

Trees - Structure and Function

Fine root dynamics in Slovenian beech forests in relation to soil temperature and water availability

--Manuscript Draft--

Trees, vol. 30, no. 2 (2016): 375-384

doi: 10.1007/s00468-015-1218-z

Manuscript Number:	TSAF-D-14-00465R4
Full Title:	Fine root dynamics in Slovenian beech forests in relation to soil temperature and water availability
Article Type:	S.I. : Root-Nagoya 2014
Keywords:	fine root ingrowth, fine root mortality, environmental factors, forest floor precipitation, evapotranspiration
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Funding Information:	
Abstract:	The ingrowth and mortality of European beech (<i>Fagus sylvatica</i> L.) fine roots (diameters < 2 mm) were studied in relation to environmental variables describing temperature and water availability at four sites, covering a range in environmental conditions likely to be encountered in Slovenian beech forests. Minirhizotron images were used to determine fine root dynamics in a stand and gap in each of the sites for twelve periods during 2007-2009 growing seasons. The environmental variables included air and soil temperatures, precipitation, forest floor precipitation, evapotranspiration, and soil water contents. For data analysis the daily mean values for each period for all variables were used. Fine root ingrowth and mortality were higher in the managed stand and gap compared to the old-growth stand and gap, but only significantly correlated with each other in the case of the managed stand. Forest floor precipitation and soil temperature were significant in explaining fine root ingrowth whereas maximal evapotranspiration, soil temperature and soil water content were more important for fine root mortality. However, the correlations were weak and inconsistent among the four sites. By including site as predictor as well as environmental variables, R ² values of 0.49 and 0.55 for ingrowth and mortality, respectively, were achieved. Despite this, the relationships between the fine root dynamics and selected environmental factors appeared relatively weak and complex, especially for fine root ingrowth, and might be partially related also to differences in successional stages of forests under study.
Response to Reviewers:	Concerning: TSAF-D-14-00465R3 Title: Fine root dynamics in Slovenian beech forests in relation to soil temperature and

water availability

Authors: Peter Železnik, PhD; Urša Vilhar, PhD; Mike Starr, PhD; Maarten de Groot, PhD; Hojka Kraigher, PhD Submitted to Trees - Structure and Function

Dear Editors,

Thank you very much again for your effort. Small changes according to Communicating Editors comments were made in text.

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Title

Fine root dynamics in Slovenian beech forests in relation to soil temperature and water availability

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Abstract

The ingrowth and mortality of European beech (*Fagus sylvatica* L.) fine roots (diameters < 2 mm) were studied in relation to environmental variables describing temperature and water availability at four sites, covering a range in environmental conditions likely to be encountered in Slovenian beech forests. Minirhizotron images were used to determine fine root dynamics in a stand and gap in each of the sites for twelve periods during 2007-2009 growing seasons. The environmental variables included air and soil temperatures, precipitation, forest floor precipitation, evapotranspiration, and soil water contents. For data analysis the daily mean values for each period for all variables were used. Fine root ingrowth and mortality were higher in the managed stand and gap compared to the old-growth stand and gap, but only significantly correlated with each other in the case of the managed stand. Forest floor precipitation and soil temperature were significant in explaining fine root ingrowth whereas maximal evapotranspiration, soil temperature and soil water content were more important for fine root mortality. However, the correlations were weak and inconsistent among the four sites. By including site as predictor as well as environmental variables, R^2 values of 0.49 and 0.55 for ingrowth and mortality, respectively, were achieved. Despite this, the relationships between the fine root dynamics and selected environmental factors appeared relatively weak and complex, especially for fine root ingrowth, and might be partially related also to differences in successional stages of the forests under study.

Keywords fine root ingrowth, fine root mortality, environmental factors, forest floor precipitation, evapotranspiration

Key Message

Fine root ingrowth and mortality of European beech are related to evapotranspiration, cumulative forest floor precipitation, soil temperature and water content, which are affected by forest management and gap creation.

1 Introduction

The response of trees, roots in particular, to climate change is one of the most important challenges facing forest ecologists. While many studies have shown the relationships between above-ground growth and climate, less is known about the growth and mortality of fine roots in relation to climate, soil temperature and soil moisture (Gill and Jackson 2000; McCormack and Guo 2014). Fine roots (roots <2 mm diameter) and mycorrhiza represent a small part of total tree biomass, but their production accounts for up to 60 % of total stand biomass production in many forests (Brunner and Godbold 2007). Fine roots are also the most dynamic and sensitive component within the overall root system (McCormack and Guo 2014) and research has found relationships between fine root dynamics, soil temperature and water availability (Joslin et al. 2000; Pregitzer et al. 2000; Tierney et al. 2003). However, while studies carried out in controlled environments have often found clear relationships between fine root dynamics and environmental factors, it has proven much more difficult to elucidate such relationships for mature or young trees under field conditions where environmental variables interact in complex ways (Kaspar and Bland 1992). Although Vogt et al. (1996), Finér et al. (2011a) and Finér et al. (2011b) were able to establish relationships between fine root production, turnover, biomass and climatic variables in forests at the global scale, detailed studies of fine root dynamics and environmental factors such as soil temperature and moisture within forest sites have produced conflicting results and/or weak relationships. This lack of strong relationships between fine root dynamics and environmental factors has usually been taken to indicate the dominance of endogenic factors, primarily inherent phenology, over environmental (exogenic) factors (Hendrick and Pregitzer 1997; Tierney et al. 2003).

The European beech is a mesic long-lived species of great economic and ecological importance to forestry in Central Europe and is tolerant of a wide range of soils and soil moisture conditions (Knoke and Seifert 2008; Leuschner et al. 2006). However, the growth and competitive ability of beech might be adversely affected by expected climate change, particularly drought (Bolte et al. 2007; Geßler et al. 2007; Meier and Leuschner 2008). Drought stress is more likely to occur on shallow soils, such as in this study. Nevertheless, the results from empirical studies concerning the relationships between beech fine root dynamics and temperature and moisture conditions are contradictory or illusive. In a study, using data compiled from beech stands from across Europe, Finér et al. (2007) reported negative, but non-significant, correlations between fine root biomass and both mean annual temperature and mean annual precipitation. The results from studies in controlled environments or at the stand level have been more definitive however. Soil temperature was found to be an important environmental factor for fine root formation and growth in European beech seedlings (Štraus et al. 2014). In a study carried out in beech forests in the Italian Southern Alps, the response of beech fine root mass and length showed significant interaction between soil moisture and soil temperature (Montagnoli et al. 2014). In a study carried out in a beech stand in southern Germany (Mainiero and Kazda 2006), fine root formation was only weakly affected by soil drying and remained directly correlated to soil temperature during a severe drought year, but it was concluded that beech fine root formation was still more strongly controlled by endogenous (genetic) factors than by exogenous (environmental) factors. In another study (Mainiero et al. 2010) beech fine root growth and mortality were correlated with each other, growth with soil temperature and mortality with both soil temperature and soil moisture, suggesting a strong exogenous influence on beech fine root dynamics.

In the present study we investigated the relationships between the root dynamics of beech trees growing on shallow soils in Slovenia and a number of environmental factors describing or related to soil temperature and water availability. The study was carried out in a stand and a gap in each of an old-growth and a managed forest over a two year period thereby covering a range in environmental conditions likely to be encountered in Slovenian beech forests. It was hypothesized that fine root ingrowth and mortality counts would be significantly related to soil temperature and water availability. It is hoped that the determination of such relationships will aid the development of forest growth models and increase the accuracy with which the impacts of global climate change on forest growth and carbon sequestration can be predicted (Davi et al. 2005; Dufrene et al. 2005; Morales et al. 2005; Stojanović et

al. 2013). We also investigated if the fine root ingrowth and mortality counts and relationships with the environmental factors differed among the four sites. This was done in order to indicate the effect of gap creation as a forest management practice on forest regeneration (Diaci et al. 2012; Grebenc et al. 2009; Ritter 2005; Vilhar et al. 2015).

