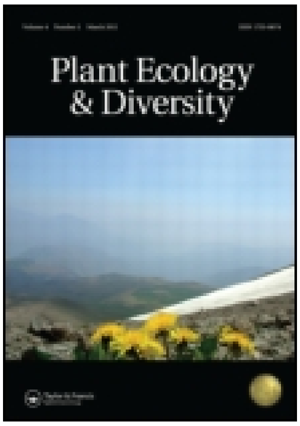

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Which processes drive fine root elongation in a natural mountain forest ecosystem?

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Background: Quantifying the dynamics of root growth is vital when characterising the role of vegetation in carbon cycling.
Aims: We examined the temporal dynamics of root growth and responses to spatial (altitude, forest patchiness and soil depth) and biological factors (root diameter and root topology) in mid-montane and upper montane coniferous forest ecosystems.
Methods: Using rhizotrons, two indicators were investigated: occurrence, i.e. the proportion of roots which had elongated since the previous measurement of root elongation (%), and daily root elongation speed (mm d^{-1}) once the elongation occurred.
Results: Spatial factors had a limited effect on root growth. Roots in the same diameter class possessed different elongation speeds and this was related to topological ranking, reflecting a disparity in physiological activity. Temporally, the occurrence of root elongation reached a peak in May–October (up to 90%) and sharply dropped after October 2010. The maximum root elongation speed (mean: 3.0 mm d^{-1}) was measured in July–August. Root growth was the most inactive in February 2011 but some roots still exhibited positive elongation speeds (mean: 0.5 mm d^{-1}). Occurrence and speed of elongation reacted differently with regard to environmental and biological factors.
Conclusions: Temporal and biological factors contributed more towards explaining the variability of root growth than spatial factors. In future studies, both occurrence and speed of elongation should be used to characterise root growth.

Keywords: *Abies alba*; altitude; *Picea abies*; rhizotron; root dynamics

Introduction

Root dynamics, that is, production, senescence, mortality and decomposition, play an essential part in the functioning of individual plants as well as terrestrial ecosystems (Vogt et al. 1996, 1998; Gill and Jackson 2000). During the whole root lifespan, root elongation speed (or 'root extension speed'), that is, the growth speed in the longitudinal direction per root, is an important indicator to quantify root dynamics (Teskey and Hinckley 1981). At the scale of an individual, root elongation is a key process that contributes to the architectural development of the whole root system (Jourdan and Rey 1997). Possessing a plastic root elongation within the soil matrix is essential for water or nutrient scavenging and uptake, so as to maintain the correct functioning of the whole plant. In several current models that describe root architecture and function, root elongation speed is one of the most fundamental parameters (Baldwin 1976; Jourdan and Rey 1997).

Variations in root elongation speed can also affect the dynamics of carbon allocation of trees by influencing the rhythm of root respiration (Farrar 1981) and shoot growth (Harris et al. 1995). Root extension favours mycorrhizal and microbial activities which, in turn, regulate root growth (Artursson et al. 2006). Root elongation is therefore a key process involved in carbon sequestration and the net primary productivity of an ecosystem. Root elongation speed can be described as analogous to the speed or efficiency of carbon sequestration by roots.

Observations of root elongation speed differ depending on the observed time scale and methodology, and are dependent on the objectives of the study being carried out. Root elongation speed can be calculated at a scale of hours focusing on, for example, the physiological responses of roots to gene expression or immediate environmental changes (Nye and Tinker 1977; Gould et al. 2004; Walter et al. 2009). For studying the impact of seasonality on root carbon sequestration, it is more suitable that root elongation speed be characterised per day (Arbez 1971). Daily root elongation speed has been documented in very early root studies, for example Crider (1928), Lyr and Hoffmann (1967) and Teskey and Hinckley (1981), and it is obtained from root growth observed in rhizotrons or minirhizotrons (Arbez 1971; Harris et al. 1995). Nevertheless, compared with root production (number of roots initiated, length or mass in a given area) and mortality (number of dead roots, length or mass in a given area), as well as their derived indicators, for example, longevity and turnover, root elongation speed is often ignored. Few studies concerning root elongation data in terms of the accretion of biomass are available, especially for small roots (Stewart et al. 2009). Joslin et al. (2001) discussed root elongation, using the

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*Corresponding author. Email: alexia.stokes@cirad.fr concept of length extension of all roots in a given area, which is similar to a root production indicator in each class of diameter, but does not take into account efficiency, that is, elongation speed at the scale of the individual (Hoffmann 1966). The spatial position and age of a root can also affect efficiency. Guo et al. (2008b) showed, for example, that the dynamics of roots of a similar thickness, but which vary in topological order, could be remarkably different and this disparity may be reflected throughout the year.

Several studies have suggested that fine roots of conifers are not dormant in winter (Hansen et al. 1997; Mao et al. 2013), and root respiration can contribute up to 10–50% of the total winter respiration (Schindlbacher et al. 2007; Ruehr and Buchmann 2010) in montane forests, despite the low value of respiration. In upper montane forests, carbon lost due to soil respiration during the winter was 50–90% of the carbon gained during the previous summer (Monson et al. 2005), suggesting major root and microbial activity in winter months. However, root dynamics in the winter are still poorly studied in upper montane ecosystems. Although several studies have highlighted the carbon consumption of roots during the winter, estimations of carbon stockage in winter are scanty. Nor are there many studies on root dynamics above an altitude of 1500 m in temperate zones (Hertel and Schöling 2011b), where seasonal low temperatures impact tree growth, particularly towards the climatic treeline, that is, the upper altitudinal limit of trees (Körner 1998).

In this study, we focused on root elongation and responses to temporal (month, season), spatial (altitude, ecological patch and soil depth) and biological factors (root diameter, root topology). Our field work was carried out in heterogeneous, naturally regenerated temperate mid-montane and upper montane forest ecosystems in the French Alps, Isère. We investigated root growth in forests at two altitudes which differed in thermal regimes, stem density and species composition. In these forests, trees are naturally grouped into clusters with a closed canopy above the cluster (called 'tree island', see Mao et al. 2012). Between the clusters are gaps or patches, which often form after, for example, tree fall during a storm or tree mortality. Root growth dynamics were measured in rhizotrons or 'root windows' (Böhm 1979; Huck and Taylor 1982). We aimed at determining which temporal, spatial and biological factors most influenced root growth in a natural mountain forest ecosystem where seasonal cold temperature constrains shoot growth. The responses of root growth to both environmental and biological factors are necessary to explore and quantify variations in carbon cycling rate and associated belowground processes, for example microbial activity. Among the studied factors (soil and air temperature, month, altitude, patch, soil depth, species and functional group), we hypothesised that over time and space, environmental factors such as modifications in soil and air temperature would explain the principal variations in root growth in these ecosystems.

