Underplanted silver fir and common beech cause changes in root stratification and morphology in mature spruce stands

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Received on February 7, 2018; Accepted on June 17, 2018

Abstract: In this study we analysed changes in distribution and morphological properties of fine roots caused by underplanting of a 110-year-old Norway spruce monoculture by silver fir and common beech. Three different stand structures were investigated: mature spruce underplanted by beech (S/b), by fir (S/f) and mature spruce with natural regeneration of spruce (S/s). We established 3 sample plots per each structure and took 5 soil cores per sample plot (45 cores in total). Soil cylinders of 5 cm diameter were taken up to 40 cm depth. Fine roots (diameter ≤ 2 mm) were extracted from the soil, classified according to tree species, weighted and scanned; their length and surface were quantified and specific root length (SRL) and specific surface area (SSA) were calculated. Root-to-root interaction of spruce and underplanted species led to differences in vertical distribution of roots towards the more homogeneous root density in investigated profile with clear shifting of beech and fir roots into deeper soil layers. Cumulative root fractions of fir and beech in upper 20 cm were lower than those of Norway spruce. The share of spruce roots in depth under 20 cm never exceeded 20%. The co-occurrence of beech and spruce in small spots was about twice as frequent as the co-occurrence of spruce with fir. We found differences in SRL and SSA between broadleaves (beech) and conifers, while the values of beech morphological parameters increased significantly, when mixed with spruce. We assume that the competitive strategy of beech is based in changing its root morphology, whereas silver fir is inclined to extend its biomass.

Keywords: fine root stratification, Norway spruce, root morphology, underplantings

Abbreviations: FRB, fine root biomass; SRL, specific root length; SSA, specific surface area of roots

Introduction

Since the middle of 18th century, the tree species composition of natural forest stands in central Europe has been considerably changed in favour of conifers. Norway spruce and Scots pine have been artificially regenerated and cultivated in the form of monoculture stands, both within and beyond their natural range (Johann et al. 2004). Apart from high susceptibility to the primary damage by abiotic and anthropic factors (Kulhavý et al. 2004), Norway spruce growing on the non-native sites also suffers from secondary damage by bark beetles and pathogens (Wermelinger 2004, Schlyter et al. 2006). However, Norway spruce still remains economically very important tree species and maintaining of its adequate proportion in forest stands is justifiable. The conversion of monocultures to stands with considerable admixture of broadleaves and/or silver fir is expected to improve the sustainability and production of ecosystems actually dominated by Norway spruce. One of the possible silvicultural strategies, appropriate to introduce sensitive, shade-tolerant broadleaves and silver fir, is the underplanting of a mature spruce stand (Löf and Oleskog 2005, Löf et al. 2007) extended in some cases with the target diameter harvesting (Kenk and Guehne 2001).
Mature spruce trees are strong competitors, which affect the growth performance and morphology of underplanted seedlings (Spiecker et al. 2004). Apart from the negative affecting, overstory may facilitate the environmental condition required by understory, and total biomass accumulation and productivity of the mixed stands can be higher than that of monocultures. Čater and Simončič (2010) found that both fine and coarse beech root biomass of underplanted beech seedlings increase by increasing mature stand density i.e. by increasing light intensity. On the single-tree level, the influence of overstory on the underplanted root systems of seedlings causes the modification of quantity (Čater and Simončič 2010), horizontal and vertical distribution (Casper and Jackson 1997, Borken et al. 2007) and morphological properties of fine roots (Ammer and Wagner 2002, Bolte and Villanueva 2006, Meinen et al. 2009, Rewald and Leuschner 2009).

Kelty (2006) supposed that species, which differ substantially in characteristics such as root depth and phenology, have a good ecological combining ability resulting in greater total stand biomass. Hendricks and Bianchi (1995) in the research of Douglas fir and Beech mixed stands concluded that root systems of both tree species might profit by temporal difference in growth. Beech as slow-growing tree species produces higher biomass due to the expansion of fine roots only after the culmination of Douglas fir height growth. Göransson et al. (2016) found an overyielding belowground of 16–41% in mixed stands of Fagus sylvatica, Betula pendula and Alnus glutinosa, depending on water availability. Brassard et al. (2013) demonstrated that both the fine root production and biomass increases in mixed stands of coniferous and broadleaves compared to monospecific stands. In contrast to this, Meinen et al. (2009) found that the fine root biomass of mixed stands was not affected by the number of tree species present, which contrasts with the more marked differences in above-ground structure among the stands.