2 Materials and methods

Statement of Human and Animal Rights

No human subjects or animals were involved in the study.

2.1 Study sites

This study was conducted in an old-growth forest, a nearby managed forest, and in one gap in each forest in south-eastern Slovenia (45°20'N, 14°30'E, 860–890 m a.s.l.). Both forests are dominated by silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) with a patchy understory of shrubs and herbs. Norway spruce (*Picea abies* (L.) Karst.), maple (*Acer pseudoplatanus* L.), elm (*Ulmus glabra* Huds.) and lime (*Tilia cordata* Mill.) make up less than 1% of total stem volume. The bedrock consists of Cretaceous limestone and the soils are shallow, well-drained Eutric Cambisols and Rendzic Leptosols (Urbančič et al., 2005) of 10 to 40 cm depth with scattered patches of bare limestone rock. The climate of the region is montane with an annual precipitation of up to 1600 mm. Generally, the area is snow-covered from late November until mid-April. The long-term (1961–1990) mean annual air temperature recorded at the nearest meteorological station (Kočevje, 45°39'N, 14°51'E, 467 m a.s.l.) is 8.3°C (Supplementary material 1), which corresponds to 5.9°C at the study site (using an environmental lapse rate of 6 °C per km).

The specific old-growth and managed forests in the study have similar elevation, aspect and slope (Table 1). In the managed forest, an irregular experimental clear-cut gap (ca. 2375 m²) was created in the winter of 2000-2001. All the trees in the experimental gap were harvested and carefully removed by horse skidding. At the time this study was carried out, beech seedlings accounted for 20 % of ground vegetation cover. In the old-growth forest, an irregular shaped gap (ca. 710 m²) was formed as a result of a wind throw during the winter of 2002-2003. Further information about the sites and forest management is given in Vilhar *et al.* (2010).

2.2 Fine root ingrowth and mortality

Individual fine roots of beech were observed using minirhizotrons (MR). In October 2006, five transparent plastic tubes (49 mm inner diameter) were installed at 1 m intervals along an E to W transect

in each of the stands and gap centres. The tubes were installed at an angle of 45° down to bedrock, the depth of which varied from 0 to 64 cm (Kutnar and Urbančič 2006).

Images of fine roots were taken at 14-mm intervals along opposite sides of each tube. Fine root ingrowth (*RI*) and mortality (*RM*) were determined for 12 observation periods from June 2007 to September 2009 (Supplementary material 2). Winter conditions prevented measurements from late November until mid-April and therefore the 12 observation periods are restricted to the snow-free season. The images were taken using a Bartz BTC-2 minirhizotron camera system (Bartz Technology Corporation, USA) and analysed using WinRHIZO Tron MF® software (v2003c; Regent Instruments Inc., Quebec, Canada). The location and number of all dead old roots and new fine roots growing within each frame were recorded. As no other tree species were present in the vicinity of MR tubes, the tree roots observed were only of beech trees. Roots of shrubs and herbs were easily differentiated from beech roots by morphological and architectural characteristics.

All fine roots were classified as live, dead or disappeared. A root was classified 'dead' when it had become very faint or discontinuous with indistinct edges and shrivelled to a fraction of its previous width. Roots that had disappeared between consecutive observation periods were classified into two groups: roots out of sight (it was not possible to assess what had happened to them and were censored in the subsequent analysis) and roots that had probably been eaten by herbivores. Roots that had been eaten were included into dead class. The number of new ingrowing roots and of dead roots for each of the two sides of the MR tubes were counted and the count divided by the number of days in the period to give the daily mean *RI* and *RM* count (no. day⁻¹) for each observation period. As one of the tubes in the managed gap was damaged by animals, images from only 4 tubes were available for this site. Thus the total number of *RI* and *RM* values was 456 each.

2.3 Environmental measurements

Air (2 m) and soil (5 cm depth) temperatures were recorded using automatic digital air temperature sensors (i-button, Dallas semiconductor) installed at a maximum distance of 2 m from the middle of each MR transect. Temperatures were logged at 30 minute intervals throughout the study period. For each site the mean, maximum and minimum daily air and soil temperatures for each MR observation period were calculated. Missing soil temperature data were given values calculated from measured air temperature using site specific regression functions (Vilhar et al. 2006).

Daily throughfall, actual evapotranspiration and soil water content were simulated for each study site and MR observation period using the BROOK90 water balance model (Federer 1995; Hammel and Kennel 2001). The model calculates daily water fluxes (tree transpiration, evapotranspiration, interception, throughfall, soil evaporation, drainage) and soil water content at different depths. Tree transpiration and soil evaporation are calculated separately using the Shuttleworth-Wallace method (Shuttleworth and Wallace 1985) modified to separate day-time and night-time evaporation (Federer 1995). Site specific parameter values for running the model (see Supplementary material 3) had been derived by calibrating model output with measured monthly throughfall data collected during 2001-2003 and soil water content collected during 2001-2004. The parameter values were subsequently tested using monthly throughfall data collected during 2004-2007 and daily soil water content data collected during 2005-2007. Statistics describing the goodness-of-fit between measured and modelled throughfall and soil water values using the parameter values are presented in Supplementary material 4. Further details of model calibration and testing are given in Vilhar and Simončič (2012). Measured precipitation and air temperature data for the period covered in this paper were then used to simulate daily throughfall, actual evapotranspiration and soil water content values for each of the study sites. These data were then used to calculate the cumulative amount of forest floor precipitation (PFF), the maximum daily actual evapotranspiration (ET_{max}), and the mean soil water content of the 0 to 20 cm soil layer (SWC_{0-20}) for each of the RI and RM observation periods and four sites.

2.4 Statistical analysis

Spearman rank correlations (r_s) were used to assess the relationships between the fine root variables (RI and RM) and various environmental factors. Of the variables that were highly intercorrelated, those considered the most ecologically meaningful were chosen for further analysis. The non-parametric Friedman test was used to test for differences in RI , RM and the selected environmental variables between the four study sites, matching the data by observation period. The Wilcoxon signed rank test with a Holm's correction was used for post-hoc multiple comparison tests between the study sites. To investigate the relationships between RI or RM and multiple environmental variables, a general linear model (GLM) was used in which the four sites were considered as qualitative predictor variables. For the GLM the RM values were log transformed to improve normality and reduce heteroscedasticity. Selection of the environmental variables was achieved using the stepwise backwards selection method.

GraphPad Prism version 6.04 for Windows (GraphPad Software 2014) and R statistics software (R Development Core Team 2013) were used to carry out the statistical analysis.

3 Results

3.1 Fine root dynamics

RI and *RM* were generally higher in the managed stand and gap compared to the old-growth stand and gap (Table 2). Statistical testing revealed that *RI* in the old-growth gap was significantly ($p < 0.05$) lower than in the managed stand and gap and that *RM* in both the old-growth stand and gap was significantly lower from that in the managed stand and gap. *RI* and *RM* were only significantly correlated with each other in the case of the managed stand ($r_s = 0.691$, $p = 0.015$), although the correlation between *RI* and *RM* was nearly significant in the case of the old-growth gap site, but negatively ($r_s = -0.385$, $p = 0.053$).

