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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).

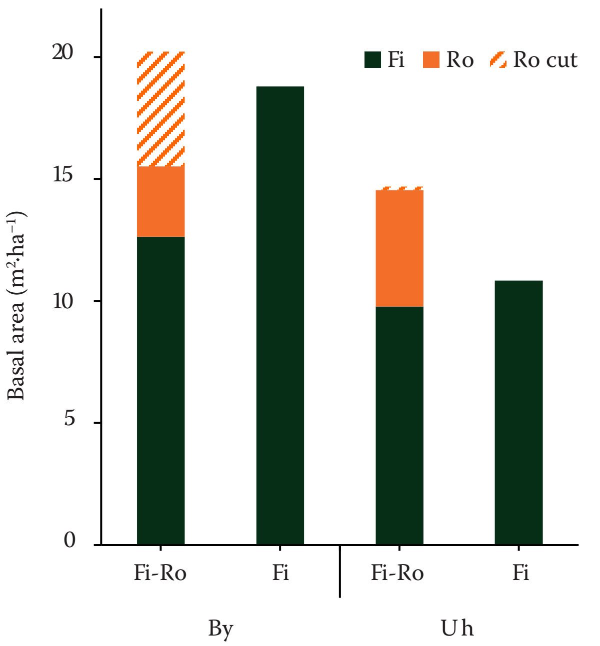

Figure 1. Mixture overyielding illustrated with larger basal areas of mixed treatments (Fi-Ro) and monospecific treatments (Fi) on 20-year-old By and 17-year-old Uh research plots

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 ($BS = BCC / CEC \times 100$); Fi-Ro – fir-rowan; Fi – fir