The change in the stratification of fine roots is an important adaptation mechanism to soil conditions (Meier and Leuschner 2008) or root to root interaction (Gale and Grigal 1987, Jackson et al. 1996). Segregation of root systems in both vertical and horizontal directions can significantly reduce the competition between species as shown by several plant communities (Hutchings and John 2003). Spatial and temporal separation is also described by Casper and Jackson (1997) as traits that strongly influence belowground competitive ability.

Besides niche partitioning, the morphological plasticity of fine roots is an excellent adaptation mechanism of plant to changes in the soil environment (Ostonen et al. 2007, Borja et al. 2008, Brunner et al. 2009). Trees that suffer from strong interspecific or intraspecific competition tend to have higher specific root length (SRL), and bigger specific root surface area or number of root tips per root length unit. Fujii and Kasuya (2008) found nearly double the value of specific fine root length of Pinus densiflora grown in an intensely competitive environment of dense Chamaecyparis obtusa, compared to environment with reduced competition. According to Bolte et al. 2013, beech is able to raise significantly its SRL, while growing with spruce competitors. To the contrary, Meinen et al. (2009) reported that tree species were rather conservative regarding the morphological plasticity of their roots and also the vertical fine root distribution patterns.

Our study was focused on finding differences in root mass, their stratification and morphological properties of fine roots of underplanted silver fir (Abies alba), European beech (Fagus sylvatica) seedlings and naturally regenerated Norway spruce (Picea abies) saplings growing under the canopy of a mature Norway spruce monoculture. The main objectives of this study were: (i) to quantify the mass of fine roots according to vitality (dead mass and biomass) and tree species and its stratification in soil profile, (ii) to evaluate the root to root interaction between underplantings and mature spruce stand, and (iii) to describe the fine root morphological traits of all three species and the modification of these traits by root to root interaction.

Materials and Methods

Study site

The 100-year-old pure Norway spruce stand is located in northern Slovakia within the Oravské Beskydy Mts. (49°23’N 19°10’E, 850–900 m a.s.l.). The mean annual precipitation (1981–2010) is 1160 mm and the mean annual temperature 5.2°C. The bedrock is formed by flysch with the dominance of sandstones, and the soil type is gleyic cambisol. In this region, pure Norway spruce stands were established artificially during the 19th century, and nowadays the second generation of spruce monocultures reaches the end of their cutting cycle. The proportion of Norway spruce in tree species composition in original Medio-European acidophilous beech forests (Luzulo-Fagetum - according to Natura 2000) should not exceed 35%,
In each plot, we recorded the location of all stems in mature stand using the polar coordinates. For each living stem, we measured dbh (diameter at breast height), height, crown base height, and crown radii in four cardinal directions. Using this data, the basic characteristics of the mature stand were calculated (Table 1).

Fine root sampling and processing

In October 2013, during two consecutive days, we selected randomly 5 saplings on each sample plot. We located the points of fine root sampling within the crown projections at the distance of ½ of crown radius, i.e. ca. 30 cm from the root collars of the selected sapling. This sampling design guaranteed that the whole fine root sample was taken either from undisturbed soil (outside of the planting hole) and within the belowground influence zone (Casper et al. 2003) of underplanted or naturally regenerated saplings. From each sample plot, we took 5 soil cores, i.e. 15 cores per stand structure and 45 soil cores in total. All cores were taken during two consecutive days.

Soil cores were taken with a hollow drill (the inner diameter of 50 mm) up to 40 cm of mineral soil depth and then divided into the sections that corresponded to the whole humus layer and 0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm mineral soil layers. The humus horizon was analysed as a whole and separately. The soil sections were considered as “small spots”, i.e. as small-scale spatial frame for the evaluation of interspecific root-to-root interaction.