Materials and methods

Study sites and vegetation

Our study sites were located near Chamrousse, Isère, in the French Alps. We chose plots in mixed, mature, naturally regenerated forests at 1400 m (mid-montane forest, 45° 07′ N, 5° 51′ E) and 1700 m (upper montane forest, 45° 06′ N, 5° 53′ E) where *Abies alba* Mill. and *Picea abies* (L.) Karst. were dominant. The basal area was 41–56 m^2 ha^{-1} at 1400 m and 27–33 m^2 ha^{-1} at 1700 m, respectively. Regarding the tree composition, *A. alba* (56–72%), *P. abies* (9–28%), and *Fagus sylvatica* L. (14–18%) were dominant at 1400 m, whereas *P. abies* (50–51%) and *A. alba* (36–38%) were dominant at 1700 m. *F. sylvatica* was not present above at 1700 m. The climatic treeline was located between 1950 m and 2000 m. Soil was acid at both sites (acid brown colluvium to mull above green schist with an abundant water supply at 1400 m and acid brown to brown podzolic above the crystalline formation at 1700 m) with a high content of rock blocks (Mao et al. 2012, 2013). More details about the two forest ecosystems are available in Mao et al. (2012, 2013).

Soil (at a depth of 0.3 m) and air temperature (at a height of 1.5 m above each rhizotron) data were monitored every 30 min during 1 year from March 2010 to April 2011 by using TidbiT v2 Water Temperature Data Loggers – UTBI-001 (Onset, USA) and HOBO Pendant® Event Data Logger – UA-003-64 (Onset, USA), respectively. Air temperature data recorded every 30 min were available from a meteorological station located at the nearby ski station of Chamrousse (http://www.meteo-chamrousse.com). This town was close to our sites at an altitude of 1785 m and air temperature data were highly correlated with measurements recorded by our logging sensors. Therefore, we extrapolated the daily air temperature and monthly soil temperature at each altitude and patch type from January 2009 to February 2010. Precipitation data were obtained from the topographical factors-based *AURELHY* model of *Météo-France* (1961–1990) (Benichou and Le Breton 1987). Potential evapotranspiration data were obtained from Lebourgeois and Piedallu (2005) in which the potential evapotranspiration was computed with Turc's equation (see Lebourgeois and Piedallu 2005) coupling *AURELHY* and *HELIOS*, a model for solar radiation (Piedallu and Gegout 2007, 2008). All above meteorological models performed computations at a scale of 1 km with satisfactory validations using observed data in France. There is an underestimation of approximately 10% for solar radiation (Piedallu and Gegout 2007); nevertheless, we used the *HELIOS* model for site characterisation only.

Installation of rhizotrons

Vertical rhizotrons were all 1.0 × 1.0 m^2 and used for analysing and modelling root elongation speed of conifers. At each altitude, four trenches were dug: two in tree islands and two in gaps (tree islands and gaps are henceforth jointly referred to as 'ecological patches', see Mao et al. 2012). Each tree island or gap had only one trench placed centrally. The installation was carried out in May 2009 at 1400 m and in July 2009 at 1700 m, except for one rhizotron in a tree island of 1400 m which was damaged and reinstalled in September 2009. During the installation of each rhizotron, along one side of the trench, a profile was cut at an angle of 15° to the vertical (sloping from top to bottom). This slight angle encouraged roots to grow downwards with close contact to the transparent window (Stepniewski et al. 1991). Roots crossing the profile were cut by using secateurs. A Plexiglas pane was placed parallel to the soil profile at a distance of ca. 0.05 m. The soil removed when the trenches were dug was sieved to 10 mm and air dried. This soil was used to fill the space between the Plexiglas, and the soil was gently compacted using a thin wooden plank, thus ensuring a good contact surface between the soil and the Plexiglas. Each Plexiglas pane was covered with black plastic and glass fibre insulating material to protect against light and variations in temperature. Each trench was then covered with wooden boards and corrugated iron to protect against rainfall and passing animals.

Measurement of root elongation

Observations of root growth were made immediately after installation of rhizotrons until March—April 2011. To avoid bias in the data due to disturbance after the installation of rhizotrons, we used only root data from March 2010 to February 2011 (denoted as the database '12 MONTHS'), that is, 8 months after the installation of rhizotrons. With regard to this duration characterised as the 'potentially disturbed stage', some studies used a maximum period of 6 months (Johnson et al. 2000; Baddeley and Watson 2005; Graefe et al. 2008), whereas other authors claimed that a duration ≥12 months was necessary to obtain typical growth dynamics data (Majdi 1996; Joslin and Wolfe 1999; Joslin et al. 2001), or even 3 years (Strand et al. 2008). To investigate the magnitude of rhizotron-triggered disturbance, we examined a period of 10 months' root growth (denoted as the database '2 WINTERS') from October 2009 to February 2010 (within the potentially disturbed stage and denoted as 'winter of 2009–2010') and from October 2010 to February 2011 (1 year after the potentially disturbed stage, and denoted as 'winter of 2010–2011'). Therefore, in the database '2 WINTERS', the effect of disturbance and year were mixed.

Root growth dynamics was measured every 2–4 weeks. A sheet of transparent plastic was placed over the Plexiglas and left in position for several months. During each inventory, root elongation was traced onto the transparent sheet with permanent colour pens, and the dates of each measurement noted. Root elongation speed was calculated on segments, therefore one root possessed several root elongation speed values belonging to different growth periods.

Root topology was quantified using an approach developed by Fitter (1982), which has been widely adopted in other studies (Pregitzer et al. 2002; Guo et al. 2008a; Valenzuela-Estrada et al. 2008; Huang et al. 2010). In this approach, each distal root is considered as a 1st order root. A root in which two ith order roots link is considered as a (i+1)th root and so on. In our study, the 3rd order was the maximum order and 3rd order roots were few, since most branched roots possessed a simple herringbone branching topology. Therefore, we combined all the 2nd and 3rd order roots to form a class '>1st order roots' to be compared with a class containing 1st order roots only. Root diameter was not measured precisely on each segment, as roots were classified into three classes:^{1}]0, 1] mm,]1, 2] mm and]2, 5] mm as in Matamala et al. (2003). The classification of root diameter was initially made using vernier callipers with a precision of 0.01 mm and then was made visually. Elongation can occur only when the root is a distal root, that is, a 1st order root. Therefore, a '>1st order' root was no longer a distal root and this order should be considered as its 'potential order'.

