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A belowground perspective of temperate old-growth forests: Fine root system structure in beech primeval and production forests

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ABSTRACT

Old-growth forests differ from managed forests by a generally higher biodiversity, larger carbon stores, and greater heterogeneity of aboveground structures. It is not known whether the aboveground structural diversity of old-growth forests is mirrored in root system structure, e.g. by greater root biomass, the occurrence of root gaps, and a different fine root morphology. We studied the fine root system of beech (roots < 2 mm in diameter) in three development stages (initial, optimum, terminal) of a primeval beech (*Fagus sylvatica*) forest in the Slovakian Carpathians and compared it to a nearby beech production forest close to harvest. We conducted root coring to 30 cm depth in 16 plots (84 sampling locations) with subsequent detailed analysis of fine root bio- and necromass, and fine root morphology. Despite lower aboveground wood mass, the production forest had on average about 15% larger beech fine root biomass and necromass totals than the primeval forest, though the differences were not significant. Contrary to expectation, the spatial variation of fine root biomass in the 0–30 cm layer in the structurally diverse primeval forest was not higher than in the more homogeneous production forest. Also, fine root morphology did not differ between primeval and production forest.

Across the three primeval forest stages, fine root biomass tended to peak in the optimum stage, but the difference was not significant, and no alteration in fine root morphology across the stages was detected. Fine root necromass increased significantly from the initial to the terminal stage, pointing at higher fine root mortality and/or reduced root decomposition in forest patches with many senescent trees and canopy gaps. Yet, soil fertility did not decrease toward the terminal stage of forest development. From the fine root biomass data, no root gaps could be detected in the terminal stage, perhaps due to rapid gap colonization by beech saplings. We conclude that the structural differences between the fine root systems of beech primeval and production forest were relatively small. Canopy heterogeneity seems to be a less important factor determining root distribution in the primeval forest than soil heterogeneity, which can be high in production forests as well.

1. Introduction

The few remaining old-growth or primeval forests of the temperate zone have received considerable attention in recent time due to their rich and unique biodiversity, their value as study objects for understanding forest dynamics processes, and their putative role in the carbon cycle (Korpel, 1995; Kucbel et al., 2012; Glatthorn et al., 2017a). These forests have usually been associated with the occurrence of large trees of high age, high deadwood amounts, and the presence of canopy gaps of variable size, when compared to managed forests (Oliver and Larson, 1996; Wirth et al., 2009). Gaps originating either from the death of individual trees or external disturbance events are an important structural element of old-growth forests (Drössler et al., 2016; Feldmann et al., 2018a). Gaps can promote the establishment and growth of tree seedlings and saplings and the turnover of tree generations, thus driving forest dynamics. In production forests, the natural disturbance regime is usually overlain by management operations, which alter the population structure and density of the stand, create artificial canopy gaps, and often lead to topsoil disturbance and soil compaction, when harvesters are used (Ampoorter et al., 2012). Moreover, many production forests in the temperate zone, especially in Europe, are planted and thus represent cohorts of even-aged trees. Understanding the effects of management on the functioning of forest ecosystems is important in the face of climate warming and associated putative threats to forest health. Management could potentially increase the stress exposure of forests, for example, if it creates cohort stands which use up resources more completely, disturbs the soil, or creates a stressful microclimate with lower air humidity. Alternatively, management may decrease drought stress by reducing stem density or removing the shrub layer, thereby reducing water consumption and

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Table 1
Soil chemical characteristics of the primeval forest plots (initial, optimum, terminal stage; each 4 per stage) and the production forest (n = 4) in Kyjov. Per plot, each four samples were collected at 0–10 cm depth which were pooled for analysis. CEC – cation exchange capacity. SOC – soil organic carbon. P_{resin} – resin-exchangeable P. base saturation – proportion of Ca, K and Mg in CEC.

	pH		Total N	SOC	C/N ratio	P_{resin}	CEC	Base saturation
Forest type	H_2O	KCl	mg g^{-1}	mg g^{-1}		µg g^{-1}	µmol_c g^{-1}	%
Primeval								
Initial	4.13	3.83	5.9	81.9	13.7	2.72	170.4	25.3
Optimum	3.97	3.74	6.3	87.8	13.8	3.56	169.2	15.1
Terminal	3.85	3.66	7.5	104.4	13.9	3.78	213.6	9.3
Production	3.89	3.67	5.3	76.5	14.3	2.32	161.3	9.4

drought stress (D'Amato et al., 2013). Management effects can be assessed by comparing several stands with different management intensity, or by contrasting managed and unmanaged (primeval) forests, which represent a valuable reference.