3.2 Environmental variables

Using measured climatic data and BROOK90 simulated data, 19 environmental variables describing or related to soil temperature and water availability were derived for each site and observation period (Supplementary material 5a). The Spearman correlation analysis revealed significant and positive correlations between air and soil temperatures for each of the four sites ($p < 0.05$) (Supplementary material 5b). However, while the amount of precipitation reaching the forest floor was significantly and negatively correlated with mean and maximum air temperature at all four sites, the amount of precipitation reaching the forest floor was not correlated to minimum air temperature or to soil temperature at 5 cm depth. The amount of precipitation reaching the forest floor was not correlated to mean daily actual evapotranspiration but was strongly correlated with the maximum daily actual evapotranspiration at all four sites. The mean soil water content during each observation period was strongly and negatively correlated with the maximum daily actual evapotranspiration and positively to the amount of precipitation reaching the forest floor at all four sites. The relative soil water deficits showed the opposite signed correlations with the other environmental variables compared to those with soil water contents.

On the basis of the correlation analysis and consideration of the ecological relevance of the factors, the following environmental variables were selected for further analysis: the amount of precipitation reaching the forest floor (*PFF*), maximum daily evapotranspiration (ET_{max}), mean daily soil temperature at 5 cm depth (ST_5), and the daily mean soil water content of the 0-20 cm layer (SWC_{0-20}) (Table 2). As expected

the gaps had significantly greater PFF than the stands. Both stands also had significantly higher ET_{max} values compared to the gaps. SWC_{0-20} significantly differed among the four sites, but was higher in the gaps compared to the stands. However, ST_5 values were about 2 °C higher in the managed than in the old-growth sites and the differences were statistically significant.

3.3 Root dynamics and environmental variables

Scatter plots of RI and RM plotted against the four selected environmental variables are shown in Figure 1. The Spearman correlation analysis showed that RI was significantly and negatively correlated to PFF and SWC_{0-20} at all four sites and positively correlated to ET_{max} and ST_5 (Supplementary material 5b). The general linear model (GLM) using only ST_5 and SWC_{0-20} as predictors resulted in a model that was significant ($P=0.022$) but with a low R^2 value (0.16). However, the GLM which included site as a predictor variable showed that RI was also correlated to PFF and to ST_5 (Table 3; Supplementary material 6). There was a negative correlation between RI and PFF , which was statistically significant only in the case of the old-growth stand ($p=0.037$), and a positive correlation between RI and ST_5 which was statistically significant only in the managed gap ($p=0.005$). The inclusion of site as a predictor variable along with PFF and ST_5 into the GLM explained 49% of the variation in RI and there was a good agreement between observed and modelled RI values (Figure 2a).

The Spearman correlation analysis showed that RM was negatively correlated with SWC_{0-20} and ST_5 and positively with ET_{max} (Supplementary material 5b). The GLM showed that RM was significantly related to ET_{max} , SWC_{0-20} and ST_5 , explaining 55% of the variation in RM (Table 3). In contrast to the GLM model for RI , the model for RM indicated a consistent response to each of the four selected environmental factors at all four sites (Table 3; Supplementary material 6). The regression intercepts decreased in the order: managed gap, managed stand, old-growth stand, and old-growth gap. The plot of observed RM against modelled values showed good agreement (Figure 2b).

4 Discussion

We considered that the four sites (a forest stand and a gap in each of an old-growth forest and a managed forest) and the length of the study period (3 years) in our study would cover the range in environmental conditions typical for beech trees growing on shallow soils in Slovenia and thereby enable us to explore the relationships between fine root dynamics and temperature and water availability factors. Accordingly, we did find a range in air and soil temperatures, water supply to the soil and soil

water contents, and in the ingrowth (*RI*) and mortality (*RM*) of beech tree fine roots. We also found that beech fine root ingrowth and mortality, when calculated across all four sites, were significantly correlated to soil temperature and to soil water contents and deficits. However, the direction and significance of the simple correlations differed among the four sites when calculated separately. But by including site as a predictor variable we were able to produce general linear models (GLM) for fine root ingrowth and mortality having R^2 values of 49% and 55% respectively.

The differences in forest floor precipitation, evapotranspiration and soil water content we observed between the stands and gaps could logically be explained by the greater interception, transpiration and soil water extraction by the roots of the canopy trees in the stands compared to the gaps (Ritter et al. 2005; Vilhar and Simončič 2012). The higher soil temperatures in the gaps than in the stands can be attributed to the reduced shading of the soil, and the greater air temperatures in the managed forest compared to the old-growth forest can be explained by the differences in radiation and microclimate related to the differences in stem volume, basal area and ground vegetation cover, and possibly also clay content of the soil, all of which were lower in the managed stand (Vilhar et al. 2015; Vilhar et al. 2006).

RI showed greater variation than *RM*, but both *RI* and *RM* were greater in the managed stand than in the old-growth stand, indicating that management has an important effect on the rooting dynamics of beech. *RI* and *RM* were positively and significantly correlated to variables describing temperature, including soil temperature, and negatively to variables describing soil water contents (including positive correlations to relative soil water deficits). Correlations to water supply (precipitation, the amount of rainfall reaching the forest floor) and to evapotranspiration, however, were not significant. It is generally considered that, as long as other environmental factors (soil moisture and soil fertility) are not limiting, tree root growth increases with temperature (Pregitzer et al. 2000). However, this increase in root growth with temperature is likely to occur only up to optimal temperature and then decrease even when other environmental factors are not limiting. In a study carried out in the Southern Alps (nearby our study), this optimal soil temperature for beech would appear to be around 14 °C (Montagnoli et al 2014). With the exception of the old-growth gap, maximum soil temperatures did exceed 14°C on some days in some of our twelve observations period, and therefore may have reduced the strength of the simple correlation between *RI* and soil temperature. However, the strength of the correlation of *RI* and *RM* with soil temperature in our study may have also been weakened by limiting soil water contents as soil water

contents and relative soil water deficits were respectively negatively (although non-significantly) and positively (significantly) correlated to soil temperatures. Thus, the highest soil temperatures tended to occur when the soil water contents were the lowest and the deficits of plant available water were the highest.

It is generally considered that trees increase fine root production when subject to decreases in precipitation or soil water availability and increasing drought, resulting in increased root:shoot ratios, fine root biomass and net production (Joslin et al. 2000). This would explain the negative correlation with soil water content and positive correlation with soil water deficits we observed for *RI*. However, the empirical evidence of such an increase in root production related to decreases in precipitation, soil water availability (increases in soil water deficits) is conflicting (Joslin et al. 2000; Hertel et al. 2013 and references therein). As soil water contents and deficits were correlated to soil temperature, the increase in *RI* with decreasing soil water contents and increasing deficits may therefore be an artefact due to this covariance and the *RI* response of beech is mostly determined by soil temperature. This would support the conclusion by Mainiero and Kazada (2006) that increasing soil temperatures overrules the effect of soil drying and that fine root formation in beech is controlled by the seasonal development of soil temperature.

Fine root mortality also generally appears to increase with soil temperature, although how and understanding the interactions with soil moisture and soil fertility are still to be clarified (Pregitzer et al. 2000, McCormack and Guo 2014). Root mortality and longevity responses to soil water availability and drought are variable, with both increases and decreases being reported (Joslin et al. 2000; Leuschner et al. 2004). However, the response of fine roots to drought may depend more on the duration of drought rather than simply to low soil water contents (Leuschner et al. 2004). Nevertheless, the lifespan of fine roots, as with soil temperature, might be expected to depend on the soil water contents, with longevity initially increasing with increasing water contents before reaching an optimum and then declining with the development of anoxic conditions (McCormack and Guo 2014). The increase in *RM* with decreasing soil water contents (increasing soil water deficits) we observed would thus indicate that the relationship with soil water contents and deficits is an artefact and more to do with the increase in soil temperature, as discussed above for *RI*. A weak response of beech fine root mortality to drought was shown in the study carried out by Mainiero and Kazada (2006) during a year of extreme drought. They found beech fine root mortality was not correlated to either soil temperature or soil moisture.