In the laboratory, roots were washed out from the mineral soil or picked from the litter,
respectively. We separated and further processed only fine roots (with diameter below 2 mm) and categorized as live or dead according to the macroscopic or microscopic criteria (Leuschner et al. 2001). Live roots were classified and separated by the tree species (spruce, beech, and fir) considering differences in fine root features as root morphology, topology, colour and ramification (Leuschner et al. 2001, Meinen et al. 2009). Distinctions between tree species were unambiguous, but roots of natural regeneration of spruce cannot be distinguished from roots of mature spruce stand. Therefore, all parameters of fine roots for S/s plots were quantified for “spruce” – regardless of the generation (mature spruce vs. natural regeneration). All classified fine roots were immediately scanned using high-resolution Epson Expression 10000 XL scanner (1200 dpi). Root length, volume, surface and number of root tips were determined on all living roots using the WinRhizo 2009c™ software. After scanning, the roots were dried for 72 hours at the temperature of 75°C and weighed to the nearest 0.1 mg. The live fine root mass (hereafter “biomass” or “fine root biomass” FRB) and dead root mass (hereafter “necromass”) were quantified in g m\(^{-2}\). Specific root length (SRL) was provided in m per g of dry weight of fine roots, specific surface area (SSA) in cm\(^2\) per g of dry fine roots and both parameters were determined for living roots of each tree species. Processing and scanning of all samples was finished in December 2013.

Data analysis

One-way ANOVA and Tukey test were used to test for significant differences in fine root biomass among the stand structure. Differences between FRB of fir and FRB of beech as well as those between SRL and SSA of pure and mixed spots for every tree species were tested by Student t-test for independent samples. The probability of fit to a normal distribution was tested by the Kolmogorov-Smirnov test. The homogeneity of variances was tested by Levene’s test. All statistical analyses were conducted with the Statistica 6.0 package. To fit and compare the distributions of FRB in the soil profile we used the equation by Gale and Grigal (1987):

\[
y = 1 - \beta^x
\]

where \(y\) is the cumulative root fraction, \(x\) is the depth, and \(\beta\) is the „extinction parameter“, that characterizes the shape rooting distribution.

Result

Fine root mass (FRB) and its vertical distribution

Total fine roots mass in whole soil profile ranged between 274.0 g m\(^{-2}\) (S/s structure) and 354.0 g m\(^{-2}\) (S/b structure) and did not differ significantly between the stand structures (\(F(2.42) = 0.91; p = 0.41\)). Fine root biomass of Norway spruce did not differ between stand structures significantly. On the contrary to spruce, the differences between FRB of beech and FRB of fir was significant (\(t(28) = 2.13; p = 0.045\)) despite high variability (Table 2). FRB of Norway spruce was still significantly accumulated in the layer up 0–10 cm (56.3–68.1% of total FRB), while the FRB of underplantings was evenly distributed in the upper half of study soil profile (Fig. 1).

Comparison of the increase in cumulative fine root fractions with the soil depth, based on the asymptotic equation \(y = 1 - \beta^x\) (Gale and Grigal 1987, Jackson 1996) revealed the differences between Norway spruce and underplantings in the vertical distribution of fine roots, unaffected by their quantity. The decrease of beech and fir FRB with increasing depth was always markedly slower than the decrease of FRB of Norway spruce in all stand

### Table 2. Mean fine root masses (± standard error) according to tree species and vitality in three stand structures. ANOVA was calculated separately for total mass and FRB of spruce.

| Stand structure   | Fine root biomass (g m\(^{-2}\)) | Dead root mass (g m\(^{-2}\)) | Total mass (g m\(^{-2}\)) |
|-------------------|----------------------------------|-------------------------------|---------------------------|
|                   | Spruce  | Fir   | Beech | Spruce  | Fir   | Beech | Spruce  | Fir   | Beech |
| Spruce/spruce (S/s) | 247 ± 35 α | 27 ± 6 | 274 ± 39 A | | | | |
| Spruce/beech (S/b)   | 278 ± 43 α | 33 ± 13 * | 354 ± 48 A | | | | |
| Spruce/fir (S/f)    | 196 ± 32 α | 102 ± 34 * | 328 ± 41 A | | | | |

Identical letters (Latin for total mass and Greek for spruce biomass) represent homogenous groups according to Tukey test (\(p<0.05\)). Differences between FRB of beech and FRB of fir were tested by t-test for independent samples (* represents \(p<0.05\)).
structures (Fig. 2). The calculated extinction coefficients $\beta$ indicate that half of fir and beech FRB was concentrated in the top 12 cm or 13 cm respectively. The half of Norway spruce FRB was located close to the mineral soil surface (up to 3.0–5.5 cm), and more than 90% of FRB was located in the layer 0–20 cm.

