

PART OF A SPECIAL ISSUE ON FUNCTIONAL–DEVELOPMENTAL PLANT CELL BIOLOGY

Tree root dynamics in montane and sub-alpine mixed forest patches

Y. Wang¹, J. H. Kim^{1,2}, Z. Mao¹, M. Ramel¹, F. Pailler¹, J. Perez¹, H. Rey¹, S. Tron³,
C. Jourdan⁴ and A. Stokes^{1,*}

¹University Montpellier, INRA, CNRS, IRD, CIRAD, AMAP, 34000 Montpellier, France, ²Max Planck Institute of Biogeochemistry, Jena, Germany ³ÖGUT, Austrian Society for Environment and Technology, Vienna, Austria and ⁴CIRAD, UMR Eco&Sols – Ecologie Fonctionnelle & Biogéochimie des Sols & Agroécosystèmes (Montpellier SupAgro-CIRAD-INRA-IRD), 2 Place Viala, 34060 Montpellier, France

*For correspondence. E-mail alexia.stokes@cirad.fr

Received: 21 November 2017 Returned for revision: 22 December 2017 Editorial decision: 29 January 2018 Accepted: 2 February 2018
Published electronically 28 February 2018

- **Background and Aims** The structure of heterogeneous forests has consequences for their biophysical environment. Variations in the local climate significantly affect tree physiological processes. We hypothesize that forest structure also alters tree root elongation and longevity through temporal and spatial variations in soil temperature and water potential.
- **Methods** We installed rhizotrons in paired vegetation communities of closed forest (tree islands) and open patches (canopy gaps), along a soil temperature gradient (elevations of 1400, 1700 and 2000 m) in a heterogeneous mixed forest. We measured the number of growing tree roots, elongation and mortality every month over 4 years.
- **Key Results** The results showed that the mean daily root elongation rate (RER) was not correlated with soil water potential but was significantly and positively correlated with soil temperature between 0 and 8 °C only. The RER peaked in spring, and a smaller peak was usually observed in the autumn. Root longevity was dependent on altitude and the season in which roots were initiated, and root diameter was a significant factor explaining much of the variability observed. The finest roots usually grew faster and had a higher risk of mortality in gaps than in closed forest. At 2000 m, the finest roots had a higher risk of mortality compared with the lower altitudes.
- **Conclusions** The RER was largely driven by soil temperature and was lower in cold soils. At the treeline, ephemeral fine roots were more numerous, probably in order to compensate for the shorter growing season. Differences in soil climate and root dynamics between gaps and closed forest were marked at 1400 and 1700 m, but not at 2000 m, where canopy cover was more sparse. Therefore, heterogeneous forest structure and situation play a significant role in determining root demography in temperate, montane forests, mostly through impacts on soil temperature.

Key words: Root elongation, initiation, longevity, *Picea abies*, *Abies alba*, altitude, growth.

INTRODUCTION

Tree fine root growth and mortality are studied increasingly with regard to carbon cycling and sequestration (Norby and Jackson, 2000; Phillips *et al.*, 2012; Brunner *et al.*, 2013). Studies are usually limited to individual species' responses to various environmental conditions. Below-ground plant community responses to resource supply or constraints are rarely studied but are providing important clues as to how communities respond to changes in land use and climate (Prieto *et al.*, 2015, 2016). Heterogeneous forest ecosystems should be investigated in a similar holistic manner in order to predict and model forest responses to climate variability (Kitajima *et al.*, 2010; Kubisch *et al.*, 2017). The structure of a forest community will also affect local climatic conditions, especially with regard to open and closed canopies that alter the biophysical environment both above- and below-ground. Examining the dynamics of tree root growth and mortality within a context of temporal and spatial variations in the biophysical environment is a major step to understanding how forest communities respond to changes in below-ground climatic conditions.

Responses of root elongation and longevity to climatic variations have usually been studied at the species level (Barlow and Rathfelder, 1985), or artificially in growth chambers (Lahti *et al.*, 2005; Alvarez-Uria and Körner, 2007), which do not reflect the true conditions found in natural or mixed forests (Kubisch *et al.*, 2017). Tree roots in heterogeneous temperate forest ecosystems can initiate and elongate during the winter, even when mean daily air temperatures are below freezing, as long as the soil temperature does not drop below 0 °C (Mao *et al.*, 2013a; Radville *et al.*, 2016). Optimal soil temperatures for conifer root growth vary from 6 to 15 °C [*Picea abies* (L.) Karst] and from 10 to 20 °C (*Abies* sp.) (Lopushinsky and Ma, 1990; Lyr, 1996; Alvarez-Uria and Körner, 2007; Nagelmüller *et al.*, 2016), but periods of low or zero activity occur throughout the year (Mao *et al.*, 2013a; Wang *et al.*, 2018). However, few studies have characterized and quantified root active and dormant periods in the field, partially because of the relatively short duration of experimental studies on root growth and the assumption that root dormancy is synchronous with that of shoot dormancy (Eissenstat *et al.*, 2005; Graefe *et al.*, 2008; Abramoff and Finzi, 2015; Radville *et al.*, 2016).

If root activity and elongation are influenced by seasonal changes in soil temperature, it is likely that root longevity is also affected. Kitajima *et al.* (2010) found that in a mixed Californian forest, tree root turnover rate was higher in thinner roots and in warmer and wetter soils. However, Kubisch *et al.* (2017) showed that in *Pinus cembra* growing at the treeline, higher fine root turnover occurred in colder areas compared with that in warmer soil. Longevity is also linked to the time of root initiation during the year (Geng *et al.*, 2014). Therefore, spatial or temporal variations in soil temperature or moisture content linked to season or the forest structure should alter root demography.