As previously mentioned, the correlations between *RI* and *RM* and the environmental variables differed among the four sites. The positive effect of soil temperature on *RI* and *RM* was largely driven by the relationship from the managed gap; the correlations for the other sites were either weak or negative. That the relationships between fine root dynamics and the environmental factors differed among the four sites was clearly shown by the GLM analysis in which site was included as a predictor variable. It was only in the GLM analysis with site as a predictor variable that water supply (rainfall and the amount of water reaching the forest floor, *PFF*) and evapotranspiration (ET_{max}) became important.

Studies done in coniferous and mixed coniferous broad-leafed forests have shown that fine-root biomass, production and turnover varies with tree and stand age, stand development and ecosystem successional stage (Børja et al. 2008; Campbell et al. 1998; Finér et al. 1997; Makkonen and Helmisaari 2001; Sun et al. 2015; Vogt et al. 1987; Yuan and Chen 2012). In contrast, Finér et al. (2011a; 2011b) in a meta analysis showed that age related parameters explain very little of the variation in tree fine root dynamics. The age of the trees in both the old-growth and managed forests in our study varied considerably. While the age of the trees are not known, there is certainly more very old trees in the old-growth stand than in the managed stand, but even there the trees are of varying age due to the traditional group-shelterwood forest management that has been carried out. Nevertheless, the old-growth forest has a more complex structure than the managed forest, being a mosaic of decline and juvenile development phases (Bončina and Diaci 1998) with a high amount of coarse woody debris at various stages of decay (Kraigher et al. 2002). The resulting mixture in the growth status of the trees and associated micro-climates and environments might, at least partially, account for the difference we observed in beech fine root dynamics among the old-growth and managed sites. Furthermore, the interaction between exogenous (environmental) and endogenous factors may vary between sites (Tierney et al. 2003). Thus the same environmental factor can affect the growth and mortality of fine roots differently at different sites and at different levels of other related factors.

In conclusion, our study showed that the ingrowth and mortality of beech fine root dynamics in Slovenia forests are affected by environmental conditions, especially soil temperature. The effect of soil water content and soil water deficits on beech fine root dynamics appeared to be an artefact and rather due to covariance with soil temperature. Nevertheless the relationships with environmental variables were rather weak and differed between sites. Whilst differences in the environmental variables were mainly related to differences between the stands and gaps, the differences in *RI* and *RM* were more related to

the type of forest, i.e. old-growth versus managed. The response of beech tree fine roots to environmental factors is clearly complex and prediction remains elusive.

Author contribution Statement

Peter Železnik: data collection; paper concept and approach; drafting of text; revision and editing

Urša Vilhar: modelling; paper concept and approach; drafting of text, graphs and tables; revision and editing

Mike Starr: paper concept and approach; checking of data; drafting of text, graphs and tables; revision and editing

Maarten de Groot: statistical analysis; paper concept and approach; partial drafting of text, graphs and tables

Hojka Kraigher: research project preparation and management; supervision of PhD thesis

5 Acknowledgements

The study was part of a Ph.D. study, the 5th EU FP project Nature-based management of beech in Europe (NAT-MAN 648 QLK-CT99-1349), ManFor C. BD project, titled “Managing forests for 649 multiple purposes: carbon, biodiversity and socio-economic wellbeing” (LIFE09ENV/IT/000078), EUFORINNO - »European Forest Research and Innovation« (Reg.Pot No. 315982), several projects within the Programme group “Forest biology, ecology and technology”, and finalized within the project “Carbon dynamics in forest soils and the rhizosphere” financed by the Ministry of Education, Science and Sport of the Republic of Slovenia. We would also like to thank anonymous reviewers for their constructive comments.

6. Conflict of Interest:

The authors declare they have no conflict of interest.

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Figure 1. Relationships between fine root ingrowth (RI) (No. day^{-1}) and a) forest floor precipitation (PFF), b) maximum evapotranspiration (ET_{max} , mm day^{-1}), c) soil temperature at 5 cm depth (ST_5), d) soil water content in 0-20 cm layer (SWC_{0-20} , mm) and fine root mortality (RM) No. day^{-1} and e) forest floor precipitation (PFF), f) maximum evapotranspiration (ET_{max} , mm day^{-1}), g) soil temperature at 5 cm depth (ST_5) and h) soil water content in 0-20 cm layer (SWC_{0-20} , mm) for the two stands and gaps ($n=48$). Triangles are for old-growth site and circles are for the managed site; open symbols indicate gap and filled symbols indicate stand.

Figure 2. Observed and predicted a) fine root ingrowth (RI) and b) fine root mortality (RM) (No. day^{-1}) result of general linear model ($n = 48$). Triangles are for old-growth sites and circles are for the managed sites; open symbols indicate stands and filled symbols indicate gaps. Black 1:1 lines indicate a perfect fit between the observed and the modelled values.

