spruce for normal forest establishment. One of the ways to maintain pine and spruce in the lowlands is to mix them, with the potential benefit of increased production (Remeš, Kozel 2006; Bielak et al. 2014; Švec et al. 2015; Ruiz-Peinado et al. 2021).

Production potential. The production potential of forest stands is influenced by several factors, whether abiotic, biotic, or internal – genetic dispositions (Schweingruber 1996). The structure, growth, and production and very existence of the forest depends on these factors (Vacek et al. 2023). Specific habitat and stand conditions and management practices play a crucial role (Poleno et al. 2007). In general, stands under 50 years of age grow faster, and stands of higher age grow more slowly. Faster growth of forest tree species has been attributed to a range of factors such as increased nitrogen deposition (De Vries et al. 2014), increased CO$_2$ concentration (Soulé, Knapp 2006), the effect of climate change (Nemani et al. 2003; Čermák et al. 2019), or the influence of management measures (Poleno et al. 2009; Lindner et al. 2010).

On the site of interest described in this study, research has already been conducted by Remeš and Kozel (2006), who report a stock of broadly comparable production characteristics from spruce and pine stands in conversion with interspersed fir, oak, and beech. The range of stock was set at 366–378 m^3·ha^{-1}, i.e. the upper range of stock was 101 m^3 lower than in our study (which is 351–479 m^3·ha^{-1}). The production of mixed stands of pine and spruce is also described in studies by Pretzsch and Schütze (2016) or Ruiz-Peinado et al. (2021) in their research across Europe, where they concluded that it is such mixed stands that achieve a statistically significant increase in production compared to monocultures. Pretzsch and Biber (2016) have found up to a 35.9% increase in the production of mixed stands of pine and spruce with beech compared to monocultures. Their conclusions are confirmed by our work, in which we found that the variants from mixing 75% pine and 50% Scots pine are the most favorable in terms of stand stock and basal area. The production characteristics for Scots pine under given habitat and stand conditions in the Czech Republic are comparable to Vacek et al. (2016) and Čihák and Vejpustková (2021). Similar production characteristics of Scots pine and Norway spruce from the Říčany Forest District are reported by Bílek et al. (2013), depending on the nature-friendly management methods and the conversion process. While the number of trees in our case ranged from 256 trees·ha^{-1} in a spruce monoculture to 512 trees·ha^{-1} in a stand with an equal proportion of spruce and pine, Bílek et al. (2013) set the range at 288–476 trees·ha^{-1}. The same was true for stock (273–346 m^3·ha^{-1}) and basal area (24.2–27.6 m^2·ha^{-1}). For stands under conversion to a selection forest, Saniga and Szanyi (1998) reported a range of 270–725 trees·ha^{-1}, and Réh (1978) reported a similar range of 348–985 trees·ha^{-1}. The aforementioned differences in the production characteristics of the conversion stands can be justified by how conversion to a selective forest was initiated. In our case, it was introduced after a partial disruption of the forest stands (Remeš, Kozel 2006), while in the works of Saniga and Szanyi (1998) and Réh (1878), for example, the models are based on the assumption of a homogeneous closed stand.

Structure and diversity. Similar to our case, a predominantly random horizontal structure and only slightly clustered structure was found in other stands at Klokočná (Vacek et al. 2007). This also applied to a height and diameter structural differentiation, which was low in monocultures and medium in mixed forest stands. In terms of overall diversity, in our case, monocultures achieved a complex *B* index of structural variability ranging from 2.573–3.329 (monotonous structure) and mixed forests from 4.661–5.960 (uniform structure). In other stands at Klokočná, the monocultures showed uniform to irregular structure, and the mixed stands showed heterogeneous structure (Vacek et al. 2007). Similar results were also found at School Forestry Enterprise Kostelec nad Černými lesy during the conversion of spruce stands to selective forest (Remeš 2006). Here, the horizontal structure of the stands was random to slightly regular. Also, the height and diameter structural differentiation was low, and the structural variability was also monotonous.

Gallo et al. (2020) attribute differences in the structure and diversity of pine stands in Spain and the Czech Republic to different forest management practices. On the other hand, Bílek et al. (2016), comparing different pine stands in the Czech Republic and Poland, document relatively little difference in the structure of stands managed with close-to-nature principles and unmanaged stands. Vacek et al. (2017, 2020), contrastingly, note a pronouncedly irregular to rich structure of relict mixed pine stands, which in this context, is due to two main factors of heterogeneous stand structure – natural gap formation and the existence of natural regeneration. Therefore, these findings confirm that the management method also has a substantial influence on stand diversity, so in our case, management according to selection principles positively influences the heterogeneity of the environment.