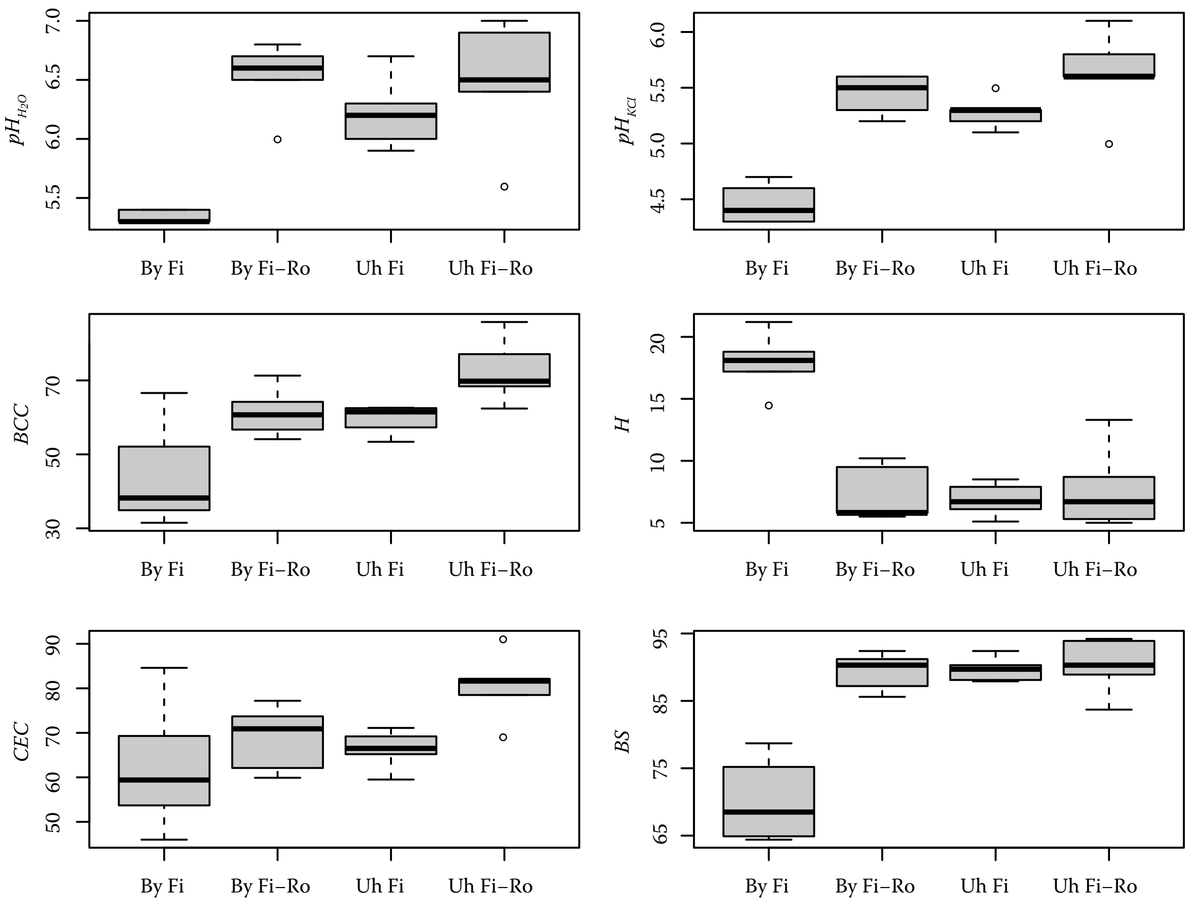

Figure 2. Forest floor qualitative properties according to plot and treatment: soil acidity and sorption complex

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 ($BS = BCC / CEC \times 100$) (%); By – Bystré; Uh – Uhřínov; Fi – fir; Fi-Ro – fir-rowan

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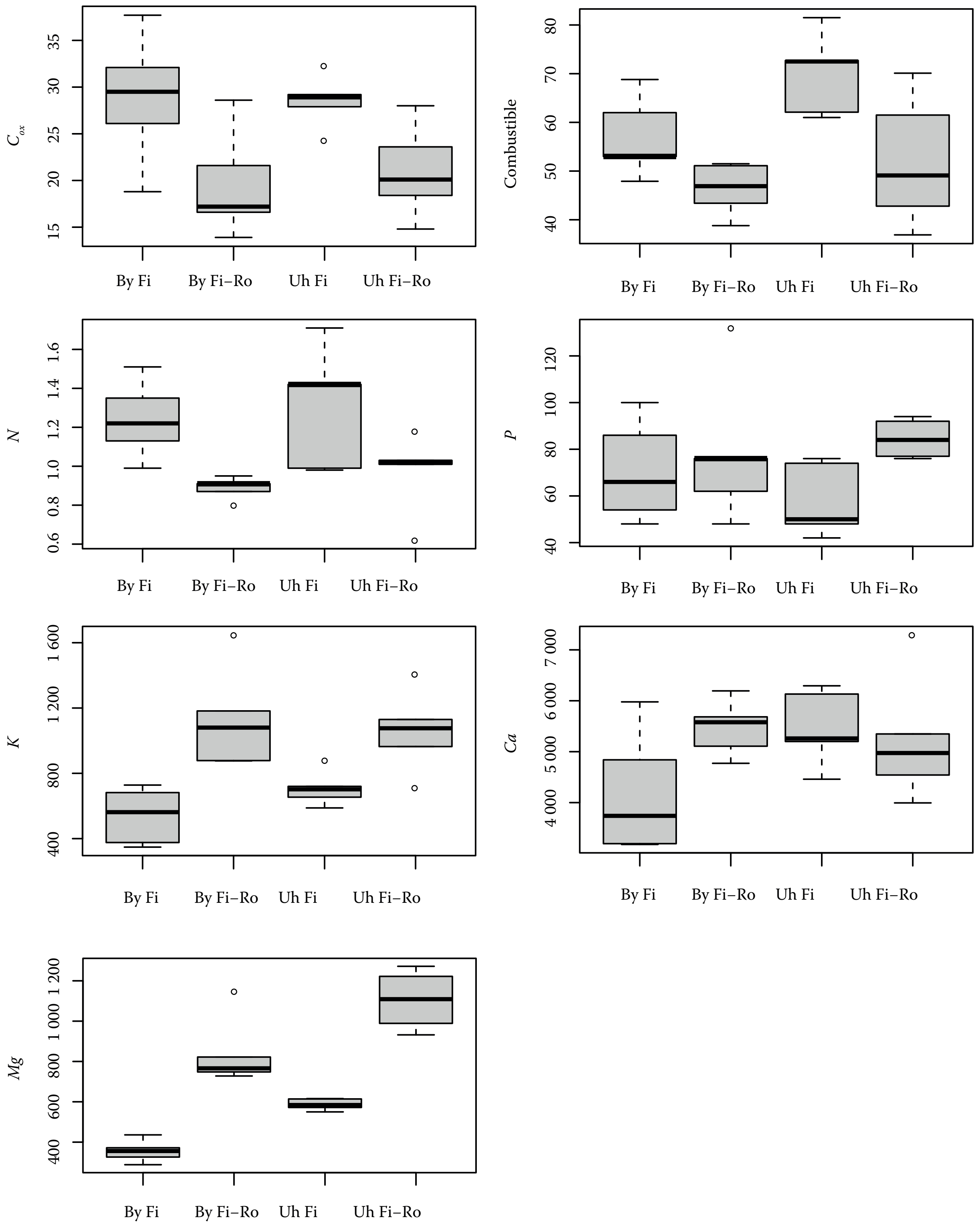