Comparative studies on the structure and dynamics of temperate primeval forests have mostly focused on the aboveground compartment, while the root system has largely been ignored. Given that about 30–50 percent of a tree's annual carbon gain is invested in the root system (Scarascia-Mugnozza et al., 2000; Leuschner and Ellenberg, 2017) and a considerable proportion of soil organic matter is typically derived from roots (Rasse et al., 2005; Comas and Eissenstat, 2009), the belowground compartment is of high functional significance for forest ecosystems. While several studies have examined the effects of forest harvesters on tree root growth (e.g. Heilman, 1981; Gebauer and Martinková, 2005), it is not known, whether forest management more generally has a long-term impact on the size and structure of the root system. The root system of primeval forests could differ from that of managed forests in several ways. (1) Due to a generally higher standing aboveground biomass, primeval forests could have larger and more deep-reaching root systems than production forests of the same species. (2) It could also be that the large canopy heterogeneity in primeval forests is associated with a similarly high heterogeneity in the root system, i.e. as a belowground reflection of the highly variable size of trees and leaf areas. Pockets with high root density could occur next to patches with low root density, and canopy gaps could correspond to root gaps. (3) This spatial heterogeneity could result in changes in root density across different forest development stages. We would expect higher root density in the initial (pole-sized) and optimum stages of the forest cycle, where trees have higher growth rates and stem densities are high, while root density should be lower in the terminal stages with tree senescence and death and the formation of larger gaps. Change in rooting patterns with stand dynamics could also result from soil properties that change from the initial to the terminal stage (Kutsch et al., 2009). These questions have not been addressed in a study with a systematic design.

We conducted an in-depth study of the fine root system (roots < 2 mm in diameter) of European beech (*Fagus sylvatica* L.) in a primeval forest and a nearby production forest in the Carpathians of eastern Slovakia in order to (i) search for differences in stand fine root biomass between managed and unmanaged beech forests, (ii) examine changes in fine root biomass across the different stages of the natural forest cycle, (iii) investigate the spatial heterogeneity of the fine root system in a primeval forest, in particular with respect to the occurrence of root gaps, and (iv) assess the evidence for possible differences in fine root morphology between managed and primeval forests.

2. Methods

2.1. Study site and sampling design

The study was conducted in the forest reserve Kyjov and a nearby production forest of European beech (*Fagus sylvatica*) in the Vihorlat Protected Landscape Area south of the city of Snina in eastern Slovakia (western Carpathian Mountains; 48°53′ N, 22°06 E). The Kyjov Reserve is considered a primeval forest at montane elevation (700–870 m a.s.l.), which apparently has not been affected by human intervention for several centuries (Korpel, 1995). It is part of the UNESCO World Heritage Site 'Primeval Beech Forests of the Carpathians and Ancient Beech Forests of Germany'. The directly adjacent production forest is an age-class forest (ca. 90–100 yr old) shortly before harvest. Both stands can be assigned to the Fagetum dentarietosum glandulosae community (Bohn et al., 2003) with a sparse herb layer. The climate of the site is humid and cool (5.2–5.7 °C mean annual temperature, 950–1000 mm mean annual precipitation). The slightly sloping terrain (11–12°) faces north- to eastwards. The primeval forest consists of 99% beech, while the production forest contains a few *Acer pseudoplatanus* L., *A. platanoides* L. and *Fraxinus excelsior* L. trees (proportion of beech stems: 94%). The soils are acid Dystric Cambisols with moderate to low base saturation (topsoil pH_{H2O} around 4; base saturation 25%) developed in clayey loam on Andesite as bedrock, covered on top by a 3 cm thick organic moder layer (see Table 1). The topsoil consists of 33% sand, 42% silt and 25% clay. Due to the fine particle-rich soil texture, the water storage capacity is moderate to high. Despite largely different forest structure, primeval and production forest are similar in stem density, stand basal area, mean diameter at breast height, and dominant height (Table 2). Measurement of stand leaf area index with optical and leaf mass-based methods gave similar values for both stands (range 6.1–8.4 m^2 m^{-2}; Glatthorn et al., 2017b).

The primeval forest consists of a small-scale mosaic of patches assignable to the initial, optimum or terminal stages of a natural forest development cycle according to the definition given in Feldmann et al. (2018b). The stages differ in important characteristics of above-ground stand structure (Table 3). The production forest with its cohort structure is much more homogenous and at the time of investigation resembles most the optimum stage of the primeval forest.

In the context of a detailed study of aboveground forest structure, a rectangular grid of 40 circular sampling plots of 500 m^2 (25.24 m in diameter) had been established in the primeval forest with a plot distance of 65 m. In the production forest, which was smaller in size, only 10 plots were established in a rectangular grid of 50 m net width (Glatthorn et al., 2017b). Feldmann et al. (2018b) used stem diameter and stem volume to assign the trees on the inventory plots in the forest

Table 2
Stand structural characteristics of the primeval and production forest in Kyjov, averaged over all three development stages (after Glatthorn et al., 2017a, 2017b).

Forest type	Dominant height [m]	Basal area [m^2 ha^{-1}]	Mean diameter at breast height [cm]	Average stem density [n ha^{-1}]	Mean LAI [m^2 m^{-2}]
Primeval	30.3 ± 0.8	35.3 ± 13.1	37.3 ± 9.5	329 ± 91	7.4 ± 1.9
Production	31.6 ± 0.1	33.8 ± 7.9	36.7 ± 0.8	330 ± 98	6.1 ± 1.3