Radial growth and climate. A negative year was found for pine at Klokočná, with minimal growth in 1976 due to low precipitation during the growing season (especially in June). In comparable habitat and stand conditions in the Týniště region, this was the case in 1975 and 1980 (Vacek 2016). At our study site, a positive effect of average monthly temperature on radial growth was found in February and March of the current year and a negative effect in May of both the current and previous year. In the Týniště region, under similar habitat and stand conditions, the relationship between temperature and radial growth was statistically positive in March of the current year and positive for precipitation in November and December of the previous year, and in February to April and June of the current year (Vacek et al. 2016).

In contrast to the Klokočná site we monitored, a significant negative year with minimum growth was found for spruce in a nearby stand in comparable habitat and stand conditions at Kostelec nad Černými lesy in 1977, i.e. the year after the minimum increment of Scots pine. The average tree ring width in spruce at this site was 2.31 mm (Brabec et al. 2023), while at the Klokočná site, we monitored it at 3.34 mm. At Klokočná, temperature had a greater effect on the radial growth of both tree species compared to precipitation, especially during the growing season. One of the crucial months influencing radial growth for both species was July of the current year, which is consistent with several conclusions from various studies, with diverse habitat conditions in different forest stands (Rybníček et al. 2010; Remeš et al. 2015; Sidor et al. 2015). In contrast, in a nearby spruce stand near Kostelec nad Černými lesy, there was no statistically significant correlation of mean diameter increment with monthly temperatures. For monthly precipitation in relation to radial growth, a statistically conclusive positive correlation was found in June and July of the previous year and a negative correlation in August of the current year (Brabec et al. 2023).

Drought, in particular, has thus emerged as a determinant of radial growth and vigor of Scots pine and Norway spruce under conditions of advancing climate change (Augustaitis et al. 2007; Bogino et al. 2009; Putalová et al. 2019; Lubojacký, Knížek 2021; Brichta et al. 2023). Moreover, trees damaged by browsing and bark stripping, which is very common in spruce compared to pine, suffer more from lack of precipitation and reduced growth (Cukor et al. 2019a, b; 2022). Especially in response to drought, perhaps it is the use of selection principles that will ultimately allow for greater plasticity and mitigation of negative impacts related to climate change in this context (Vacek et al. 2016).

CONCLUSION

In the context of the climatic fluctuations of the last decades and the increasing adaptability of forest stands under Central European conditions, it is increasingly necessary to reflect on silvicultural options for the essential commercial tree species. In many places, Scots pine and Norway spruce are beginning to fail when managed traditionally, but this does not mean that these two now semi-fragile species cannot be combined into mixed stands.

Based on our results, we conclude that mixed stands of Scots pine and Norway spruce are not only significantly more resilient to various environmental factors, have a diverse structure and biodiversity, and offer opportunities for mixing with other tree species but are also significantly more productive and have higher carbon sequestration compared to monocultures. This is, of course, also linked to the economic benefits of mixed forests in terms of higher profits, long-term sustainability, and reduced production uncertainty. These benefits can also be enhanced by interspersing other tree species due to the higher heterogeneity of such stands. However, given the wide range of both species, it is necessary to continue research into these forms of mixing, with as large a sample of study sites as possible, evenly across the range of pine and spruce. In conclusion, however, it should be stressed that within the framework of the different ecological requirements of the species present, mixed forests must not be managed as monocultures.

Acknowledgment: Acknowledgment belongs to the Czech Hydrometeorological Institute for providing the climatic data set. Also, we would like to thank Jitka Šišáková, an expert in the field, and Richard Lee Manore, a native speaker, for checking English.

REFERENCES

Abdullah H., Skidmore A.K., Darvishzadeh R., Heurich M. (2019): Sentinel-2 accurately maps green attack stage of European spruce bark beetle (*Ips typographus* L.) compared with Landsat-8. Remote Sensing in Ecology and Conservation, 5: 87–106.

Albrich K., Rammer W., Seidl R. (2020): Climate change causes critical transitions and irreversible alterations of mountain forests. Global Change Biology, 26: 4013–4027.

Aleksandrowicz-Trzcińska M., Drozdowski S., Brzeziecki B., Rutkowska P., Jabłońska B. (2014): Effects of different methods of site preparation on natural regeneration of *Pinus sylvestris* in Eastern Poland. Dendrobiology, 71: 73–81.

Aleksandrowicz-Trzcińska M., Drozdowski S., Wołczyk Z., Bielak K., Żybura H. (2017): Effects of reforestation and site preparation methods on early growth and survival of Scots pine (*Pinus sylvestris* L.) in south-eastern Poland. Forests, 8: 1–17.

Aleksandrowicz-Trzcińska M., Drozdowski S., Studnicki M., Żybura H. (2018): Effects of site preparation methods on the establishment and natural-regeneration traits of Scots pines (*Pinus sylvestris* L.) in northeastern Poland. Forests, 9: 717.

Allen C.D., Breshears D.D., McDowell N.G. (2015): On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere, 6: 1–55.