Figure 3. Forest floor qualitative properties and dry mass (*DM* in g·m^{-2}) according to plot and treatment: C_{ox} (%), combustible matter (%), *N* (%) and nutrients by Mehlich III (mg·kg^{-1})

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

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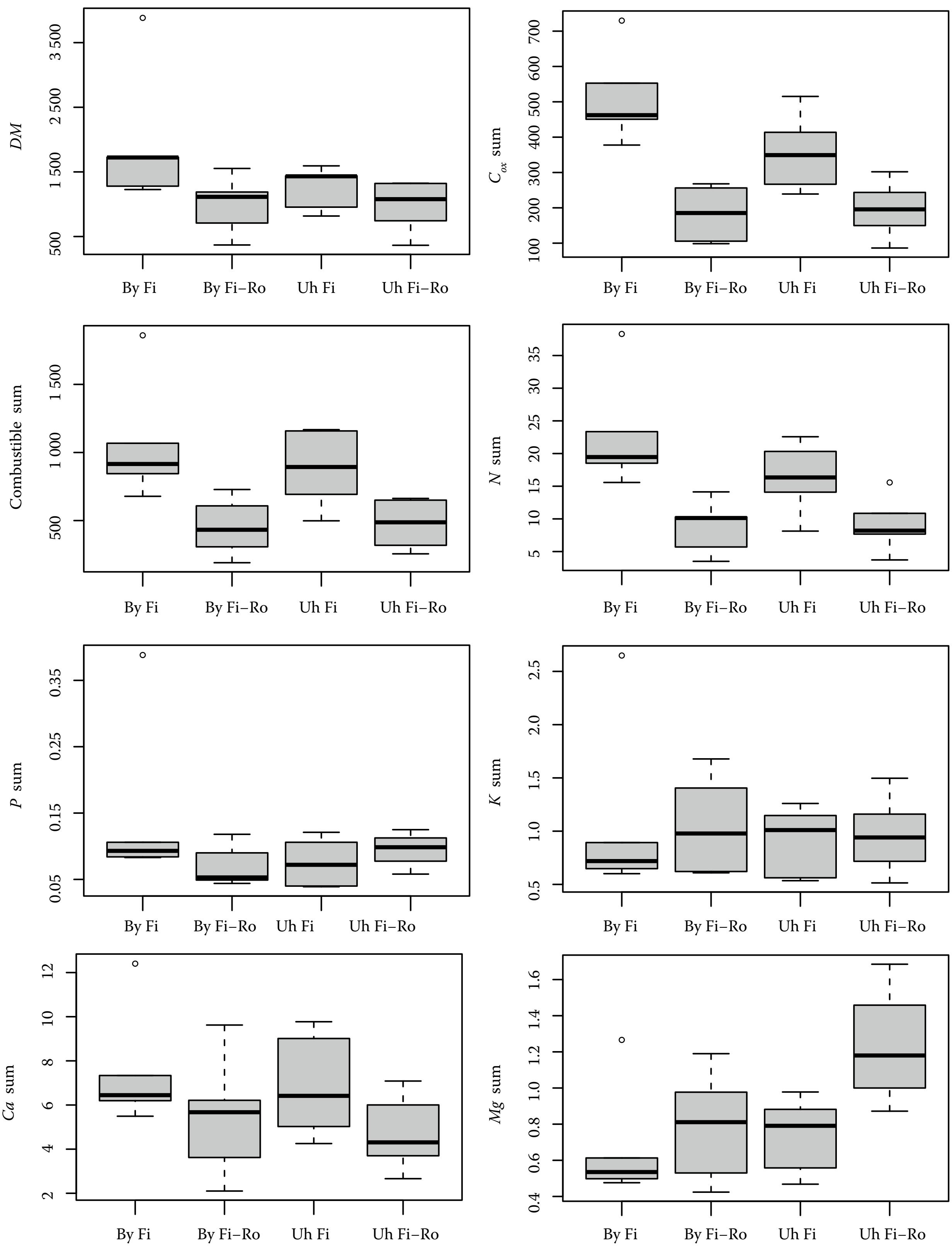