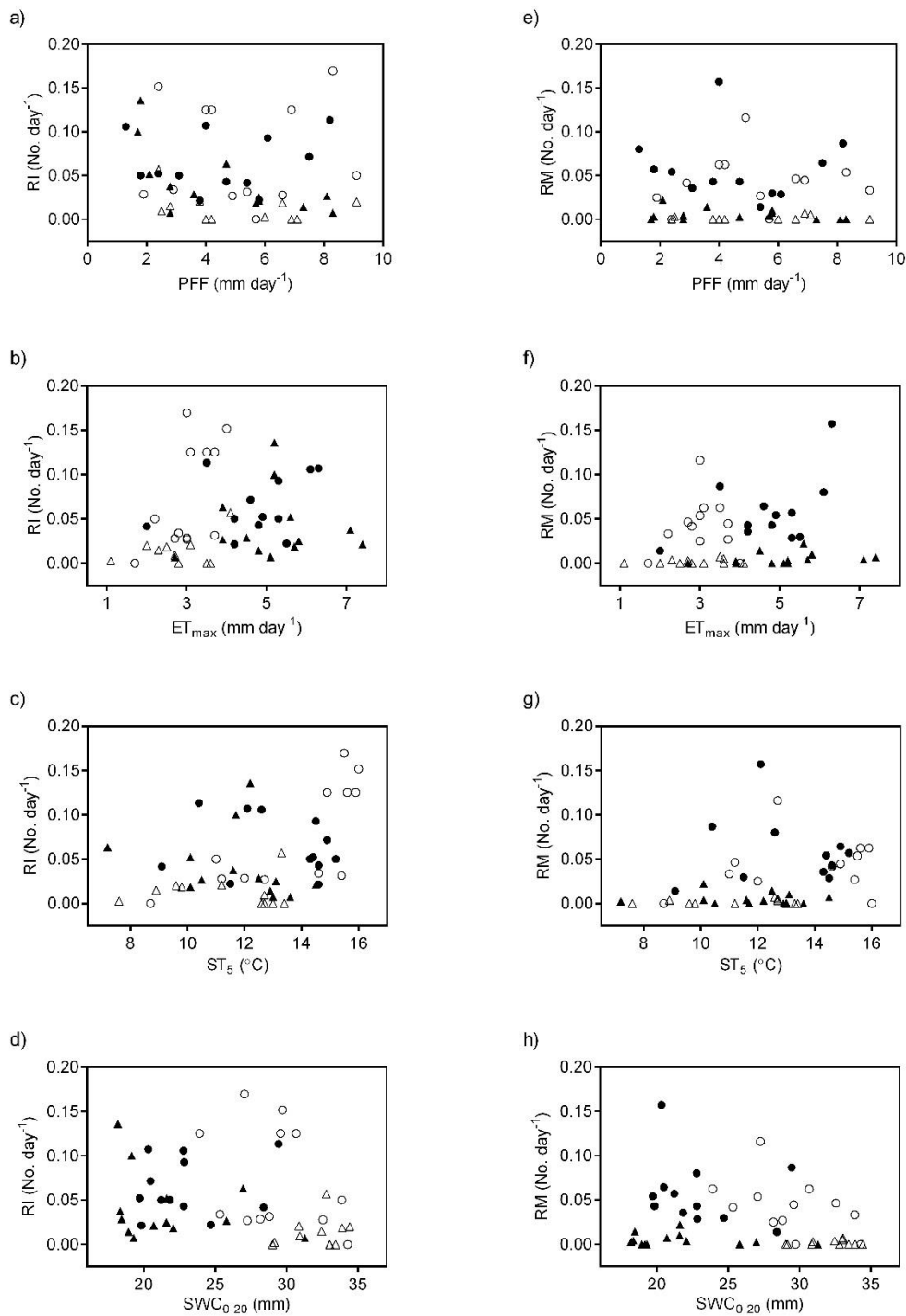


Figure 1. Relationships between fine root ingrowth (RI) (No. day⁻¹) and a) forest floor precipitation (PFF), b) maximum evapotranspiration (ET_{max} , mm day⁻¹), c) soil temperature at 5 cm depth (ST_5), d) soil water content in 0-20 cm layer (SWC_{0-20} , mm) and fine root mortality (RM) No. day⁻¹) and e) forest floor precipitation (PFF), f) maximum evapotranspiration (ET_{max} , mm day⁻¹), g) soil temperature at 5 cm depth (ST_5) and h) soil water content in 0-20 cm layer (SWC_{0-20} , mm) for the two stands and gaps ($n=48$). Triangles are for old-growth site and circles are for the managed site; open symbols indicate gap and filled symbols indicate stand.

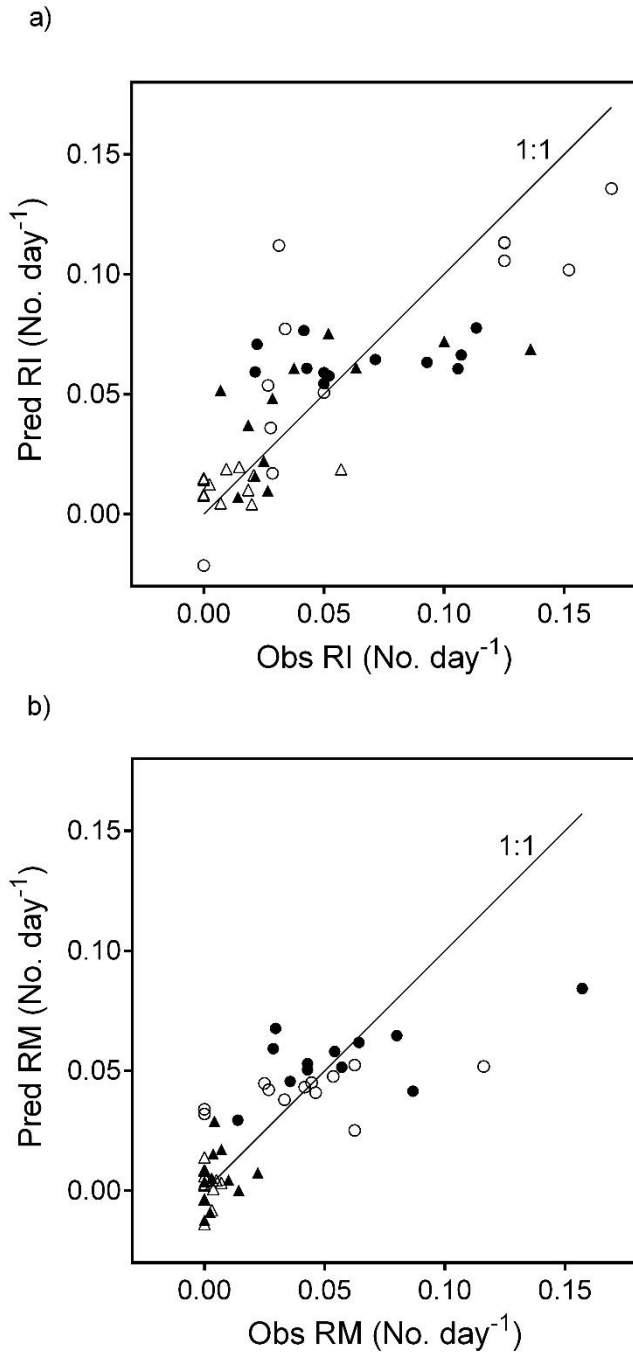


Figure 2. Observed and predicted a) fine root ingrowth (*RI*) and b) fine root mortality (*RM*) (No. day⁻¹) result of general linear model ($n = 48$). Triangles are for old-growth sites and circles are for the managed sites; open symbols indicate stands and filled symbols indicate gaps. Black 1:1 lines indicate a perfect fit between the observed and the modelled values.

Table 1: General characteristics of the study site forests and soil.

Study site	Forest						Soil					
		Average tree height (m)	Average diameter at breast height (cm)	Stem volume ($\text{m}^3 \text{ha}^{-1}$)	Basal area ($\text{m}^2 \text{ha}^{-1}$)	Ground vegetation cover (%)	Depth (cm)	pH (H_2O)	Org. Mat. (%)	N (%)	Stoniness (% vol)	Soil texture class
Managed	Stand	20	10-45	255	37	20	32.2	6.1	8.4	0.4	24.4	Loam
	Gap	0.1-0.5	<10	-	-	6	31.3	5.9	11.2	0.4	22.3	Loam
Old-growth	Stand	27	41-50	746	49	22	32.6	5.7	8.5	0.4	29.7	Clay loam
	Gap	0.3-1.8	<10	-	-	62	29.9	5.8	8.9	0.3	23.1	Clay loam

Table 2: Median, minimum and maximum values of minirhizotron observation period mean daily fine root ingrowth (RI , No. day⁻¹), fine root mortality (RM , No. day⁻¹), forest floor precipitation (PFF , mm day⁻¹), maximum evapotranspiration (ET_{max} , mm day⁻¹), soil temperature at 5 cm depth (ST_5 , °C) and soil water content in 0-20 cm layer (SWC_{0-20} , mm) for the four study sites ($n=12$). Significant differences in median values between sites are indicated by different letters (Friedman test, matching by minirhizotron observation period).