Andrzejczyk T. (2006): Rębnia przerębowa w drzewostanach sosnowych. Sylwan, 150: 52–60. (in Polish)

Augustaitis A., Augustaitiene I., Deltuvas R. (2007): Scots pine (*Pinus sylvestris* L.) crown defoliation in relation to the acid deposition and meteorology in Lithuania. Water, Air, and Soil Pollution, 182: 335–348.

Barta M., Lalik M., Rell S., Kunca A., Horáková M.K., Mudrončenková S., Galko J. (2019): Hypocrealean fungi associated with *Hylobius abietis* in Slovakia, their virulence against weevil adults and effect on feeding damage in laboratory. Forests, 10: 634.

Bauhus J., Forrester D.I., Gardiner B., Jactel H., Vallejo R., Pretzsch H. (2017): Ecological stability of mixed-species forests. In: Pretzsch H., Forrester D., Bauhus J. (eds): Mixed-Species Forests: Ecology and Management. Berlin, Springer: 337–382.

Bielak K., Dudzińska M., Pretzsch H. (2014): Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.) can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. Forest Systems, 23: 573–589.

Bílek L., Remeš J., Švec O., Zahradník D. (2013): On the way to continuous cover forest at middle elevations – The question of forest structure and specific site characteristics. Journal of Forest Science, 59: 391–397.

Bílek L., Vacek S., Vacek Z., Remeš J., Král J., Bulušek D., Gallo J. (2016): How close to nature is close-to-nature pine silviculture? Journal of Forest Science, 62: 24–34.

Biondi F., Waikul K. (2004): Dendroclim 2002: AC++ program for statistical calibration of climate signals in tree ring chronologies. Computers and Geosciences, 30: 303–311.

Bogino S., Fernández Nieto M.J., Bravo F. (2009): Climate effect on radial growth of *Pinus sylvestris* at its southern and western distribution limits. Silva Fennica, 43: 609–623.

Brabec P., Vacek Z., Vacek S., Štefančík I., Cukor J., Weatherall A., Gallo J., Slávik M., Sitková Z., Putalová T. (2023): Growth-climate responses of *Picea sitchensis* (Bong.) Carr. versus *Picea abies* (L.) Karst. in the British Isles and Central Europe. Central European Forestry Journal, 69: 167–178.

Brichta J., Bílek L., Linda R., Vítámvás J. (2020): Does shelterwood regeneration on natural Scots pine sites under changing environmental conditions represent a viable alternative to traditional clear-cut management? Central European Forestry Journal, 66: 104–115.

Brichta J., Vacek S., Vacek Z., Cukor J., Mikeska M., Bílek L., Šimůnek V., Gallo J., Brabec P. (2023): Importance and potential of Scots pine (*Pinus sylvestris* L.) in 21st century. European Forestry Journal, 69: 3–20.

Bublinec E. (1994): Koncentrácia, akumulácia a kolobeh prvkov v bukovom a smrekovom ekosystéme. Bratislava, VEDA: 85. (in Slovak)

Bunn A., Mikko K. (2018): Chronology Building in dplR. Vienna, R Foundation for Statistical Computing: 13.

Buras A., Schunk C., Zeiträg C., Herrmann C., Kaiser L., Lemme H., Straub C., Taeger S., Gößwein S., Klemmt H., Menzel A. (2018): Are Scots pine forest edges particularly prone to drought-induced mortality? Environmental Research Letters, 13: 025001.

Camarero J.J., Gazol A., Sangüesa-Barreda G., Cantero A., Sánchez-Salguero R., Sánchez-Miranda A., Granda E., Serra-Maluquer X., Ibáñez R. (2018): Forest growth responses to drought at short- and long-term scales in Spain: Squeezing the stress memory from tree rings. Frontiers in Ecology and Evolution, 6: 9.

Caudullo G., Tinner W., de Rigo D. (2016): *Picea abies* in Europe: Distribution, habitat, usage and threats. In: San-Miguel-Ayanz J., de Rigo D., Caudullo G., Houston Durrant T., Mauri A. (eds): European Atlas of Forest Tree Species. Luxembourg, Publications Office of the European Union: 114–116.

Čermák P., Kolář T., Žid T., Trnka M., Rybníček M. (2019): Norway spruce responses to drought forcing in areas affected by forest decline. Forest Systems, 28: e016.

Čihák T., Vejpustková M. (2021): Produkční charakteristiky borovice lesní v České republice na základě informací z druhého cyklu Národní inventarizace lesů (2011–2015). Zprávy lesnického výzkumu, 66: 126–137. (in Czech)

Čížek J., Kratochvíl F., Peřina V. (1959): Přeměny monokultur. Praha, SZN: 191. (in Czech)

Clark P.J., Evans F.C. (1954): Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology, 35: 445–453.

Cook E.R., Holmes R.L. (1984): Program ARSTAN user manual. Tucson, Laboratory of Tree-Ring Research, University of Arizona: 15.