Figure 4. Dry matter (*DM*), combustible matter, and nutrient pools in the forest floor according to plot and treatment in g·m^{-2}

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

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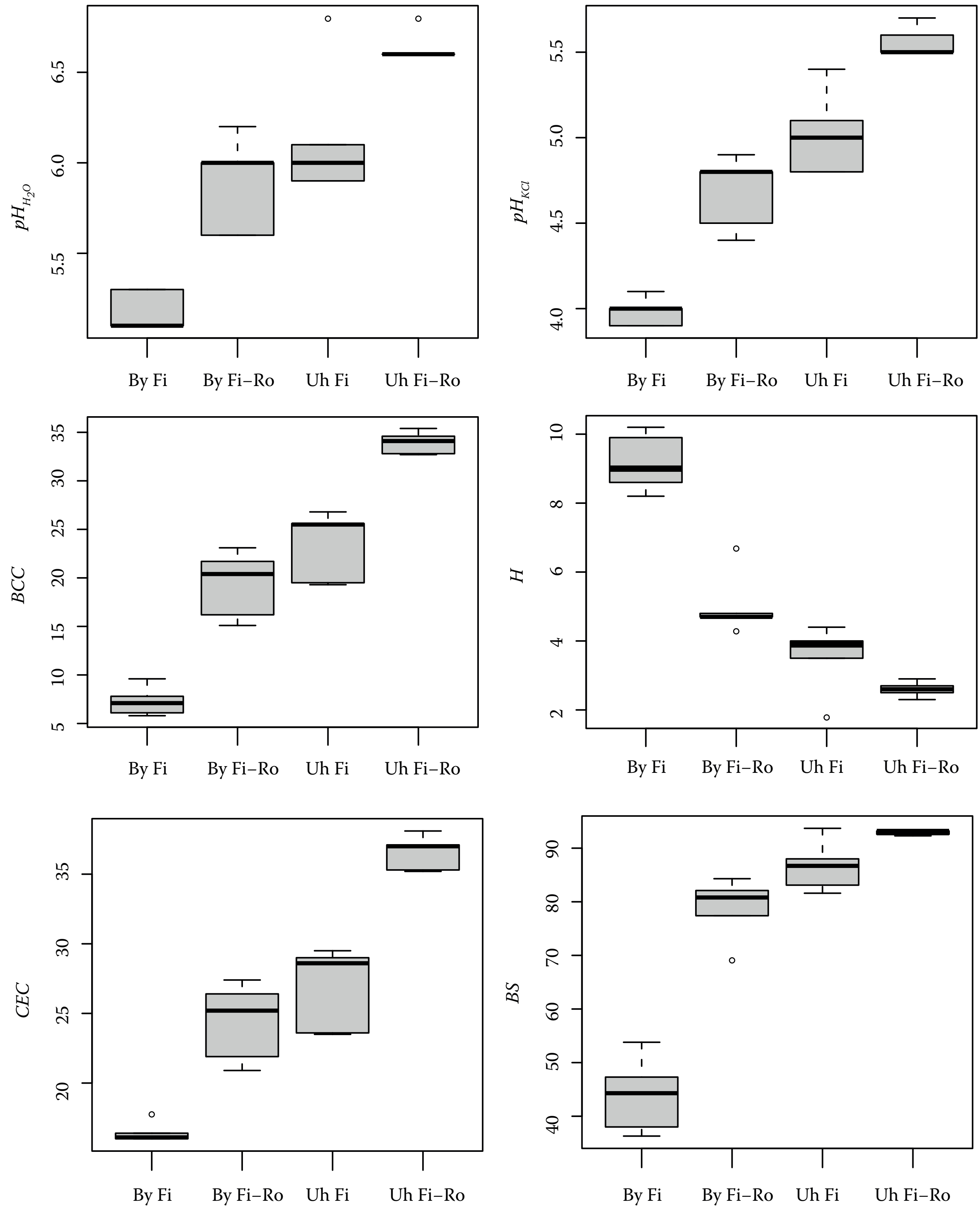