Variable	Managed stand			Managed gap			Old-growth stand			Old-growth gap			Friedman chi-squared	p-value
	median	min	max	median	min	max	median	min	max	median	min	max		
RI	0.05 ^a	0.02	0.11	0.04 ^a	0.00	0.17	0.03 ^{ab}	0.01	0.14	0.01 ^b	0.00	0.06	17.2	< 0.001
RM	0.05 ^a	0.01	0.16	0.04 ^a	0.00	0.12	0.00 ^b	0.00	0.02	0.00 ^b	0.00	0.01	27.5	< 0.001
ST_5	14.3 ^a	9.1	15.2	14.7 ^b	8.7	16.0	11.9 ^a	7.2	14.5	12.6 ^b	7.6	13.4	27.3	< 0.001
PFF	4 ^a	1	8	5 ^b	2	9	4 ^a	2	8	5 ^b	2	9	31.8	< 0.001
ET_{max}	5 ^a	2	6	3 ^b	2	4	5 ^a	4	7	3 ^b	1	4	31.3	< 0.001
SWC_{0-20}	22 ^a	20	29	29 ^a	24	34	20 ^b	18	27	33 ^b	29	34	34.9	< 0.001

Table 3: Coefficients of the general linear model using the stepwise backwards selection method relating fine root ingrowth (RI) and mortality (RM) (No. day^{-1}) to environmental variables and site as qualitative predictor variable ($n=48$; adjusted R^2 value is for the whole model). For calculating the predicted value of RI and RM for the different sites the separate site specific intercepts (managed stand intercept = 0) should be added to the model intercept. In case of the interaction terms in RI , the site specific slope coefficient of the environmental variable should be added to the slope coefficient of the variable (managed stand slope coefficient=0).

Dependent variable	Independent variables ^a	Coefficient	SE	t	P	Adjusted R^2
Fine root ingrowth (RI)	Intercept	0.092	0.079	1.166	0.251	0.492
	Site(managed gap)	-0.332	0.104	-3.203	0.003	
	Site(old-growth stand)	0.052	0.100	0.522	0.605	
	Site(old-growth gap)	-0.062	0.103	-0.601	0.552	
	PFF	0.002	0.005	0.341	0.735	
	ST_5	-0.003	0.005	-0.513	0.611	
	Site(managed gap) * PFF	0.006	0.007	0.899	0.375	
	Site(old-growth stand) * PFF	-0.012	0.007	-1.879	0.068	
	Site(old-growth gap) * PFF	-0.004	0.006	-0.630	0.532	
	Site(managed gap) * ST_5	0.023	0.007	3.447	0.001	
	Site(old-growth stand) * ST_5	-0.002	0.007	-0.273	0.786	
	Site(old-growth gap) * ST_5	0.002	0.007	0.310	0.758	
Fine root mortality (RM)	Intercept	0.14	0.055	2.554	0.015	0.553
	Site(managed gap)	0.026	0.016	1.679	0.101	
	Site(old-growth stand)	-0.070	0.011	-6.250	<0.001	
	Site(old-growth gap)	-0.012	0.016	-0.735	0.466	
	PFF	0.002	0.002	1.414	0.165	
	SWC_{0-20}	-0.004	0.002	-2.239	0.031	
	ET_{max}	0.010	0.004	2.304	0.027	
	ST_5	-0.005	0.002	-2.054	0.047	

^a PFF = amount of precipitation to forest floor during MR observation period, ST_5 = mean daily soil temperature at 5 cm depth during MR observation period, ET_{max} = maximum daily actual evapotranspiration during MR observation period, SWC_{0-20} = mean daily soil water content of 0-20 cm layer

List of supplementary material

Supplementary material 1: Monthly air temperature (°C) and precipitation (mm), recorded at Kočevje meteorological station for 1971- 2000 (mean), 2007, 2008 and 2009.

Supplementary material 2: Start and end dates of the twelve minirhizotron observation periods used in the study.

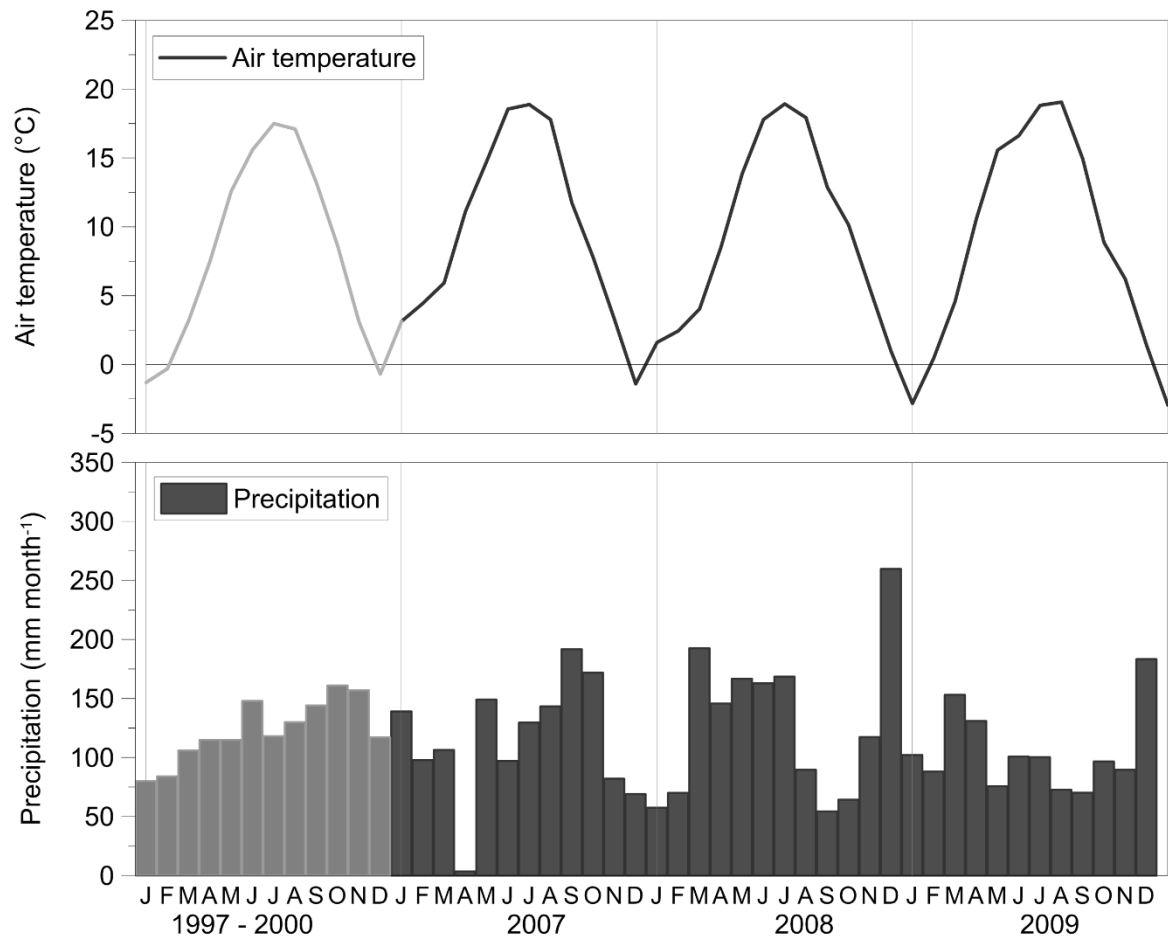
Supplementary material 3: BROOK90 model parameter values used to simulate throughfall, evapotranspiration and soil water contents for this study.

Supplementary material 4: Linear regression ($y = a + bx$) coefficients, coefficient of determination (r^2), index of agreement (D), root mean square error (RMSE), and sample size (n) describing the goodness-of-fit between BROOK90 simulated (y) and measured (x) values for the soil water contents (0-40 cm layer) and throughfall (mm) for two calibration periods.

Supplementary material 5: a) Explanation of all environmental variables investigated in this study, and b) Spearman rank correlations (r_s) between 18 environmental variables and fine root ingrowth (RI , No. day⁻¹) and mortality (RM , No. day⁻¹) across all 12 minirhizotron observation periods and 4 sites (n=48). Significant ($p \leq 0.05$) correlations are in bold.

