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Journal of Forest Science

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Support for silver fir (*Abies alba* Mill.) in managed forests

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Historical flashback. Local names such as "Jedlová, Jedlina, Jedlí, Jedlany", but also "Jedlá" (see https://wwwinfo.mfcr.cz/ares/obce/obce_abc_J.html.cz) are derived from the Czech genus name "jedle" for silver fir (*Abies alba* Mill.). The number of such names is very small, which corresponds with the very small share of firs in Czech forests. This is also supported by the archive files, dated back to the 12th and 13th centuries, which report only a few names related to fir (Nožička 1957). Nevertheless, silver fir had been an important component of a woody species mosaic until the support of its regeneration via silvicultural systems of that time ceased (see Dreslerová 2012).

The issue. Changes in management and/or air pollution contributed to a species-specific decline, which led to a mere 0.9% share of silver fir in the Czech Republic at the turn of the century (Ministry of Agriculture 2001). Management of the silver fir was rather neglected in the last few decades, which was also attributable to the vulnerability of young firs to frost (Vaněk et al. 2016) or its palatability for cloven-hoofed game (Diaci et al. 2011; Červený 2016; Liška, Šrůtka 2016; Vitasse et al. 2019; van Beeck Calkoen 2022). The silver fir is an ideal component of stand mixtures at suitable sites (Horáček 2016) and belongs among the most universal species capable of functioning as a stand stabilizer (Mauer, Houšková 2016). A limiting factor for renewal success is fencing, which can help establish large patches of regeneration even if only a few parent fir trees are present in the stand (Dobrovolný, Martiník 2016).

Silver fir is a rare species in Central Europe nowadays. Let's learn more about the fir thus helping it cover larger areas of forested land again.

Supported by National Agency for Agricultural Research (NAZV) at Ministry of Agriculture under project QK1910292 "Approaches for supporting silver fir in managed forests in the Czech Republic".

Good news and research needs. The signs of a fir recovery have been observed both in Czechia or abroad since 1990s (Bošela et al. 2014; Dmyterko, Bruchwald 2015). The fir responded positively not only to air pollution reduction but also to the increased temperature in the temperate forest domain (Gazol et al. 2015). Compared to spruce, fir exhibits larger resistance to drought stress (Zang et al. 2015; Gazol, Camarero 2016; Vitali et al. 2017; Dănescu et al. 2018); it can be, therefore, used appropriately in areas of spruce decline (Martiník, Dušek 2015). However, there is a need to pay attention to the biotic pests of silver fir. As the fir share increases in the forested lands of the Czech Republic, one can expect a rising number of pests, of which we have no relevant information except a few records. As for the mutual relationship between the fir and its growing environment, there are still just a few studies dealing with nutrition or litterfall nutrient return. Besides, the published results on the fir foliar nutrients (Dušek et al. 2020) or forest floor of the fir litterfall origin (Třeštík, Podrázský 2017) seemed to differ slightly from Norway spruce. In other words, there is a need to put more pieces in the puzzle as the climate shifts change the growth conditions of the forests, and the species-specific pests feed on them to such an extent that alternative woody species composition proposals are needed.

Answering some research questions. Readers will find some answers in this thematic issue of Journal of Forest Science. The authors looked for solutions not only on the species level but also for information on provenances' performance, which would help change the forest management paradigm. The experience with fir in the Moravian Sudetes is presented by Fulín et al. Another project presented by Vejpustková et al. deals with how the fir coped with drought. Article about the nutrition of fir compared to Norway spruce was written by Novotný and the nutrient return in fir-rowan plantation was the interest of Kacálek et al.

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Evaluation of silver fir provenances at 51 years of age in provenance trials in the Předhoří Hrubý Jeseník and Nízký Jeseník Mts. regions, Czech Republic

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Abstract: In 2021, measurements were done at two international provenance research trials for silver fir originating from the same series of experiments. The investigation was carried out in the location Vítkov and Úsov, where both trials were established. Biometric data (tree height, diameter at breast height) were measured and qualitative traits (stem shape, occurrence of stem forking, stem damage, bark pattern, and defoliation) were assessed during the early mature stage of the experiment. Overbark stem volume and per-hectare standing volume were also calculated. Sixty-five provenances of domestic and foreign origin were evaluated in both trials. Although the results do not indicate unequivocally the most suitable or most productive provenance in the trials, provenances of Czech origin including the ones originating from the surrounding natural forest areas perform consistently better than the average. The least productive provenances, on the other hand, were those from parts of Bulgaria, Austria, and especially Italy, which achieved the poorest results even in stem shape. In Czech conditions, therefore, Italian fir provenances have not proved so successful as they have in the United Kingdom.

Keywords: *Abies alba*; provenance plot; production; phenotypic characteristics; variability

Silver fir (*Abies alba* Mill.) is one of the basic tree species of Central Europe, extending from the Pyrenees to the Balkan Peninsula (Farjon 2010; Praciak et al. 2013). In terms of the elevation distribution, fir is the most widespread in forest altitudinal zones 2–6, which roughly cover the altitudinal range of 290–850 m a.s.l. (Málek 1983). It is the fourth most abundant coniferous tree species in the Czech Republic, with representation of 1.2% (Ministry of Agriculture 2021). Moreover, (Podrázský et al. 2018) an advantage of its cultivation is its good effect on soil improvement. In the past, at the time

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when significant anthropogenic influences started to occur, its representation even reached an average of 19.8% (Ministry of Agriculture 2015). The greatest expansion of fir in Europe was recorded during the 14th–16th centuries, when it gradually came to occupy the area at the expense of beech. However, in the last century, repeated dieback of silver fir in its northern natural range has been recorded, which has reduced its abundance (Málek 1983). Having such a large natural range, the area of which is also discontinuous in nature (Musil, Hamerník 2007), different provenances developed over the long term while adapting to local environmental conditions. Genetic characterization of silver fir in the Czech lands was carried out by Cvrčková et al. (2015) and Fulín et al. (2016), of foreign authors for example Longauer (2001), Paule et al. (2001) and Loungauer et al. (2003) dealt with this topic. Silver fir variability allows it to respond to changing conditions and naturally persist in woodlands, as shown by its fluctuation in the past. Morphological variability of silver fir was assessed in several publications, e.g. by Dobrowolska (2008) and Skrzyszewska and Chłanda (2009). Moreover, in the Balkans, hybridization between silver fir and Greek fir (*Abies cephalonica* Loudon) occurred in the contact zone of their natural ranges, resulting in hybridogenous Macedonian fir (*Abies* × *borisii regis* Mattf.) (Novotný et al. 2022). The genus *Abies* is therefore often used in breeding programmes dealing with interspecies hybridization. Hybridization trials have been conducted for a long time, for example by Kormuťák (1985), Greguss (1988), Kobliha and Pokorný (1990), and Kobliha et al. (2013). Provenance trials are also carried out to investigate adaptability and use in forestry while focusing on both native and introduced tree species. From the evaluated research areas, current real data are obtained that are informative for resolving economic, breeding, or legislative situations. Provenance trials specifically on fir trees were conducted in the Czech Republic for example by Šindelář et al. (2008), Kýval et al. (2012), and Čáp et al. (2013), and in neighbouring countries for instance by Paule (1986), Larsen and Mekic (1991), Mihai et al. (2018), and Gunia (2019).

The aim of this paper is to evaluate the growth and morphological characteristics of silver fir provenances at intermediate felling age at two sites in northern Moravia and Silesia and which reflect the variability, resistance, and ecological requirements of the tree species since their establishment. Differences in characteristics between individual provenances will indicate the suitability of silver fir subpopulations planted within a given environment.

MATERIAL AND METHODS

In the 1970s, international cooperation began regarding the exchange of reproductive material for silver fir and foreign firs. The Forestry and Game Management Research Institute obtained seed lots representing 153 provenances, which were also evaluated for seed quality. Twenty provenance trials were planted between 1973 and 1977 from the material grown from these seeds, 14 of these trials were with silver fir only and the remaining 6 trials were mixed with native and non-native firs. Due to the limited amount of seed, a varying number of provenances and repetitions were planted. The repetition was usually done four times, but in some cases only three times. Thus, after the planting and fencing of all trials, the 1973–1977 *Abies* research series was created, from which the trials of silver fir provenances at Šternberk, Úsov-Veleboř No. 70 and Vítkov, Kerhartice No. 71 were measured in 2021 (Figure 1). Both trials were established in the same way using the double grid method with plot size set at 10 m × 10 m. The seedlings were planted at 2 m × 1 m spacing with 50 trees in each plot. A total 6 050 seedlings were planted at research site 70, which consists of 121 plots of 25 provenances with 4 repetitions and 7 provenances with 3 repetitions, for a total of 32 provenances (Table 1). The trial size is 1.3 ha, exposure is southeastern, slope is 10–20%, and altitude is 400–420 m. The habitat conditions are based on the subsoil of Quaternary loam and stone sediment and soil type Dystric Cambisol. The forest type at the site is designated 3K3 – acidic oak-beech woodland with Luzula cover (Viewegh et al. 2003). Annual rainfall total is 551–600 mm and mean annual temperature is in the range of 8.1–10 °C. At research site 71, the total number of fir trees planted was 9 600, corresponding to 192 plots with 48 silver fir provenances (Table 1) with 4 repetitions. The trial is 1.92 ha in size with southern exposure, slope of 12–33%, and altitude of 400–450 m. The habitat conditions are based upon culm greywacke with shale and the soil type is predominantly Mesobasic Cambisol with Gley and Ranker. The forest type on the site is designated 3S1 – lush oak-beech woodland with Oxalis. Annual rainfall total

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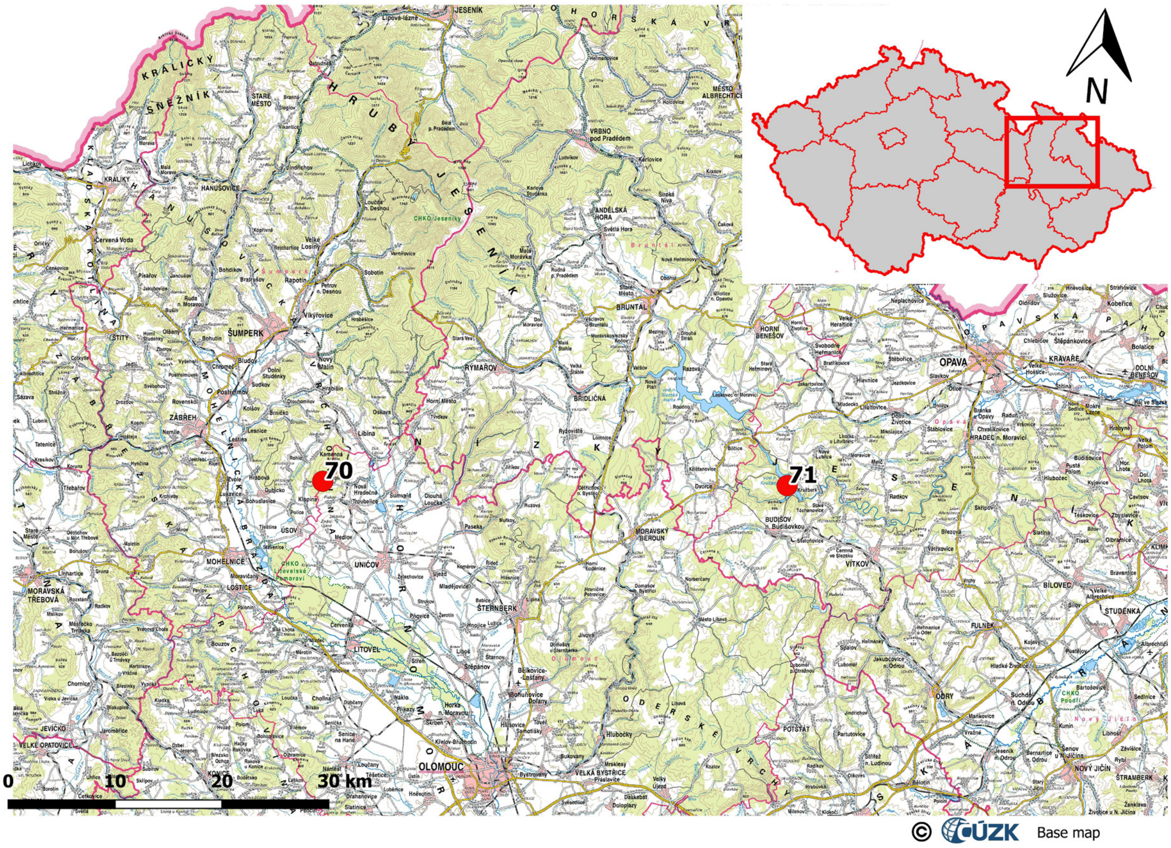

Figure 1. Display of research trials No. 70 (Úsov) and No. 71 (Vítkov) in the Czech Republic

is 651–700 mm and mean annual temperature is in the range of 7.1–9 °C.

In the provenance trials, biometric data of each tree were measured, namely the diameter at breast height (*DBH*) was read twice perpendicularly using a millimetre calliper (Haglöf, Sweden), and the tree height using a Vertex VL ultrasound hypsometer (Haglöf, Sweden) to the nearest 0.1 m. From these parameters, the overbark volume was calculated according to the volumetric formula for fir (Petráš, Pajtík 1991) and subsequently the per-hectare standing volume of provenances was calculated. Qualitative traits were also evaluated, such as stem shape (1 – completely straight; 2 – unilaterally curved at near-ground level; 3 – unilaterally curved along the entire length; 4 – strongly curved in S-shape; 5 – multiply curved, crooked), the occurrence of stem forking (1 – continuous; 2 – forking in the upper third; 3 – in the second third; 4 – in the lower third; 5 – shrubby, 3 or more stems at near-ground level), damage to the stem (1 – no damage; 2 – damaged only in the upper part; 3 – multiply damaged in the past, good overgrowth; 4 – multiply damaged in the past, poor overgrowth; 5 – damaged in the lower part of the stem (mechanical, fungi), bark pattern (1 – smooth; 2 – scaly; 3 – ridged; 4 – deeply ridged) and defoliation 1–5 (by increments of 20%). Trait indices were calculated for each provenance as medians of tree classification rankings.

Height and *DBH* data sets from the Úsov and Vítkov provenance trials were evaluated using a one-factor analysis of variance ($\alpha = 0.05$), and Tukey-Kramer multiple comparisons test was performed in NCSS 10 (Version 10.0.6, 2015). The null hypothesis was rejected. Multidimensional principal component analysis (PCA) and cluster analysis (CLU) methods were used to reveal the structure and association between the studied traits. By combining both methods, a biplot was created, which combines the advantages of both analyses and better creates a visual image. For the calculation of PCA and CLU (using Statistica, Version 12, 2013; PAST, version 2.07, Hammer et al. 2001), the data was reduced so that the individual traits of the assessed provenances were represented by their medians.

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Table 1. Description of site characteristics of parent stands of provenances present in our research trials

State	Provenance		Trial		Longitude (E)	Latitude (N)	Altitude (m a.s.l.)	Average annual temperature (°C)	Average year precipitation (mm)	European forest zones*	Natural forest region	Climatype**	Former silvicultural region
	code	name	70 (Úsov)	71 (Vítkov)									
CZ	1–15	Kamenice n. L. – Losy	X	X	15°14'	49°21'	680	5.4	729	3.13.0	16	6	II
	16–30	Jihlava – Popice	X	–	15°31'	49°21'	600	7.5	603	3.13.0	16	6	II
	32	Nýrsko – Dešenice	X	X	13°13'	49°17'	500	7.4	650	3.05.4	12	6	Ib
	35	Petrohrad – Oráčov	–	X	13°28'	50°08'	400	7.2	526	3.05.4	9	6	II
	36	Červené Poříčí – Kaliště	–	X	13°27'	49°32'	500	6.8	583	3.06.0	6	6	II
	43	Vsetín – Hošťálková	–	X	17°57'	49°21'	490–530	7.0	833	6.07.0	41	7	IV
	48	VLS Plumlov – Stínava	–	X	16°58'	49°20'	400	7.5	597	3.14.0	30	7	IV
	49	Přibyslav – Hamry	–	X	15°54'	49°33'	590	6.1	744	3.13.0	16	6	II
	51	VLS Lipník n.Bečvou – Podhoří	X	X	17°25'	49°35'	600	6.0	811	3.05.1	39	7	IV
H	52	Sopron – School Forest District	X	–	16°53'	47°65'	450	9.8	760	6.10.0	–	10	–
CZ	59	Velké Karlovice – Vranča	–	X	18°13'	49°12'	590–680	6.5	1 045	6.07.0	41	7	IV b
	64	Dobříš – Chouzavá	–	X	14°12'	49°50'	420	7.3	605	3.07.0	10	6	II
	68	Vyšší Brod – Běleň	X	X	14°20'	48°38'	680	6.2	810	3.05.4	13	6	I b
	70	Ždírec n. Doubravou – Maleč	X	X	15°42'	49°47'	400	7.3	789	3.13.0	16	6	II
	71	Plumlov – Ruprechtov	X	X	16°58'	49°20'	450–510	7	655	3.14.0	30	7	IV
	74	Milevsko – Klučenice	–	X	14°14'	49°34'	380	7.8	577	3.12.0	10	6	II
	75	Rájec-Jestřebí – Černá Hora	–	X	16°39'	49°18'	350	7.7	612	3.14.0	30	6	IV
	76	Nýrsko – Suchý Kámen	X	–	13°06'	49°16'	620	6.7	751	3.05.4	12	6	I b
	81	Vyšší Brod – Vítkův Kámen	–	X	14°15'	48°37'	800–900	5.4	1063	3.05.4	13	6	I b
	82	Vizovice – Bratřejov	X	X	17°56'	49°13'	550	6.6	946	6.07.0	38	7	IV
	85	Kašperské Hory – Kašperské Hory	–	X	13°34'	49°10'	800	5.5	854	3.05.4	13	6	I b
	86	VLS Hořovice – Strašice	X	–	13°48'	49°44'	650 (530)	6.1	789	3.07.0	7	6	I b
	87	VLS Hořovice – Jince	X	–	13°58'	49°46'	520-540	6.9	556	3.07.0	7	6	I b
	88	VLS Hořovice – Mirošov	X	–	13°42'	49°42'	620	6.3	783	3.07.0	7	6	I b
	90	Prachatice – Včelná	–	X	13°51'	49°01'	750–1 020	5	790	3.05.4	13	6	I b

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Table 1. to be continued

State	Provenance code	Provenance name	Trial 70 (Úsov)	Trial 71 (Vítkov)	Longitude (E)	Latitude (N)	Altitude (m a.s.l.)	Average annual temperature (°C)	Average year precipitation (mm)	European forest zones*	Natural forest region	Climatype**	Former silvicultural region
A	93	Wörschachwald – Steiermark	X	X	14°06'	47°34'	1 100–1 200	5.3	1 600	5.04.3	–	4	–
	94	Schneegattern – Kobernsusserwald	X	–	13°23'	48°00'	550–750	7	1 200	5.01.3	–	4	–
	95	Gröbming – Steiermark	X	X	13°53'	47°27'	850	6.5	1 350	5.04.3	–	4	–
	96	Thal – Wechselgebiet	X	–	16°11'	47°36'	550	8.5	850	5.03.0	–	4	–
CZ	101	Velké Karlovice – Brodská	–	X	18°11'	49°22'	700–760	5.6	1 212	6.07.0	41	7	IV b
	106	Kácov – Psáře	–	X	14°58'	49°46'	420	7.5	603	3.12.0	16	6	II
	130	Nasavrky – Podhůra	–	X	15°48'	49°51'	370	7.6	711	3.13.0	16	6	II
BG	131	Pirin – Razlog	–	X	23°24'	41°49'	1 600	4.7	1 549	6.26.0	–	10	–
	132	Rila – Borovec	X	X	23°36'	42°14'	1 600	5.1	988	6.26.0	–	10	–
D	146	Schwarzwald mit Baar – Schönmünzach	X	–	7°59'	48°35'	530–650	5.8	1 833	3.32.0	–	4	–
	147	Schwäb.-Fränkischer Wald – Geschwend	X	X	9°45'	48°57'	480–530	7.2	1 000	3.21.0	–	4	–
	148	Schwarzwald mit Baar – Gengenbach	X	X	8°01'	48°24'	465–740	6.0	1 707	3.32.0	–	4	–
	149	Ostbayer - Viechtach	X	X	12°55'	49°05'	700–780	6.5	1 364	3.05.4	–	6	–
CZ	186	Šternberk – Řídeč	–	X	17°17'	49°46'	380–500	6.6	745	3.05.1	29	7	IV
	194	Karlovice – Karlovice sever	–	X	17°25'	50°06'	720	5.5	974	3.05.1	27	7	I b
	198	Vítkov – Budišov n. Budišovkou	–	X	17°38'	49°50'	500–570	6	754	3.05.1	29	7	IV
	199	Krnov – Horní Benešov	–	X	17°35'	49°59'	500–600	6.5	689	3.05.1	28	7	IV
PL	203	Stary Sacz	–	X	20°36'	49°33'	300	7.8	725	6.06.4	–	7	–
CZ	205	Bílovec – Skřípov	–	X	17°54'	49°50'	440	7.0	729	3.05.1	29	7	IV
	207	Nové Město n. M.	–	X	16°04'	49°35'	630	5.9	740	3.13.0	16	6	I b
	209	Nové Město n. M. – Lísek	–	X	16°12'	49°36'	680	5.2	724	3.13.0	16	6	IV
	210	Nové Město n. M. – Cikháj	X	–	15°59'	49°39'	690	5.4	882	3.13.0	16	6	I b
	211	Nové Město n. M. – Vojnův Městec	X	–	15°55'	49°40'	660	5.5	852	3.13.0	16	6	I b