Figure 5. Mineral A horizon qualitative properties according to plot and treatment: soil acidity and sorption complex

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* × 100) (%); By – Bystré; Uh – Uhřínov; Fi – fir; Fi-Ro – fir-rowan

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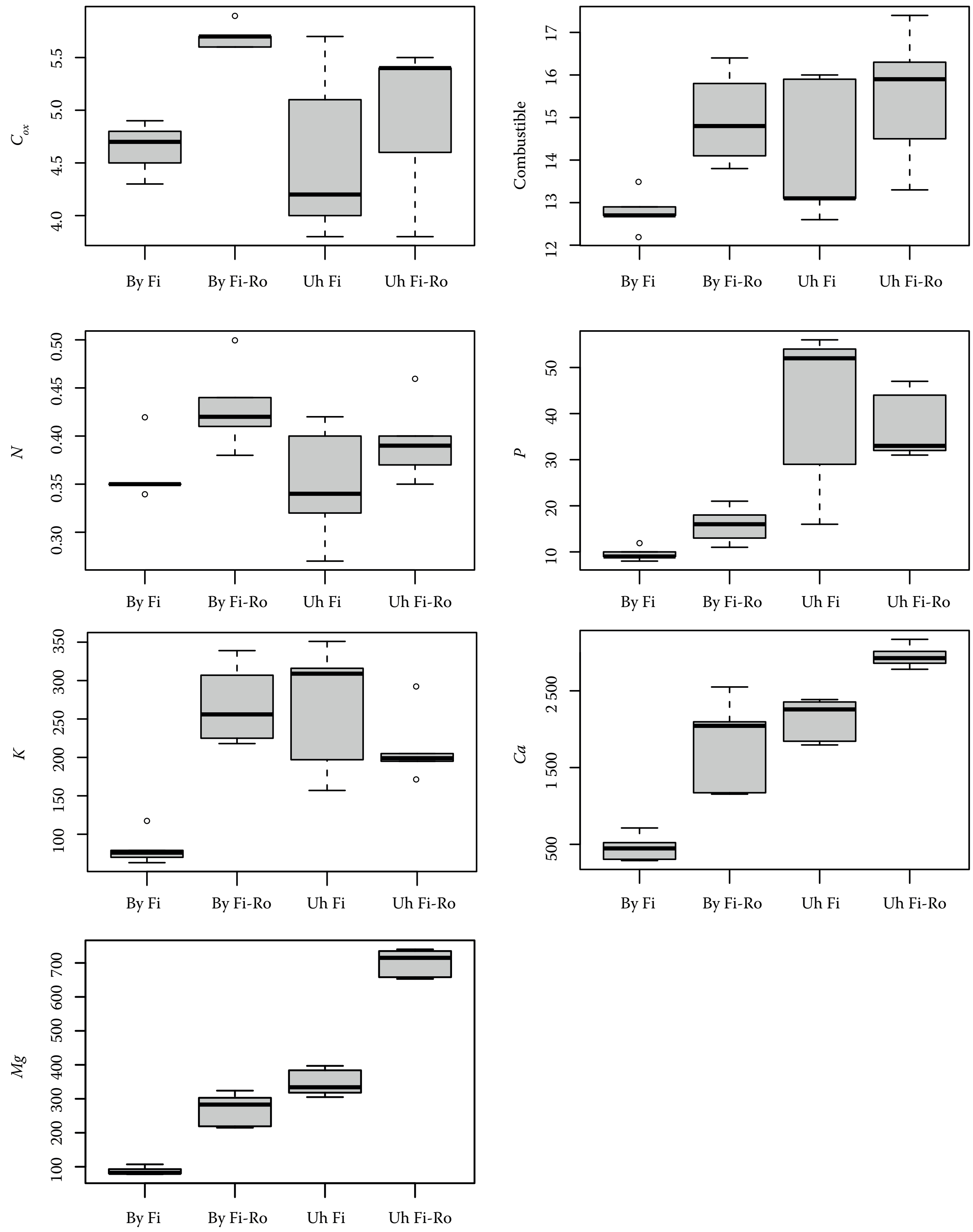