Crookston N.L., Stage A.R. (1999): Percent Canopy Cover and Stand Structure Statistics from the Forest Vegetation Simulator. Ogden, Rocky Mountain Research Station: 11.

Cukor J., Vacek Z., Linda R., Vacek S., Marada P., Šimůnek V., Havránek F. (2019a): Effects of bark stripping on timber production and structure of Norway spruce forests in relation to climatic factors. Forests, 10: 320.

Cukor J., Vacek Z., Linda R., Sharma R.P., Vacek S. (2019b): Afforested farmland vs. forestland: Effects of bark stripping by *Cervus elaphus* and climate on production potential and structure of *Picea abies* forests. PLoS ONE, 14: e0221082.

Cukor J., Vacek Z., Linda R., Vacek S., Šimůnek V., Macháček Z., Brichta J., Prokůpková A. (2022): Scots pine (*Pinus sylvestris* L.) demonstrates a high resistance against bark stripping damage. Forest Ecology and Management, 513: 120182.

D'Andrea G., Šimůnek V., Pericolo O., Vacek Z., Vacek S., Corleto R., Olejár L., Ripullone F. (2023): Growth response of Norway spruce (*Picea abies* [L.] Karst.) in central Bohemia (Czech Republic) to climate change. Forests, 14: 1215.

De Vries W., Dobbertin M.H., Solberg S., Van Dobben H.F., Schaub M. (2014): Impacts of acid deposition, ozone exposure and weather conditions on forest ecosystems in Europe: An overview. Plant and Soil, 380: 1–45.

del Río M., Pretzsch H., Alberdi I., Bielak K., Bravo F., Brunner A., Condés S., Ducey M.J., Fonseca T., von Lüpke N. et al. (2016): Characterization of the structure, dynamics, and productivity of mixed-species stands: Review and perspectives. European Journal of Forest Research, 135: 23–49.

Desplanque C., Rolland C., Schweingruber F.H. (1999): Influence of species and abiotic factors on extreme tree ring modulation. Trees., 13: 218–227.

Drexhage M., Colin F. (2001): Estimating root system biomass from breast-height diameters. Forestry, 74: 491–497.

Drössler L., Agestam E., Bielak K., Dudzinska M., Koricheva J., Liziniewicz M., Löf M., Mason B., Pretzsch H., Valkonen S., Wellhausen K. (2018): Over-and underyielding in time and space in experiments with mixed stands of Scots pine and Norway spruce. Forests, 9: 495.

Durant D.T., de Rigo D., Caudullo G. (2016): *Pinus sylvestris* in Europe: Distribution, habitat, usage and threats. In: San-Miguel-Ayanz J., de Rigo D., Caudullo G., Houston Durrant T., Mauri A. (eds): European Atlas of Forest Tree Species. Luxembourg, Publications Office of the European Union: 114–116.

Dyderski M.K., Paz S., Frelich L.E., Jagodziński A.M. (2018): How much does climate change threaten European forest tree species distributions? Global Change Biology, 24: 1150–1163.

Eckenwalder J.E. (2009): Conifers of the World: The Complete Reference. Portland, Timber Press: 720.

Fabrika M., Ďurský J. (2005): Algorithms and software solution of thinning models for SIBYLA growth simulator. Journal of Forensic Sciences, 51: 431–445.

Farjon A. (2010): A Handbook of the World's Conifers. Leiden, Brill: 1111.

Flexas J., Medrano H. (2002): Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited. Annals of Botany, 89: 183–189.

Fritts H.C. (1976): Tree Rings and Climate. London, Academic Press: 567.

Füldner K. (1995): Strukturbeschreibung in Mischbeständen. Forstarchiv, 66: 235–606. (in German)

Fürst C., Vacik H., Lorz C., Makeschin F., Podrázský V., Janeček V. (2007): Meeting the challenges of processoriented forest management. Forest Ecology and Management, 248: 1–5.

Gallo J., Bílek L., Šimůnek V., Roig S., Fernández J.A.B. (2020): Uneven-aged silviculture of Scots pine in Bohemia and Central Spain: Comparison study of stand reaction to transition and long-term selection management. Journal of Forest Science, 66: 22–35.

Gallo J., Vacek Z., Vacek S. (2021): Quarter of a century of forest fertilization and liming research at the Department of Silviculture in Prague, Czech Republic. Central European Forestry Journal, 67: 123–134.

Gao Y., Markkanen T., Aurela M., Mammarella I., Thum T., Tsuruta A., Yang H., Aalto T. (2017): Response of water use efficiency to summer drought in a boreal Scots pine forest in Finland. Biogeosciences, 14: 4409–4422.

Gazol A., Camarero J.J., Anderegg W.R.L., Vicente-Serrano S.M. (2017): Impacts of droughts on the growth resilience of Northern Hemisphere forests. Global Ecology and Biogeography, 26: 166–176.