Supplementary material 6: Summary of general linear model (GLM; stepwise backwards selection method) of minirhizotron observation period mean daily fine root ingrowth (RI) and mortality (RM) (No. day⁻¹) using environmental variables and site as a qualitative predictor variable (n=48; adjusted R^2 value is for the whole model).

Supplementary material 1:



Supplementary material 2:

Study site	Period No.	Start date	End date	No. of days
Managed stand and gap	1	22.6.2007	5.7.2007	14
	2	6.7.2007	19.7.2007	14
	3	20.7.2007	2.8.2007	14
	4	3.8.2007	16.8.2007	14
	5	17.8.2007	30.8.2007	14
	6	31.8.2007	26.9.2007	27
	7	27.9.2007	11.10.2007	15
	8	16.10.2008	20.11.2008	36
	9	25.4.2009	29.5.2009	35
	10	30.5.2009	12.6.2009	14
	11	13.6.2009	7.8.2009	56
	12	8.8.2009	24.9.2009	48
Old-growth stand and gap	1	22.6.2007	5.7.2007	14
	2	6.7.2007	19.7.2007	14
	3	20.7.2007	2.8.2007	14
	4	3.8.2007	16.8.2007	14
	5	17.8.2007	30.8.2007	14
	6	31.8.2007	26.9.2007	27
	7	27.9.2007	11.10.2007	15
	8	25.10.2008	4.12.2008	41
	9	23.4.2009	19.5.2009	27
	10	20.5.2009	12.6.2009	24
	11	13.6.2009	22.7.2009	40
	12	23.7.2009	24.9.2009	64

Supplementary material 3:

Parameters ^a	Soil layer ^b	Managed										Old-growth								
		Stand					Gap					Stand			Gap					
		2001-2009	2001	2002	2003	2004	2005	2006	2007	2008	2009	2001-2009	2003	2004	2005	2006	2007	2008	2009	
Input:																				
MAXLAI		7.00	1.00	1.00	3.00	4.00	4.00	4.00	4.00	4.00	4.00	7.00	2.00	2.00	3.00	4.00	5.00	5.00	5.00	
MAXH		20.00	0.10	0.10	0.30	0.50	0.50	0.50	0.50	0.50	0.50	27.00	0.25	0.50	1.00	1.20	1.40	1.60	1.80	
GLMAX		0.53	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.53	0.80	0.80	0.80	0.80	0.80	0.80	0.80	
CVPD		2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	
PSICR		-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	-1.90	
STONEF	L1	0.10	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.10	0.15	0.15	0.15	0.15	0.15	0.15	0.15	
	L2	0.20	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.20	0.25	0.25	0.25	0.25	0.25	0.25	0.25	
	L3	0.30	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.30	0.45	0.45	0.45	0.45	0.45	0.45	0.45	
THETAF	L1	0.377	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.417	0.343	0.417	0.343	0.417	0.417	0.417	0.343	0.417	
	L2	0.243	0.283	0.283	0.283	0.293	0.283	0.283	0.283	0.283	0.283	0.216	0.283	0.329	0.283	0.283	0.283	0.329	0.283	
	L3	0.251	0.291	0.291	0.291	0.311	0.291	0.291	0.291	0.291	0.291	0.225	0.291	0.333	0.291	0.291	0.291	0.333	0.291	
THSAT	L1	0.714	0.419	0.419	0.419	0.419	0.419	0.419	0.419	0.419	0.419	0.738	0.419	0.358	0.419	0.419	0.419	0.358	0.419	
	L2	0.599	0.399	0.399	0.399	0.399	0.399	0.399	0.399	0.399	0.399	0.618	0.399	0.339	0.399	0.399	0.399	0.339	0.399	
	L3	0.565	0.365	0.365	0.365	0.365	0.365	0.365	0.365	0.365	0.365	0.571	0.365	0.344	0.365	0.365	0.365	0.344	0.365	
BEXP	L1	6.75	6.75	6.75	6.75	7.75	7.75	6.75	6.75	7.75	6.75	7.10	9.10	11.50	9.10	9.10	9.10	11.50	9.10	
	L2	6.75	6.75	6.75	6.75	7.75	7.75	6.75	6.75	7.75	6.75	7.10	9.10	11.50	9.10	9.10	9.10	11.50	9.10	
	L3	7.75	7.75	7.75	7.75	8.75	8.75	7.75	7.75	8.75	7.75	8.10	10.10	11.50	10.10	10.10	10.10	12.50	10.10	
Calibrated:																				
FRINTL		0.065	0.001	0.001	0.001	0.010	0.001	0.001	0.001	0.001	0.001	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	
FRINTS		0.060	0.001	0.001	0.001	0.010	0.001	0.001	0.001	0.001	0.001	0.060	0.050	0.050	0.050	0.050	0.050	0.050	0.050	
CINTRL		0.25	0.10	0.10	0.10	0.20	0.10	0.10	0.10	0.10	0.10	0.35	0.05	0.10	0.05	0.10	0.05	0.10	0.05	
CINTRS		0.25	0.10	0.10	0.10	0.20	0.10	0.10	0.10	0.10	0.10	0.35	0.05	0.10	0.05	0.10	0.05	0.10	0.05	
DENSEF		1.00	0.25	0.25	0.40	0.40	0.40	0.40	0.40	0.40	0.40	1.00	0.05	0.10	0.25	0.25	0.25	0.25	0.25	
QFFC		0.47	0.60	0.60	0.10	0.01	0.01	0.60	0.60	0.01	0.60	0.50	0.30	0.25	0.30	0.30	0.30	0.25	0.30	

^a MAXLAI = Maximal leaf area index, based on litterfall collections

MAXH = Maximal height (m), based on stand inventory measurements

GLMAX = Maximum leaf conductance when stomata are fully open, default value (Federer 1995)

CVPD = Vapour pressure deficit at which conductance is halved (kPa), default value (Federer 1995)

PSICR = Critical water potential at which stomata close (MPa), default value (Federer 1995)

STONEF = Stone fraction, based on soil analysis
THETAF = Volumetric soil water content at field capacity, based on soil hydrological measurements
THSAT = Volumetric soil water content at saturation, based on soil hydrological measurements
BEXP = Exponent in "matric soil water potential–soil water content" power curve relationship (Clapp and Hornberger 1978), based on soil hydrological measurements
FRINTL = Intercepted fraction of rain per unit of projected leaf area index, based on model fitting
FRINTS = Intercepted fraction of rain per unit of projected stem area index, based on calibration with measured data
CINTRL = Maximal interception storage of rain per unit of projected leaf area index, based on calibration with measured data
CINTRS = Maximal interception storage of rain per unit of projected stem area index, based on calibration with measured data
DENSEF = Canopy density multiplier, used to simulate thinned or spaced plants when compared to the original canopy, based on calibration with measured data
QFFC = Fraction of quick flow at field capacity, based on calibration with measured data

^b L1 = 0–10 cm, L2 = 10–30 cm, L3 = 30–40 cm

Supplementary material 4:

Study site		<i>a</i>	<i>b</i>	<i>r</i> ²	<i>D</i>	RMSE	n
Model fitting - soil water content 2001 - 2004							
Managed	Stand	0.69	41.10	0.47	0.725	24.84	30
	Gap	0.88	18.84	0.78	0.946	5.67	32
Old-growth	Stand	0.82	15.35	0.62	0.862	13.21	29
	Gap	1.05	-8.20	0.89	0.989	3.31	18
Model testing - soil water content 2005 - 2007							
Managed	Stand	0.57	54.72	0.57	0.580	27.54	23
	Gap	0.81	31.95	0.83	0.929	8.65	27
Old-growth	Stand	0.40	63.79	0.29	0.707	14.60	23
	Gap	0.67	58.01	0.72	0.800	13.45	27
Model fitting - throughfall 2001 - 2003							
Managed	Stand	0.67	34.82	0.53	0.849	47.83	16
Old-growth	Stand	0.87	29.99	0.48	0.797	50.95	17
Model testing - throughfall 2004 - 2007							
Managed	Stand	1.35	-4.17	0.62	0.766	74.12	16
Old-growth	Stand	1.24	20.55	0.53	0.738	82.02	16