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Table 1. to be continued

State	Provenance		Trial		Longitude (E)	Latitude (N)	Altitude (m a.s.l.)	Average annual temperature (°C)	Average year precipitation (mm)	European forest zones*	Natural forest region	Climatype**	Former silvicultural region
	code	name	70 (Úsov)	71 (Vítkov)									
PL	212	Nieskurzow	X	–	21°12'	50°50'	480	6.6	661	6.05.0	–	7	–
RO	214	Prahova-Mineciu	–	X	25°15'	46°25'	1 200	7.5	800	6.19.0	–	8	–
	217	Neamt –Gircina	X	–	26°10'	46°45	950	8.1	710	6.19.0	–	8	–
BiH	222	Gornja Stupčanica	–	X	18°46	44°07'	1 060	5.7	1 088	6.22.0	–	9	–
	224	Sokolac – Kaljina Bioštica	–	X	18°41	44°05	1 060	7.6	820	6.22.0	–	9	–
	225	Vitez – Kruščica	–	X	17°49'	44°05'	1 200	9.2	844	6.22.0	–	9	–
I	227	Popi e Bibbiena – Arezzo	X	–	11°52'	43°47'	1 000–1 100	8	2 000	9.12.0	–	5	–
	228	Vallombrosa – Reggello, Firenze	–	X	11°37'	43°43'	900–1 120	9.8	1 386	9.12.0	–	5	–
	230	Spadola e Serra San Bruno – Catanzaro	–	X	16°22'	38°32'	1 100	9.6	1 636	9.14.0	–	5	–
PL	231	Baligród	–	X	22°17'	49°20'	550	6.5	945	6.06.1	–	7	–
SK	S1	Banská Bystrica – Badín	X	X	19°02'	48°42'	800	5.2	700	6.07.0	46	7	VII
	S5	Ružomberok – Korytnica	–	X	19°16'	48°54'	750	5.6	925	6.06.4	43	7	VI b
	S6	Čierny Váh – Čierny Váh	X	–	19°56'	49°00'	850	4.8	925	6.06.4	43	7	VI b
	S9	Kriváň – Snohy	X	X	19°33'	48°36'	630	6	925	6.07.0	47A	7	VI b
	S10	Čierny Balog – Krám	X	–	19°36'	48°47'	600	5.7	675	6.07.0	47A	7	VI b
	S13	Bardejov – Zborov – Kružlov	X	–	21°08'	49°18'	580	5.3	750	6.06.1	42C	7	X
	S14	Svidník – Giraltovce – Vyšný Komárnik	–	X	21°42	49° 23'	480	5.8	750	6.06.1	41A	7	X

*according to Rubner et Reinhold (1953); **according to Svoboda (1953); CZ – Czech Republic; H – Hungary; A – Austria; BG – Bulgaria; D – Germany; PL – Poland; RO – Romania; BiH – Bosnia and Herzegovina; I – Italy; SK – Slovakia

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RESULTS

A total of 1 041 trees were evaluated in the Úsov provenance trial (Table 2). The highest numbers of surviving trees in the trial were found in Czech provenances 76 Nýrsko – Suchý Kámen (44 individuals, 22% survivors) and 86 VLS Hořovice – Strašice (42 individuals, 21% survivors). In contrast, Italian provenance 227 Popi e Bibbiena – Arezzo (18 individuals, 9% survivors), Czech provenance 211 Nové Město n. M. – Vojnův Městec (19 individuals, 10% survivors) and Austrian provenance 93 Wörschachwald – Steiermark (16 individuals, 11% survivors) had the lowest values. A total of 1 420 trees were measured in the Vítkov provenance trial (Table 3). With 55 individuals (28% survivors), Czech provenance 75 Rájec-Jestřebí – Černá Hora had the highest number of surviving trees. This was followed by Bulgarian provenance 131 Pirin – Razlog (53 individuals, 27% survivors). Italian provenance 228 Vallombrosa – Reggello, Firenze (5 individuals, 3% survivors) and Polish provenance 231 Baligród (7 individuals, 4% survivors) had the lowest values.

The median height of all trees in the Úsov trial was calculated to be 22.0 m. The best provenance in terms of height was Czech provenance 71 Plumlov – Ruprechtov, with median height of 23.4 m. This was followed by Slovak provenance S10 Čierny Balog – Krám and German provenance 149 Ostbayer – Viechtach, with the same median height of 23.1 m. The lowest median height of 18.6 m was recorded for Bulgarian provenance 132 Rila – Borovec and the second shortest provenance (at 19.7 m) was Czech provenance 82 Vizovice – Bratřejov. In the second trial, Vítkov, an overall median height of 23.0 m was recorded. Within the provenance trial, the highest median height was measured in Czech provenance 194 Karlovice – Karlovice sever with a result of 25.5 m, and the second highest measured height of 24.9 m was in Czech provenance 70 Ždírec n. Doubravou – Maleč and Slovak S5 Ružomberok – Korytnica provenances. In contrast, the lowest height values were recorded for foreign provenances, namely from Austria 93 Wörschachwald – Steiermark (18.4 m) and from Italy 230 Spadola e Serra San Bruno – Catanzaro (18.9 m).

The second data set was for *DBH*. The median *DBH* value of all trees in the trial was found to be smaller in the Úsov provenance trial, at 22.9 cm, than in the Vítkov trial, at 25.7 cm. In the Úsov trial, the largest diameters by provenance were recorded for Czech provenance 16–30 Jihlava – Popice, with median value of 25.5 cm, followed by provenance 87 VLS Hořovice – Jince, with median *DBH* of 24.7 cm. Contrarily, the lowest values in the trial were measured for Italian provenance 227 Popi e Bibbiena – Arezzo, with median diameter of 20.5 cm, and Bulgarian provenance 132 Rila – Borovec, with median value of 20.6 cm. The largest median diameter of 31.9 cm was recorded for the Vítkov trial for Czech provenance 194 Karlovice – Karlovice sever and Polish provenance 231 Baligród, at 29.5 cm. At the other extreme, Austrian provenance 93 Wörschachwald – Steiermark had a median value of 17.4 cm and Bulgarian provenance 131 Pirin – Razlog had median diameter of 21.8 cm. From both trials, provenances from abroad, mainly from Bulgaria, had the lowest *DBH* values.

After calculating the mean stem volume (over-bark volume), the overall median was 0.50 m^3 in the Úsov trial, and in the Vítkov trial it was greater by 0.13 m^3 (0.63 m^3). The highest median values in the Úsov trial were found in Czech provenance 16–30 Jihlava – Popice, with a volume of 0.64 m^3, and provenances 87 VLS Hořovice – Jince from the Czech Republic and S10 Čierny Balog – Krám from Slovakia with the same median volume of 0.59 m^3. A smaller median volume was recorded for Bulgarian provenance 132 Rila – Borovec (at 0.35 m^3) and Italian provenance 227 Popi e Bibbiena – Arezzo (0.38 m^3). In the Vítkov provenance trial, the largest median value of stem volume was found to be 1.03 m^3 for Czech provenance 194 Karlovice – Karlovice sever and Polish provenance 231 Baligród, with median value of 0.89 m^3. By contrast, the smallest volumes were recorded for Austrian provenance 93 Wörschachwald – Steiermark, with median value of 0.25 m^3.

The calculated standing volume averaged 435.5 $m^3 \cdot ha^{-1}$ in the Úsov trial, with the largest standing volume reached by the provenances from the Czech Republic 87 VLS Hořovice – Jince (at 662.5 $m^3 \cdot ha^{-1}$) and from the Slovak Republic S10 Čierny Balog – Krám (609.1 $m^3 \cdot ha^{-1}$). The smallest standing volumes were found for Italian provenance 227 Popi e Bibbiena – Arezzo (170.5 $m^3 \cdot ha^{-1}$) and Czech provenance 211 Nové Město n. M. – Vojnův Městec (238.5 $m^3 \cdot ha^{-1}$). In the second study trial, Vítkov, the average standing volume was 487.0 $m^3 \cdot ha^{-1}$. The largest standing volume was cal-

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Table 2. Results of biometric and phenotypic data from trial No. 70 (Úsov)

State	Provenance code	Provenance name	No of individuals (% of survivors)	Median tree height (m)	Median of *DBH* (cm)	Mean stem volume[1] (m^3)	Standing volume ($m^3 \cdot ha^{-1}$)	Stem form index[2]	Occurrence of stem forking index[2]	Stem damage index[2]	Bark pattern index[2]	Defoliation index[2]
CZ	1–15	Kamenice n. L. – Losy	28 (14)	22.5	24.4	0.58	406.4	1	1	1	1	1
	16-30	Jihlava – Popice	25 (13)	22.8	25.5	0.64	400.1	1	1	1	1	1
	32	Nýrsko – Dešenice	40 (20)	22.0	22.6	0.49	485.9	1	1	1	1	1
	51	VLS Lipník n.Bečvou – Podhoří	37 (19)	20.2	22.3	0.43	395.6	1	1	1	1	1
H	52*	Sopron – School Forest District	23 (15)	22.6	24.0	0.53	403.9	1	1	1	1	1
CZ	68	Vyšší Brod – Běleň	36 (18)	22.3	22.3	0.50	450.0	1	1	1	1	1
	70	Ždírec n. Doubravou – Maleč	31 (16)	23.0	23.9	0.58	446.7	2	1	1	1	1
	71	Plumlov – Ruprechtov	39 (20)	23.4	23.7	0.55	538.6	1	1	1	1	1
	76	Nýrsko – Suchý Kámen	44 (22)	22.3	22.9	0.49	537.4	1	1	1	1	1
	82	Vizovice – Bratřejov	40 (20)	19.7	23.4	0.45	452.3	1	1	1	1	1
	86	VLS Hořovice – Strašice	42 (21)	22.9	24.1	0.55	579.3	1	1	1	1	1
	87*	VLS Hořovice – Jince	34 (23)	22.6	24.7	0.59	662.5	2	1	1	1	1
	88	VLS Hořovice – Mirošov	40 (20)	21.9	22.5	0.52	516.8	1	1	1	1	1
A	93*	Wörschachwald – Steiermark	16 (11)	22.1	22.1	0.45	240.4	1.5	1	1	1	1
	94	Schneegattern – Kobernsusserwald	39 (20)	21.7	22.5	0.49	480.5	2	1	1	1	1
D	95*	Gröbming – Steiermark	22 (15)	23.0	23.5	0.57	417.7	1	1	1	1	1
A	96	Thal – Wechselgebiet	31 (16)	20.6	21.9	0.42	322.7	1	1	1	1	1
BG	132	Rila – Borovec	37 (19)	18.6	20.6	0.35	327.9	1	1	1	1	1
D	146*	Schwarzwald mit Baar – Schönmünzach	30 (20)	22.2	24.2	0.56	558.0	1	1	1	1	1
	147	Schwäb.-Fränkischer Wald – Geschwend	35 (18)	22.8	23.3	0.54	476.4	1	1	1	1	1
	148	Schwarzwald mit Baar – Gengenbach	34 (17)	22.9	23.3	0.52	442.2	1	1	1	1	1
	149*	Ostbayer – Viechtach	26 (17)	23.1	23.1	0.52	453.7	1	1	1	1	1

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Table 2. to be continued

State	Provenance code	Provenance name	No of individuals (% of survivors)	Median tree height (m)	Median of *DBH* (cm)	Mean stem volume[1] (m^3)	Standing volume ($m^3 \cdot ha^{-1}$)	Stem form index[2]	Occurrence of stem forking index[2]	Stem damage index[2]	Bark pattern index[2]	Defoliation index[2]
CZ	210	Nové Město n. M. – Cikháj	30 (15)	21.7	24.4	0.55	415.7	2	1	1	1	1
	211	Nové Město n. M. – Vojnův Městec	19 (10)	21.6	22.4	0.50	238.5	2	1	1	1	1
PL	212	Nieskurzow	29 (15)	19.8	22.4	0.40	290.5	1	1	1	1	1
RO	217	Neamt –Gircina	26 (13	22.9	22.9	0.54	352.3	1	1	1	1	1
IT	227	Popi e Bibbiena – Arezzo	18 (9)	20.1	20.5	0.38	170.5	1	1	1	1	1
SK	S1	Banská Bystrica – Badín	38 (19)	22.7	22.2	0.48	456.0	1	1	1	1	1
	S6	Čierny Váh – Čierny Váh	41 (21)	22.4	22.2	0.47	481.8	1	1	1	1	1
	S9	Kriváň – Snohy	41 (21)	20.0	21.5	0.39	399.8	1	1	1	1	1
	S10*	Čierny Balog – Krám	31 (21)	23.1	24.3	0.59	609.1	1	1	1	1	1
	S13	Bardejov – Zborov – Kružlov	39 (20)	22.7	23.0	0.54	526.5	1	1	1	1	1
Summary values			1 041 (17)	22.0	22.9	0.50	435.5	1	1	1	1	1

*only 3 repetitions of plots; [1]stem volumes were calculated using to volume equations of Petráš and Pajtík (1991); [2]stem shape (1 – completely straight; 2 – unilaterally curved at near-ground level; 3 – unilaterally curved along the entire length; 4 – strongly curved in S-shape; 5 – multiply curved, crooked), the occurrence of stem doubling (1 – continuous; 2 – doubling in the upper third; 3 – in the second third; 4 – in the lower third; 5 – shrubby, 3 or more stems at near-ground level), damage to the stem [1 – no damage; 2 – damaged only in the upper part; 3 – multiply damaged in the past, good overgrowth; 4 – multiply damaged in the past, poor overgrowth; 5 – damaged in the lower part of the stem (mechanical, fungus)], bark pattern (1 – smooth; 2 – scaly; 3 – ridged; 4 – deeply ridged) and defoliation 1–5 (by increments of 20%); CZ – Czech Republic; H – Hungary; A – Austria; BG – Bulgaria; D – Germany; PL – Poland; RO – Romania; SK – Slovakia

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Table 3. Results of biometric and phenotypic data from trial No. 71 (Vítkov)

State	Provenance code	Provenance name	No of individuals (% of survivors)	Median tree height (m)	Median of *DBH* (cm)	Mean stem volume[1] (m^3)	Standing volume ($m^3 \cdot ha^{-1}$)	Stem form index[2]	Occurrence of stem forking index[2]	Stem damage index[2]	Bark pattern index[2]	Defoliation index[2]
CZ	1–15	Kamenice n. L. – Losy	28 (14)	24.0	28.5	0.80	561.3	1	1	1	1	1
	32	Nýrsko – Dešenice	44 (22)	24.0	26.5	0.69	763.5	1	1	1	1	1
	35	Petrohrad – Oráčov	40 (20)	22.8	23.7	0.56	556.9	2	1	1	1	1
	36	Červené Poříčí – Kaliště	39 (20)	20.9	25.1	0.56	544.0	1	1	1	1	1
	43	Vsetín – Hošťálková	34 (17)	23.3	28.2	0.78	660.6	1	1	1	1	1
	48	VLS Plumlov – Stínava	47 (24)	20.7	24.4	0.51	598.4	2	1	1	1	1
	49	Přibyslav – Hamry	40 (20)	24.2	27.8	0.82	817.5	1	1	1	1	1
	51	VLS Lipník n.Bečvou – Podhoří	43 (22)	22.6	24.7	0.55	590.3	2	1	1	1	1
	59	Velké Karlovice – Vranča	24 (12)	23.1	23.3	0.50	302.3	1	1	1	1	1
	64	Dobříš – Chouzavá	41 (21)	24.4	29.2	0.87	895.6	2	1	1	1	1
	68	Vyšší Brod – Běleň	32 (16)	24.3	28.5	0.84	669.8	1	1	1	1	1
	70	Ždírec n. Doubravou – Maleč	30 (15)	24.9	27.8	0.80	601.6	1	1	1	1	1
	71	Plumlov – Ruprechtov	38 (19)	24.0	25.8	0.67	636.0	1	1	1	1	1
	74	Milevsko – Klučenice	44 (22)	24.2	25.9	0.68	744.4	2	1	1	1	1
	75	Rájec-Jestřebí – Černá Hora	55 (28)	21.0	22.3	0.43	588.7	2	1	1	1	1
	81	Vyšší Brod – Vítkův Kámen	31 (16)	21.2	24.2	0.50	388.3	2	1	1	1	1
	82	Vizovice – Bratřejov	34 (17)	23.6	27.7	0.78	660.7	1	1	1	1	1
	85	Kašperské Hory – Kašperské Hory	33 (17)	23.8	28.7	0.74	611.4	1	1	1	1	1
	90	Prachatice – Včelná	23 (12)	24.2	26.2	0.74	423.6	1	1	1	1	1
A	93	Wörschachwald – Steiermark	24 (12)	18.4	17.4	0.25	151.3	2	1	1	1	1
D	95	Gröbming – Steiermark	20 (10)	24.8	25.2	0.63	317.5	1	1	1	1	1
CZ	101	Velké Karlovice – Brodská	29 (15)	23.9	28.1	0.73	526.0	1	1	1	1	1
	106	Kácov – Psáře	45 (23)	21.3	23.6	0.51	568.9	2	1	1	1	1
	130	Nasavrky – Podhůra	46 (23)	22.0	25.7	0.61	702.1	2	1	1	1	1
BG	131	Pirin – Razlog	53 (27)	20.4	21.8	0.46	612.3	1	1	1	1	1
	132	Rila – Borovec	23 (12)	22.8	26.2	0.63	364.4	1	1	1	1	1

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Table 3. to be continued

State	Provenance code	Provenance name	No of individuals (% of survivors)	Median tree height (m)	Median of *DBH* (cm)	Mean stem volume[1] (m³)	Standing volume (m³·ha⁻¹)	Stem form index[2]	Occurrence of stem forking index[2]	Stem damage index[2]	Bark pattern index[2]	Defoliation index[2]
D	147	Schwäb.-Fränkischer Wald – Geschwend	39 (20)	22.3	24.0	0.55	537.9	1	1	1	1	1
	148	Schwarzwald mit Baar – Gengenbach	22 (11)	23.0	22.6	0.51	279.8	2	1	1	1	1
	149	Ostbayer – Viechtach	14 (7)	24.4	28.8	0.84	292.3	1	1	1	1	1
CZ	186	Šternberk – Řídeč	25 (13)	23.2	25.4	0.70	435.2	1	1	1	1	1
	194	Karlovice – Karlovice sever	12 (6)	25.5	31.9	1.03	308.8	1	1	1	1	1
	198	Vítkov – Budišov n. Budišovkou	14 (7)	24.6	24.6	0.64	223.8	1.5	1	1	1	1
	199	Krnov – Horní Benešov	20 (10)	23.1	26.7	0.68	340.2	1	1	1	1	1
PL	203	Stary Sacz	23 (12)	21.8	24.7	0.57	327.0	1	1	1	1	1
CZ	205	Bílovec– Skřípov	25 (13)	22.2	26.0	0.63	391.4	1	1	1	1	1
	207	Nové Město n. M.	10 (5)	23.5	27.3	0.72	180.9	2	1	1	1	1
	209	Nové Město n. M. – Lísek	31 (16)	23.7	26.3	0.68	526.3	1	1	1	1	1
BiH	222	Gornja Stupčanica	25 (13)	23.1	26.8	0.65	405.3	1	1	1	1	1
	224	Sokolac – Kaljina Bioštica	30 (15)	21.1	24.5	0.53	399.3	1	1	1	1	1
	225	Vitez – Kruščica	27 (14)	22.9	25.2	0.61	410.4	1	1	1	1	1
I	228	Vallombrosa – Reggello, Firenze	5 (3)	21.6	22.6	0.48	60.2	1	1	1	1	1
	230	Spadola e Serra San Bruno – Catanzaro	14 (7)	18.9	23.9	0.45	159.1	3	1	1	1	1
PL	231	Baligród	7 (4)	23.6	29.5	0.89	155.5	1	1	1	1	1
SK	S1	Banská Bystrica – Badín	31 (16)	23.1	26.2	0.66	511.5	1	1	1	1	1
	S5	Ružomberok – Korytnica	41 (21)	24.9	27.2	0.78	799.5	1	1	1	1	1
	S9	Kriváň – Snohy	29 (15)	23.7	26.8	0.72	522.0	1	1	1	1	1
	S14	Svidník – Giraltovce – Vyšný Komárnik	36 (18)	24.3	28.9	0.85	765.0	1	1	1	1	1
Summary values			1420 (15)	23.0	25.7	0.63	487.0	1	1	1	1	1

For abbreviation explanations, see Table 2

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culated for Czech provenance 64 Dobříš – Chouzavá (at 895.6 m^3·ha^{-1}), followed by another Czech provenance 49 Přibyslav – Hamry (817.5 m^3·ha^{-1}). The lowest standing volume values were calculated for Italian provenance 228 Vallombrosa – Reggello, Firenze, with only 60 m^3·ha^{-1}, followed by Austrian provenance 93 Wörschachwald – Steiermark with the volume of 151.3 m^3·ha^{-1}.

