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Root growth dynamics of three beech (*Fagus sylvatica* L.) provenances

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ABSTRACT

European beech (*Fagus sylvatica* L.) is commercially and ecologically important tree species in Central European forests but its intra-specific variability in drought and temperature tolerance might endanger its future distribution in Europe. Beech phenological and growth traits have been studied in large-scale international beech provenance trials, yet the growth and turnover of its fine roots (FR) has not been included among the observations. FR growth dynamics and FR architectural traits of three beech provenances in the international beech provenance trial Straza/Kamenski hrib, established in Slovenia in 1998, and from a natural beech regeneration site growing at its border, were studied from 2007 to 2010. We studied FR biomass using soil cores (SC), root production using ingrowth soil cores (IC), and root longevity using minirhizotrons (MR). Significant differences in FR biomass (live and dead) between the provenance P37 and other provenances were discovered in SC, FR biomass of P37 being significantly higher than FR biomass of latter, which could be connected with overall excellent growth performance of P37 due to favourable environmental conditions at trial. Values of specific root length (SRL) in IC varied significantly among P37 and P54. The turnover rates in IC were at the end of the experiment close to MR results. Median MR-based longevities of FR varied between 625 and 934 days. Survival curve of the slowest growing provenance (considering its aboveground characteristics) was significantly different from the other two, median longevities of the latter being higher. Death of FR, older than two years, occurred most likely in the winter. Our results suggest that there are significant differences in FR longevity among provenances, which might contribute to their adaptation to future environmental conditions. Furthermore, the calculated annual C investment into FR growth per ha differs up to twofold between provenances, contributing to different C dynamics of their future stands.

1. Introduction

European beech (*Fagus sylvatica* L.; hereafter beech) is gaining importance in Central Europe as a substitute for coniferous species (Geßler et al., 2007). Beech survived the last glaciation in the refuge situated in today's Slovenia (Magri et al., 2006) and still thrives here. It represents a third of the Slovenian total growing stock and grows on 89% of the total forest area (Ficko et al., 2008). However, owing to its sensitivity to drought (Geßler et al., 2007), altered precipitation and temperature regimes (Prislan et al., 2013), its physiological performance, growth and competitiveness may be adversely affected by the predicted climate change (IPCC, 2014). Since high intra-specific plasticity was observed in beech regarding its phenology (Robson et al., 2010) and wood production (Prislan et al., 2013), choosing tree provenances with high adaptability potential for regeneration is important for the survival and growth of future forests. Adaptation to macroclimate, which is the scientific basis for the current European Union directive for marketing of forest reproductive material, recommendations for its use, conservation of forest genetic resources and strategies for adaptation to and mitigation of the expected effects of climate change, can best be studied in large-scale international provenance trials (Mátyás et al., 2009a). Adaptability of root systems is especially important, as soil is heterogeneous in terms of water and nutrient availability, but has so far not been part of the traits studied in these trials.

The main belowground characteristic of beech is its very dense system of fine and coarse roots which rapidly decrease in diameter (Kutschera and Lichtenegger, 2002; Seletković et al., 2003), which seems to be maintained regardless of site conditions (Leuschner et al.,

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2001a). Beech is also regarded as a good below-ground competitor (Leuschner et al., 2001b; Seletković et al., 2003). The density of beech fine roots (FR) is greatest in organic horizons and quickly decreases with depth (Leuschner et al., 2001b; Kutschera and Lichtenegger, 2002; Curt and Prévosto, 2003).

Tree roots contribute from 14 to 27 t C ha^{-1} to the belowground forest carbon (C) pool (Brunner and Godbold, 2007). Although tree FR (traditionally classified as roots with diameter ≤2 mm) in forest ecosystems contribute only 10–20% to the C stock of all roots (Jackson et al., 1997), this contribution is significant, as their longevity can range from months to several years depending on the species and the environmental conditions (Brunner et al., 2013; Hansson et al., 2013; McCormack et al., 2015). Differences in FR longevity are thus of great importance to carbon and nutrient cycles and influence ecosystem C balance (Norby and Jackson, 2000; Matamala et al., 2003), belowground biodiversity and overall ecosystem functioning (Bardgett and van der Putten, 2014; Wieder, 2014).