Radial growth was not taken into account in this study. For roots <1 mm in diameter, Eissenstat and Achor (1999) found that 1st and 2nd order roots from citrus trees (*Citrus* spp. and close relatives, for example *Poncirus trifoliata* (L.) Raf.) did not undergo secondary growth. Wells and Eissenstat (2003) showed that the diameter of roots between 0 and 1 mm did not tend to increase with root longevity. Hishi (2007) also pointed out that the growth in diameter from the interval]0, 1] mm to >1 mm occurred rarely. Therefore, secondary growth (increase in root diameter) might occur in the upper data values of the class]1, 2] mm. In our study, root diameter was always estimated at the time when the root was elongating. Therefore, roots]2, 5] mm in diameter impacting the Plexiglas pane might be those from the class]1, 2] mm where secondary growth had already occurred before the roots touched the Plexiglas.

Identifying the plant species to which a root belongs is difficult, especially in rhizotrons where destructive sampling cannot be carried out (Tosti and Thorup-Kristensen 2010). In our case, we could only identify if roots growing in rhizotrons belonged to coniferous or herbaceous plants. We were not able to distinguish between roots of *A. alba* and *P. abies* but Ladefoged (1939), cited by Riedacker (1976), found that there was a major difference in the speed of root elongation between these two species of conifers when soil temperature was >12 °C. As we did not take tree species into account, variability in our data may be higher than expected, particularly in the summer months, although soil temperature rarely exceeded 12 °C (Figure 1). For root elongation speeds of conifers, only data for conifers with roots growing in vertical rhizotrons were included in the database '12 MONTHS' and '2 WINTERS'.

Statistical analyses

Perennial plants can display continuous root growth (Mainiero et al. 2010), therefore a mean root elongation speed was calculated to describe growth. However, root growth was not necessarily continuous. Therefore,

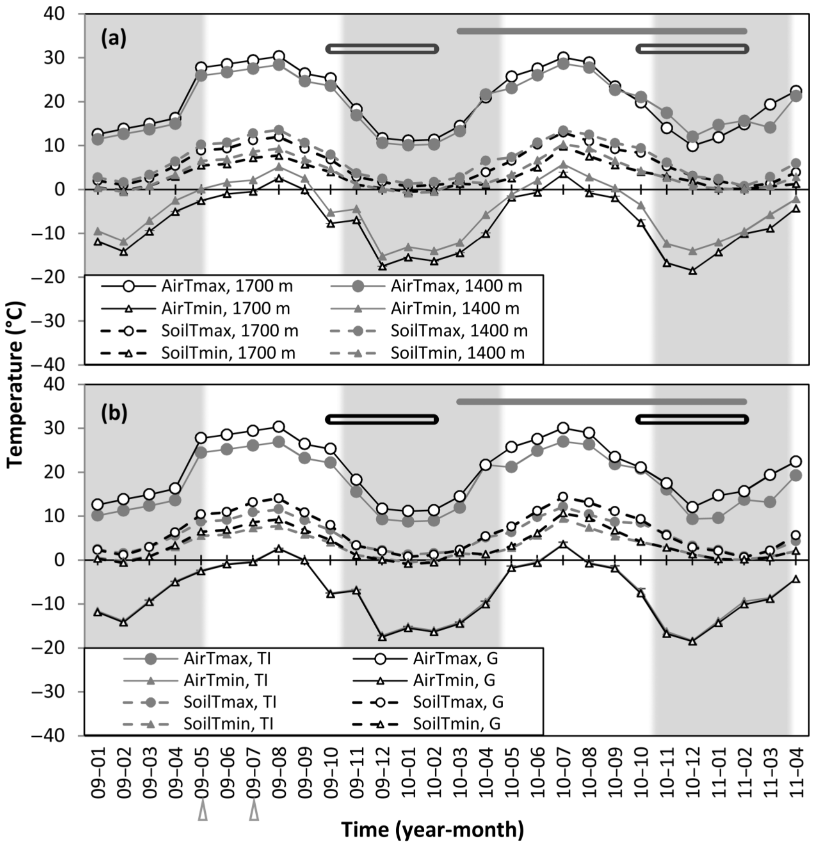

Figure 1. Ranges of monthly air and soil temperatures as a function of different altitudes (a) and ecological patches (b), near Chamrousse, Isère, French Alps. Grey and white background colours highlight the growing period and dormant (with regard to aboveground activity) seasons. The growing season lasted from 30 April to 13 October in 2009 and from 15 April to 16 October in 2010. In (b), TI and G denote 'tree island' and 'gap', respectively. Two thick horizontal lines denote the month in the databases '12 MONTHS' (grey bar) and '2 WINTERS' (double black line bar), respectively. Triangles indicate the month in which rhizotrons were installed: May 2009 at 1400 m and July 2009 at 1700 m.

we needed to take into account periods of dormancy for individual roots. These periods are interpreted as zero-populations in root elongation speed data. Classical statistical models, for example generalised linear models (GLM), are not suitable for analysing this type of data, as the data distributions are skewed to the left due to the large zero-population, even after transformations, for example logarithmic and inverse transformations. In this study, we used a two-part model (Fletcher et al. 2005) and we fitted root elongation speed data in two steps with all environmental, biotic and experimental factors as covariates. Firstly, we modelled the probability of occurrence of root elongation against non-occurrence applying a GLM with logistic distribution. Secondly, we modelled the daily root elongation speed (mm d^{-1}) only when the elongation occurred, and only by applying a GLM with a normal distribution. Root elongation speeds were normalised using a logarithmic transformation. Regarding the occurrence (%) of root elongation, theoretically, the longer the duration between inventories of root growth, the higher the occurrence of root elongation is expected. In our study, the values of R^2 of correlations between this duration and occurrence were very low (data not shown). Therefore, we assumed that the duration between inventories used in this study did not have an impact on data collection, especially with regard to occurrence of root elongation, that is, the proportion of roots which had elongated since the previous measurement.

In order to select the ideal models, we used Bayesian information criterion (BIC) (Schwarz 1978) that can measure the relative goodness of fit of a statistical model. For root elongation speed, analysis of variance (ANOVA) was used so as to evaluate the contribution rate (ρ, %) of each concerned factor to the variability of the root elongation speed. ρ was obtained with the following equation:

$$\rho_A = \frac{SS_A - f_A \times MS_e}{SS_T} \times 100\% \tag{1}$$

where ρ_A is the contribution rate to the variability of root elongation speed of the factor A, SS_A and f_A are the sums-of-squares and the degrees of freedom of the factor A, respectively, MS_e is the mean of residuals, SS_T is the total sum-of-squares, that is, the sum of sum-of-squares of all factors plus residuals. In addition, Pearson's correlations between the mean daily root elongation of all roots and monthly soil and air temperature, were carried out for the database '12 MONTHS'. Correlations were performed using data from the current and previous months.

All statistical analyses were carried out using R 2.13.0 (Ihaka and Gentleman 1996, see also http://www.r-project.org/). Only data collected during March 2010–February 2011 were used for the validation.