The evaluation of morphological traits of silver fir in both trials showed low variability, especially for stem forking, stem damage, bark pattern, and defoliation, where the median value for provenances was the same everywhere, that is to say 1, indicating mainly a straight stem without damage, smooth bark, and crown defoliation between 0% and 20%. The only more variable trait was stem shape. In the Úsov trial, only 5 provenances were distinguished: 70 Ždírec n. Doubravou – Maleč, 87 VLS Hořovice – Jince, 94 Schneegattern – Kobernsusserwald, 210 Nové Město n. M. – Cikháj, and 211 Nové Město n. M. – Vojnův Městec. These had median value of 2 – unilaterally curved at near-ground level. In one provenance, 93 Wörschachwald – Steiermark, the median value was 1.5, which marked the range between unilaterally curved stem at near-ground level and straight stems. The other provenances had a median value of 1 – straight stem. In the Vítkov trial, the evaluation of stem shape was similar. Italian provenance 230 Spadola e Serra San Bruno – Catanzaro had the poorest shape score of 3 – unilaterally curved along its entire length, followed by 12 provenances: 35 Petrohrad – Oráčov, 48 VLS Plumlov – Stínava, 51 VLS Lipník n. Bečvou – Podhoří, 64 Dobříš – Chouzavá, 74 Milevsko – Klučenice, 75 Rájec-Jestřebí – Černá Hora, 81 Vyšší Brod – Vítkův Kámen, 93 Wörschachwald – Steiermark, 106 Kácov – Psáře, 130 Nasavrky – Podhůra, 148 Schwarzwald mit Baar – Gengenbach, and 207 Nové Město n. M., which reached a median value of 2 – unilaterally curved stem at near-ground level, and provenance 198 Vítkov – Budišov n. Budišovkou reached a value of 1.5, which again marked the range between unilaterally curved stems at near-ground level and straight stems. Most of the other provenances were evaluated at a median value of 1 – straight stem.

In examining multivariate statistics for the Úsov provenance trial, tree height, *DBH*, stem shape, and mortality proved to be significant indicators in the biplot (Figure 2). Other indicators such as occurrence of stem forking, stem damage, bark pattern and defoliation are not statistically significant (α = 0.05). Two outlying provenances, 227 Popi e Bibbiena – Arezzo from Italy and 132 Rila – Borovec from Bulgaria, stand out promi-

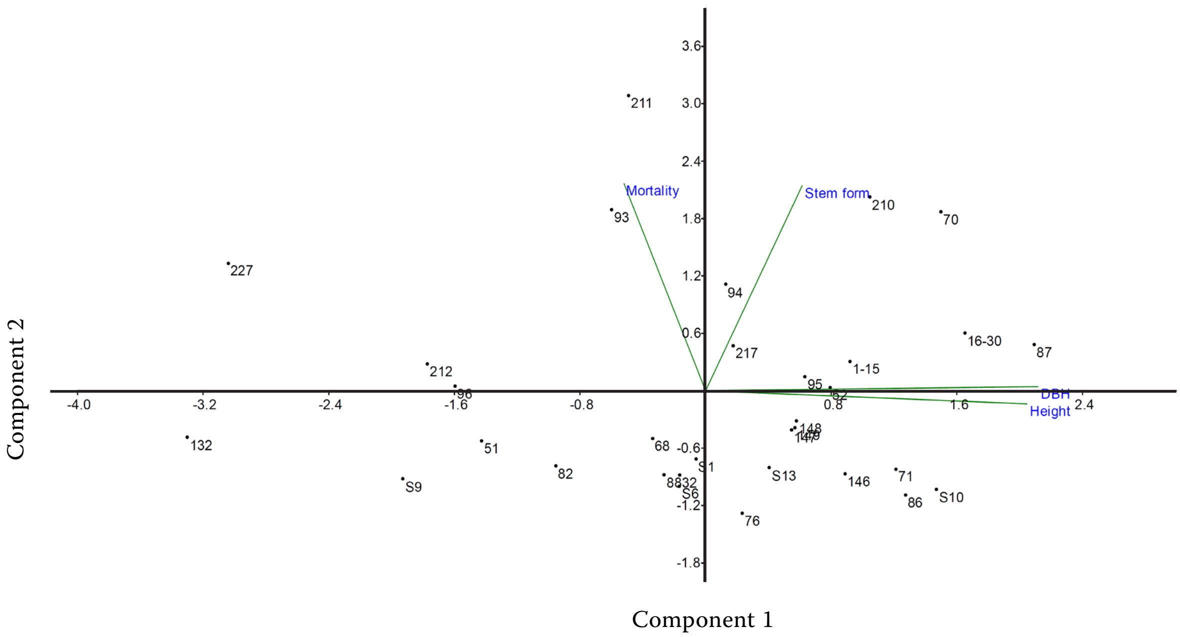

Figure 2. Biplot from the measured data of research trial No. 70 (Úsov)

For provenance codes, see Table 1.

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nently as differentiated groups. Another group is composed of provenances 211 Nové Město n. M. – Vojnův Městec from the Czech Republic and 93 Wörschachwald – Steiermark from Austria. Closer clustering is visible in the three German provenances 147 Schwäb.-Fränkischer Wald – Geschwend, 148 Schwarzwald mit Baar – Gengenbach, and 149 Ostbayer – Viechtach. Overall, the distribution of the other provenances is more or less evenly spread over the three quadrants. The biplot (Figure 3) created from the data obtained from the Vítkov trial has the same significant indicators as from the previous plot. Similarly to Úsov, two provenances are clearly differentiated, namely 93 Wörschachwald – Steiermark from Austria and 230 Spadola e Serra San Bruno – Catanzaro from Italy. Provenance 228 Vallombrosa – Reggello, Firenze from Italy also stands off slightly from the main cluster, but this is not so obvious as for the previously named two provenances. In the second quadrant, provenances 194 Karlovice – Karlovice sever (CZ), 231 Baligród (PL) and 149 Ostbayer – Viechtach (D) stand out as a separate group. The other provenances are mostly evenly distributed in all quadrants and create no visibly separated group. When comparing the two biplots overall, they show a similar distribution of provenances, and also most importantly, the separation of the Italian provenances as an individual group from all other provenances.

DISCUSSION

Quantitative and qualitative parameters of silver fir from provenance trials No. 70 (Úsov) and No. 71 (Vítkov) can be compared with the published results from other silver fir provenance trials in the territory of the Czech Republic that had been established in a similar manner (Čáp et al. 2009, 2011, 2013; Šindelář et al. 2006; Kýval et al. 2012). It is possible to compare the frequency of surviving individuals, or their mortality, by region and, sometimes, even by provenance. The highest numbers of individuals in both provenance trials are recorded mainly in Czech provenances; the only exception in the Vítkov trial being Bulgarian provenance 131 Pirin – Razlog with 53 trees, which is confirmed by results from the Pivoň, Trhanov provenance trial (Kýval et al. 2012), where this Bulgarian fir dominated over the Czech provenances with the lowest mortality. On the contrary, the lowest numbers of surviving individuals were recorded in Italian provenances and one Austrian provenance 93 Wörschachwald – Steiermark. Similar results were obtained in other provenance trials Hůrky, Písek (Čáp et al. 2013), Nové Hrady,

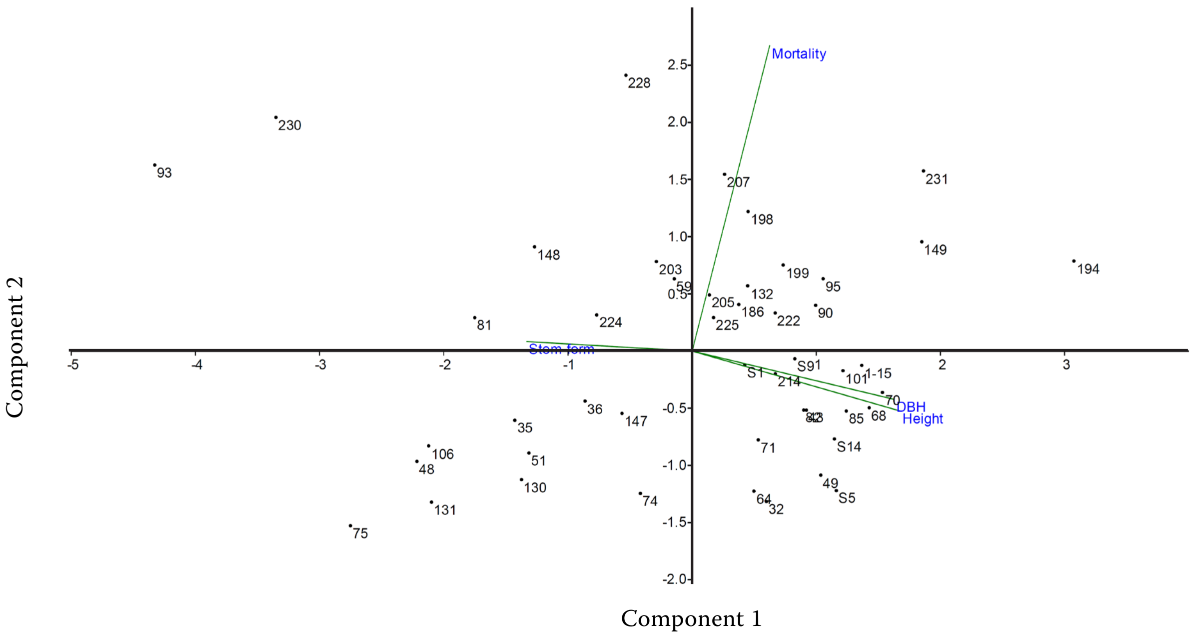

Figure 3. Biplot from the measured data of research trial No. 71 (Vítkov)

For provenance codes, see Table 1.

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Konratice (Šindelář et al. 2006), and Pivoň, Trhanov (Kýval et al. 2012).

In the evaluation of tree heights by provenance, the best results were achieved by Czech provenances from the vicinity of the provenance trials, that is from Plumlov and Ždírec nad Doubravou. Contrarily, the lowest trees were of Austrian (93 Wörschachwald – Steiermark), Italian (230 Spadola e Serra San Bruno – Catanzaro), Bulgarian (132 Rila – Borovec), and Czech (82 Vizovice – Bratřejov) provenances. There is also partial agreement with Čáp et al. (2009), who stated that the tallest trees were found in the Czech provenance from Plumlov and the lowest in the Austrian, Romanian, and Czech provenances. The evaluation of the poorest-growing provenances is also confirmed by the results of Čáp et al. (2011).

In the evaluation of *DBH* and mean stem volume, the best provenances proved to be Czech provenances and in one case also Polish provenance (provenance 231 Baligród), but this is due to the high mortality of trees in the trials and therefore higher light increment. Again, the provenances from Bulgaria, Italy, and Austria proved to have the smallest increment, which is confirmed by the results of Čáp et al. (2009, 2011). Regarding the forest stand volume, which was greatest for the Czech provenances from the Brdy area and lowest for the Italian provenances, similar results were obtained by Kýval et al. (2012), with a difference being that the largest standing volume was in the Czech provenance Losy (Kamenice nad Lipou).

In terms of morphological traits, a significant difference was found only in stem shape, which was assessed as straight in most provenances except for two provenances from Austria and three Czech provenances from the Vysočina region. These provenances have the majority of stems with unilateral curvature at near-ground level. In comparison with Čáp et al. (2011), where the Austrian provenances were best and the German and Czech provenances the poorest, and Kýval et al. (2012), where a Slovak provenance was best and a French fir provenance the poorest, the best and poorest provenances in terms of the quality of stem shape are not clearly confirmed in our case. Thus, it can be concluded that the results of the stem shape index from different trials are influenced by local factors (the environment) so that their original inherited features are suppressed. Considering the other morphological traits (occurrence of stem forking, stem damage, bark pattern and defoliation) evaluated in the measured provenance trials of silver fir, which had identical median values (1), two influencing factors for this result can be inferred, namely the implementation of thinning to unify the stand and moderate evaluation of quality traits by the evaluator.

In the evaluation of results, tree height, *DBH*, mortality and stem shape were the main variables of interest for the evaluation of the analyses. No statistical differences were found for the other indicators and therefore they were not used in the PCA and CLU. When assessing the differences in provenances using multivariate statistics, the provenances from the south of the Czech Republic, falling according to the classification by Rubner and Reinhold (1953) into the Inner Alps – Eastern Subregion (5.04.3), Central Bulgarian Mountains (6.26.0), Northern Apennine Mountain Forest (9.12.0), and Southern Apennine Mountain Forest (9.14.0) were the most distinct. Similar findings were reported also by Šindelář et al. (2006) and Čáp et al. (2009, 2011), where 5 – Alpine region, 6 – Eastern and Southern European region of oak and beech woodlands, and 9 – Southern European region of hardwood and chestnut forests were distinguished from the other regions based on the lowest values for tree heights.

From the overall evaluation of the measured provenance trials Úsov and Vítkov, the provenances from Italy performed most poorly. That is in contrast to provenance trials in the UK, which show that Italian provenances from Calabria are thriving (Kerr et al. 2015). Even Danish trials with Italian fir provenances suggest that had the trees not suffered from frost damage, their growth would have been rated very well (Hansen, Larsen 2004). A possible reason for the unsuccessful growth of Italian provenances at both our sites may be due to the continental climate. It is also interesting to note that Italian, Austrian, and Bulgarian provenances originating from altitudes higher than 1 000 m a.s.l. suffered in the study trials and did not achieve any good growth results. The combination of the two factors may be decisive for the growth development of some foreign provenances in the Czech Republic. Another reason for the differences in provenances is the reduced phenotypic diversity and adaptability of silver fir in central Europe (Larsen 1986) compared to the southwestern and southeastern parts of its natural range due to postglacial development. Confirmation of this

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hypothesis was provided by Bergmann et al. (1990), who provided evidence of the diversity of individual provenances by means of enzyme analyses (genetic level). Significant differences in the geographic distribution of silver fir have also been recorded by genetic analyses (Longauer 2001; Paule et al. 2001; Longauer et al. 2003). The differentiation of this tree species has arisen during its evolution by adaptation to local climatic and habitat conditions. A summary more detailed description confirming the differentiation of silver fir regarding the genetic structure, development and adaptation is also presented in the review by Dobrowolska et al. (2017).

CONCLUSION

The Forestry and Game Management Research Institute deals with issues affecting the forest environment and seeks methods to improve its condition for future generations. One of the many activities of the Forest Tree Species Biology and Breeding Department is long-term provenance trials of native and non-native tree species. Investigations in two international provenance trials in the northern part of Moravia and Silesia in the Czech Republic showed that, at stand age of 51 years, provenances from Plumlov and Ždírec nad Doubravou (i.e. Czech provenances from the surrounding area) were the most prominent. In terms of *DBH*, best performing were the Czech provenances from Vysočina and Jeseníky. The standing volume as the best aggregate measure reflecting the survival, tree height and *DBH* was found to be the greatest in the fir from the Brdy area in the Czech Republic. On the contrary, firs from Bulgaria, Austria, and Italy performed most poorly. In evaluating the qualitative traits, the differentiation among provenances in stem shape was significantly evident, and differences among the other traits evaluated were statistically insignificant in this case. The evaluation of stem shape from both plots was excellent for most provenances (straight stem), except for Czech provenances from the vicinity of Nové Město na Moravě, as well as one Austrian and one Italian provenance, which more often produced a curved stem. Overall, the Italian provenances were the poorest in terms of production and quality. Long-term provenance research shows that it can be recommended to grow silver fir from local sources of reproductive material and provenances of the Brdy area.

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Nutrition of silver fir (*Abies alba* Mill.) and its comparison with Norway spruce (*Picea abies* L. H. Karst) from the same forest sites in the Czech Republic

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Abstract: Forests in central Europe were affected by heavy bark beetle outbreak during the years 2014–2022. Decline of Norway spruce brought other species of forest trees, including the fir, to the fore. The nutritional level of silver fir is one of the studied topics. Needles in 14 Norway spruce (NS) – silver fir (SF) mixed forest stands from 4 regions in the Czech Republic have been sampled to survey their nutrition level. Nutrition of NS is often near or below the deficiency limit, while nutrition of SF was assessed as sufficient or good. Differences between both regions and tree species were found. SF drew more nutrients from the soil profile than NS on the same forest site. Differences between NS and SF in nutrient concentrations in needles were significant for N, Ca, Mg, Zn and S and non-significant for P and K.

Keywords: mixed forest; mixed forest nutrition; nitrogen; nitrogen to main nutrient ratio; nutrients ratio; trees nutrition

According to palaeoecological studies, silver fir was a very common tree species within the European continent in the past (Wick, Möhl 2006; Tinner et al. 2013; Birks, Tinner 2016). A decrease in its representation in forests can be explained and the most important explanations include: (*i*) land-use pressure, specifically excessive anthropogenic fire and site browsing disturbance; (*ii*) forest management using clearcuts and oriented to even-aged unmixed stands; and (*iii*) sensitivity to abiotic and biotic factors, particularly SO_2 pollution and climate change (Schütt et al. 1984; Uhlířová, Kapitola 2004; Elling et al. 2009; Hájek et al. 2016; Mauri et al. 2016; Ugarković et al. 2021).

Silver fir tolerates a wide variety of soil types with different nutrient content and alkalinity conditions, except compact and hydromorphic soils. It usually requires deep, aerated and humid soils, as well as high air humidity. It roots deeper than most other conifer species and is also less affected by wind throws. The fir demand for oxygen content in the soil is relatively low; for example, it can grow in deeper and wetter soils than Norway spruce. It is a typical shade-tolerant species, and in open areas, it suffers from frost and bark scorch (Meister 1999; Macías et al. 2006; Mauri et al. 2016).

The proportion of silver fir in forests stands has decreased from 18% to 0.9% in the last 200–250 years in the Czech Republic (Vacek et al. 2002; Uhlířová, Kapitola 2004), and in 2000–2020, its proportion changed from 0.9% to 1.2% (Ministry of Agriculture 2021). More detailed information about the silver

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fir in the Czech Republic can be found in Novák and Dušek (2021). Increasing the share of fir in forest stands is desirable for several reasons: (*i*) silver fir is an ecological and functional tree species, which stabilises soil and retains water; (*ii*) it is less vulnerable to wind and snow or ice breakage than Norway spruce; (*iii*) it is a very important tree species for maintaining high biodiversity in forest ecosystems; (*iv*) fir has wide plasticity to environmental conditions and the ability to coexist with many tree species in mixtures due to its ability to survive long periods in the understorey and to respond when light conditions become more favourable; and (*v*) silver fir is also an economically important tree species (Schütz 2002; Tinner et al. 2013; Mauri et al. 2016; Dobrowolska et al. 2017; Podrázský et al. 2018; Schwarz, Bauhus 2019; Walder et al. 2021). This explains the increased interest in silver fir and its ecological requirements as well as the possibility of increasing its share in forest stands. One of the studied aspects is the nutrition of silver fir and its comparison with other tree species. This topic is the main aim of this paper to assess the nutrition of silver fir in comparison with Norway spruce growing on the same forest sites.

MATERIAL AND METHODS

Sampled plots. Plots for needle sampling were selected in regions where mature fir stands were present and grew together with Norway spruce or other tree species (Table 1, Figure 1). Needle sampling was carried out in 2020 and 2021. Each forest stand was sampled only once. During these two years, Norway spruce died on a few sites due to bark beetle outbreak, and needles were not sampled on these plots.

Foliage sampling. Needle sampling to define their nutrient level and air pollution load was undertaken in autumn (September–October). Five specific trees were sampled for each plot. Three branches of the top part of the crown (from the upper third of the tree crown) were taken from each tree. Rope techniques were used to climb to the treetops. For each plot, a pooled sample of the current-year needles was created. These foliar samples were prepared in accordance with ICP Forests methodology (Rautio et al. 2020). As a result of sampling, we had pooled samples from each forest stand for each tree species. Only in the Město Albrechtice forest district we sampled five forest stands (Table 1).

Laboratory analyses. The samples of the assimilation organs were prepared in accordance with standard methods (Rautio et al. 2020). The amount of elements in the foliage (K, Ca, Mg and P) was determined using ICP-OES after needle decomposition in a microwave oven. The total S and N content was determined using the Leco CNS element analyser (Elementar Analysensysteme GmbH, Germany).