Figure 6. Mineral A horizon qualitative properties according to plot and treatment: C_{ox} (%), combustible matter (%), *N* (%) and nutrients by Mehlich III (mg·kg^{-1})

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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REFERENCES

Augusto L., Ranger J., Binkley D., Rothe A. (2002): Impact of several common tree species of European temperate forests on soil fertility. Annals of Forest Science, 59: 233–253.

Bartoš J., Kacálek D. (2006): Elaboration of afforestation projects – possibilities of tree species composition. In: Neuhöferová P. (ed.): Zalesňování zemědělských půd – výzva pro lesnický sektor. Sborník referátů. Kostelec nad Černými lesy, Jan 17, 2006: 73–80. (in Czech)

Beneš J. (2008): Anthracological analyses in archaeology and paleoecology. Archeologické rozhledy, 60: 75–92. (in Czech)

Caduff M.E., Brožová N., Kupferschmid A.D., Krumm F., Bebi P. (2022): How large-scale bark beetle infestations influence the protective effects of forest stands against avalanches: A case study in the Swiss Alps. Forest Ecology and Management, 514: 120201.

Carnol M., Bazgir M. (2013): Nutrient return to the forest floor through litter and throughfall under 7 forest species after conversion from Norway spruce. Forest Ecology and Management, 309: 66–75.

Čater M., Diaci J. (2017): Divergent response of European beech, silver fir and Norway spruce advance regeneration to increased light levels following natural disturbance. Forest Ecology and Management, 399: 206–212.

Čavlović J., Bončina A., Božić M., Goršić E., Simončič T., Teslak K. (2015): Depression and growth recovery of silver fir in uneven-aged Dinaric forests in Croatia from 1901 to 2001. Forestry: An International Journal of Forest Research, 88: 586–598.

CGS (2019): Geoscience maps. Available at: https://mapy.geology.cz/geo/ (in Czech)

Chládek J., Novotný P. (2007): Various pioneer tree species comparison for utilization in conditions of the Orlické hory Mts. immission area. Zprávy lesnického výzkumu, 52: 226–233. (in Czech)

De Groote S.R.E., Vanhellemont M., Baeten L., De Schrijver A., Martel A., Bonte D., Lens L., Verheyen K. (2018): Tree species diversity indirectly affects nutrient cycling through the shrub layer and its high-quality litter. Plant and Soil, 427: 335–350.

Den Herder M., Kouki J., Ruusila V. (2009): The effects of timber harvest, forest fire, and herbivores on regeneration of deciduous trees in boreal pine-dominated forests. Canadian Journal of Forest Research, 39: 712–722.

Diaci J., Rozenbergar D., Anic I., Mikac S., Saniga M., Kucbel S., Visnjic C., Ballian D. (2011): Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. Forestry: An International Journal of Forest Research, 84: 479–491.

https://doi.org/10.17221/180/2022-JFS

Dobrowolska D., Bončina A., Klumpp R. (2017): Ecology and silviculture of silver fir (*Abies alba* Mill.): A review. Journal of Forest Research, 22: 326–335.

Dušek D., Kacálek D., Novák J., Slodičák M. (2020): Foliar nutrients in current and one-year-old needles of naturally-regenerated Norway spruce and silver fir saplings. Zprávy lesnického výzkumu, 65: 146–152. (in Czech)

Elling W., Dittmar C., Pfaffelmoser K., Rötzer T. (2009): Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. Forest Ecology and Management, 257: 1175–1187.