Greenwood S., Ruiz-Benito P., Martínez-Vilalta J., Lioret F., Kitzberge T., Alle C.D., Fensham R., Laughlin D.C., Kattge J., Bönisch G., Kraft N.J.B., Jump A.S. (2017): Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. Ecology Letters, 20: 539–553.

Grissino-Mayer H.D., Holmes R.L., Fritts H.C. (1992): International Tree-Ring Data Bank Program Library: User's Manual. Tuscon, Laboratory of Tree-Ring Research, University of Arizona: 106.

Haberstroh S., Werner C., Grün M., Kreuzwieser J., Seifert T., Schindler D., Christen A. (2022): Central European 2018 hot drought shifts Scots pine forest to its tipping point. Plant Biology, 7: 1186–1197.

Halaj J., Grék J., Pánek F., Petráš R., Řehák J. (1987): Rastové tabuľky hlavných drevín ČSSR. Bratislava, Príroda: 361. (in Slovak)

Hanewinkel M., Pretzsch H. (2000): Modelling the conversion from even-aged to uneven-aged stands of Norway spruce (*Picea abies* L. KARST.) with a distance-dependent growth simulator. Forest Ecology and Management, 134: 55–70.

Hanewinkel M., Cullmann D.A., Schelhaas M.J., Nabuurs G.J., Zimmermann N.E. (2013): Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change, 3: 203–207.

Hartl-Meier C., Zang C., Büntgen U., Esper J., Rothe A., Göttlein A., Dirnböck T., Treydte K. (2014): Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest. Tree Physiology, 35: 4–15.

Hlásny T., Krokene P., Liebhold A., Montagné-Huck C., Müller J., Qin H., Raffa K., Schelhaas M.-J., Seidl R., Svoboda M., Viiri H. (2019): Living with Bark Beetles: Impacts, Outlook and Management Options. From Science to Policy 8. Joensuu, European Forest Institute: 50.

Hlásny T., Zimová S., Merganičová K., Štěpánek P., Modlinger R., Turčáni M. (2021): Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. Forest Ecology and Management, 490: 119075.

Holuša J., Foit J., Knížek M., Schovánková J., Lukášová K., Vanická H., Trombík J., Kula E. (2019): The bark beetles *Orthotomicus laricis* and *Orthotomicus longicollis* are not pests in Central Europe: A case study from the Czech Republic. Bulletin of Insectology, 72: 253–260.

Horgan T., Keane M., McCarthy R., Lally M., Thompson D., O'Carroll J. (2003): A Guide to Forest Tree Species Selection and Silviculture in Ireland. Dublin, National Council for Forest Research and Development (COFORD): 255.

Jaehne S.C., Dohrenbusch A. (1997): Ein Verfahren zur Beurteilung der Bestandesdiversität. Forstwissenschaftliches Centralblatt, 116: 333–345. (in German)

Jansson M., Fors H., Lindgren T., Wiström B. (2013): Perceived personal safety in relation to urban woodland vegetation – A review. Urban Forestry & Urban Greening, 12: 127–133.

Johnson O., More D. (2006): Collins Tree Guide. London, Collins: 464.

Knibbe B. (2007): PAST4: Personal Analysis System for Treering Research, Version 4.2. Vienna, SCIEM: 161.

Knížek M., Liška J., Véle A., Zahradník P., Lubojacký J. (2021): Ochrana borovice lesní (*Pinus sylvestris* L.) před podkorním a dřevokazným hmyzem. Certifikovaná metodika, Lesnický průvodce 9/2021. Strnady, Výzkumný ústav lesního hospodářství a myslivosti: 120. (in Czech)

Komonen A., Schroeder L.M., Weslien J. (2011): *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. Journal of Applied Entomology, 135: 132–141.

Kovalevskii S.B., Krol A., Myroniuk V., Kovalevskyi S.S., Vysotska N., Khromulyak O., Yurchenko V. (2022): Growth of Scots pine (*Pinus sylvestris* L.) stands on soils with close bedding of crystalline parent rocks in Central Polissya, Ukraine. Central European Forestry Journal, 68: 72–77.

Kraft G. (1884): Beiträgezur zur lehre von den durchforstungen, schlagstellungen und lichtungshieben. Hannover, Klindworth: 147. (in German)

Krakau U.K. Liesebach M., Aronen T., Lelu-Walter M.A., Schneck V. (2013): Scots Pine (*Pinus Sylvestris* L.). Managing forest ecosystems. In: Pâques L.E. (ed.): Forest Tree Breeding in Europe: Current State-of-the-Art and Perspectives. Dordrecht, Springer: 267–323.