Results

Climatic data

Henceforth, the terms 'growing' and 'dormant' season are used when referring to aboveground organs only. The growing season is defined as the period when the daily mean air temperature was continuously >0 °C. In this present study, it lasted from 30 April to 13 October in 2009 and from 15 April to 16 October in 2010 (Figure 1). The period between two growing seasons is the 'dormant' season (Figure 1). The seasonality of monthly soil temperature was similar to that of monthly air temperature during the growing season, but with a lag of approximately 1–2 months compared with air temperature in the dormant season (Figure 1). The correlations between the maximum, mean and minimum values of monthly soil and air temperature were high ($R^2 \geq 0.75$, Table 1(b), zone *iii*). With regard to inter-annual variations, the ranges of temperature in 2010 were similar to those in 2009, that is, between −17 °C and +30 °C for air temperatures and between −0.5 °C and 14 °C for soil temperatures. However, the two years differed slightly with regard to the month when these values occurred. During the growing season, peaks in 2010 occurred in August and they preceded the peaks in 2009 by 1 month (Figure 1). In the dormant season, extreme air temperatures occurred in December in both years, but the lowest values in soil temperature occurred in January and February, also for both years.

Daily soil temperature was significantly related to altitude and ecological patch (data not shown) but when monthly averages of soil temperature were calculated, no significant relationships were found with any other variable. In gaps at 1700 m, the amplitude of seasonal variation (maximum–minimum) in air temperatures was approximately 3 °C greater than in gaps at 1400 m as well as in tree islands at 1700 m. However, differences in soil temperature between gaps and islands were negligible, regardless of altitude and season.

Total annual precipitation at 1400 m and 1700 m was 1239 mm and 1337 mm, respectively (estimated with the *AURELHY* model using data collected over a period of 40 years). Compared with temperature, the distribution of precipitation was more homogeneous without a marked dry season (Figure 2). The minimum value for precipitation occurred in July (87 mm) whilst the maximum value occurred between November and December and often as snowfall events (115 mm at 1400 m and 126 mm at 1700 m, Figure 2). As evapotranspiration demonstrated a high seasonality but with inverse trends (Figure 2), the period with the least available water in the soil probably occurs in July.

Occurrence and speed of root elongation

For conifer root growth data in the '12 MONTHS' database, the BIC selected the best models for occurrence and speed of root elongation speed which contained the following terms: month, diameter and topology (Table 2). Besides these three terms, soil depth was uniquely included for elongation speed (Table 2). The ρ indicated that month was the most significant factor to explain the variability of root elongation speed, and soil depth was the least significant factor (Table 2). However, the sum of ρ of all four factors reached <50%, indicating a high variability in our data.

Root elongation was highly seasonal: the occurrence of root elongation augmented sharply from March 2010, reached a peak in May–October (up to 90%) and dropped quickly after October, with the minimum value in February

Table 1. R^2 of Pearson correlations between the mean daily root elongation of all roots, air (AirT) and soil temperatures (SoilT) using data from the database '12 MONTHS' grouped by altitude. All correlations are positive. The three zones denote correlations (*i*) between elongation indicators (light grey), (*ii*) between elongation indicators and temperature indicators (medium grey) and (*iii*) between temperature indicators (dark grey) from top to bottom, left to right. Indicators used in correlations: occurrence of root elongation, elongation speed, monthly maximum, mean and minimum values of monthly soil and air temperatures. In (a), correlations were made between root data of the actual month (only occurrence is shown) and root and temperature data of the previous month (Month-1); in (b), correlations were carried out by using root and temperature data of the actual month. Asterisks indicate significant correlations (where *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Underlined values indicate the best correlations and only their equations are presented in this study. In (a) − denotes that the correlation was not made because it was biologically meaningless.

	Actual month		Actual month							
R^2	Occurrence	R^2	Occurrence	Elo. speed	SoilT-max	SoilT-mean	SoilT-min	AirT-max	AirT-mean	AirT-min
(a) Month-1		**(b)** Actual month								
Occurrence	– *i*	Occurrence	1	*i*						
Elo. speed	–	Elo. speed	0.35***	1						
SoilT-max	0.41*** *ii*	SoilT-max	0.47***	0.73*** *ii*	1					*iii*
SoilT-mean	0.37***	SoilT-mean	0.45***	0.82***	0.96***	1				
SoilT-min	0.33***	SoilT-min	0.39***	0.85***	0.90***	0.98***	1			
AirT-max	0.53***	AirT-max	0.43***	0.61***	0.81***	0.74***	0.70***	1		
AirT-mean	0.47***	AirT-mean	0.46***	0.71***	0.90***	0.89***	0.86***	0.92***	1	
AirT-min	0.58***	AirT-min	0.39***	0.60***	0.83***	0.80***	0.75***	0.90***	0.94***	1

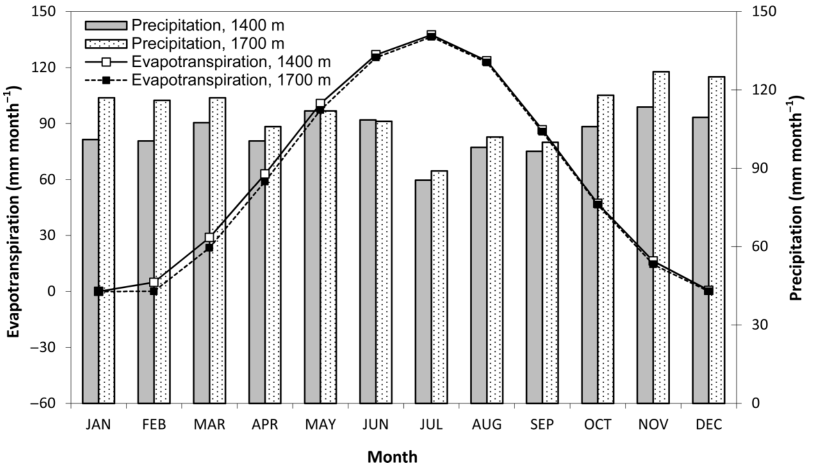

Figure 2. Monthly precipitation and evapotranspiration at altitudes of 1400 m and 1700 m, near Chamrousse, Isère, French Alps.

Table 2. Bayesian information criterion selected best models fitted using '12 MONTHS' database with F values. The reference class is March 2010,]2, 5] mm, 1st order and]0.0, 0.2] m for month, diameter, topology and soil depth, respectively. The columns 'z value' and 't value' show the results of Wald tests and Student's *t*-tests, respectively. For root elongation speed, the F and ρ values show the F value and contribution rate (%) to the variability of root elongation speed from ANOVA, respectively. Asterisks indicate significant correlations (where *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Data are not available for November 2010.