Data analyses. Exploratory data analysis was carried out to identify outliers or extreme values. After

Table 1. Main characteristics of sampled plots

Locality	Code	Sampled species	Age in 2020	Soil type	Altitude (m a.s.l.)	Coordinates	
						N	E
Tábor	TA1	fir, spruce	98	dystric cambisols	441	49.37031	14.67157
	TA2		135	eutric cambisols	460	49.40468	14.56528
	TA3		127	haplic cambisols	410	49.41124	14.63623
Rožmitál	ROZ1	fir, spruce	116	dystric cambisols	590	49.55465	13.80564
	ROZ2		195	dystric cambisols	775	49.56654	13.78048
	ROZ3		113	dystric stagnic cambisols	705	49.55021	13.76718
M. Albrechtice	MA1	fir	115	dystric cambisols	340	50.23428	17.57684
	MA2		137	haplic cambisols	450	50.18584	17.61807
	MA3	fir, spruce	124	haplic podzols	540	50.21188	17.53056
	MA4		169	dystric cambisols	640	50.1519	17.50676
	MA5		187	dystric cambisols	710	50.1238	17.40442
Vítkov	VT1	fir, spruce	126	dystric cambisols	490	49.76294	17.68828
	VT2		123		615	49.78469	17.58132
	VT3		83		715	49.78295	17.54618

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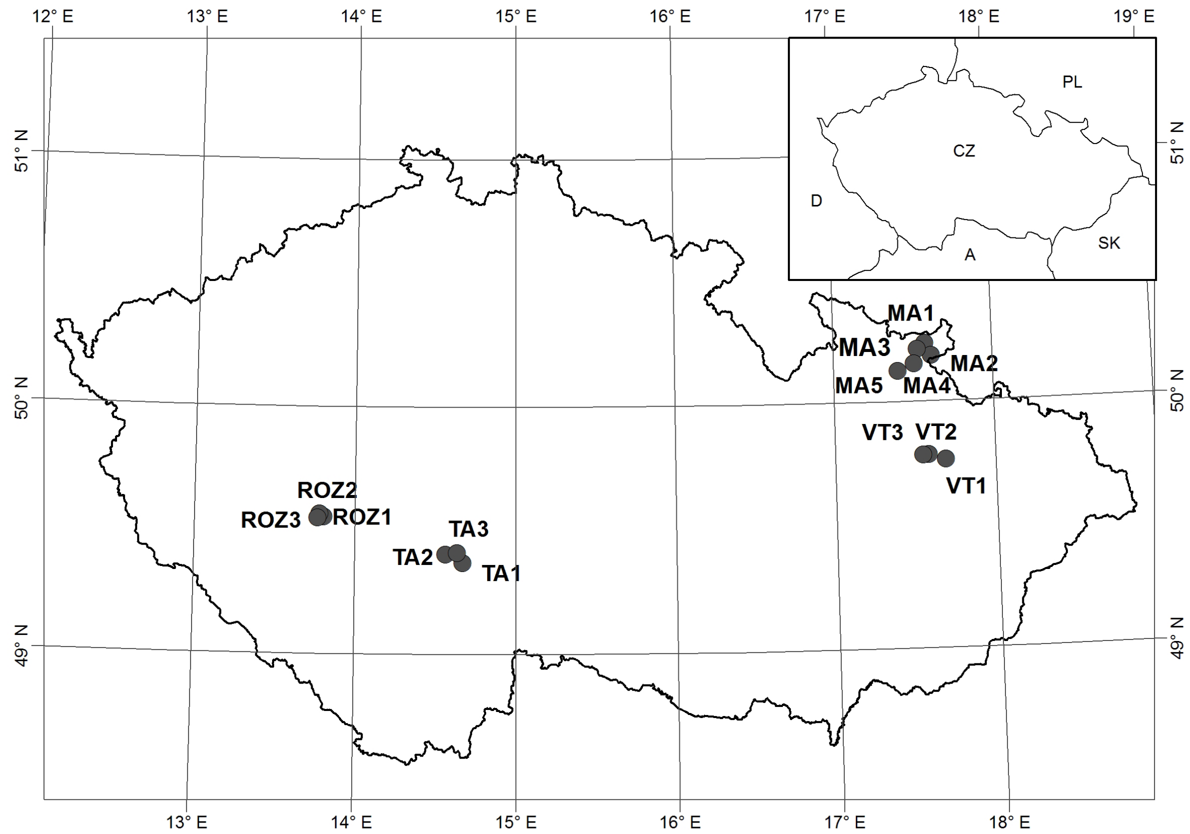

Figure 1. Location of sampled plots within the Europe and within the Czech Republic

carrying out the exploratory data analysis, normality was tested using the Shapiro-Wilk *W* test. Datasets were tested as independent samples; then, parametric tests (Student's *t*-test), if normality was not rejected, or nonparametric tests (Mann-Whitney *U* test), in case normality was rejected, were performed after the Shapiro-Wilk *W* test was used. All statistical evaluations of the data were subsequently conducted using the Statistica 12 CZ programme (Version 12, 2013).

RESULTS AND DISCUSSION

Nutrition of silver fir (SF). The nitrogen concentration in current-year needles varied between 12 $g{\cdot}kg^{-1}$ and 18 $g{\cdot}kg^{-1}$. The median nitrogen concentration was above 14 $g{\cdot}kg^{-1}$ for the analysed trees and plots (Figure 2). This is comparable with previous studies carried out in Germany, Poland or Slovakia (Bäumler et al. 1995; Maňkovská et al. 2004), as well as with a study from the Czech Republic (Novotný et al. 2010; Dušek et al. 2020).

The median of phosphorus concentration was between 1.2 $g{\cdot}kg^{-1}$ and 1.4 $g{\cdot}kg^{-1}$, and the concentration varied between 0.8 $g{\cdot}kg^{-1}$ and 2.6 $g{\cdot}kg^{-1}$. This matches the values from Bäumler et al. (1995) and Maňkovská et al. (2004). In Novotný et al. (2010), who focused on silver fir growing in the Bohemian Forest (Šumava) at high elevations, the phosphorus concentration of current-year needles was higher than in samples from other regions of the Czech Republic. The potassium concentration in current-year needles varied between 5 $g{\cdot}kg^{-1}$ and 8 $g{\cdot}kg^{-1}$ (median above 6.5 $g{\cdot}kg^{-1}$). This is a lower value than that reported by Bäumler et al. (1995) and Maňkovská et al. (2004), but it is still above the limit of deficiency determined by Hüttl (1986). This is very important because potassium is responsible for the regulation of the water regime, as well as for frost resistance.

Magnesium is a very mobile and flexible nutrient, and coniferous species can relocate it from older needles to current-year needles, which are most photosynthetically active. We found concentrations between 1 $g{\cdot}kg^{-1}$ and 3 $g{\cdot}kg^{-1}$. These values showed a sufficient or good level of magnesium nutrition.

Calcium is bound to the cell walls and is not as flexible as other main nutrients. This means that

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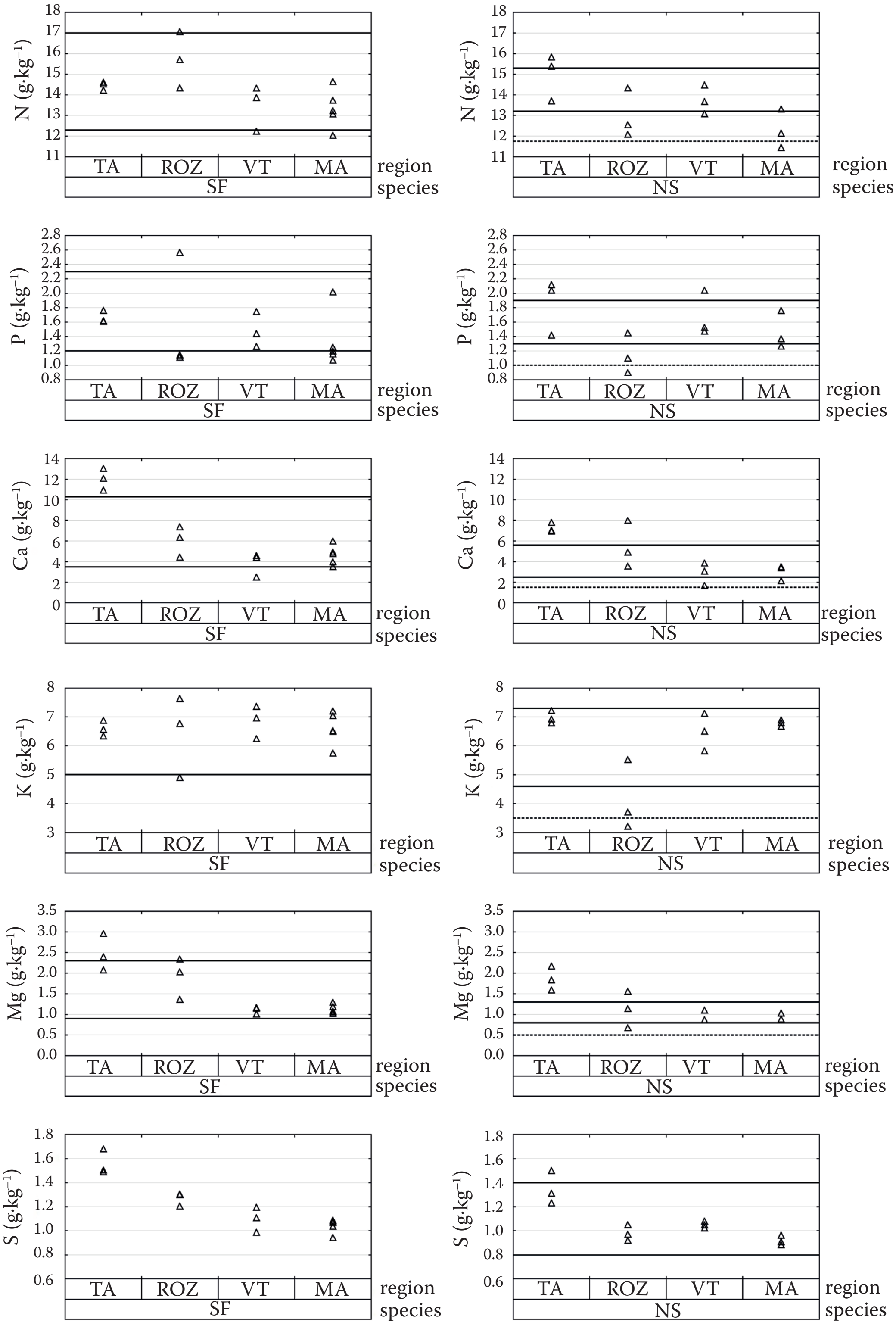

Figure 2. Variability plots with factors "species" and "region" for nutrients concentration in current year needles – the area between the two black lines is the range of optimal nutrition, below the dashed line, the tree species is in the deficiency range [lines are shown according to Göttlein et al. (2011)]

SF – silver fir; NS – Norway spruce; TA – Tábor; ROZ – Rožmitál; VT – Vítkov; MA – M. Albrechtice

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its concentration usually rises with the age of the needles. The concentration in current-year needles varied between 2 g·kg^{-1} and 13 g·kg^{-1} (median about 5 g·kg^{-1}). Similar results were reported by Bäumler et al. (1995) and Maňkovská et al. (2004).

We observed huge variability in nutrient concentrations between the sampled regions (Figure 2). The highest concentration of elements (Ca, Mg, P, S) was found in samples from the Tábor municipal forest. Large differences between regions were also observed in the concentrations of magnesium. Regions also differ partly in the concentration of calcium and potassium.

Nutrition of Norway spruce (NS). The nitrogen concentration in current-year needles varied between 1.1 g·kg^{-1} and 1.6 g g·kg^{-1}. The nitrogen concentration below 1.3 g·kg^{-1} is considered as a low concentration (Materna 1963; Göttlein et al. 2011); see Figure 2.

The phosphorus concentration in current-year needles was very different according to regions, and varied between 0.9 g·kg^{-1} and 2.1 g·kg^{-1}. In the Rožmitál region it was below the deficiency limit 1.2 g·kg^{-1} (Figure 2).

The lowest potassium concentration in NS current-year needles was found also in the Rožmitál locality, where it was between 3.2 g·kg^{-1} and 5.5 g·kg^{-1}. However, in other sampled regions, its concentration ranged between 5.8 g·kg^{-1} and 7.2 g·kg^{-1} in current-year needles (Figure 2).

The highest magnesium concentration was found in the Tábor locality (between 1.6 g·kg^{-1} and 2.2 g·kg^{-1}), and it was comparable with the other three sampled regions (0.7–1.6 g·kg^{-1}). The lower calcium concentration values were about 2.0 g·kg^{-1}, which was near the deficiency limit (Figure 2).

A decrease of sulphur content in Norway spruce needles (Lomský et al. 2012, 2013; Novotný et al. 2017) is connected with the reduction of SO_2 pollution during the 1990s (Hůnová et al. 2004, 2014). Nowadays, sulphur is often assessed as nutrient in-

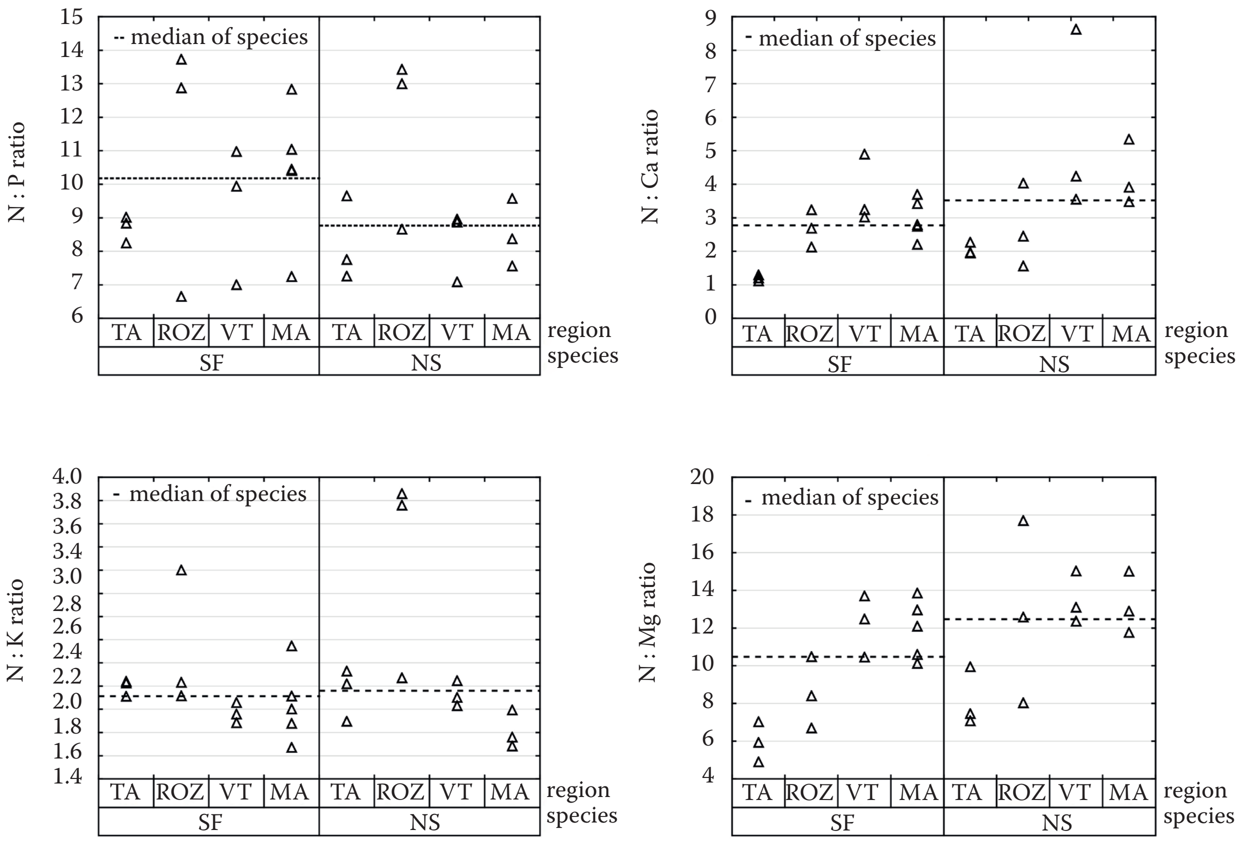

Figure 3. Variability plots for ratio between nitrogen and selected macro nutrients in current year needles categorized according to tree species and locality

SF – silver fir; NS – Norway spruce; TA – Tábor; ROZ – Rožmitál; VT – Vítkov; MA – M. Albrechtice

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stead of as stress element, especially when the sulphur concentration drops below 1 g·kg^{-1}. We found a decrease of sulphur concentration near to or below this value within all localities except Tábor (Figure 2).

Comparison of nutrient content in silver fir (SF) and Norway spruce (NS) needles. NS nutrition was similar but not the same as that of SF. The biggest differences were observed between SF and NS in the concentration of nitrogen, magnesium, and partly calcium. The nutrient concentrations found in NS needles were usually lower than in SF needles. These differences were probably associated with the rooting system of the evaluated tree species; SF is able to use deeper soil layers to draw water and nutrients in comparison with NS. If assessed according to Göttlein at al. (2011), the nutrition level was sufficient for SF. Nutrition of NS was in the range of latent nutrient deficiency especially for nitrogen and phosphorus.

Although the concentration of selected macronutrients differed between the evaluated tree species, the ratio of nitrogen to other main nutrients was similar. The ratio between nitrogen and other nutrients was used to determine the balance according to ICP Forests thresholds (Figure 3).

Statistically significant differences in the nutrition between SF and NS were found at the significance level of < 0.001 for nitrogen, magnesium and sulphur, at the significance level of < 0.01 for calcium, non-significant differences were found for phosphorus and potassium using the Mann-Whitney *U* test.

CONCLUSION

Different tree species have various abilities and efficiencies for nutrient uptake from the soil and have different demands and requirements for the amount of nutrition. This means that tree species growing on the same forest site can differ significantly in the nutrition level. Differences ranged from 5% to 200%. Differences greater than 100% were surprising because samples were taken in mixed or immediately adjacent spruce-fir stands. Therefore, we assumed that differences in soil conditions were not significant and that differences in nutrition levels would not be so huge. The reason for this could be explained by different amounts and architectures of roots; Norway spruce has a flat root system and its main rooting zone usually covers a depth between 0 cm and 40 cm of mineral soil. The roots of silver fir reach much deeper and are able to obtain nutrients from almost the whole soil profile. This means that in general, silver fir has a higher amount of nutrients at its disposal compared to Norway spruce, regardless of whether they are growing on the same site. The next reason could be different demands for the supply of nutrients. We concluded that silver fir grows well on the same forest sites as spruce and is able to gain sufficient nutrients from the whole soil profile. Symptoms of nutrient deficiency could most probably be visible only on acidic and poor sites where the mineral soil (or its top layer) is strongly acidic, and base cations are depleted or leached to the deeper soil layers.

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The increasing drought sensitivity of silver fir (*Abies alba* Mill.) is evident in the last two decades

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Abstract: Silver fir (*Abies alba* Mill.) is still counted among drought-tolerant tree species. However, its ability to cope with the recent extremely dry period has not yet been sufficiently studied. The objective of research was to analyse differences in the climate-growth response between silver fir, Norway spruce (*Picea abies* L. Karst.) and European larch (*Larix decidua* Mill.) growing in areas with large-scale disintegration of spruce stands. In 2019–2021, the increment cores were sampled at 16 sites along the altitudinal gradient of 340–775 m a.s.l. in different regions of the Czech Republic affected by bark beetle outbreak. The radial growth pattern of fir was compared with that of spruce or larch growing under the same site conditions. In fir, the missing rings were frequently recorded during the period of peak SO_2 pollution load in 1966–1985, but they were rarely identified in recent years. In spruce and larch, missing rings were less common and occurred mainly in the recent dry period after 2015. Fir was less sensitive to summer drought compared to larch and especially to spruce, which showed high sensitivity to summer drought regardless of the altitude. The significant positive response of fir to summer precipitation was recorded at sites up to 450 m a.s.l., however, its sensitivity to drought has increased in the last two decades. Hence, when considering the wider use of fir, it is necessary to respect its ecological requirements as much as possible in order to preserve its vitality and production potential in changing climatic conditions.

Keywords: Czech Republic; dendrochronology; European larch; growth; Norway spruce

Forest ecosystems have been under heavy pressure from environmental changes (Allen et al. 2010; Seidl et al. 2017). The rise in air temperatures, more frequent and intense periods of drought and heat waves affect forest trees significantly (Senf et al. 2020). Species that grow in limiting ecological conditions, whether it is at the xeric edge of their distribution range or outside their ecological niches, are prone to drought-induced dieback (Camarero et al. 2013; Gazol et al. 2015; Gazol, Camarero 2016). In addition, climate scenarios predict a continued significant rise in temperatures by 2050, negatively affecting tree performance (Buras, Menzel 2019). Therefore, the key issue for forest management is the resistance and resilience of individual tree species to drought.