Ledermann T., Neumann M. (2005): Ergebnisse vorläufiger Untersuchungen zur Erstellung von Biomassefunktionen aus Daten alter Dauerversuchsflächen. In: Deutscher

Verband Forstlicher Forschungsanstalten, Sektion Ertragskunde, Beiträge zur Jahrestagung 2005, Freising, May 9–11, 2005: 143–152. (in German)

Leštianska A., Fleischer Jr P., Merganičová K., Fleischer Sr P., Nalevanková P., Střelcová K. (2023): Effect of provenance and environmental factors on tree growth and tree water status of Norway spruce. Forests, 14: 156.

Leuschner C., Ellenberg H. (2017): Ecology of Central European Forests: Vegetation Ecology of Central Europe, Volume 1. Berlin, Springer: 972.

Lindner M., Maroschek M., Netherer S., Kremer A., Barbati A., Garciagonzalo J., Seidl R., Delzon S., Corona P., Kolström M., Marchetti M., Lexer M. (2010): Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management, 259: 698–709.

Liška J., Knížek M., Véle A. (2021): Evaluation of insect pest occurrence in areas of calamitous mortality of Scots pine. Central European Forestry Journal, 67: 85–90.

Lubojacký J., Knížek M. (2021): Podkorní hmyz. In: Knížek M., Liška J. (eds): Výskyt lesních škodlivých činitelů v roce 2020 a jejich očekávaný stav v roce 2021. Zpravodaj ochrany lesa – Supplementum 2021. Strnady, Výzkumný ústav lesního hospodářství a myslivosti: 22–36. (in Czech)

Matías L., Jump A.S. (2012): Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: The case of *Pinus sylvestris*. Forest Ecology and Management, 282: 10–22.

Mikeska M., Vacek S., Prausová R., Simon J., Minx T., Podrázský V., Malík V., Kobliha J., Anděl P., Matějka K. (2008): Typologické vymezení, struktura a management přirozených borů a borových doubrav v ČR. Kostelec nad Černými lesy, Lesnická práce: 450. (in Czech)

Mikulenka P., Prokůpková A., Vacek Z., Vacek S., Bulušek D., Simon J., Šimůnek V., Hájek V. (2020): Effect of climate and air pollution on radial growth of mixed forests: *Abies alba* Mill. vs. *Picea abies* (L.) Karst. Central European Forestry Journal, 66: 23–36.

Nemani R.R., Keeling C.D., Hashimoto H., Jolly W.M., Piper S.C., Tucker C.J., Myneni R.B., Running S.W. (2003): Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science, 300: 1560–1563.

Novák J., Dušek D., Kacálek D., Slodičák M., Souček J. (2017): Pěstební postupy pro borové porosity 1. a 2. lesního vegetačního stupně. Strnady, Lesnický průvodce: 28. (in Czech)

O'Reilly-Wapstra J.M., Moore B.D., Brewer M., Beaton J., Sim D., Wiggins N.L., Iason G.R. (2014): *Pinus sylvestris* sapling growth and recovery from mammalian browsing. Forest Ecology and Management, 325: 18–25.

OECD (2006): Safety Assessment of Transgenic Organisms: OECD Consensus Documents, Vol. 2. Paris, OECD Publishing: 448.

Petráš R., Pajtík J. (1991): Sústava česko-slovenských objemových tabuliek drevín. Lesnícky časopis, 37: 49–56. (in Slovak)

Petráš R., Košút M., Oszlányi J. (1985): Listová biomasa stromov smreka, borovice a buka. Lesnícky časopis, 31: 121–135. (in Slovak)

Plíva K. (2000): Trvale udržitelné obhospodařování lesů podle souborů lesních typů. Brandýs nad Labem, ÚHÚL: 200. (in Czech)

Podrázský V., Remeš J. (2007): Změny kvality a množství nadložního humusu při přirozeném zmlazení bukových porostů na území Školního lesního podniku Kostelec nad Černými lesy. Zprávy lesnického výzkumu, 52: 118–122. (in Czech)

Podrázský V., Remeš J. (2010): Effects of the species composition change on the humus form state in the forest stands on the territory of the University Training Forest at Kostelec nad Černými lesy. Zprávy lesnického výzkumu, 55: 71–77.

Podrázský V., Remeš J., Kratochvíl J. (2005): Vývoj půdního chemizmu ve smrkových lesních ekosystémech na území ŠLP Kostelec nad Černými lesy. Zprávy lesnického výzkumu, 50: 198–201. (in Czech)

Poleno Z., Vacek S., Podrázský V., Remeš J., Mikeska M., Kobliha J., Bílek L. (2007): Pěstování lesů II. Teoretická východiska pěstování lesů. Kostelec nad Černými lesy, Lesnická práce: 464. (in Czech)

Poleno Z., Vacek S., Podrázský V., Remeš J., Štefančík I., Mikeska M., Kobliha J., Kupka I., Malík V., Turčáni M., Dvořák J., Zatloukal V., Bílek L., Baláš M., Simon J. (2009): Pěstování lesů III. Praktické postupy pěstování lesů. Kostelec nad Černými lesy, Lesnická práce: 952. (in Czech)

Praciak A., Pasiecznik N., Sheil D., van Heist M., Sassen M., Sousa Correia C., Dixon C., Fyson G.E., Rushforth K., Teeling C. (2013): The CABI Encyclopedia of Forest Trees. Wallingford, CABI: 536.