		Occurrence of root elongation (%)			Root elongation speed (mm d^{-1})		
Factor	Class	Estimate	Std. error	z value	Estimate	Std. error	t value
(intercept)		1.63	0.26	6.23***	−0.34	0.03	−10.74***
month	April	0.91	0.19	4.67***	0.01	0.04	0.22
	May	1.73	0.22	7.77***	0.22	0.03	6.41***
	June	1.85	0.22	8.52***	0.31	0.03	9.54***
	July	1.65	0.33	5.04***	0.58	0.04	14.17***
	August	1.6	0.22	7.25***	0.57	0.03	17.21***
	September	2.09	0.19	11.07***	0.5	0.03	16.79***
	October	2.13	0.2	10.87***	0.29	0.03	9.55***
	December	−0.32	0.24	−1.35	−0.08	0.05	−1.68
	January	−0.64	0.27	−2.32*	−0.15	0.05	−2.84**
	February	−0.74	0.31	−2.40*	−0.38	0.06	−6.16***
						F = 138.81***, ρ = 32.49%	
diameter	]1, 2] mm	−1.54	0.22	−6.90***	−0.2	0.02	−11.83***
	]0, 1] mm	−2.34	0.24	−9.78***	−0.38	0.02	−19.18***
						F = 170.76***, ρ = 8.00%	
topology	>1st order	1.96	0.38	5.21***	0.17	0.02	7.95***
						F = 74.56***, ρ = 1.73%	
soil depth	]0.2, 0.4] m	–	–	–	0.05	0.02	2.87**
	]0.4, 0.6] m	–	–	–	0.13	0.02	7.43***
	]0.6, 0.8] m	–	–	–	0.16	0.02	6.65***
	]0.8, 1.0] m	–	–	–	0.30	0.03	9.87***
						F = 36.70***, ρ = 3.37%	
						Residuals : ρ = 54.41%	

2011 (<45%). With regard to root elongation speed, the minimum speed occurred also in February 2011 (Table 2). However, the seasonality of root elongation speed differed from that of occurrence, although the correlation between the two indicators was significant ($R^2 = 0.35$, Table 1(b), zone *i*). Elongation speed did not augment sharply until May and it reached a peak in July–August (at a monthly soil temperature of ca. 11 °C and mean monthly air temperature of 15 °C) with an average value of approximately 3 mm d^{-1}, but the range of variations was large and dependent on several factors (Figures 3 and 4).

Pearson's correlations between the two indicators of root elongation and temperature were significant ($P < 0.01$) but R^2 values for occurrence were generally lower (Figure 5). Simultaneous monthly soil temperatures were best correlated with the elongation speed, whereas the air temperatures of the previous month (i.e. Month-1) were most significantly correlated with the occurrence of root elongation (Figure 5). Minimum air temperature correlated best with occurrence of root elongation ($R^2 = 0.58$, Table 1(a), zone *ii* and Figure 5) and minimum soil temperature correlated best with the elongation speed ($R^2 = 0.85$,

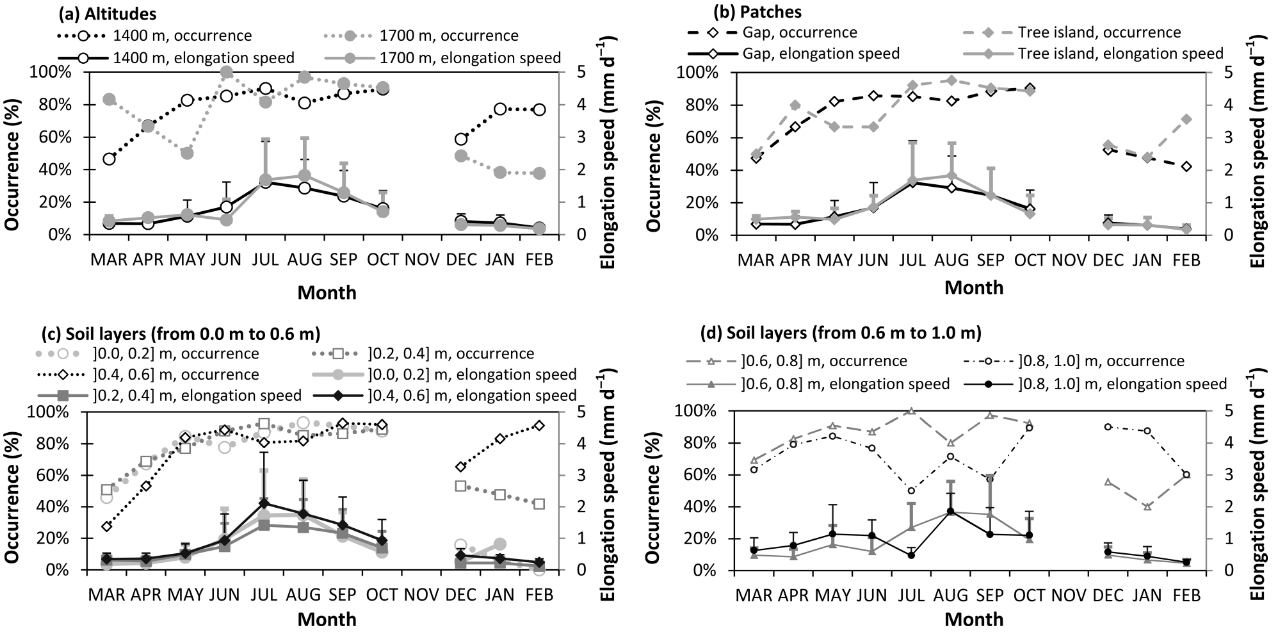

Figure 3. Occurrence of root elongation (%) and daily elongation speed (mean + standard deviation, mm d^{-1}) in *Picea abies* and *Abies alba* near Chamrousse, Isère, French Alps from March 2010 to February 2011 (i.e. database '12 MONTHS') as a function of spatial factors: (a) altitudes (1400 m, 1700 m), (b) patches (tree island, gap), (c) soil depth (0.0–0.6 m) and (d) soil depth (0.6–1.0 m).

Table 1(b), zone *ii* and Figure 5), compared with correlations with maximum or mean temperatures.