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In Europe, silver fir is a key tree species for maintaining a high biodiversity of forest ecosystems thanks to its shade tolerance, plasticity to environmental conditions and ability to coexist with many tree species (Dobrowolska et al. 2017). In relation to the predicted climate changes, the higher resistance of fir to drought (Zang et al. 2014) and the ability to withstand low temperatures during the winter (Savill et al. 2016) are important. At the same time, however, it is necessary to take into account the higher sensitivity of fir to low air humidity (Guicherd 1994) and late frosts (Úradníček et al. 2009).

The vast decline of Norway spruce and Scots pine (*Pinus sylvestris* L.) has been observed in recent years in the Czech Republic and other Central European countries (Bošela et al. 2021; Haberstroh et al. 2022). The primary cause was recurrent droughts with subsequent activation of biotic pests and pathogens (Cienciala et al. 2017). In the regions of North Moravia and the Bohemian-Moravian Highlands, with intense spruce dieback, we observed survival of vital silver fir populations.

Previous dendroecological studies proved that silver fir is more drought tolerant than Norway spruce, European larch or European beech (*Fagus sylvatica* L.) (van der Maaten-Theunissen et al. 2012; George et al. 2019; Vitasse et al. 2019a) and similarly drought tolerant to Douglas fir (*Pseudotsuga menziesii* /Mirb./ Franco) (Vitali et al. 2017). However, the fir ability to cope with the recent dry period, which has been extreme in duration and intensity, has not yet been sufficiently studied.

Here, we analyse the growth pattern and spatiotemporal variation in the climate-growth response of Silver fir (Sf), Norway spruce (Ns) and/or European larch (El) growing in mixed stands distributed in different regions of the Czech Republic along the altitudinal gradient between 340 m a.s.l. and 775 m a.s.l., which corresponds with the altitudinal zone of intensive spruce dieback. The aim of the study was to confirm or refute differences between the studied tree species in terms of sensitivity to drought and to assess the temporal stability of the climate-growth relationship. We hypothesize that even fir trees have recently become more sensitive to rising temperatures and lack of precipitation due to chronic drought stress, which is gradually leading to the depletion of the tree internal reserves.

MATERIAL AND METHODS

Study sites. The study was carried out in the Czech Republic in five different regions (Table 1, Figure 1). The regions of Město Albrechtice and Černá Hora represent areas where large-scale disintegration of spruce stands has already occurred, while in Tábor, Rožmitál and Písek, the decline of spruce still has a patchy character. The original intention was to compare the growth dynamics of fir and spruce, but due to the high mortality of spruce in the Město Albrechtice region, it was necessary to include larch in the comparison, because spruce was no longer available at altitudes up to 500 m a.s.l.

In each region, 2–5 mature stands where fir occurred in a mixture with spruce or larch were chosen. A total of 16 sample sites were selected (Table 1, Figure 1) covering an altitude gradient of 340–775 m a.s.l. and representing nutrient-medium, nutrient-rich and moist sites according to forest ecosystem classification (Viewegh et al. 2003). According to the Köppen-Geiger climate classification, all sites are in the Dfb category, i.e. humid continental climate with warm summers (Beck et al. 2018). Most sites belong to the upper colline vegetation belt, sites MA5, ROZ2 and ROZ3 can be classified as submontane (Chytrý 2017). The sites, except MA5, are characterized by mean annual temperatures between 8.6 °C and 9.3 °C and total annual precipitation ranging between 588 mm and 705 mm. Site MA5 is cooler and wetter, with a mean annual temperature of 7.8 °C and annual precipitation of 859 mm (Figure 2). The climatic characteristics were calculated based on monthly temperature means and monthly precipitation sums obtained from Climatic Research Unit gridded Time Series (CRU TS) with 0.5° resolution (Harris et al. 2020) for the assessed period 1962–2018. Standard forest management is applied in all stands with the exception of MA5, which is located in a nature reserve. Most of the managed stands are single-layered, even-aged, 100–135 years old, established by artificial regeneration with regular thinning application. The two oldest stands, ROZ2 and MA4, probably originated from natural regeneration. Site MA4 was the only one recorded with an age difference between tree species, where fir was about 50 years older than larch and spruce.

Data collection. Increment cores were collected in 2019–2021 during the dormant season. At least

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Table 1. Basic characteristics of sample sites

Region	Site	Coordinates		Altitude (m a.s.l.)	Forest type complex	Stand age (years)	Species sampled
		latitude	longitude				
Tábor	TB1	49.3703	14.6716	441	4H	98	Sf, Ns
	TB2	49.4047	14.5653	460	3S	135	
	TB3	49.4112	14.6362	410	4A	127	
Rožmitál	ROZ1	49.5546	13.8056	590	5O	116	Sf, Ns
	ROZ2	49.5665	13.7805	775	6S	195	
	ROZ3	49.5502	13.7672	705	5K	113	
Písek	PS1	49.2861	14.2886	430	3H	108	Sf, Ns
	PS2	49.2940	14.2919	410		108	
Černá Hora	CH1	49.5690	16.7636	610	5K	99	Sf, Ns
	CH2	49.5661	16.7951	540	4S	107	
	CH3	49.5644	16.7763	540	5U	120	
Město Albrechtice	MA1	50.2343	17.5768	340	4B	115	Sf, El
	MA2	50.1858	17.6181	450	4S	137	Sf, El
	MA3	50.2119	17.5306	540	4S	124	Sf, Ns, El
	MA4	50.1519	17.5068	640	4A	169	Sf, Ns, El
	MA5	50.1238	17.4044	710	5B	187	Sf, Ns

3H – loamy oak-beech; 3S – nutrient-medium oak-beech; 4A – stony-colluvial lime-beech; 4H – loamy beech; 4S – nutrient-medium beech; 4B – nutrient-rich beech; 5B –nutrient-rich fir-beech; 5K – acidic fir-beech; 5O – nutrient-medium beech-fir; 5U – moist ash-maple floodplain; 6S – nutrient-medium spruce-beech; Sf – silver fir; Ns – Norway spruce; El – European larch

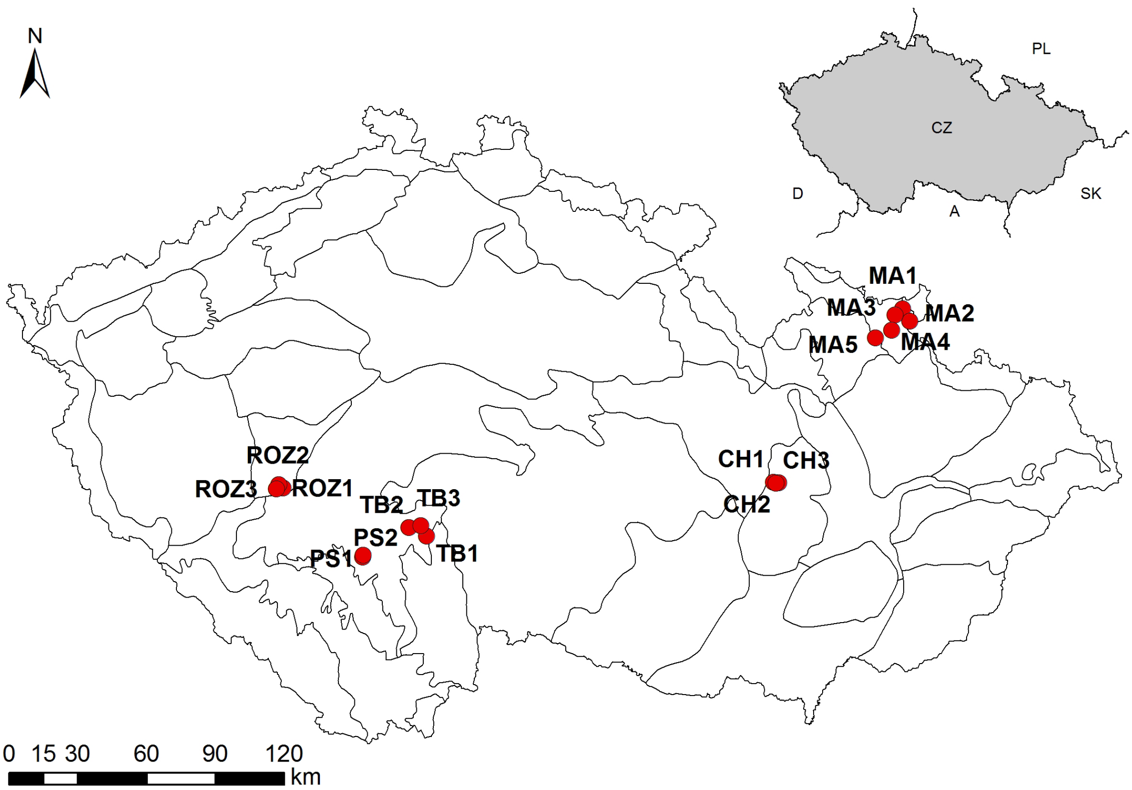

Figure 1. Localization of sample sites against the background of the forest nature areas of the Czech Republic

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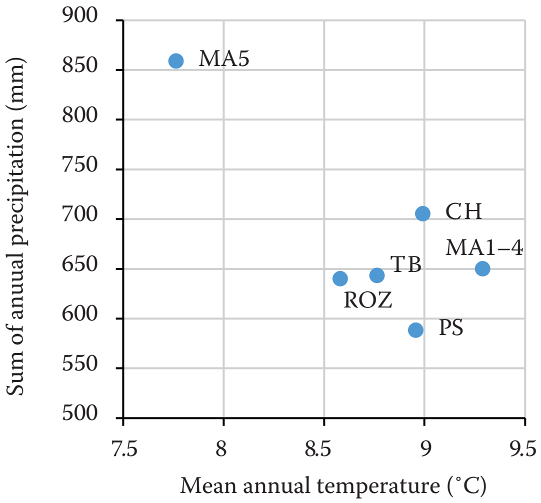

Figure 2. Climograph showing mean annual temperatures and total annual precipitation for individual regions/sites

20 dominant or codominant trees per tree species were selected in each stand; thus, we obtained two or three tree sets for each site. Two cores per tree were taken at breast height (1.3 m above ground) using a Haglöf increment borer (Haglöf, Sweden). To avoid compression wood, core sampling was performed along the contour line. Tree-ring widths (*TRW*) were measured to the nearest 0.01 mm, using the TimeTable measuring stage (VIAS, Austria).

Data processing and chronology development. Ring-width series were visually crossdated and statistically verified using the PAST 4 (Knibbe 2004) and COFECHA programme (Grissino-Mayer 2001). Successfully crossdated series were included in the final dataset. Anomalies in tree-ring formation, such as partly and completely missing rings (Bräuning et al. 2016), were detected during this stage. The occurrence of missing rings and growth decline were used as indicators of stress periods. Basic statistics of raw tree-ring measurements are shown in Table 2.

In order to remove both age-related trends in *TRW* and other non-climatic noise, we performed individual-based detrending using a cubic smoothing spline with a 64% variability cut-off at the mean segment length of a given tree set. The remaining autocorrelation was eliminated by autoregressive modelling in ARSTAN software (Cook, Krusic 2005). The resulting residual chronologies were aggregated in site-species-level chronologies by calculating the biweight robust means. For each chronology mean sensitivity and expressed population signal (*EPS*) were calculated (Table 2). *EPS* quantifies how well a chronology based on a finite number of trees represents a theoretical infinite population. For all chronologies in the common period 1962–2018, the *EPS* reached a value higher than 0.85, which means that the chronologies represent the population signal with sufficient quality (Wigley et al. 1984).

Principal component analysis (PCA) was used to detect similarities in growth patterns of different tree species growing in different regions. PCA was carried out based on the covariance matrix of the residual tree-ring chronologies. The number of significant principal components was selected based on those with eigenvalues greater than 1 (Kaiser rule).

Climate-growth relationship. The gridded monthly climatic data from the CRU TS dataset with 0.5° resolution (Harris et al. 2020) were used for the growth-climate response analysis. The selected climate series corresponded to the closest grid point to each sample site. In addition to average monthly temperatures and monthly precipitation totals, climatic variables related to drought stress such as the Standardized Precipitation Evapotranspiration Index – *SPEI* (Vicente-Serrano et al. 2010) and self-calibrating Palmer Drought Severity Index – *scPDSI* (Wells et al. 2004) were derived from the CRU TS dataset.

Long-term growth-climate relationships were evaluated for each tree set using a simple correlation analysis (Pearson's correlation coefficient) for the period 1962–2018. Monthly climatic variables entered the analysis in sequence from April of the previous year to August of the current year, i.e. the observation year for growth parameters. In addition to the monthly data, we also calculated the seasonal average for the summer months (June–August) to determine correlations with *TRW* indices.

To assess the temporal stability of the climate-growth relationship, we computed moving correlations. The method is based on progressively shifting the period of a fixed number of years across time to compute the correlation coefficients. In this study, we chose a window of 20 years starting with the period 1962–1981. Standardized *TRW*s were gradually correlated with seasonal climatic values related to drought stress, such as the mean temperatures, the sum of precipitation, *SPEI* and *scPDSI* during the peak growing season (June–August).

All statistical analyses were performed in OriginPro software (Version 9.9, 2022).

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Table 2. Basic characteristics of raw tree-ring measurements and residual tree-ring chronologies

Region	Site	Species	No. of trees/ series	Raw measurements					Residual chronology	
				Mean *TRW* (mm)	Proportion of missing rings (%)	Series intercorrel. vs. mean	Mean sensitivity	1st order autocorrel.	Mean sensitivity	*EPS*
Tábor	TB1	Sf	19/35	1.88	0.92	0.618	0.305	0.68	0.237	0.96
		Ns	20/32	2.14	0.24	0.625	0.279	0.68	0.236	0.96
	TB2	Sf	19/32	1.85	1.96	0.706	0.313	0.77	0.289	0.97
		Ns	18/32	1.81	0.76	0.667	0.326	0.65	0.258	0.96
	TB3	Sf	16/30	1.65	3.72	0.681	0.298	0.78	0.254	0.96
		Ns	16/27	2.09	0.40	0.683	0.322	0.62	0.267	0.95
Rožmitál	ROZ1	Sf	20/37	2.02	2.42	0.601	0.261	0.83	0.214	0.96
		Ns	25/48	2.21	0.23	0.513	0.215	0.78	0.164	0.94
	ROZ2	Sf	13/23	1.63	1.05	0.636	0.279	0.79	0.244	0.94
		Ns	19/36	1.47	0.10	0.610	0.249	0.79	0.187	0.95
	ROZ3	Sf	22/43	1.81	0.97	0.602	0.255	0.81	0.188	0.95
		Ns	19/36	1.93	0.08	0.621	0.208	0.73	0.153	0.95
Písek	PS1	Sf	16/30	1.88	0.00	0.713	0.261	0.73	0.260	0.96
		Ns	15/29	2.82	0.00	0.688	0.327	0.60	0.266	0.94
	PS2	Sf	19/34	2.29	0.00	0.636	0.321	0.68	0.259	0.96
		Ns	15/29	2.82	0.00	0.592	0.327	0.60	0.266	0.94
Černá Hora	CH1	Sf	15/27	1.83	2.28	0.592	0.320	0.76	0.241	0.93
		Ns	14/27	2.03	0.00	0.632	0.238	0.57	0.197	0.95
	CH2	Sf	18/32	2.03	0.25	0.604	0.262	0.74	0.192	0.93
		Ns	10/20	2.48	0.00	0.705	0.259	0.73	0.247	0.94
	CH3	Sf	11/21	1.80	1.67	0.614	0.267	0.83	0.227	0.90
		Ns	9/15	2.23	0.00	0.615	0.218	0.69	0.168	0.90
Město Albrechtice	MA1	Sf	14/26	2.04	2.32	0.624	0.311	0.79	0.252	0.94
		El	15/30	1.78	0.82	0.668	0.339	0.75	0.321	0.95
	MA2	Sf	19/37	1.32	1.76	0.652	0.324	0.71	0.294	0.97
		El	16/30	1.22	0.51	0.608	0.330	0.61	0.269	0.94
	MA3	Sf	21/39	1.49	1.41	0.687	0.267	0.83	0.250	0.97
		Ns	19/34	1.93	0.27	0.633	0.264	0.73	0.231	0.96
		El	19/35	1.85	0.17	0.663	0.269	0.68	0.232	0.96
	MA4	Sf	18/33	1.09	2.77	0.672	0.277	0.80	0.246	0.96
		Ns	18/33	1.65	0.05	0.576	0.239	0.74	0.189	0.94
		El	16/30	1.14	0.96	0.654	0.276	0.78	0.231	0.96
	MA5	Sf	11/21	1.80	2.29	0.648	0.275	0.82	0.245	0.93
		Ns	13/21	1.82	0.71	0.560	0.263	0.85	0.214	0.91

TRW – tree-ring width; *EPS* – expressed population signal; Sf – silver fir; Ns – Norway spruce; El – European larch

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RESULTS

Growth dynamics. Ring-width chronologies of fir and spruce show synchronous year-to-year fluctuations within the given region as well as between different regions. Mean ring-width series for individual tree species calculated based on a pooled dataset from all sample sites illustrate the major differences in growth dynamics between tree species (Figure 3). Series of fir and spruce have a synchronous course until the end of the 1950s. Later, from the 1960s to the 1980s, fir experienced a deep growth depression, followed by a period of intensive regeneration in the 1990s. The increase in fir growth was interrupted by a drought in 2003, after which growth stagnated or decreased. Spruce showed its first growth reduction in the period 1992–1995 and then a steep growth decline after 2003 with an increasing occurrence of missing rings. Inter-annual ring-width variations in larch differ from those of both fir and spruce. However, similarly like in spruce, there was also a growth decline after 2003 in larch, but it had a lower intensity.

Missing rings are most common in fir (Figure 4, Table 2). The anomalies in tree-ring formation were recorded with a similar frequency in all re-

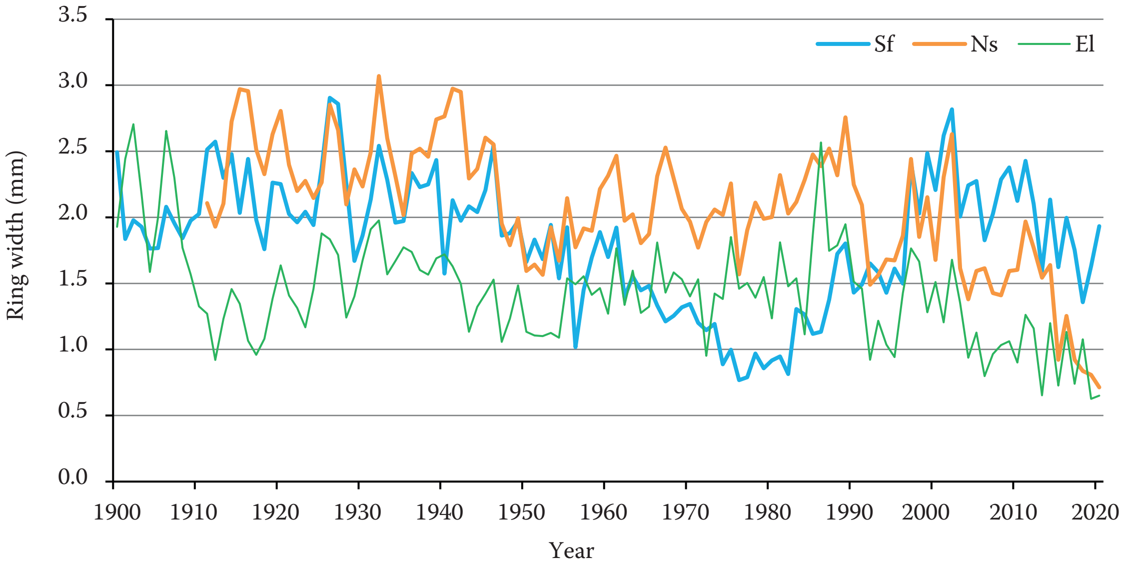

Figure 3. Mean ring-width series for silver fir (Sf), Norway spruce (Ns) and European larch (El)

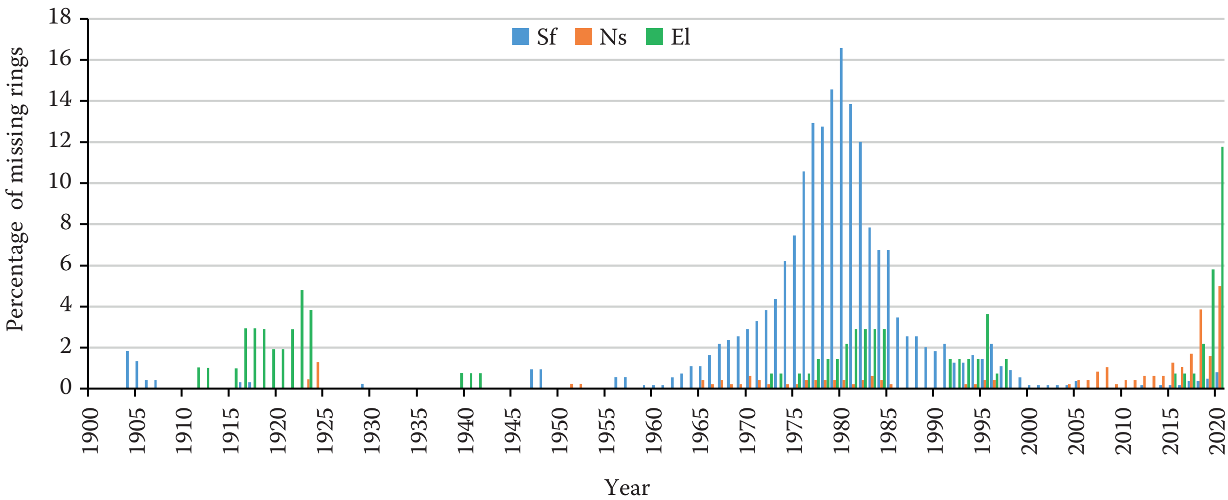

Figure 4. Occurrence of missing rings in individual years for silver fir (Sf), Norway spruce (Ns) and European larch (El)

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gions with the exception of Písek, where no missing rings were determined. Here, fir has also shown almost no growth decline since 1960. In other regions, missing rings in fir mostly occurred in the period 1966–1985 but they were rarely identified in recent years (Figure 4). Missing rings were much less common in spruce and larch than in fir. In spruce, they occurred mainly in the last dry period after 2003, with a steep increase after a dry year in 2015. For larch, missing rings occurred in several periods: 1915–1923, 1976–1984, 1991–1996 and after 2015, with the most missing rings recorded in 2019 and 2020.