**Interspecific competition.**

The co-occurrence of fir and spruce fine roots in small spots (100 cm$^3$ of soil volume) was rather infrequent compared to beech and spruce roots interaction. From all the samples containing fir roots, only 28% contained also Norway spruce roots, while the co-occurrence of beech and spruce was approximately two times more frequent (Table 3). In mixed stand structures, the frequency of co-occurrence of spruce and underplantings roots was not significantly influenced by soil depth. Biomass of spruce fine roots was always higher when growing in pure (single-species) spots, although the differences between pure and mixed (two-species) spots were significant only in the S/f stand structure. Opposite to beech, higher FRB of fir was found on pure spots.

In the plots with underplantings, significant differences in response of fine root morphology of
underplanted beech and fir to the presence of spruce roots were found. For beech, we found significant ($p = 0.037$) difference between pure and mixed spots in the case of SRL. SRL of Silver fir and Norway spruce remained constant, unaffected by the presence of other tree species. The presence of roots of other tree species affected the specific surface area (SSA) only on beech spots ($p = 0.048$). Although the relative differences in SSA of beech were smaller than in SRL, SSA on beech spots was almost two times higher than SSA of conifers (Fig. 3).

**Discussion**

The total fine root mass of investigated plots were within the range reported for the pure or coniferous dominated forest of temperate zone by Finér et al. (2007), Finér et al. (2011) and Konôpka and Lukac (2013). According to Table 2, the proportion of dead fine root mass from total mass was low and reaches only 9.2–12.1%. The total biomass (biomass of spruce and underplanted species) to necromass ratio reached very high values of 7.24–9.80. In Scots pine stands with comparable FRB, Makkonnen and Helmisaari (1998) found high seasonal differences in of biomass to necromass ratios, which varied between 0.17 and 5.82. In pure spruce stands on soils with different acidity, Godbold et al. (2003) confirmed low values of biomass to necromass ratio (0.5–1.1). Necromass is considered to be the most variable compartment of the total fine root mass (Brunner et al. 2013) due to the different decay speed of particular thickness fraction and seasonal pedoclimatic variability in temperate forests. Therefore the mass and morphological parameters of live roots are of more informational value for the analysis of influence of underplantings admixture.
Although the underplanted tree species did not affect the total spruce FRB (Table 2), they markedly affected vertical distribution in its belowground competition zone (Casper et al. 2003, Swinning and Weiner 1998). The shape of the vertical distribution of spruce FRB in all stand types was similar to the conspicuous maximum in 0–10 cm soil layer. However, stand types differed in the absolute value of this maximum (Fig. 1) and in the proportion of FRB in 0–10 cm soil layer on total spruce FRB. The weight ratio of spruce roots in the first two layers (0–10 cm, 10–20 cm) was approximately the same (3:1) on both plots with underplantings, but 6:1 on the pure spruce plot. Considering the foundation that the lowest total FRB in S/s and more than 2/3 of FRB concentrated above the 10 cm in soil layer, we assume that FRB of Norway spruce in the uppermost soil layer was elevated also by the roots of spruce natural regeneration. Both underplanted tree species had a similar shape of the distribution of fine roots even in different FRB in the soil profile, and a clear shift to the layer 10–20 cm was evident. Even though the influence of the vertical distribution of fine roots by the different type of root system (Köstler et al. 1968) cannot be excluded also in the youngest growth stages, growth performance of fine roots was mainly affected by the other factors such as nitrogen content (Hertel 1999), water availability (Brunner et al. 2009), or belowground competition (Curt and Prévosto 2003, Bolte and Villanueva 2006).