Pretzsch H. (2006): Wissen nutzbar machen für das Management von Waldökosystemen. Allgemeine Forst Zeitschrift für Waldwirtschaft und Umweltvorsorge, 61: 1158–1159. (in German)

Pretzsch H., Biber P. (2016): Tree species mixing can increase maximum stand density. Canadian Journal of Forest Research, 46: 1179–1193.

Pretzsch H., Schütze G. (2016): Effect of tree species mixing on the size structure, density, and yield of forest stands. European Journal of Forest Research, 135: 1–22.

Průša E. (2001): Pěstování lesů na typologických základech. Kostelec nad Černými lesy, Lesnická práce: 594. (in Czech)

Putalová T., Vacek Z., Vacek S., Štefančík I., Bulušek D., Král J. (2019): Tree-ring widths as an indicator of air pollution stress and climate conditions in different Norway spruce forest stands in the Krkonoše Mts. Central European Forestry Journal, 65: 21–33.

Reddy A.R., Chaitanya K.V., Vivekanandan M. (2004): Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. Journal of Plant Physiology, 161: 1189–1202.

Réh J. (1978): Technika pestovania lesa vo výbernej sústave hospodárenia. In: Vyskot M. et al.: Pěstění lesů. Praha, SZN: 360–412. (in Slovak)

Reich P.B., Oleksyn J. (2008): Climate warming will reduce growth and survival of Scots pine except in the far north. Ecology Letters, 11: 588–597.

Reineke L.H. (1933): Perfecting a stand density index for even-aged forests. Journal of Agricultural Research, 46: 627–638.

Remeš J. (2006): Transformation of even-aged spruce stands at the School Forest Enterprise Kostelec nad Černými lesy: Structure and final cutting of mature stand. Journal of Forest Science, 52: 158–171.

Remeš J., Kozel J. (2006): Structure, growth and increment of the stands in the course of stand transformation in the Klokočná Forest Range. Journal of Forest Science, 52: 573–546.

Remeš J., Bílek L., Novák J., Vacek Z., Vacek S., Putalová T., Koubek L. (2015): Diameter increment of beech in relation to social position of trees, climate characteristics and thinning intensity. Journal of Forensic Sciences, 61: 456–464.

Remeš J., Pulkrab K., Bílek L., Podrázský V. (2020): Economic and production effect of tree species change as a result of adaptation to climate change. Forests, 11: 431.

Ruiz-Peinado R., Pretzsch H., Löf M., Heym M., Bielak K., Aldea J., Barbieto I., Brazaitis G., Drössler L., Godvod K. et al. (2021): Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) productivity along a climatic gradient across Europe. Forest Ecology and Management, 482: 118834.

Rybníček M., Čermák P., Žid T., Kolář T. (2010): Radial growth and health condition of Norway spruce (*Picea abies* (L.) Karst.) stands in relation to climate (Silesian Beskids, Czech Republic). Geochronometria, 36: 9–16.

Saniga M., Szanyi O. (1998): Modely výberkových lesov vo vybraných lesných typoch a geografických celkoch Slovenska. Vedecké štúdie TU vo Zvolene, 4/1998/A. Zvolen, Technická univerzita Zvolen: 48. (in Slovak)

Schweingruber F.H. (1996): Tree Rings and Environment Dendroecology. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research: 609.

Seidl R., Rammer W., Lexer M. (2011): Climate change vulnerability of sustainable forest management in the Eastern Alps. Climatic Change, 106: 225–254.

Sevik H., Topacoglu O. (2015): Variation and inheritance pattern in cone and seed characteristics of Scots pine (*Pinus sylvestris* L.) for evaluation of genetic diversity. Journal of Environmental Biology, 36: 1125.

Sidor C.G., Popa I., Vlad R., Cherubini P. (2015): Different tree-ring responses of Norway spruce to air temperature across an altitudinal gradient in the Eastern Carpathians (Romania). Trees, 29: 985–997.

Šimůnek V., Vacek Z., Vacek S. (2020): Solar cycles in salvage logging: National data from the Czech Republic confirm significant correlation. Forests, 11: 973.

Souček J., Tesař V. (2008): Metodika přestavby smrkových monokultur na stanovištích přirozených smíšených porostů: Certifikovaná metodika. Lesnický průvodce, 4: 37. (in Czech)

Souček J., Špulák O., Dušek D. (2018): Metodika přeměny a přestavby borových monokultur na stanovištích přirozených smíšených porostů: Certifikovaná metodika. Lesnický průvodce, 15: 35. (in Czech)

Soulé P.T., Knapp P.A. (2006): Radial growth rate increases in naturally occurring ponderosa pine trees: A late-20th century CO_2 fertilization effect? New Phytologist, 171: 379–390.