The PCA revealed that ring-width chronologies were relatively similar. The first principal component (PC1) retained 43.5% of the total variance and represented the tree-ring width variability common to all species growing in different regions, since it was strongly related to all tree sets (Figure 5A). The signal captured in PC1 indicates a high common variance in tree growth driven by climatic factors. PC2 (14.5%) divided chronologies into groups according to the tree species and was positively related to larch and spruce and negatively to fir chronologies. It points to a higher similarity in the growth pattern of spruce and larch and to the dissimilarity of fir. PCA loadings on PC3 were differentiated mainly by region (Figure 5B), separating the eastern Moravian regions from the western Bohemian regions. However, PC3 retains only 9.9% of the overall variance. This means that regional affiliation explains only a small part of the common variability in tree growth.

Climate-growth relationship

The correlation analysis showed a significant ($P < 0.05$) positive effect of higher temperatures during the winter and early spring on the growth of fir in sites at an altitude above 700 m a.s.l. and in a moist site CH3 located in a cool valley position. Summer temperatures had no effect on fir growth in any of the sample sites (Figure 6A). Similarly, for larch, there was no significant effect of summer temperatures on most sites. However, a negative effect of high spring temperatures in the previous year was obvious for larch trees. On the other hand, spruce growth was negatively affected mainly by high temperatures during the summer of the current year and in September of the previous year in lower sites up to 550 m a.s.l.

The growth of all three species was positively related to precipitation totals in the summer months of the current year (Figure 6B). They clearly had a significant ($P < 0.05$) positive effect on the growth of spruce at all sample sites across the altitude gradient studied and then also on the growth of larch, with the exception of the highest site, MA4. By contrast, for fir, a significant ($P < 0.05$) relationship with summer precipitation was observed only at two sites in lower locations.

The relationship of growth to the *SPEI* index followed the same pattern as the relationship of growth to precipitation and confirms the higher sensitivity to summer drought in spruce and larch compared to fir (Figure 6C).

The relationship of growth to the *scPDSI* corroborated strong limitation of spruce growth by the

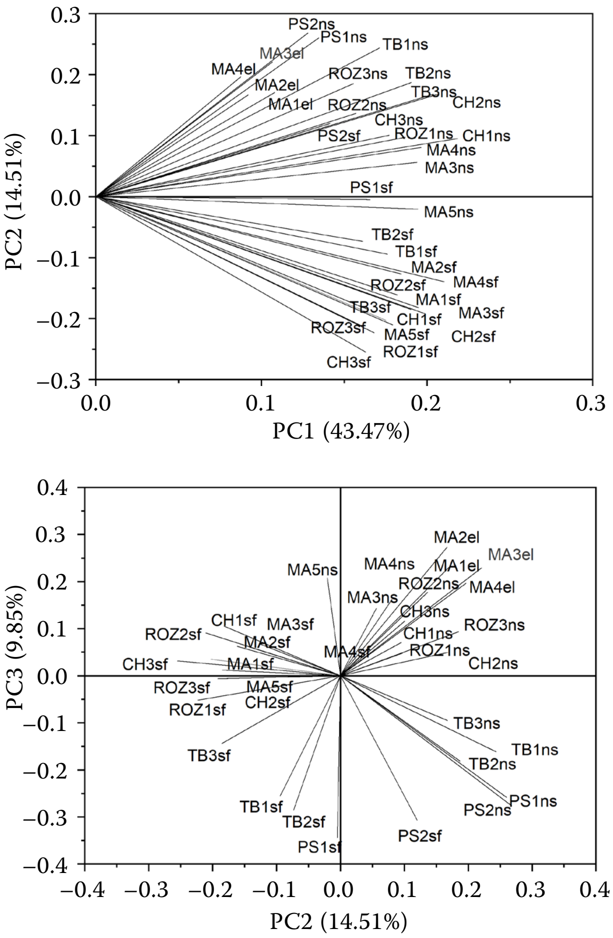

Figure 5. PCA loading plots of residual tree-ring chronologies for the common period 1962–2018; (A) PC1 against PC2; (B) PC2 against PC3; percentage indicates the proportion of the variance explained by a given principal component, the vector name consists of the site name (e.g. MA4) and tree species code (sf – Silver fir, ns – Norway spruce, el – European larch)

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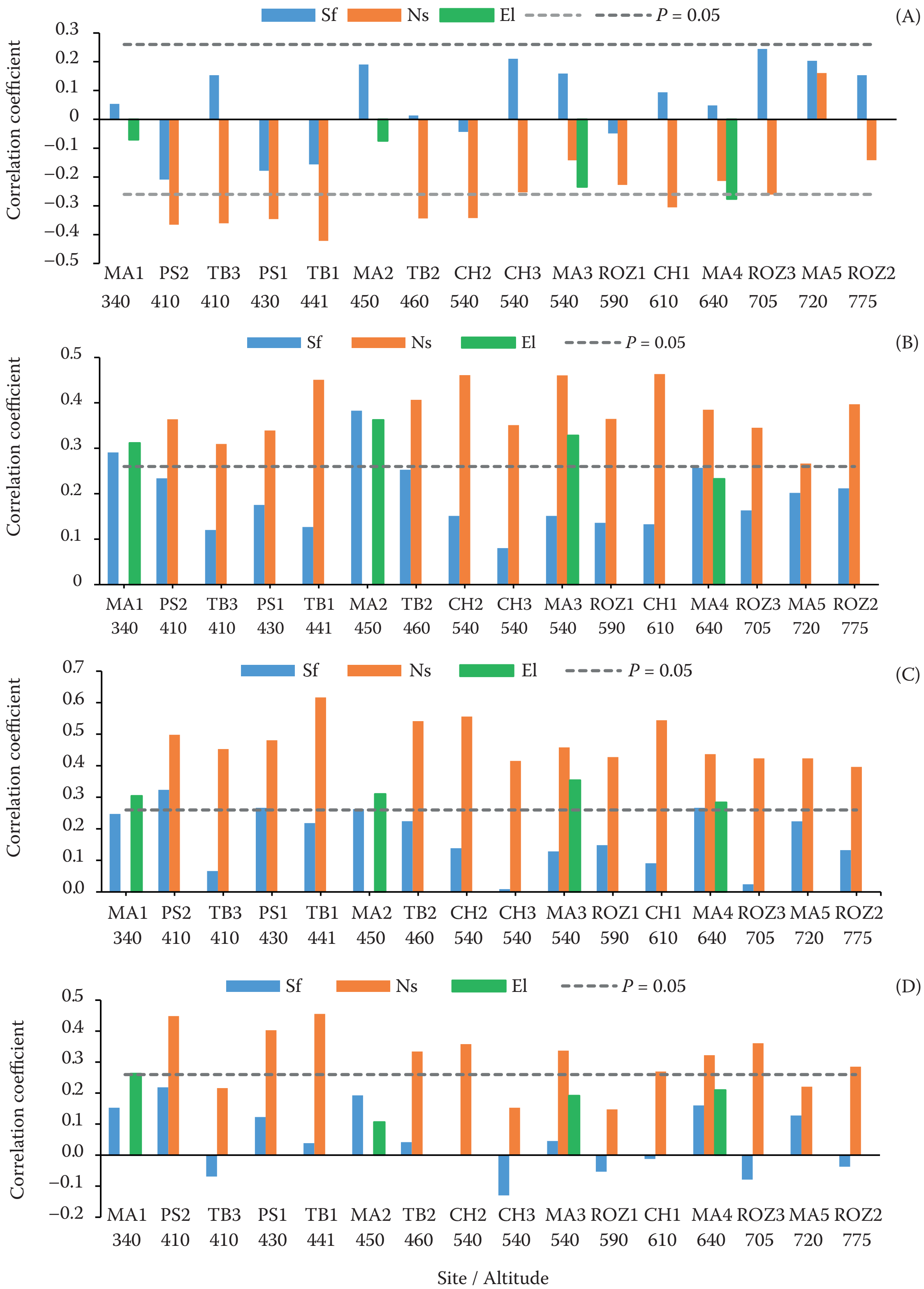

Figure 6. Correlation of silver fir (Sf), Norway spruce (Ns) and European larch (El) growth with summer (A) temperatures, (B) precipitation totals, (C) Standardised Precipitation Evapotranspiration Index (*SPEI*) and (D) self-calibrated Palmer Drought Severity Index (*scPDSI*) for the common period 1962–2018; the dashed line indicates the limit for statistically significant values ($P = 0.05$)

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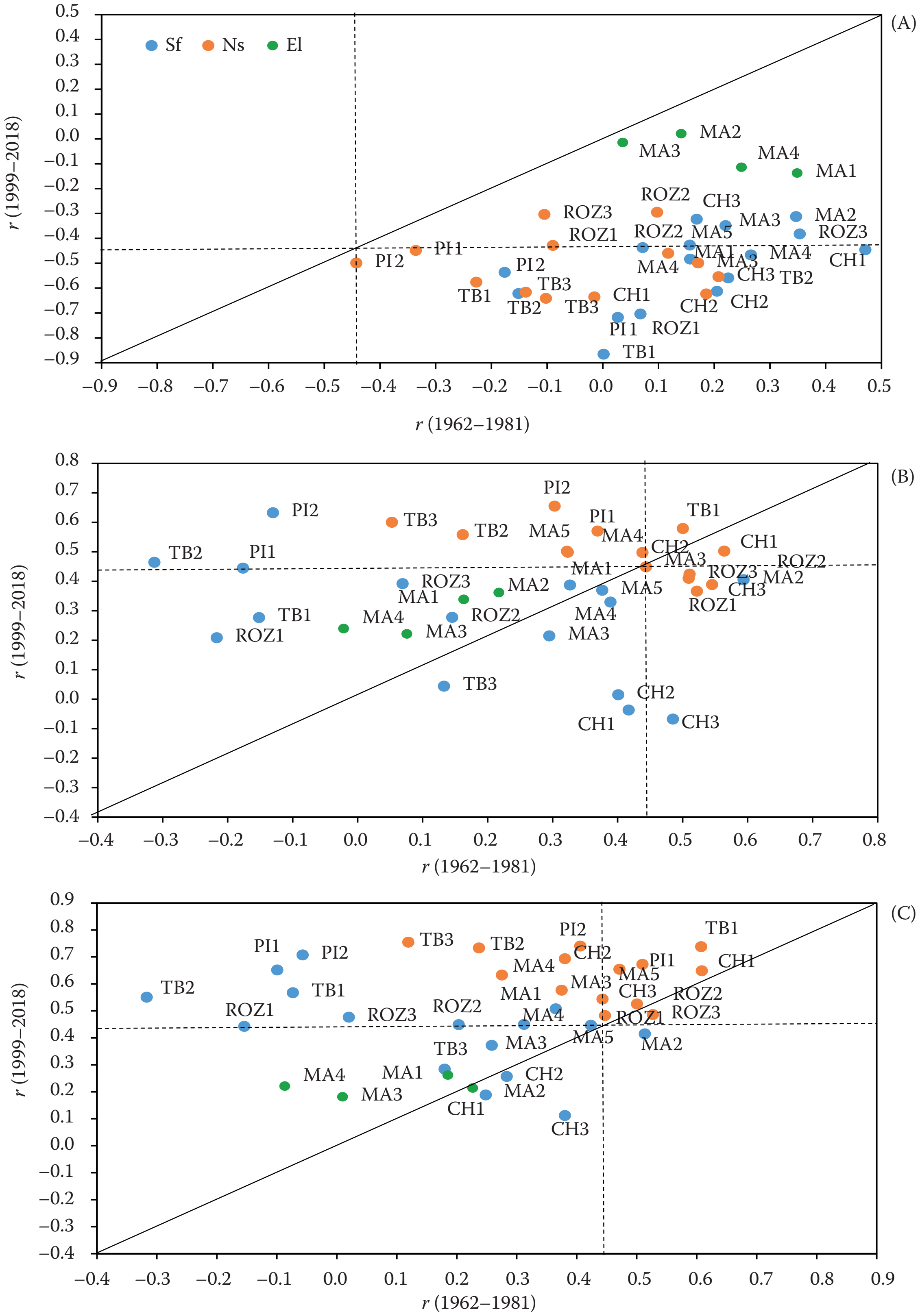

Figure 7. Overall stability of the individual climate-growth relationships expressed by correlation values for summer (A) temperatures, (B) precipitation and (C) Standardised Precipitation Evapotranspiration Index (*SPEI*) for the 1999–2018 (on the y-axis) and previous 20-year period 1962–1981 (on the x-axis), vertical and horizontal dashed lines indicate significance levels ($P = 0.05$), and the solid diagonal line represents a perfect stationary response

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dry summer period, while larch and fir were less responsive (Figure 6D).

The temporal stability of the climate-growth relationship was studied using moving correlations. We focused on seasonal climatic values related to drought stress. The overall individual stability at the site- and tree-species levels can be seen in Figure 7, which illustrates the shift in the climate-growth relationship between the two 20-year periods 1962–1981 and 1999–2018. Scattering of the correlation values around the diagonal line represents the theoretical perfect stationary response. The growth response to summer temperatures was unstable at both the individual and the global level, resulting in an asymmetrical displacement of the cloud of points (Figure 7A). While in the period 1962–1981 the relationship of growth to summer temperatures was insignificant for all tree species and sites, and the values of correlation coefficients reached positive values, in the period 1999–2018, spruce and fir showed a statistically significant ($P < 0.05$) negative relationship with temperatures at most sites. The growth response of larch did not change significantly.

The response to summer precipitation was individually unstable but overall stable with the individual responses symmetrically divided by the diagonal line (Figure 7B). Spruce growth was significantly ($P < 0.05$) positively related to precipitation in both periods at most sites, whereas for larch and most fir populations the correlations were insignificant in both time windows. However, a distinct shift in the growth response of fir was obvious for the *SPEI* index (Figure 7C). The fir became more sensitive to drought in the recent 20-year period.

DISCUSSION

In this study, we focused on spatiotemporal changes in the growth response to climate depending on tree species and regional affiliation. Analyses were restricted to trees > 100 years old to avoid the age-related effect on the climate-growth relationship (Carrer, Urbinati 2004), and the stands were selected at sites well supplied with nutrients to eliminate the effect of site quality.

For spruce at site CH1, the resulting chronology reached less than 60 years, although the age of the stand was around 100 years. This was due to the frequent occurrence of stem rot in spruce trees at this lower site. Therefore, we analysed the growth pattern for the period 1962–2018, which was common to all sites and tree species.

The observed deep growth depression in fir from the early 1960s to the late 1980s corresponds to the findings of other studies from different parts of Europe (Becker et al. 1989; Elling et al. 2009; Gazol et al. 2015; Vitali et al. 2017; Bošela et al. 2018). The growth decline was probably the result of exposure to atmospheric pollution, in particular to sulphur dioxide, to which fir is sensitive (Elling et al. 2009; Mikulenka et al. 2020). With 3 150 kilotons in 1985, SO_2 emissions in the Czech Republic were the highest in Europe (Hůnová 2020). Pollution had a clear effect on the growth pattern of fir during this period and may have modified the growth response to climatic factors (Rydval, Wilson 2012; Kolář et al. 2015).

The vitality of silver fir has increased since the end of 1980s in many stands in Central and Western Europe (Büntgen et al. 2014; Gazol et al. 2015; Bošela et al. 2018) due to a decrease in SO_2 emissions, air warming with constant precipitation and an increase in nitrogen deposition (Elling et al. 2009; Büntgen et al. 2014). Our study shows that the increase in fir growth was interrupted by a drought in 2003 (Ciais et al. 2005), after which growth stagnated or decreased.

Spruce growth failed during the hot and dry periods in the first half of the 1990s (Brázdil et al. 2009). After an extreme drought in 2003, followed by several dry years with further extremes in 2015 (Ionita et al. 2017) and 2018 (Salomón et al. 2022), there was a rapid decline in spruce growth in most locations with an increasing occurrence of failures in tree-ring formation, which indicates severe drought stress (Bräuning et al. 2016). The correlation analysis also clearly indicated high sensitivity of spruce to drought across the altitude gradient. Also, van der Maaten-Theunissen et al. (2012) and Vitali et al. (2017) detected higher sensitivity of spruce to summer droughts compared to that of co-occurring silver fir, regardless of the elevation.

Silver fir is generally more resistant to drought than Norway spruce, larch and European beech (reviewed in Vitasse et al. 2019b). However, Cailleret and Davi (2011) reported higher sensitivity of silver fir to summer water stress compared to beech under mountain conditions in the Mediterranean area. Our study confirmed higher drought tolerance in fir compared with larch and particularly spruce. The fir tree has a deep taproot system (Úradníček et el. 2009) that allows it to use water from deeper soil

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layers. In addition, this species controls its transpiration efficiently via the rapid closure of its stomata in response to a vapour-pressure deficit (VPD) increase (Nourtier et al. 2014). Both functional traits allow fir to cope with dry periods.

In the entire period 1962–2018, fir showed lower sensitivity to summer drought, however, in the most recent 20-year period, the susceptibility of fir to summer temperatures and *SPEI* values has increased. In 1999–2018, the highest positive correlation with *SPEI* was recorded in the Písek region. Here, we observed the mortality of fir trees after the drought in 2018. This means that even the relatively drought-resistant fir may currently experience local decline due to drought stress in Central European conditions. So far, the decline of silver fir triggered by drought has been reported mainly from southwestern Europe, where fir populations grow at their xeric distribution limit (Macias et al. 2006; Linares, Camarero 2012). However, drought-induced tree decline and mortality are complex phenomena. Trees weakened by drought are susceptible to secondary stressors, including pests and pathogens (Mattson, Haack 1987; Gaylord et al. 2013). Also, nutritional imbalances may accelerate the decline and death of climatically stressed trees (Hevia et al. 2019; Gonzáles de Andrés et al. 2022). Silver fir shows humus forms with lower surface humus accumulation, but with soil chemistry very comparable with that of Norway spruce (Podrázský et al. 2018). The importance of impaired nutrition may increase in the future, as the concentration of nutrients in foliage is decreasing in the long term on a European scale (Jonard et al. 2015).

CONCLUSION

Fir is a vital tree species that showed a remarkable ability to recover from a decline period in the 1970s and 1980s when air pollution peaked. In recent years, the strongest abiotic stressor has been climate change manifested by periods of drought and an increased frequency of extreme events. Compared to European larch and Norway spruce, silver fir is more resistant to a lack of precipitation, however, its sensitivity to drought has increased in the last two decades, and in some sites at a lower elevation, fir is currently showing symptoms of decline, even in the central part of its distribution range.

Due to the intense dieback of spruce and pine stands, fir appears to be a promising coniferous tree species that certainly has a high potential for use in mixed temperate forests in Central European conditions. However, it is necessary to apply cautious forest management with respect to the ecological requirements of this tree species.

The selected sites do not represent the entire ecological amplitude of the investigated tree species, which can be considered a weak point of the study. The selection was restricted to the altitudinal zone up to 800 m a.s.l., i.e. the zone with large-scale disintegration of spruce stands. Future research should focus also on sites in the montane zone, as changes in the growth-climate relationship can be expected even there. In this study, larch was studied only at a limited number of sites. More attention should be paid to this tree species in subsequent studies as it is expected to be more widely used in mixed forests of the temperate zone.

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Positive effect of fir-rowan intimate mixture on new forest floor and topsoil following afforestation

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Abstract: Litterfall of silver fir contributes to development of forest floor similarly like Norway spruce litterfall does. The nutrient return to soil can be intensified by mixing these conifers with other tree species whose effects on soil are positive; our study deals with European rowan. The study aimed at firs and rowans in alternating rows (Fi-Ro) compared to the monospecific plantation of fir (Fi) at two former meadow sites with the stands of 20 and 17 years of age, respectively. Both organic forest floor and its mineral subsurface were sampled. Rowan admixed to the silver fir plantation improved both the uppermost layer and the topsoil as higher pH, more favourable soil-sorption properties and higher plant available magnesium were found below Fi-Ro compared to Fi. Fine dry matter was higher below Fi, which was reflected in higher organic carbon (C_{ox}), combustible matter and nitrogen pools. Besides the effects of trees on the soil, silvicultural issues such as renewal costs and tree species performance in monospecific and mixed stands were presented and discussed.