The altitude, ecological patch and interaction term was non-significant. Curves of both occurrence and speed of root elongation crossed between different altitudes and ecological patches (Figure 3(a)). For root elongation speed, the standard deviations in these data were generally superior to 1 mm d^{-1}, suggesting a high spatial variability (Figure 3(a) and (b)). Roots in the deeper soil layers grew significantly faster according to GLM (Table 2, mean elongation speed = 0.63–0.79 mm d^{-1} for the]0.0, 0.4] m soil depth and 0.84–0.86 mm d^{-1} for the]0.6, 1.0] m soil depth; GLM, t = 2.87–9.87 for soil layers below]0.0, 0.2] m, $P < 0.001$). However, soil depth interacted significantly with season (Figure 3(c) and (d)). We identified a temporal lag in the elongation speed between shallower (]0.0, 0.6] m) and deeper (]0.6, 1.0] m) soil layers (Figure 3(c) and (d)). However, no significant effect of soil depth was found with regard to the occurrence of root elongation (Table 2), all curves of which crossed and were close to each other during the growing season (Figure 3(c) and (d)). During the dormant season, the occurrence of root elongation tended to be greater for roots in the deeper soil layers (Figure 3(c) and (d)).

With regard to root diameter, in general both occurrence and speed of root elongation were lower in finer roots, i.e.]2, 5] mm >]1, 2] mm >]0, 1] mm (Table 2, Figure 4(a)). The 2nd and 3rd order roots had a greater occurrence (98%) and speeds (1.68 mm d^{-1}) of root elongation compared with that of 1st order roots (62% and 0.69 mm d^{-1}, Table 2). The effect of interaction between diameter and topology was represented in our data despite its absence in BIC-selected models (Table 2). The effect of diameter on the occurrence of root elongation was significant for 1st order roots (Figure 4(b)) but not for >1st order roots (Figure 4(c)). Inversely, diameter affected more significantly the elongation speed of >1st order roots (Figure 4(c)) but not that of 1st order roots (Figure 4(b)). For roots]2, 5] mm in diameter, the mean elongation speed of >1st order roots in summer was almost double that of 1st order roots, but this gap decreased for roots in the class]0, 1] mm (Figure 4(b) and (c)).

Root growth during the winter of 2009–2010, that is, 5 months after rhizotron installation, was significantly more active (84% mean occurrence and 0.5 mm d^{-1} mean elongation speed) than that during the following winter (59% mean occurrence and 0.28 mm d^{-1} mean elongation speed) in terms of both occurrence (GLM, $z = -3.4$ for the winter of 2010–2011, $P < 0.001$, Figure 6) and elongation speed (GLM, $t = -12.8$, $P < 0.001$, Figure 6).

Discussion

Root elongation and climatic factors

It is widely recognised that root growth activity in temperate forests is strongly dependent on season (Pregitzer et al. 2000; Giardina et al. 2005). The seasonal variation in root elongation illustrates how species respond to their surrounding environment over time. At our sites, month appeared to be the most dominant factor influencing root elongation compared with other factors, as month and season strongly reflected air and soil temperatures. In other words, our results showed that temperature was one of the most dominant factors driving plant growth in mid-montane and upper montane ecosystems.

Monthly mean minimum air temperature explained 58% of the variance in the mean occurrence of root elongation and the monthly mean minimum soil temperature

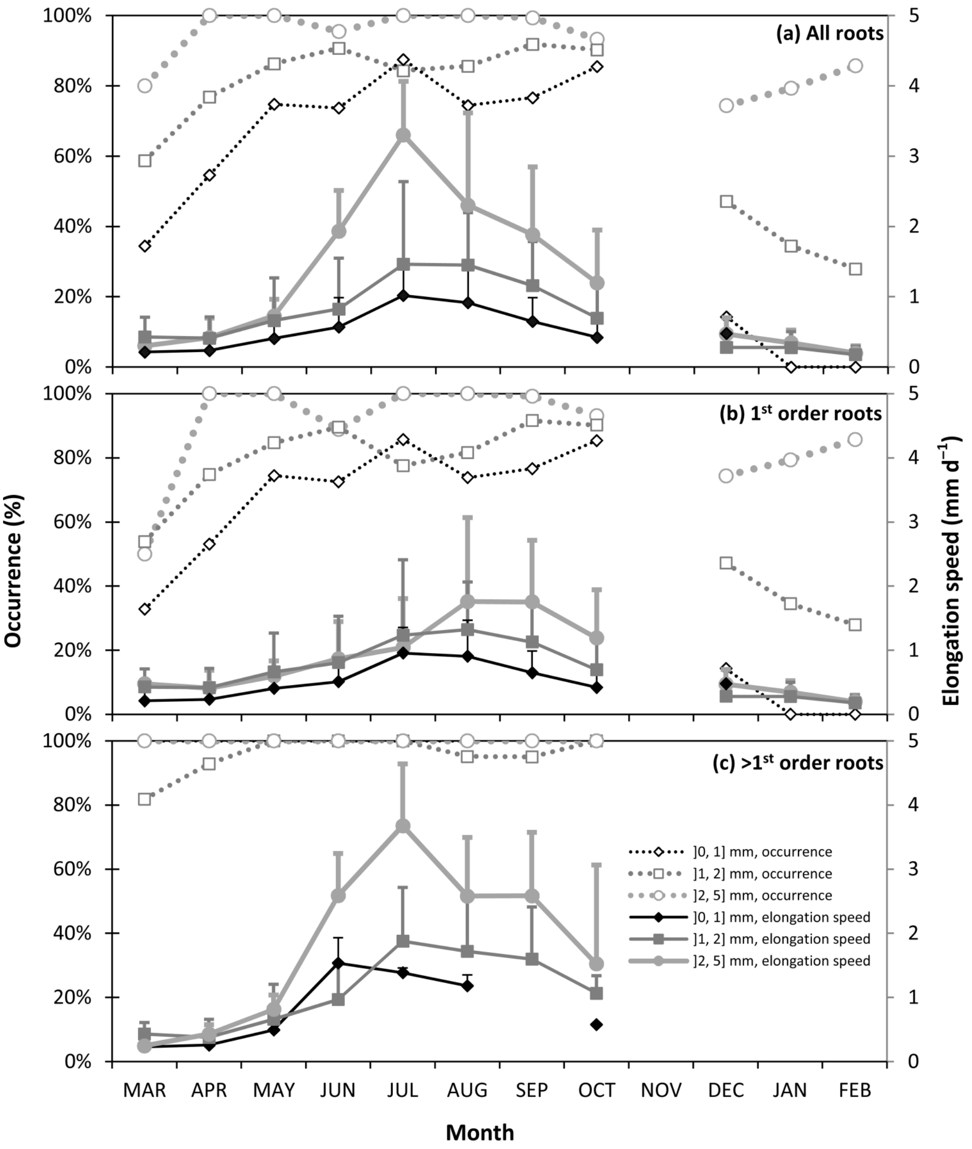

Figure 4. Occurrence of root elongation (%) and elongation speed (mean + standard deviation, mm d^{-1}) in *Picea abies* and *Abies alba* near Chamrousse, Isère, French Alps from March 2010 to February 2011 (i.e. using data from the database '12 MONTHS') as a function of (a) diameter of all roots, (b) diameter of 1st order roots and (c) diameter of >1st order roots. >1st order roots (278 segments) were less numerous than 1st order roots (2031 segments) and no longer existed after November 2011.