The admixture of fir and beech into the pure spruce stand leads to an increase of rooting homogeneity in the entire soil profile by two complementary ways: (a) underplantings occupy deeper soil layers than pure spruce stands and (b) spruce increases the concentration of its roots in deeper soil layers, even if its total biomass (in whole soil profile) is lower than that of the pure plots. Our results are in line with the findings that the formation of forest stand composed of several tree species leads to a change in the stratification of fine roots rather than to fine root overyielding (Hendricks and Bianchi 1995, Schmid and Kazda 2002). On the other hand, Meinen et al. (2009a) and Meinen et al. (2009b) found, that tree species diversity affected neither stand fine root biomass nor their vertical distribution patterns. The shift of fine roots of beech under spruce roots is often evident (Schmid and Kazda 2002, Čater and Simončič 2010, Kalliokoski et al. 2010). Rewald and Leuschner (2009) reported that beech seems to be superior competitor belowground in a variety of Central European mixed forests. Schmid and Kazda (2002) found that in mixed spruce-beech forests on stagnic kambisol, spruce fine roots were even more concentrated to the uppermost soil layers, in contrast to pure spruce stand. Beech fine roots were evenly distributed in the entire soil profile or were often located in deeper soil layers under spruce roots, and lead to shallower root system of spruce. In our case the concentration of FRB in pure spruce plots was highest in the uppermost soil layer. The admixture of other tree species even in very low share of aboveground biomass leads to a more homogenous rooting density on whole soil profile. Bolte et al. (2013) observed that the changes of vertical routing patterns occurred mainly in the two-species systems, mixtures of conifers with broadleaves or of early- or mid-successional tree species with late-successional species. The rooting variations of beech were considered by Bolte and Villanueva (2006) as the main reason for niche partitioning of tree species in soil space, i.e. for changes in the stratification of their fine roots in soil. As a consequence of the reconstruction in the stand surveyed in our study, rapid increase of ecological importance of plastic rooting beech and subsequently the replacement of more conservative rooting Norway spruce as dominant tree species by underplantings is to be anticipated. We assume that these changes will impact belowground competition in the overlap zones stronger than the increase of the tree species richness, e.g. the formation of mixed underplanting groups of fir and beech.

Even that different distribution of FRB of spruce and underplanted species was found (Fig. 1), the occurrence of both spruce and underplantings fine roots in small spots was not rare. We found that beech roots often occurred together with spruce roots, whereas the co-occurrence of fir and spruce was less frequent. Inter- and intraspecific segregation of root systems in time and space are frequently recorded (Hutching and John 2003). Niche differentiation is considered as mechanism by which plants try to reduce the intensity of mutual competition (de Kroon et al. 2003). Our results indicate that niche partitioning is a commonly present in underplantings of Silver fir. In more than 70% of cases, fir roots occurred without presence of spruce roots. Overlapping of beech was approximately as common as niche partitioning. Research focused on competition of broad-leaved tree species by Rewald and Leuschner (2009) found that fine root systems of different tree species seems not territorial, but broadly overlapping. The relationship of underplanted fir and mature spruce can be considered as a weak competition of fine root system within belowground zones influenced by the underplanted trees. Beech is, compared to silver fir, stronger competitor under mature Norway spruce stands. Beech occurred more frequently in mutual niches with spruce than fir and was able to establish and
increase the concentration of its fine roots in spots with higher concentration of spruce roots (Table 3).

In many cases, elimination of competition asymmetry by changing roots allocation may be more important in determining the competitive interactions than physiological mechanisms. Plasticity in growth form (e.g. increasing of SRL) in response to neighbours is another way of adaptation to avoid or at least reduce competitive suppression (Schwinning and Weiner 1998). We found that both strategies were present in both underplanted tree species, albeit in different level. Morphological adaptation of fine roots of all tree species and their high concentration in small spots can be considered as an attempt to obtain nutrients in nutrient-rich patches (Schenk 2006) in heterogenous soil environment. In our case, the morphological parameters of fine roots (Fig. 3) of fir and spruce were not different in the mixed and pure soil patches. A significant difference of SRL and SSA was found in beech. In all cases, SRL were significantly higher in beech compared to conifers, which corresponds with Ostonen et al. (2007), who stated that evergreen conifers have thicker roots and lower SRL than coexisting deciduous tree species. Our results confirmed that beech effectively replaced lower biomass with higher length and larger surface of roots, i.e. higher values of SRL and SSA to the border, where there was no significant difference in the length of the fine roots of beech and spruce in either mixed or pure soil patches.

**Conclusion**

The admixture of sufficient tree species such as silver fir or common beech in form of underplantings in mature spruce monocultures causes changes in the stratification as well as in the fine root morphology of Norway spruce, beech and fir. Even though the overyielding in total FRB was not detected, the FRB of mature spruce was not significantly affected by beech or fir. We assume, that shifting of fine root of fir and beech into deeper soil layers and thus placing their beneath spruce fine roots can be explained by the effort of underplantings to facilitate their requirements for soil resources.

**Acknowledgements:** This project was financially supported by the Slovak scientific and grant agency (VEGA), grant nr.: 1/0492/17/8 – “Regeneration processes of mixed deciduous and mountain spruce natural forests and possibility of their use in the conversion of commercial spruce forests”.

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