Hamberg L., Lehvävirta S., Kotze D.J., Heikkinen J. (2015): Tree species composition affects the abundance of rowan (*Sorbus aucuparia* L.) in urban forests in Finland. Journal of Environmental Management, 151: 369–377.

Häsler H., Senn J. (2012): Ungulate browsing on European silver fir *Abies alba*: The role of occasions, food shortage and diet preferences. Wildlife Biology, 18: 67–74.

Kacálek D., Špulák O., Dušek D., Kuneš I., Balcar V. (2013): Species-specific properties of forest floor under mountain conditions. Austrian Journal of Forest Science, 130: 45–59.

Kappen H. (1929): Die Bodenazidität. Berlin, Springer Verlag: 363. (in German)

Klopčič M., Jerina K., Boncina A. (2010): Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: Are red deer an important factor? European Journal of Forest Research, 129: 277–288.

Klopčič M., Mina M., Bugmann H., Bončina A. (2017): The prospects of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst) in mixed mountain forests under various management strategies, climate change and high browsing pressure. European Journal of Forest Research, 136: 1071–1090.

Kopáček J., Cudlín P., Fluksová H., Kaňa J., Picek T., Šantrůčková H., Svoboda M., Vaněk D. (2015): Dynamics and composition of litterfall in an unmanaged Norway spruce (*Picea abies*) forest after bark-beetle outbreak. Boreal Environment Research, 20: 305–323.

Kupka I., Dimitrovský K. (2006): Silvicultural assessment of reforestation under specific spoil bank conditions. Journal of Forest Science, 52: 410–416.

Lasota J., Błońska E., Wanic T., Zwydak M. (2014): The trophic requirements of selected underwood species occurring in forests. Leśne Prace Badawcze – Forest Research Papers, 75: 181–191.

Mauer O., Houšková K. (2017): Zpevňující funkce jedle bělokoré. In: Kacálek D., Mauer O., Podrázský V., Slodičák M. (eds): Meliorační a zpevňující funkce lesních dřevin. Kostelec nad Černými lesy, Lesnická práce: 300. (in Czech)

Mauri A., de Rigo D., Caudullo G. (2016): *Abies alba* in Europe: Distribution, habitat, usage and threats. In: San-Miguel-Ayanz J., de Rigo D., Caudullo G., Houston Durrant T., Mauri A. (eds.): European Atlas of Forest Tree Species. Luxembourg, Publishing Office of the EU: 48–49.

Mehlich A. (1984): Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis, 15: 1409–1416.

Moravčík P., Podrázský V. (1992): Biomass and nutrients accumulation in mountain ash stands located near Pomezní Boudy in Krkonoše Mts. Opera Corcontica, 29: 123–137. (in Czech)

Ministry of Agriculture (2002): Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2001. Prague, Ministry of Agriculture of the Czech Republic: 104. (in Czech)

Ministry of Agriculture (2022): Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2021. Prague, Ministry of Agriculture of the Czech Republic: 47. (in Czech)

Opletal M., Domečka K. (1983): Synoptic geological map of the Orlické hory Mts. Scale 1: 100 000. Prague, Ústřední ústav geologický: 1.

Podrázský V., Ulbrichová I. (2001): Importance of rowan tree as an ameliorative tree species. In: Slodičák M., Novák J. (eds): Actual Problems of Silviculture in Mountain Forests. 3rd Czech-Slovak Scientific Symposium, Opočno, Sept 13–14, 2001: 25–30. (in Czech)

Podrázský V., Remeš J., Ulbrichová I. (2006): Regeneration rate of forest soils in mountain position from the point of view of the surface humus. Zprávy lesnického výzkumu, 51: 230–234. (in Czech)

Polách R., Špulák O. (2022): Prosperity of silver fir planted under preparatory stands of pioneer broadleaves of different stocking and age. Zprávy lesnického výzkumu, 67: 269–277.

Przybylska K., Bujoczek L. (2006): Procesy odnowieniowe w reglu górnym Gorczańskiego Parku Narodowego. Ochrona Beskidów Zachodnich, 1: 109–123. (in Polish)

Robakowski P., Łukowski A., Ye Z.P., Kryszewski A., Kowalkowski W. (2022): Northern provenances of silver fir differ with acclimation to contrasting light regimes. Forests, 13: 1164.