explained 85% of the variability in the mean elongation speed. Both occurrence and speed of root elongation were positively and significantly correlated with air and soil minimum temperatures, suggesting that the lower boundary of temperature was an essential driver of root growth compared with maximum or mean temperatures. Contrary to air temperature, where there was a time lag of one month between the minimum temperature required for root growth, with an influence on root extension, soil temperature appeared to have an instantaneous effect on root growth. Several studies have shown that root growth occurs at an optimal soil temperature (Björkman 1981; Moorby and Nye 1984; Stoneman and Dell 1993) with a minimum temperature limit (Riedacker 1976), and both root extension rate and production correlates positively with soil temperature (Macduff and Wild 1986; Xiong et al. 2000). The minimum soil temperature for root growth of *P. abies* and *A. alba* is usually 2–4 °C and the optimum between 10–32 °C (Lyr and Hoffmann 1967).

Compared with temperature indicators, it appears that in our study, precipitation played a secondary role in root growth. The root elongation speed attained a maximum value in July, even though both precipitation and water balance reached minimum values at the same period. It is known that water stress can lead to a decrease in root elongation speed (see Pregitzer et al. 2000). This observation suggests that at our site water supply was not limited during the summer of 2010 and the depletion of soil water did not restrict root growth.

Root elongation is a complex process and makes observed root data statistically and biologically difficult to interpret. By introducing the occurrence and speed of

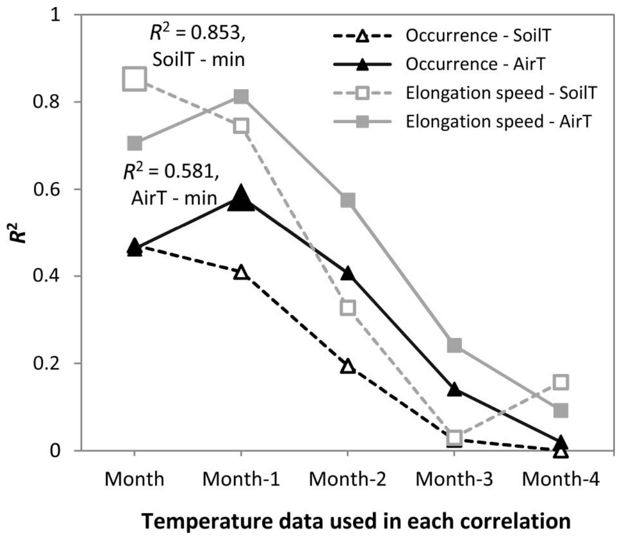

Figure 5. The highest R^2 between the root elongation (occurrence and elongation speed) and monthly air and soil temperature data (temperature of the actual month and previous of n months, $n \in [1, 4]$), near Chamrousse, Isère, French Alps. Each point denotes the highest R^2 among the maximum, mean and minimum temperatures. Peak points for occurrence and abundance are marked with larger symbols with values and the corresponding indicator noted. Root data were grouped into classes depending on altitude. The best correlations were found between the occurrence of root elongation (O) in *Picea abies* and *Abies alba* and monthly minimum air temperature of the previous month ($T_{a\text{-}min,\ Month\text{-}1}$): $O = 0.02\ T_{a\text{-}min,\ Month\text{-}1} + 0.87$ ($R^2 = 0.58$) and daily root elongation speed (S) and monthly minimum soil temperature of the actual month ($T_{s\text{-}min,\ Actual\ month}$): $S = 0.14\ T_{s\text{-}min,\ Actual\ month} + 0.20$ ($R^2 = 0.85$).

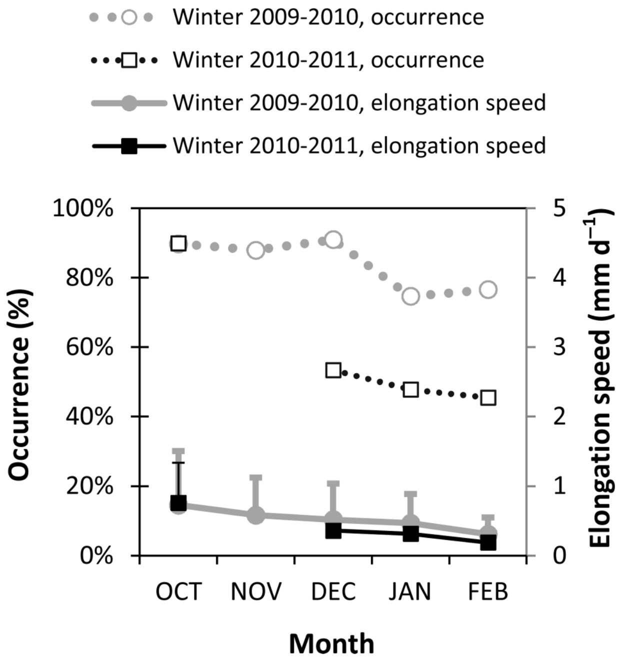

Figure 6. Occurrence of root elongation (%) and daily elongation speed (mean + standard deviation, mm d^{-1}) in *Picea abies* and *Abies alba* near Chamrousse, Isère, French Alps between winter 2009–2010 and winter 2010–2011 (October–February, i.e. using data from the database '2 WINTERS').

root elongation, we attempted to describe root elongation in two steps. The key point is to separate non-elongating and elongating roots, as only the latter are concerned with the speed of growth. Both indicators made statistical analyses more robust by dividing root elongation into two separate GLMs, and resulted in more meaningful different biological concepts. The occurrence and speed of root elongation reacted differently to temperature indicators. This result was consistent with the disparity between both indicators in terms of the monthly variation. In particular, root elongation speed appeared to be more sensitive to month and temperatures than occurrence. We suggest that in future studies, both indicators should be used to characterise root growth instead of using simple mean or median values of observed root growth data.

Spatial and environmental effects on root growth

In our study, although the effect of altitude and patch was significantly related to daily temperature data, their impact was limited with regard to variations in monthly air and soil temperatures. Not all spatial environmental factors were significantly related to monthly air and soil temperatures, thus indicating that they play a secondary role in explaining the variability in root elongation compared with temporal and biological factors.