Keywords: broadleaves; conifers; fertility; nutrient return; organic layers; planted forest

Silver fir (*Abies alba* Mill.) is one of the most important native trees of Central Europe, especially in the mountains (Mauri et al. 2016). However, unlike Norway spruce, silver fir covers only a small part of the forested area in the Czech Republic. The long-term decrease of the fir share is reflected in a continual reduction of the fir pollen content found in peat profiles by Rybníčková (1966) and Šantrůčková et al. (2010) in the Orlické hory Mts. and in the Šumava Mts., respectively. The oldest reasons for the decline in the fir share date back to the medieval use of silver fir for industrial purposes (Beneš 2008). The trend went on as the fir showed a decline since the 19th century (Volařík, Hédl 2013), thus reaching 2.9% in the 1950s and the value even dropped to 0.9% at the very end of the 1990s (Ministry of Agriculture 2002); one of the key decline factors was pollution by SO_2 (Elling et al. 2009, Čavlović et al. 2015). Silver fir was, therefore, either appreciated or disdained by foresters and timber industry (Senn, Suter 2003). Since the turn of centuries, the fir share rose to 1.2% in the Czech forests (Ministry of Agriculture 2022).

Silver fir demands deeper soils compared to Norway spruce (Úradníček et al. 2010). Although it is listed among soil-improving and soil-stabi-

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lising tree species in the Czech Republic (Decree No. 298/2018 Coll.), its content of nutrients in needles (Dušek et al. 2020) and also in forest floor (Třeštík, Podrázský 2017) can be comparable with Norway spruce. In live fir trees, the nutrient content can differ according to the canopy condition as for the highest total nitrogen (N_{tot}) in the open and the lowest under canopy reported by Čater and Diaci (2017). Augusto et al. (2002) considered silver fir as an acidifier comparable with Douglas fir and these two species impacted soil pH slightly better than spruce and pine; and all the conifers were worse compared with deciduous broadleaves. As for the stabilisation function, on waterlogged sites the silver fir root system architecture is affected by the groundwater table and the rooting is shallow (Mauer, Houšková 2017). Owing to negligible or no difference in the soil-improving function between silver fir and Norway spruce (Třeštík, Podrázský 2017), there is a potential of the more efficient nutrient return in mixtures with deciduous broadleaves. There are no general rules for effects of mixed stands on nutrient return and availability (Augusto et al. 2002), which is the reason why it is necessary to study the relationships of mixtures and biogeochemical cycles, particularly (De Groote et al. 2018). This applies not only to mixtures of commercial trees but also the trees such as silver fir accompanied by nursing pioneer species like European rowan.

The rowan soil-improving litterfall nutrient return was reported previously by e.g. Carnol and Bazgir (2013), Kacálek et al. (2013) or Kopáček et al. (2015). Further reasons to use rowan lie in its low demands on soil as it prefers and/or tolerates acidic sites, in capability to nurse commercial species and also in its natural range from lowlands to mountains (Úradníček et al. 2010; Lasota et al. 2014) and it can even dominate in the subalpine sites (e.g. Przybylska, Bujoczek 2006). Being comparable with birch, rowan acidified the soil less than willow, alder, oak and beech (Carnol, Bazgir 2013). In formerly air-polluted conditions, similar birch and rowan (Kacálek et al. 2013) or slightly worse rowan than birch (Podrázský, Ulbrichová 2001; Podrázský et al. 2006) effects on acidic soils were reported.

The objective of the paper is to study new forest-floor and topsoil properties following afforestation of the two meadows where monospecific silver fir and alternating rows of silver fir and European rowan treatments were compared. It was hypothesized that admixture of rowan improves a nutrient return to soil compared to monospecific fir, which is also reflected in soil chemical characteristics.

MATERIAL AND METHODS

Study sites. Forest floor and topsoil were sampled below 20-year-old and 17-year-old stands on two afforested meadows; research plots lie within cadastral areas of the villages of Bystré (thereinafter By) and Uhřínov (thereinafter Uh) in the Orlické hory Mts. southwestern foothills, Czech Republic. Mesoclimate attributes were calculated from 2019, 2020 and 2021 measurement campaigns on the By and Uh plots; the air temperatures were similar whereas Uh showed more precipitation than By (data from automated meteorological loggers: for By present at the site, for Uh situated to the northeast ca 1 km apart; Table 1).

On both research plots, a mixture established as alternating fir and rowan planting rows (Fi-Ro) was studied compared to the control plot represented by monospecific fir (Fi) plantation. A spacing of plantation rows was 1.6 m. Initial planting densities were 5 000 plants·ha^{-1} and 3 000 plants·ha^{-1} and the areas of square-plot treatments were 220 m^2 and 400 m^2 at By and Uh sites, respectively.

Plantation performance. Since the planting, heights and diameters (root-collar at the beginning, later DBH) were measured. Fir accompanied by rowan was supressed and basal areas of the mixed treatments were larger compared to monospecific fir. In By stand, rowan competed with fir to such an extent that firs had to be released from rowan wolf trees using thinning (see Ro cut, Figure 1).

Soil sampling. Forest floor layers (litter – L, fermenter layer – F, humus – H into one sample) were completely collected using a metal frame 25 cm × 25 cm in size to enclose all organic dry matter per unit area. The uppermost mineral soil (A horizon) was sampled from within the frame using a garden trowel. Both treatments were sampled five times at both study sites in autumn 2021, i.e. at the plantation ages of 20 and 17 years at By and Uh, respectively.

The dry forest floor was sieved through a 2-mm mesh to get a fine fraction of the dry matter (*DM_fine*) and weighed. The *DM_fine* was considered an organic-matter compartment that was likely to have important implications for the uppermost forest soil fertility. In both organic and mineral soil samples were analysed properties such

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Table 1. Site attributes of the research plots with Fi-Ro and Fi treatments; mezoclimate attributes are presented as both annual (y.) and growing-period (g.) values

Study sites	Coordinates	Afforestation year	Mean air temperature y. / g. (°C)	Total precipitation y. / g. (mm)	Altitude (m a.s.l.)	Aspect	Slope	Forest site	Bedrock*
By	50.33°N, 16.25°E	2002	8.3 / 14.3	795 / 495	510	NW	9°	nutrient-medium beech	phyllite, green schist
Uh	50.23°N, 16.33°E	2005	8.0 / 14.0	900 / 575	530	SE	14°		diorite, amphibolite

*geology was investigated by the authors and verified using maps by Opletal and Domečka (1983) and CGS (2019); Fi-Ro – fir-rowan; Fi – fir; By – Bystré; Uh – Uhřínov

as organic carbon (C_{ox}), combustible matter, Kjeldahl nitrogen, pH in water and potassium chloride, parameters of the soil sorption complex [base cation content *BCC*, cation exchange capacity *CEC*, hydrogen cations ($H = CEC – BCC$) and % of base saturation ($BS = BCC / CEC \times 100$) analysed according to Kappen (1929)] and also plant-available nutrients using the Mehlich III soil test extractant (Mehlich 1984).

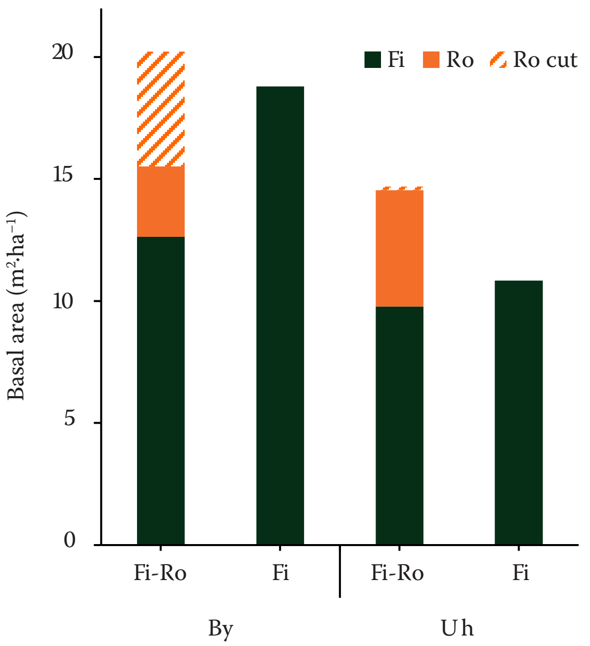

Figure 1. Mixture overyielding illustrated with larger basal areas of mixed treatments (Fi-Ro) and monospecific treatments (Fi) on 20-year-old By and 17-year-old Uh research plots

Fi – fir; Ro – rowan; Ro cut – rowan removed; By – Bystré; Uh – Uhřínov

Data analysis. The nutrient pools of the forest floor samples were computed using fine matter dry weights (*DM_fine*). The properties of both soil layers were tested for differences between the two treatments. The data for each variable were tested using the Shapiro-Wilk test for normality and by Levene's test for homogeneity of variance across groups. One outlier in P and Mg contents in humus was excluded. Analyses were performed in the R statistical computing environment (Version 4.2.1, 2022). Subsequently, even when only two groups and two treatments were compared, ANOVA with a randomized block design was used with plot as blocking factor. A linear model was computed using the lm function (stats package), and type II ANOVA table outputs were evaluated. The normality of model residuals was checked. The analysed differences were considered to be significant when $P \leq 0.05$.

RESULTS

Forest floor. The Fi-Ro treatment does differ from the Fi treatment in terms of many qualitative properties of the newly developed forest floor. The admixture of rowans had significant (mostly highly significant) positive effects on soil pH and properties of the sorption complex (Table 2, Figure 2) and also higher concentrations of potassium and magnesium (Figure 3). On the other hand, monospecific firs manifested more C_{ox} carbon, combustible matter and nitrogen. More favourable properties of the forest floor such as pH, sorption complex and magnesium concentration were found at the Uh study site (Table 2; Figures 2 and 3).

Significantly finer dry mass of forest floor was found below the monospecific fir canopy (Table 3,

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Table 2. Test of the significance of differences (*P*-values) of the analysed qualitative soil properties in the forest floor and the A horizon below the two treatments Fi-Ro and Fi (ANOVA, fixed factor – treatment; blocking factor – plot)

Properties	Forest floor		Topsoil (A horizon)	
	treatment	plot	treatment	plot
pH_{H_2O}	**0.001**	0.4	< **0.001**	< **0.001**
pH_{KCl}	< **0.001**	**0.002**	< **0.001**	< **0.001**
BCC	**0.002**	**0.005**	< **0.001**	< **0.001**
H	**0.01**	**0.008**	< **0.001**	< **0.001**
CEC	**0.03**	0.09	< **0.001**	< **0.001**
BS	**0.004**	**0.003**	< **0.001**	< **0.001**
C_{ox}	**0.002**	0.8	**0.01**	0.1
Combustible	**0.003**	**0.04**	**0.007**	0.1
N	**0.002**	0.4	**0.01**	0.3
P	0.1	0.7	0.8	< **0.001**
K	< **0.001**	0.7	0.09	0.1
Ca	0.3	0.3	< **0.001**	< **0.001**
Mg	< **0.001**	< **0.001**	< **0.001**	< **0.001**

Bold – $P \leq 0.05$; *BCC* – base cation content; *CEC* – cation exchange capacity; *H* – hydrogen cations (*H* = *CEC* – *BCC*); *BS* – % of base saturation (*BS* = *BCC* / *CEC* × 100); Fi-Ro – fir-rowan; Fi – fir

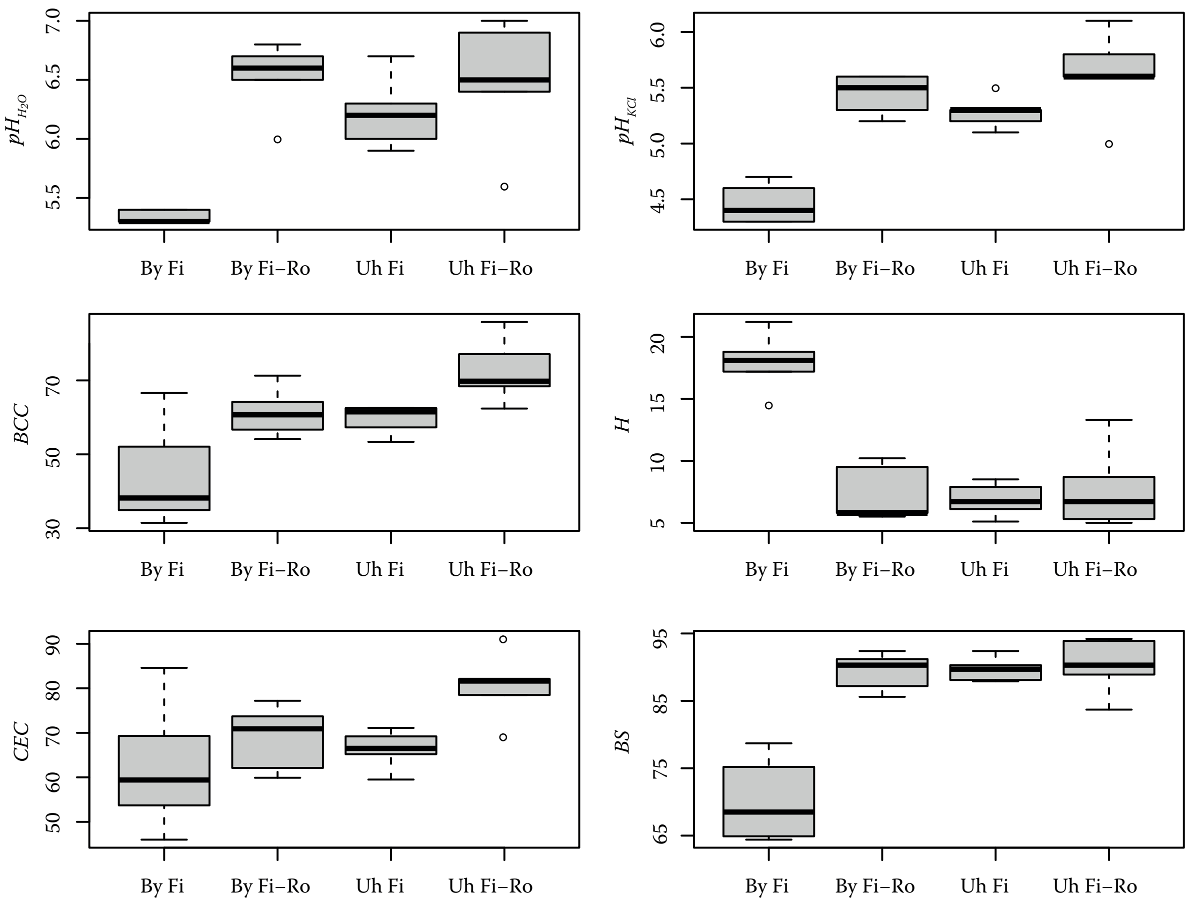

Figure 2. Forest floor qualitative properties according to plot and treatment: soil acidity and sorption complex

BCC – base cation content (meq·100 g^{-1}); *CEC* – cation exchange capacity (meq·100 g^{-1}); *H* – hydrogen cations (*H* = *CEC* – *BCC*) (meq·100 g^{-1}); *BS* – base saturation (*BS* = *BCC* / *CEC* × 100) (%); By – Bystré; Uh – Uhřínov; Fi – fir; Fi-Ro – fir-rowan

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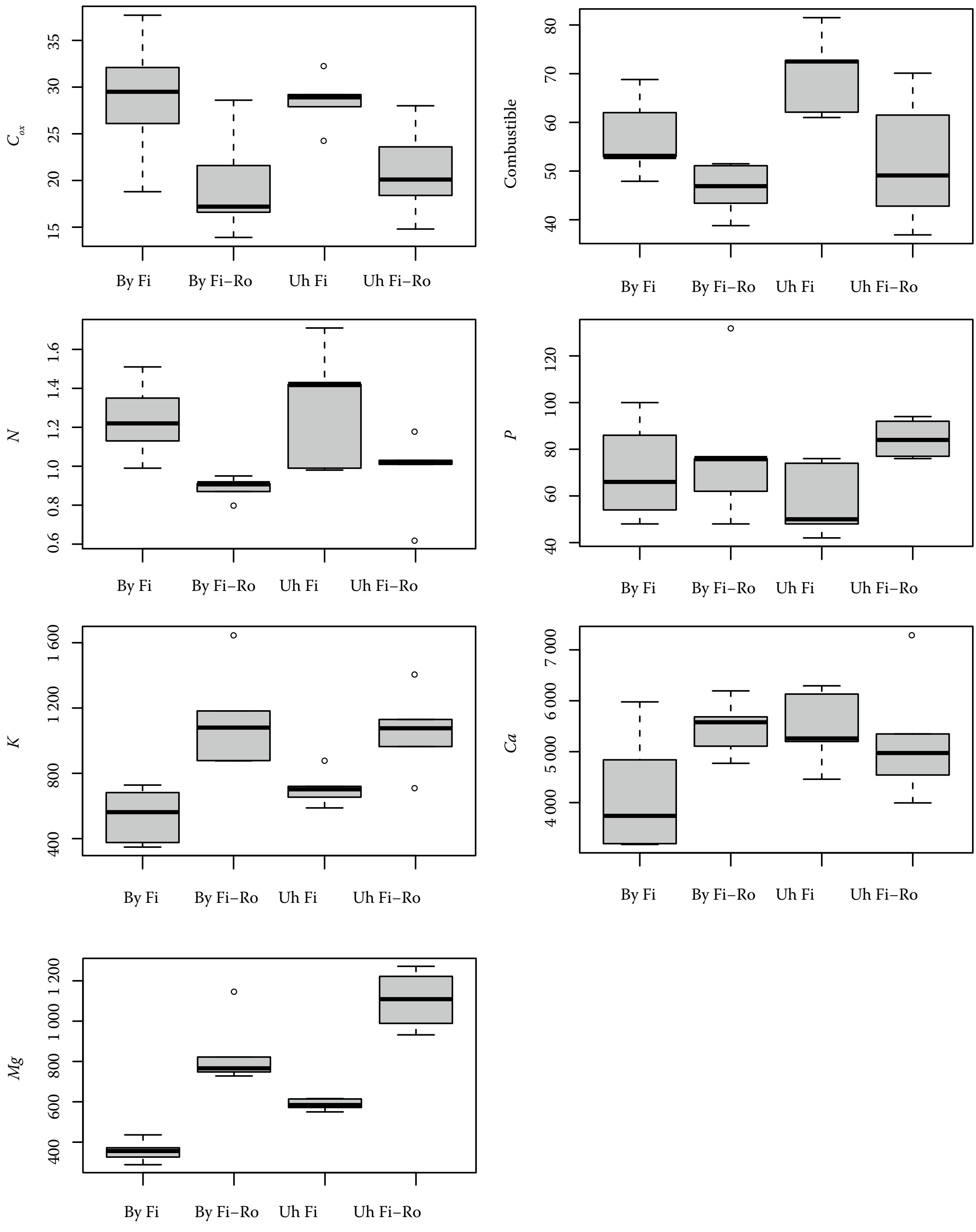

Figure 3. Forest floor qualitative properties and dry mass (*DM* in g·m^{-2}) according to plot and treatment: C_{ox} (%), combustible matter (%), *N* (%) and nutrients by Mehlich III (mg·kg^{-1})