Spathelf P., Ammer C. (2015): Forest management of Scots pine (*Pinus sylvestris* L.) in northern Germany – A brief review of the history and current trends. Forstarchiv, 86: 59–66.

Spiecker H., Hansen J., Klimo E., Skovsgaard J.P., Streba H., Teuffel K.V. (2004): Norway spruce conversion – Options and consequences. European Forest Institute Research Report 18. Leiden, Brill: 269.

Stanturf J.A., Palik B.J., Dumroese R K. (2014): Contemporary forest restoration: A review emphasizing function. Forest Ecology and Management, 331: 292–323.

Švec O., Bílek L., Remeš J., Vacek Z. (2015): Analysis of operational approach during forest transformation in Klokočná Range, Central Bohemia. Journal of Forest Science, 61: 148–155.

Sydorenko S., Voron V., Koval I., Sydorenko S., Rumiantsev M., Hurzhii R. (2021): Postfire tree mortality and fire resistance patterns in pine forests of Ukraine. Central European Forestry Journal, 67: 21–29.

Taeger S., Zang C., Liesebach M., Schneck V., Menzel A. (2013): Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenances. Forest Ecology and Management, 307: 30–42.

Tangwa E., Pechanec V., Brus J., Vyvlecka P. (2022): Spatial shifts in species richness in response to climate and environmental change: An adaption of the EUROMOVE model in the Czech Republic. Diversity, 14: 235.

Teuffel K., Baumgarten M., Hanewinkel M., Sauter U.H., Spiecker H., von Wilpert K. (2005): Waldumbau: Für eine zukunftsorientierte Waldwirtschaft. Berlin, Springer: 422. (in German)

Usoltsev V.A., Merganičová K., Konôpka B., Tsepordey I.S. (2022): The principle of space-for-time substitution in predicting *Picea* spp. biomass change under climate shifts. Central European Forestry Journal, 68: 174–189.

Vacek S., Simon J., Remeš J., Podrázský V., Minx T., Mikeska M., Malík V., Jankopvský L., Turčáni M., Jakuš R., Schwarz O., Kozel J., Valenta M., Lička L., Hlásný T., Zúbrík M., Krejčí F., Třešňák J., Hofmeister Š. (2007): Obhospodařování bohatě strukturovaných a přírodě blízkých lesů. Kostelec nad Černými lesy, Lesnická práce: 447. (in Czech)

Vacek S., Vacek Z., Bílek L., Simon J., Remeš J., Hůnová I. (2016): Structure, regeneration and growth of Scots pine (*Pinus sylvestris* L.) stands with respect to changing climate and environmental pollution. Silva Fennica, 50: 1564.

Vacek Z., Vacek S., Eşen D., Yildiz O., Král J., Gallo J. (2020): Effect of invasive *Rhododendron ponticum* L. on natural regeneration and structure of *Fagus orientalis* Lipsky forests in the Black Sea region. Forests, 11: 603.

Vacek Z., Linda R., Cukor J., Vacek S., Šimůnek V., Gallo J., Vančura K. (2021a): Scots pine (*Pinus sylvestris* L.), the suitable pioneer species for afforestation of reclamation sites? Forest Ecology and Management, 485: 118951.

Vacek Z., Prokůpková A., Vacek S., Bulušek D., Šimůnek V., Hájek V., Králíček I. (2021b): Mixed vs. monospecific mountain forests in response to climate change: Structural and growth perspectives of Norway spruce and European beech. Forest Ecology and Management, 488: 119019.

Vacek Z., Vacek S., Cukor J. (2023): European forests under global climate change: Review of tree growth processes, crises and management strategies. Journal of Environmental Management, 332: 117353.

van der Maaten-Theunissen M., van der Maaten E., Kahle H.-P. (2013): Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. Annals of Forest Science, 70: 185–193.

Viewegh J., Kusbach A., Mikeska M. (2003): Czech forest ecosystem classification. Journal of Forest Science, 49: 74–82.

Vítámvás J., Bílek L., Ulbrichová I., Bažant V., Dreslerová J., Vacek Z. (2019): Vzcházení, přežívání a kořenový systém semenáčků borovice lesní (*Pinus sylvestris* L.) při různých intenzitách slunečního záření a závlahy. Zprávy lesnického výzkumu, 64: 102–110. (in Czech)

Vorčák J., Merganič J., Saniga M. (2006): Structural diversity change and regeneration processes of the Norway spruce natural forest in Babia hora NNR in relation to altitude. Journal of Forensic Sciences, 52: 399–409.

Yamaguchi D.K. (1991): A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research, 21: 414–416.

Received: June 30, 2023
Accepted: August 18, 2023