We observed a typical distribution of tree species at our field sites, in that at 1700 m tree density was nearly half that at 1400 m, and 1700 m was beyond the altitudinal limit of *F. sylvatica*. The proportion of cold-hardy *P. abies* was significantly higher at the higher elevation site, whereas that of *A. alba* decreased. However, there were no significant differences in either the occurrence of root elongation or elongation speed between the two altitudes. Our results are complementary to a study by Hertel and Schöling (2011b), who carried out a meta-analysis of root production along increasing elevations in the European Alps. Hertel and Schöling (2011a), focusing on root biomass and production along an altitudinal gradient from 390 m to 1100 m in northern Germany, found the highest fine root biomass in a *P. abies* forest at 1100 m, which resulted in the highest relative fine root to stem biomass allocation. Therefore, our results could also indicate the occurrence of acclimation processes of roots at a higher altitude to the restriction of aboveground development (Hertel and Schöling 2011a).

As with altitude, ecological patch had no effect on root elongation. In contrast, root distribution at the same field sites has been shown to be spatially highly variable and a function of several spatial factors, for example altitude, forest patchiness and soil depth (Mao et al. 2012). Therefore, as also observed by Hendrick and Pregitzer (1992), spatial variations in root growth dynamics might be less variable than root distribution. With an increase in soil depth, root growth may augment because in deeper soil layers there is less physical disturbance from above ground (Boone et al. 1978). However, there are lower nutrient reserves in deeper soil (Lambers et al. 1998), which is also often more compacted (Taylor and Ratliff 1969; Bengough et al. 2011), and both these factors can hinder root growth. In our study, soil depth had a limited effect on root elongation speed and no effect on the occurrence. We suppose therefore that in deeper soil layers, the positive effect of less physical disturbance from above ground might be offset against the negative effect due to increasing soil compaction and decreasing nutrition reserves. In the dormant season, root elongation tended to be more favoured deeper in the soil, probably because deeper soil temperatures were more stable than in the superficial layers and not subjected to freezing and thawing cycles. Similarly, the temporal lag in the elongation speed between shallow and deeper soil layers may have been due to a greater sensitivity to environmental disturbance, as shallower layers were subjected to freezing and thawing at the beginning or end of winter.

Root growth in winter

Root elongation during the winter of 2009–2010 was greater than that during the winter of 2010–2011, even though soil and air temperatures were lower. Although roots of deciduous and evergreen species can grow during the winter with a speed of 0.5–9.0 mm d^{-1} (Crider 1928), this temperature is usually considered too low to maintain normal root growth over a long period (Riedacker 1976). However, in our study, root growth was maintained over several months during the winter period following the rhizotron installation. Joslin and Wolfe (1999) attributed higher root production during the growing season (from 16–21 April to 17–21 October) after the installation of minirhizotrons to the consequences of root pruning and nutrient release in nearby soil microsites. Our results showed that if disturbance does increase root production, it is independent of season. We found that simultaneous to this increase in occurrence and speed of root elongation, production increased during the winter of 2009–2010 (Mao et al. 2013). Therefore, if this increase in growth activity is induced through root pruning or nutrient release, the data measured during the first 8 months after installation of a rhizotron may be analysed but should not be used to describe natural growth dynamics in carbon sequestration studies. In our case, long-term root observations would be needed to confirm if 8 months was appropriate as a potentially disturbed stage.

Root elongation, especially the occurrence, was much less active during the winter of 2010–2011, suggesting a significant reduction in the effect of soil disturbance during the second year after rhizotron installation. This low occurrence could be partially attributed to root mortality due to low temperatures. Ruess et al. (1998) and Coleman et al. (2000) found the greatest rate of root mortality during the winter in a broadleaf forest in Alaska. According to Ruess et al. (2003), the low root survivorship over winter could be a typical characteristic in high-elevation ecosystems, probably due to freezing soil. However, we prefer to be as prudent as possible before attributing the low occurrence of root elongation to root mortality. In contrast, our roots tended to maintain a low mortality in the winter of 2010–2011 and peak mortality occurred in summer and autumn months (Mao et al. 2013). Hendrick and Pregitzer (1993) also observed lower root mortality in dormant seasons in temperate broadleaved forests. Wells and Eissenstat (2001) found that winter mortality was highly dependent upon root diameter, and that roots of]0.5, 1] mm in diameter possessed 50% lower mortality than those of]0, 0.3] mm. We believe that the low soil temperature greatly restricted root activities such as production (Mao et al. 2013), elongation (this study) and respiration (Ruehr and Buchmann 2010). However, temperature was not low enough to cause root mortality, as it was seldom <0 °C at a depth of 0.3 m, due to the presence of an insulating snow cover.

Influence of root system architecture on elongation

In our study, thicker and higher-order roots had significantly higher elongation speeds, and hence faster carbon fixation rates. We also showed that roots in the same diameter class but differing in order, possessed different patterns of seasonality with regard to occurrence and speed of root elongation, reflecting a disparity in physiological activity. Nevertheless, the topological order can also be considered as a simple diameter effect, as each diameter class could be divided into several sub-classes and most 1st order roots possessed a smaller sub-class than that of $>$1st order roots (Wells et al. 2002; Valenzuela-Estrada et al. 2008; Huang et al. 2010). There have been several debates on the selection of root diameter and topological parameters, with regard to the indicator which best expresses root physiological activity. In the characterisation of root longevity and turnover, it appears that root lifespan is extremely sensitive to root order (Guo et al. 2008a, 2008b) even though diameters can be similar. However, our results showed that root elongation was more sensitive to diameter compared with topology, as the former had a greater ρ value than the latter. This result might be attributed to the fact that only three orders were found with few large order roots. Therefore, we suggest taking into consideration both the indicators diameter and topology in studies on root growth dynamics.

Conclusions

Based on root data obtained in rhizotrons, this study examined the temporal dynamics of two indicators of root growth, occurrence and speed of elongation, and their responses to spatial (altitude, forest patchiness and soil depth) and biological factors (root diameter and root topology) in mid-montane and upper montane coniferous forest ecosystems. We characterised the seasonality of root growth for both the aboveground growing season and dormant season. In particular, we observed winter root growth and attributed it to the presence of insulating snow cover, which maintained soil temperature at >0 °C. Observations over a longer time period would be needed to investigate the amplitude of inter-annual variations in root growth. From measurements of root density (Mao et al. 2012) and root elongation dynamics, we showed that spatial factors had a small influence on growth. This result suggests that when studying root seasonal dynamics, it is more useful to sample in 'time' than in 'space'. Biologically, the effect of interaction between root diameter and topology was observed, thus demonstrating the need to take into account both indicators in rhizotron-based studies. By means of separating non-elongating and elongating roots, we characterised root growth using two indicators: occurrence and speed of elongation. Both indicators were linked, but reacted differently to environmental and biological factors. We suggest that in future studies, both indicators be used when studying root growth.

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Note

1. According to the international standard ISO 31–11, $]x, y]$ denotes a left half-open interval from x (excluded) to y (included).

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