Rouvinen S., Kouki J. (2011): Tree regeneration in artificial canopy gaps established for restoring natural structural variability in a Scots pine stand. Silva Fennica, 45: 1079–1091.

Rybníčková E. (1966): Pollen-analytical reconstruction of vegetation in the upper regions of the Orlické hory Mountains, Czechoslovakia. Folia Geobotanica et Phytotaxonomica, 1: 289–310.

Šach F. (2004): Ameliorating and stabilizing tree species at forest regeneration. In: Peňáz J., Martinek J. (eds): Main Assignments of Silviculture at the Beginning of 21st Century. 5th Czech-Slovak Scientific Symposium, Křtiny, Sept 14–16, 2004: 287– 296. (in Czech)

https://doi.org/10.17221/180/2022-JFS

Šantrůčková H., Vrba J., Křenová Z., Svoboda M., Benčoková A., Edwards M., Fuchs R., Hais M., Hruška J., Kopáček J., Matějka K., Rusek J. (2010): Co vyprávějí šumavské smrčiny – Průvodce lesními ekosystémy Šumavy. Vimperk, Správa Národního parku a Chráněné krajinné oblasti Šumava: 153. (in Czech)

Senn J., Suter W. (2003): Ungulate browsing on silver fir (*Abies alba*) in the Swiss Alps: Beliefs in search of supporting data. Forest Ecology and Management, 181: 151–164.

Špulák O., Kacálek D. (2020): Spontaneous development of early successional vegetation improves Norway spruce forest soil after clear-cutting and renewal failure: A case study at a sandy-soil site. Journal of Forest Science, 66: 36–47.

Svoboda M., Matějka K., Kopáček J. (2006): Biomass and element pools of understory vegetation in the catchments of Čertovo Lake and Plešné Lake in the Bohemian Forest. Biologia, 61: 509–521.

Tesař V., Tesařová J. (1996): Odrůstání smrku s jeřábem v mladých uměle založených porostech v Krkonoších. In: Vacek S. (ed.): Monitoring, výzkum a management ekosystémů na území Krkonošského národního parku. Opočno, Apr 15–17, 1996: 201–209. (in Czech)

Třeštík M., Podrázský V. (2017): Soil improving role of the silver fir (*Abies alba* Mill.): A case study. Zprávy lesnického výzkumu, 62: 182–188. (in Czech)

Úradníček L., Maděra P., Tichá S., Koblížek J. (2010): Woody Plants of the Czech Republic. Kostelec nad Černými lesy, Lesnická práce: 368.

Van Beeck Calkoen S.T.S., Deis M.H., Oeser J., Kuijper D.P.J., Heurich M. (2022): Humans rather than Eurasian lynx (*Lynx lynx*) shape ungulate browsing patterns in a temperate forest. Ecosphere, 13: e3931.

Van Nevel L., Mertens J., De Schrijver A., De Neve S., Verheyen K. (2014): Can shrub species with higher litter quality mitigate soil acidification in pine and oak forests on poor sandy soils? Forest Ecology and Management, 330: 38–45.

Vaněk P., Mauer O., Houšková K. (2016): Evaluation of the growth of European beech, Norway spruce and silver fir planted under the stands of European mountain ash. Zprávy lesnického výzkumu, 61: 25–34. (in Czech)

Vitali V., Büntgen U., Bauhus J. (2017): Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. Global Change Biology, 23: 5108–5119.

Vitasse Y., Bottero A., Rebetez M., Conedera M., Augustin S., Brang P., Tinner W. (2019): What is the potential of silver fir to thrive under warmer and drier climate? European Journal of Forest Research, 138: 547–560.

Volařík D., Hédl R. (2013): Expansion to abandoned agricultural land forms an integral part of silver fir dynamics. Forest Ecology and Management, 292: 39–48.

Zeide B. (1985): Tolerance and self-tolerance of trees. Forest Ecology and Management, 13: 149–166.

Zerbe S., Meiwes K.J. (2000): On the influence of softwoods on vegetation and organic layer of spruce stands - Investigations in a two decades old birch-rowan forest in the upper Solling. Forstwisenschaftliches Centralblatt, 119: 1–19. (in German)

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