Supplementary material 5a:

Variable	Explanation	Unit	Measured or modelled	Selected for detailed analysis
T_{mean}	mean daily air temperature during period	°C	measured	-
T_{max}	maximum daily air temperature during period	°C	measured	-
T_{min}	minimum daily air temperature during period	°C	measured	-
T_5	mean daily air temperature at 5 cm above ground during period	°C	measured	-
ST_5	mean daily soil temperature at 5 cm depth during period	°C	measured	Selected
P	mean daily precipitation during period	mm	measured	-
PFF	mean daily precipitation to forest floor (stand=modelled throughfall; gap=precipitation in open) during period	mm	measured P, modelled TF	Selected
ET_{mean}	mean daily evapotranspiration sum during period	mm	modelled	-
ET_{max}	maximum daily evapotranspiration during period	mm	modelled	Selected
$TRAN/PTRAN_{mean}$	drought stress index (mean daily actual transpiration / potential transpiration) during period	0-1	modelled	-
$TRAN/PTRAN_{min}$	severe drought stress index (= minimum daily $TRAN/PTRAN$) during period	0-1	modelled	-
SWC_{0-20}	mean daily soil water content in the rooting zone (0-20 cm depth) during period	mm	modelled	Selected
$SWC_{0-20min}$	minimum daily soil water content in the rooting zone (0-20 cm depth) during period	mm	modelled	-
$RWDEF_{0-20}$	mean daily relative plant available soil water deficit in the 0-20 cm soil layer during period	0-1	modelled	-
$RWDEF_{0-20max}$	maximum daily relative plant available soil water deficit in 0-20 cm soil layer during period	0-1	modelled	-
SWC_{0-40}	mean daily soil water content in 0-40 cm layer during period	mm	modelled	-
$SWC_{0-40min}$	minimum daily soil water content in 0-40 cm layer during period	mm	modelled	-
$RWDEF_{0-40}$	mean daily relative plant available soil water deficit in 0-40 cm soil layer during period	0-1	modelled	-
$RWDEF_{0-40max}$	maximum daily relative plant available soil water deficit in 0-40 cm soil layer during period	0-1	modelled	-

Supplementary material 5b:

Variable ^a	T_{mean}	T_{max}	T_{min}	T_5	* ST_5	P	*PFF	ET_{mean}	* ET_{max}	TRAN/ PTRAN _{mean}	TRAN/ PTRAN _{min}	* SWC_{0-20}	$SWC_{0-20min}$	$RWDEF_{0-20}$	$RWDEF_{0-20max}$	SWC_{0-40}	$SWC_{0-40min}$	$RWDEF_{0-40}$	$RWDEF_{0-40max}$	RI
T_{max}	0.954																			
T_{min}	0.775	0.651																		
T_5	0.917	0.864	0.794																	
ST_5	0.906	0.835	0.837	0.876																
P	-0.330	-0.361	-0.136	-0.282	-0.144															
PFF	-0.308	-0.328	-0.157	-0.290	-0.130	0.976														
ET_{mean}	0.472	0.424	0.420	0.488	0.552	-0.125	-0.161													
ET_{max}	0.218	0.189	0.276	0.356	0.273	-0.187	-0.347	0.613												
TRAN/PTRAN _{mean}	-0.595	-0.647	-0.429	-0.635	-0.508	0.388	0.453	-0.272	-0.587											
TRAN/PTRAN _{min}	-0.428	-0.456	-0.413	-0.546	-0.387	0.302	0.412	-0.341	-0.725	0.887										
SWC_{0-20}	-0.263	-0.227	-0.294	-0.376	-0.248	0.225	0.388	-0.272	-0.788	0.675	0.793									
$SWC_{0-20min}$	-0.207	-0.198	-0.237	-0.324	-0.206	0.211	0.376	-0.317	-0.802	0.652	0.829	0.954								
$RWDEF_{0-20}$	0.302	0.266	0.326	0.421	0.286	-0.236	-0.388	0.256	0.762	-0.708	-0.798	-0.985	-0.924							
$RWDEF_{0-20max}$	0.279	0.270	0.272	0.424	0.293	-0.273	-0.413	0.297	0.762	-0.721	-0.864	-0.914	-0.934	0.927						
SWC_{0-40}	-0.267	-0.236	-0.315	-0.380	-0.260	0.203	0.375	-0.315	-0.823	0.679	0.804	0.979	0.954	-0.953	-0.893					
$SWC_{0-40min}$	0.248	0.203	0.049	0.118	0.214	0.282	0.352	0.173	-0.234	0.155	0.398	0.352	0.468	-0.319	-0.456	0.330				
$RWDEF_{0-40}$	0.408	0.379	0.435	0.523	0.396	-0.282	-0.423	0.321	0.763	-0.766	-0.853	-0.952	-0.904	0.962	0.912	-0.962	-0.297			
$RWDEF_{0-40max}$	0.244	0.236	0.318	0.402	0.275	-0.242	-0.394	0.272	0.741	-0.679	-0.852	-0.871	-0.914	0.877	0.936	-0.895	-0.515	0.907		
RI	0.304	0.281	0.138	0.349	0.344	-0.197	-0.234	0.255	0.322	-0.256	-0.200	-0.334	-0.280	0.338	0.350	-0.331	0.036	0.354	0.300	
RM	0.217	0.153	0.251	0.306	0.371	0.016	-0.009	0.148	0.211	-0.164	-0.210	-0.259	-0.228	0.305	0.379	-0.251	-0.044	0.343	0.334	0.556

^a see Supplementary material 5a for explanation

Supplementary material 6: Summary of general linear model (GLM; stepwise backwards selection method) of minirhizotron observation period mean daily fine root ingrowth (*RI*) and mortality (*RM*) (No. day⁻¹) using environmental variables and site as a qualitative predictor variable (n=48; adjusted R² value is for the whole model).

Dependent variable	Independent variables ^a	Sum of Squares	df	<i>F</i>	<i>p</i>
Fine root ingrowth (<i>RI</i>)	Intercept	0.001	1	1.358	0.251
	Site	0.021	3	6.590	0.001
	<i>PFF</i>	0.000	1	0.116	0.735
	<i>ST</i> ₅	0.000	1	0.263	0.611
	Site * <i>PFF</i>	0.009	3	2.908	0.048
	Site * <i>ST</i> ₅	0.021	3	6.853	0.001
Fine root mortality (<i>RM</i>)	Intercept	0.003	1	6.525	0.015
	Site	0.024	3	17.445	0.000
	<i>PFF</i>	0.001	1	2.000	0.165
	<i>SWC</i> ₀₋₂₀	0.002	1	5.015	0.031
	<i>ET</i> _{max}	0.002	1	5.308	0.027
	<i>ST</i> ₅	0.002	1	4.217	0.047

^a *PFF* = mean daily forest floor precipitation (mm day⁻¹), *ST*₅ = mean daily soil temperature at 5 cm depth (°C), *SWC*₀₋₂₀ = mean daily soil water content in 0-20 cm layer (mm), and *ET*_{max} = daily maximum evapotranspiration (mm day⁻¹)