By – Bystré; Uh – Uhřínov; Fi – fir; Fi-Ro – fir-rowan

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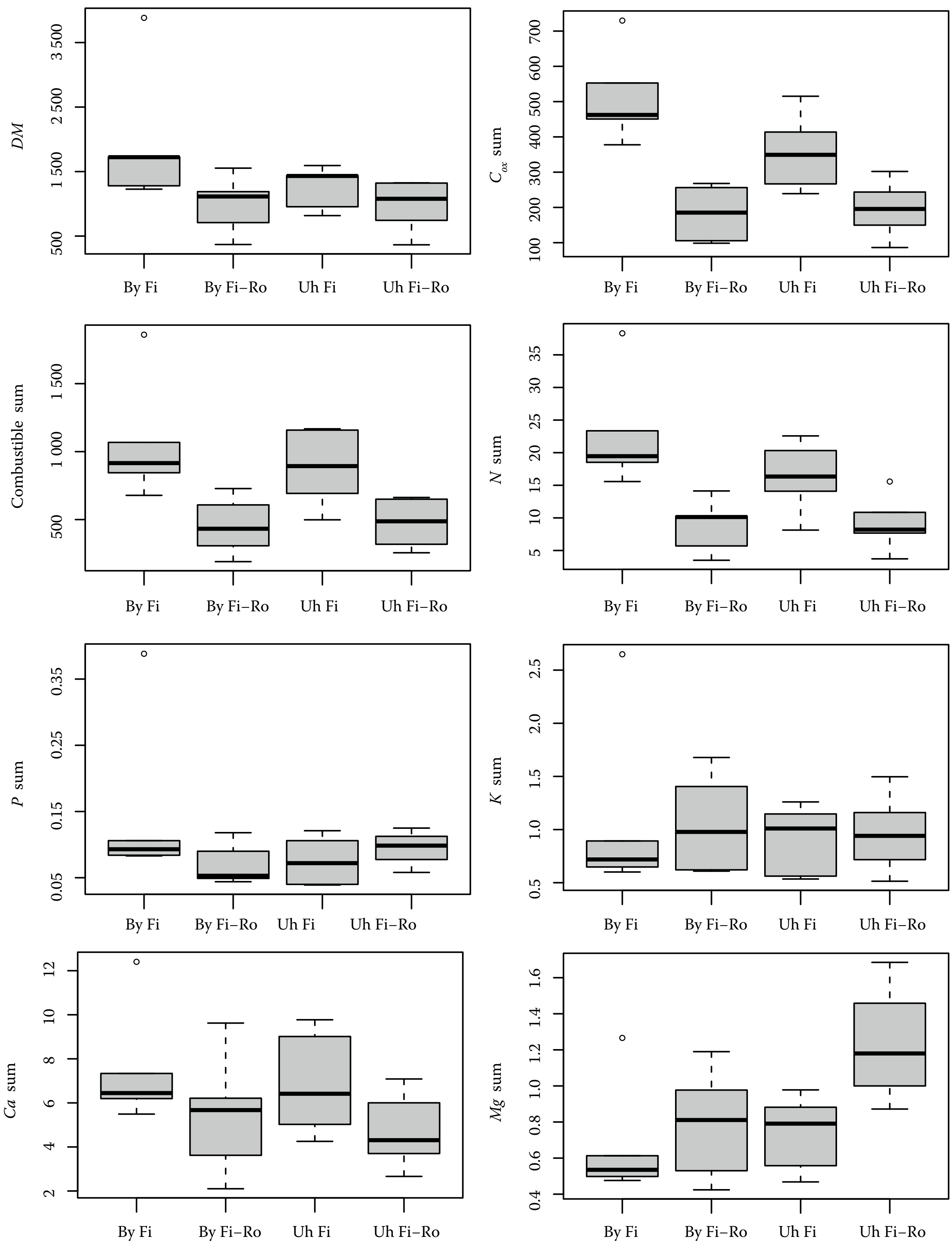

Figure 4. Dry matter (*DM*), combustible matter, and nutrient pools in the forest floor according to plot and treatment in g·m^{-2}

By – Bystré; Uh – Uhřínov; Fi – fir; Fi-Ro – fir-rowan

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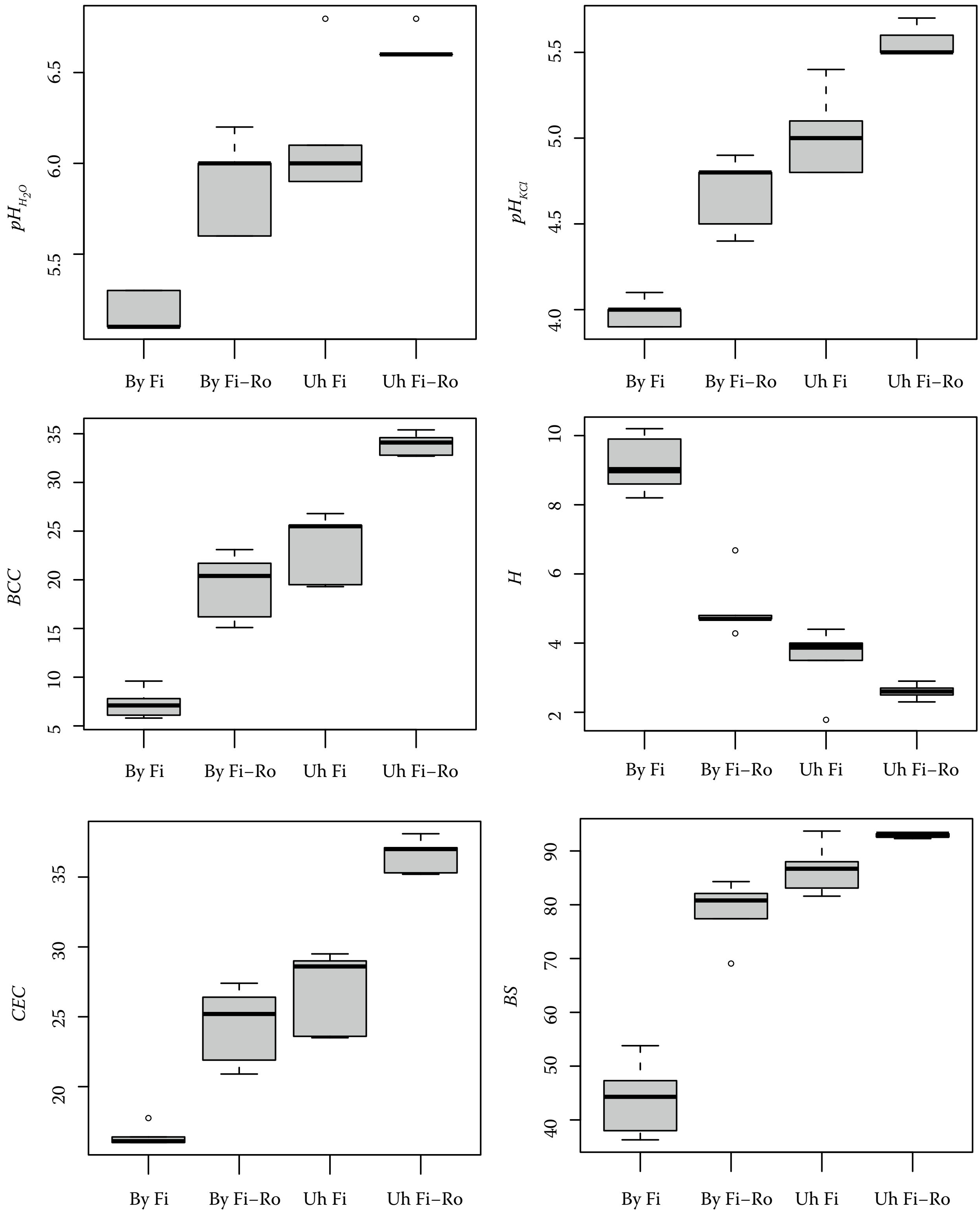

Figure 5. Mineral A horizon qualitative properties according to plot and treatment: soil acidity and sorption complex

BCC – base cation content (meq·100 g^{-1}); *CEC* – cation exchange capacity (meq·100 g^{-1}); *H* – hydrogen cations ($H = CEC - BCC$) (meq·100 g^{-1}); *BS* – base saturation ($BS = BCC / CEC \times 100$) (%); By – Bystré; Uh – Uhřínov; Fi – fir; Fi-Ro – fir-rowan

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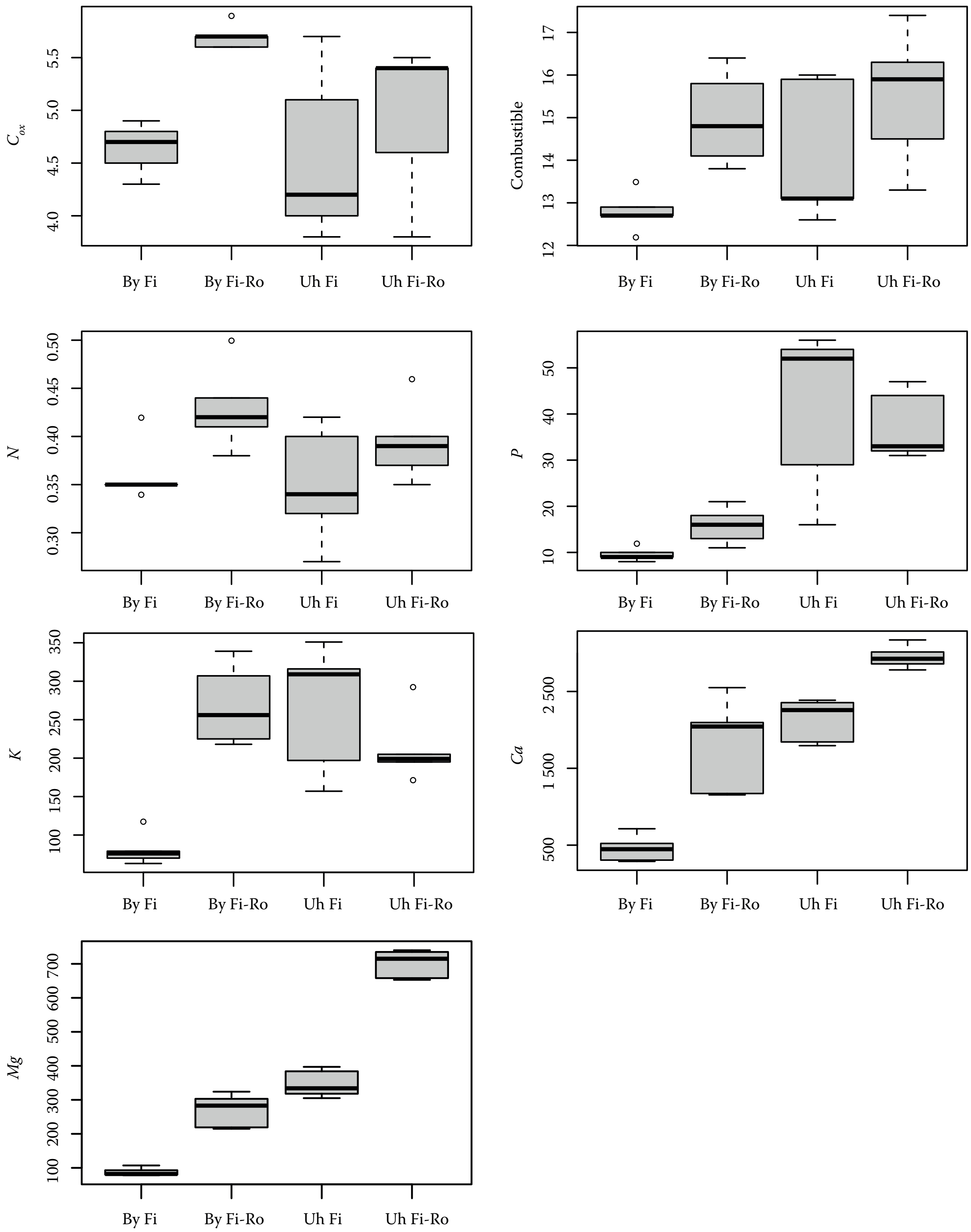

Figure 6. Mineral A horizon qualitative properties according to plot and treatment: C_{ox} (%), combustible matter (%), N (%) and nutrients by Mehlich III (mg·kg^{-1})

By – Bystré; Uh – Uhřínov; Fi – fir; Fi-Ro – fir-rowan

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Table 3. Test of the significance of differences (*P*-values) of the analysed quantitative soil properties ($g·m^{-2}$) in the forest floor: dry matter, pool of combustible matter and nutrient pools in fine dry matter (ANOVA, fixed factor – treatment; blocking factor – plot)

Value	Treatment	Plot
DM	**0.05**	0.2
C_{ox} sum	**< 0.001**	0.2
Comb sum	**0.002**	0.5
N sum	**0.001**	0.3
P sum	0.4	0.4
K sum	1.0	0.6
Ca sum	0.07	0.5
Mg sum	0.06	0.1

Bold – $P \leq 0.05$; *DM* – dry matter; *Comb* sum – pool of combustible matter

Figure 4). This was reflected in a larger pool of C_{ox}, combustible matter and nitrogen pool below fir. More calcium and magnesium in the fir fine dry matter were not statistically significant (P = 0.07; P = 0.06). There was no difference in the nutrient pools in forest floor between the two study sites.

Topsoil. The differences found in forest floor were reflected also in the very topsoil and they were even more significant. There were manifested higher pH and improved soil sorption complex properties below the mixture treatment (Table 2, Figure 5). Contrary to the organic layer, based solely on the shed plant tissues, more C_{ox}, combustible matter and nitrogen contents were found below mixtures. The pattern of magnesium contents was similar to that of the forest floor with higher values below the mixture, on the other hand calcium showed a similar pattern only in the mineral topsoil (Figure 6). Also here, the more favourable properties were found at the Uh site.

DISCUSSION

Rowan effects in monospecific and mixed stands. Effects of monospecific stands on nutrient return via litterfall are known quite well. As for forest tree species mixtures, they have opened door to further research of joint impacts of different-quality organic inputs on the soil surface. For example when mixed, also nutrient-rich shrub litterfall can improve a return of the basic nutrients (De Groote et al. 2018). Rowan foliar litterfall is high in nutrients, thus improving forest floor properties even on the relatively poor sites as reported by Carnol and Bazgir (2013) for the Ardennes, Belgium or by Kopáček et al. (2015) for the Bohemian Forest, Czech Republic. Slightly favourable impacts of the rowan on the top organic horizon were found also in conditions of formerly SO_2 polluted mountains (Moravčík, Podrázský 1992; Kacálek et al. 2013).

The impact of an unmixed rowan stand, reported by Kacálek et al. (2013), matched with our findings only partially. Unlike more forest floor nutrients found below rowan compared to conifers (Kacálek et al. 2013), Fi-Ro mixtures showed only higher potassium and magnesium contents. The concentrations of these two nutrients and phosphorus in total litterfall were found to be attributed to an increasing proportion of rowan litter also by Kopáček et al. (2015). Contrary to Fi-Ro afforestation at By and Uh sites, the increasing amounts of rowan litter enriching soil horizons in the Plešné Lake catchment followed the spruce forest die-off due to a bark beetle outbreak and were a result of natural succession of the non-intervention forest (Kopáček et al. 2015).

The actual impact of the shed rowan tissues is substantially limited by usually less biomass accumulated in rowan trees and/or its low share in the stand, which also limits the nutrient return (Podrázský, Ulbrichová 2001; Šach 2004) per unit area. On the other hand, Carnol and Bazgir (2013) found foliar litterfall amounts of rowan comparable with alder, birch, willow and spruce, and also significantly higher compared to beech and oak. When rowan fruits fallen off the stand were added to the foliar weight, it exceeded 3 $Mg·ha^{-1}·year^{-1}$, which was the greatest litterfall return among the seven investigated species (Carnol, Bazgir 2013). The importance of the species can increase over time as it can be illustrated with the abovementioned example from the Plešné Lake catchment forests where a minor share of rowan reported by Svoboda et al. (2006) turned into the increasing amounts of rowan litter enriching the soil in the catchment following the succession of the non-intervention forest (Kopáček et al. 2015).

If the woody species with nutrient-rich tissues grows in the understorey of maturing and mature stands, the effect on the properties of the upper organic layers can be various. No effect of undergrowth shrubs such as black cherry, alder buckthorn and rowan was found below pine and oak canopies (Van Nevel et al. 2014) whereas peduncu-

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lated oak, red oak and European beech (including their mixtures) litterfall from canopies undergrown with hazel, rowan, sycamore, downy birch, hornbeam, chestnut, oak, beech and buckthorn were positively influenced (De Groote et al. 2018).

Our results indicate that the proportion of rowan, as it is sharing one quarter to one half of the basal area (Figure 1) in stands of the age less than 20 years, is large enough for the soil improving effect. The ameliorative effects of rowan rows alternating with fir rows of the same age were found in both study sites though By and Uh ages slightly differ. More organic matter was found below Fi than below Fi-Ro, which is attributable to more intensive decomposition under the mixed stand. The rowan share can contribute to a faster return of base cations to the soil. There are even temporary pioneer stands mixed of birch and rowan which improved both the state of organic layers and the ground vegetation composition on formerly spruce-dominated sites following storm events (Zerbe, Meiwes 2000) or regeneration failure (Špulák, Kacálek 2020).

Silvicultural considerations. The unit price of a rowan plant was 60% of the unit price of a fir plant twenty years ago (Bartoš, Kacálek 2006). This contributed to lower costs of the established Fi-Ro plantation compared to those of Fi plantation though minimum planting density for rowan was 6 000 plants·ha^{-1} and 5 000 plants·ha^{-1} for fir at that time (Decree No. 82/1996 Coll.). The total established rowan plantation costs would be 70% of the established fir plantation costs. A further cost reduction was possible using half densities approved for soil-improving and stabilising tree species before the planting rules were changed (Decree No. 82/1996 Coll.; Appendix 8). Based on the 2022 planting stock price list of one of the largest Czech forestry nurseries, half-and-half row planting costs of rowans with fir were 60% of the fir planting costs; it reflects the lower unit price of rowans again and substantially lower planting densities required for both rowan (3 000 plants·ha^{-1}) and fir (3 500 plants·ha^{-1}) plants (Decree No. 456/2021 Coll.). This applied also to the lower unit price of similar rowan planting stocks in some forestry nurseries in Germany; the rowan price was 72% of the silver fir unit price.

Due to their growth strategies, fir and rowan can be either competitors or rowan can also be a nursing species for underplanted fir (Vaněk et al. 2016); in this case, an early thinning is needed to release fir under the rowan canopy (Polách, Špulák 2022). Rowan is capable of growing in clearcuts (Zerbe, Meiwes 2000; Chládek, Novotný 2007; Špulák, Kacálek 2020) and it is also a shade-tolerant survivor in below-canopy conditions (Chládek, Novotný 2007; Van Nevel 2014; Hamberg et al. 2015; De Groote et al. 2018). Also, the rowan sprouts from roots when parent trees are cut (Rouvinen, Kouki 2011). Silver fir also performs well in open-area and non-stressed environments (Robakowski et al. 2022) and it is a shade-tolerant species capable of sharing the environment with many tree species (Dobrowolska et al. 2017). The shade-tolerant species are better survivors when mixed with others (Zeide 1985) and silver fir is also more resistant to drought (Vitali et al. 2017). Both fir and rowan have survived very well on the formerly open area of the study sites showing just negligible mortality.

As for the rowan capability to share tree-species mixtures, for instance Hamberg et al. (2015) reported an increasing cover of rowans whereas the basal area of rowans with DBH smaller than 5 cm showed a decreasing trend as the spruce basal area got larger. The reduction of rowan abundance correlated positively with the abundance of birch and negatively with increasing abundance of broadleaves such as maple, alders, juneberry, bird cherry, oak, alder buckthorn and goat willow (Hamberg et al. 2015), which evidenced the rowan limited capability of sharing the mixed stands. This can be manifested particularly on such soils that support the performance of other trees; the rowans demand fresh moist sites of mixed coniferous forests (Lasota et al. 2014). In the 1980s and at the beginning of the 1990s, Tesař and Tesařová (1996) investigated the performance of Norway spruces mixed with rowans planted at an altitude range of 1 080–1 100 m in the Krkonoše Mts.; 2–4-year younger rowans outperformed the 14-year-old spruces. To keep spruces vigorous, they were released from above when the taller rowans were removed, but a side shelter was needed to protect them from the air-pollution flux and the recommendation aimed at the establishment of alternating strips of both woody species (Tesař, Tesařová 1996). This design is, of course, far from the intimate line plantations at By and Uh; the rowan, however, showed such a performance at By site that the thinning from above (see Ro cut, Figure 1) was needed to prevent the fir suppression.

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Another issue is to be shaping the future performance of the studied mixtures – hoofed game browsing. Silver fir belongs to the most injured woody species by the game (Senn, Suter 2003; Häsler, Senn 2012; Klopčič et al. 2017) due to its palatability (Diaci et al. 2011; Vitasse et al. 2019; Van Beeck Calkoen et al. 2022). The animals causing the most severe browsing are red deer (Klopčič et al. 2010). Therefore, the plot is still fenced in the surroundings of Uh. Contrary to Uh, the deer do not pose a threat to By site; the fencing was removed in 2012. European rowan is also one of the most palatable woody species (Van Beeck Calkoen et al. 2022; Caduff et al. 2022), which performs better when fenced (Den Herder et al. 2009) in the case of game overpopulation. Although it grows well in the open-field conditions and it tolerates poor soil (even spoil-heap substrates of brown coal mining origin), unfenced, frequently-browsed rowans can show the worst survival rates and tree quality (Kupka, Dimitrovský 2006). Similarly to monospecific stands of these two species, high palatability of the Fi-Ro mixture, and therefore increased costs of the game damage control, can be expected.

CONCLUSION

Afforestation using alternating rows of rowan and fir impacted positively on properties of the newly developed forest floor and its mineral subsurface soil as follows:

– Both forest floor and topsoil showed higher pH, better sorption complex properties and were higher in magnesium compared to monospecific fir, mixed forest floor was also higher in potassium;

– Mixing lowered the contents of C_{ox}, combustible matter and nitrogen in forest floor whereas all these properties were higher in topsoil;

– Amount of fine dry matter was higher below the monospecific fir, which was reflected in higher C_{ox}, combustible matter and nitrogen pools.

It was confirmed that the admixture of rowan to silver fir stand by alternating row planting significantly improved soil conditions and nutrient return in the two young stands.

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