In general, root systems can show considerable plasticity in their growth traits (Pregitzer et al., 1993; Kutschera and Lichtenegger, 2002; Callaway et al., 2003). Recent studies of beech root systems during summer droughts suggested high beech root growth phenotypic plasticity, whereas genotypic variation was of minor importance (Meier and Leuschner, 2008). For plants, native to or distributed over variable environments, root systems in particular are highly plastic in characteristics such as absorptive capacity, total surface area, mass to surface area ratios, rooting density, the timing of growth and placement, and architecture (Callaway et al., 2003). Recent research on influence of environmental conditions on FR growth dynamics links changes in different FR parameters (such as length, biomass and turnover) with soil temperature, precipitation, soil water content and evapotranspiration. A long-term experiment with soil warming, fertilisation and irrigation with *Picea abies* showed statistical significant influence of warmer soil on FR lifespan, shortening it (Leppälammi-Kujansuu et al., 2014). In a study on root response of *Fagus sylvatica*, performed by Montagnoli et al. (2014), fine root growth was mainly driven by soil water content and soil temperatures, and there was a clear temperature optimum of root growth. In a pot experiment, Štraus et al. (2014) observed influence of soil temperatures on belowground and aboveground parts of beech seedling while maintaining constant soil moisture. Higher soil temperature resulted in higher root biomass, specific root length (SRL) and specific root tip density. Mainiero and Kazda (2006) studied influence of soil temperature during drought and reported that temperature was shown to be directly linked to root formation while soil moisture influenced root growth to a lesser extent. In addition to this, results from studies by Mainiero et al. (2009, 2010) suggest a strong environmental control of beech fine root dynamics. Železnik et al. (2015) determined beech fine root dynamics in managed and old-growth stands under natural environmental conditions. In this study, precipitation on the forest floor, maximal evapotranspiration and soil temperatures were significant factors explaining fine root growth and mortality, whereas, soil temperature and soil water content were important for FR growth in addition to their dynamics. However, the correlations were weak and inconsistent among sites, suggesting that relationships between fine root dynamics and selected environmental factors in natural forest ecosystem are relatively weak and complex. This is supported by several studies on different tree species, which have failed to detect strong environmental control of root growth (Hendrick and Pregitzer, 1997; Joslin et al., 2001; Aspelmeier and Leuschner, 2006).

The aim of our study was to examine differences in the FR growth dynamics and architectural FR traits of different beech provenances in uniform natural environmental conditions to determine whether their growth is predominately controlled by endogenous or by exogenous factors. We investigated three beech provenances and natural beech regeneration using the methods frequently used in root research – soil cores, ingrowth soil cores and minirhizotrons.

2. Material and methods

2.1. Site and provenances

The provenance trial (PT) on Straza/Kamenski hrib is listed among the 1996/1998 series of international beech provenance trials as one of the 22 trials established in 14 European countries following a unified methodology (Von Wuehlisch et al., 1998). The trial was planted in 1998 on a fertile site with two-year old beech seedlings raised in the same nursery of 31 provenances from 15 European countries. A 1.3 ha fenced trial is designed in three blocks with 31 plots (size 10 × 10 m). On each plot, trees are planted in five rows, 10 trees per row. The distance between rows is two meters and the distance between trees in a row is one meter. Survival, height growth and phenology are measured/assessed in one or two year intervals (Mátyás et al., 2009b).

The PT is situated on the flat top of the hill Kamenski hrib (altitude 545 m) in a mixed forest of silver fir (*Abies alba* Mill. – 60%), European beech (30%), and Norway spruce (*Picea abies* (L.) Karst. – 10%). Before planting, the stand was clear-cut, tree stumps removed and the trial area fenced. All seedlings were planted within one week. Average yearly rainfall is 1275 mm while average yearly air temperature is 6.3 °C, 14.4 °C in the summer (Supplementary data 1).

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.06.024.

Early or late frosts can occur from October and into April, respectively. During winter, snow cover persists from 50 to 60 days (Pučko et al., 2004). Bedrock consists of limestone, and prevailing soils are rendzinas and cambisols.

For the analysis of roots, three provenances belonging to possibly the same genetic lineage (Magri et al., 2006) growing in a single block were selected based on the magnitude and direction of environmental change experienced because of the translocation to the PT site, i.e. ecodistance (Mátyás et al., 2009b) and their aboveground characteristics (Table 1). The Italian provenance Val di Sella (P37) and Slovenian provenance Idrija (P54) come from to PT climate conditions similar to those at PT and close to the beech optimum, while the Czech provenance Nizbor (P64) comes from the xeric and warmer part of beech distribution area. The ecodistances are also reflected in the height growth of the provenances; P37 grows best and P64 has the lowest average height growth (Alia et al., 2010). One decade of height growth measurements and ecodistances based on the Ellenberg's climate

Table 1
Growing conditions of the selected beech provenances at their place of origin and Ellenberg's climate quotient (*EQ*) with ecodistance.

Code	Country	Provenance	Flushing time	Altitude (m)	July mean temperature (°C)	Annual mean precipitation (mm)	*EQ*	Ecodistance
Local nat.reg.	Slovenia	Straza/Kamenski hrib	Not assessed	545	15.3**	1260	15.3	0
P54	Slovenia	Idrija-II/2, 14	Late	930	15.3**	2795***	5.5	9.8
P37	Italia	Val di Sella	Intermediate	1150	15.9*	1245	12.5	2.8
P64	Czech Republic	Nizbor	Early	480	17.7*	538	32.9	−17.6

* Climatic data according to WorldClim database (Hijmans et al., 2005).
** ARSO Vojsko Official meteorological station for T measurements both in close vicinity of the site P54 (reference period 1961–1990).
*** Official ARSO meteorological station for precipitation at Mrzla Rupa (reference period 1961–1990).