The structure of a heterogeneous forest affects its biophysical and climatic environment largely through the patchy nature of the canopy (Kubisch *et al.*, 2017). Naturally formed gaps in the canopy (Whitmore 1989) result in greater solar radiation and temperature at the forest floor, compared with adjacent closed canopy plots (Heithecker and Halpern, 2007; Scharenbroch and Bockheim, 2007; Yang *et al.*, 2017). Soil moisture content is higher because the water demand of the herbaceous/shrubby vegetation present is lower than under trees and because trees intercept large amounts of rainfall which does not reach the forest floor. This heterogeneity affects understorey composition (Ares *et al.*, 2010) and below-ground microbial communities (Siira-Pietikäinen *et al.*, 2001; Griffiths *et al.*, 2010). Gaps usually possess less fine tree root biomass than nearby clusters of trees (tree islands) in tropical (Denslow *et al.*, 1998; Sanford, 1990) and temperate (Wilczynski and Pickett, 1993; Bauhus and Bartsch, 1996; Müller and Wagner, 2003) forests. This decreased level of fine root biomass may be because the roots of neighbouring trees do not grow into the gap (depending on the gap size; Bauhus and Bartsch, 1996), or because a faster turnover of roots occurs in the warmer, wetter soil (McCormack and Guo, 2014). However, to our knowledge, long-term studies on fine root demography with regard to differences between gaps and closed canopy plots have not been carried out in temperate forests.

We installed rhizotrons in paired vegetation communities of closed forest (tree islands) and open patches (canopy gaps) along a soil temperature gradient (elevations of 1400, 1700 and 2000 m) in a temperate, heterogeneous mixed coniferous forest. Rooting depth in these types of forests is usually limited to the upper metre of soil (Schenk and Jackson, 2002). We examined root initiation, elongation and survival over a 4 year period. Forests were heterogeneous in terms of species, tree age and the spatial distribution of vegetation; therefore, tree root demography was representative of the tree community, not individual species. We expected that: (1) tree root elongation and longevity would be influenced by soil temperature and moisture content; and (2) tree root elongation rates would be greater and turnover faster in gaps because during the height of the growing season, soils are warmer and wetter than in tree islands. This disparity between gaps and tree islands should be reflected along the soil temperature gradient and in each type of forest community.

MATERIALS AND METHODS

Study sites

Our study was conducted in sites located at three altitudes (1400, 1700 and 2000 m, close to the treeline; Supplementary Data

Fig. S1) near Chamrousse, Isère, France (45°07'N, 5°52'E). This area comprised mixed, naturally regenerated forests which were on south-west-facing slopes. All forests were uneven aged, and tree age varied from 20 to 120 years old (Mao *et al.*, 2015; Wang *et al.*, 2018). Sites comprised three mixed, mature, naturally regenerated forests of Norway spruce [*Picea abies* (L.) Karst.], Silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.) and Mountain pine (*Pinus uncinata* Ramond ex DC.) growing at altitudes of 1400 m (Prémol forest), 1700 m (Bachat-Bouloud forest) and 2000 m (near Achard Lake, at the treeline). Species composition shifted from 1400 to 2000 m: *F. sylvatica*, the most dominant broadleaf species at 1400 m, disappeared completely at 1700 m. *Abies alba*, *P. abies* and *P. uncinata* were the most dominant species at 1400, 1700 and 2000 m, respectively. *Picea abies* was the only species present at all altitudes. *Abies alba* was absent at 2000 m, and *P. uncinata* was absent at 1400 m and sparsely distributed at 1700 m (Mao *et al.*, 2015). Tree stand basal area (SBA) and tree height decreased significantly with increasing elevation. The average maximum rooting depth of soil at the sites situated at 1400 and 1700 m attained approx. 1.0 m, but bedrock was found at 0.5 m at the site located at 2000 m. Further information about sites can be found in Supplementary Data Table S1.

We defined two types of dominant vegetation structure at each site. By investigating contrasting vegetation structure, a wide range of microclimate variables and functional groups were included in our analysis (Supplementary Data Table S1). At all three sites, closed canopy forest occurs naturally in clusters, known as tree islands (Mao *et al.*, 2012; Fig. 1). Tree islands are defined as small patches of woody vegetation embedded in a landscape of a contrasting vegetation type (Tomlinson, 1980). Between the tree islands are patches, or gaps, which refer to zones with an open canopy formed through tree mortality after, for example, a storm or tree felling. These zones are often between 20 and 100 m². Fine tree roots can grow into the gaps, depending on the size and position of structural woody roots on which they are borne (Mao *et al.*, 2013a). Due to the open canopy and increased solar radiation, herbaceous and shrubby understorey vegetation dominate in these patches (Mao *et al.*, 2012; Supplementary Data Table S1).

Climatic data and soil description

Mean monthly solar radiation was 200 MJ m⁻² in the winter and 800 MJ m⁻² in the summer (Mao *et al.*, 2015). Global precipitation data for the three sites together were obtained from the Réseau d'Observations Météo du Massif Alpin (ROMMA), station Chamrousse, (45°06'28"N, 05°52'28"E, 1800 m a.s.l.). The soil temperature within each rhizotron was recorded monthly in different soil layers (0.1, 0.4 and 0.9 m at 1400 and 1700 m, and 0.1 and 0.4 m at 2000 m) using a manual thermometer (HANNA HI 93510, Hanna Instruments, Inc., USA) from March 2010 to November 2013. Air temperatures were monitored every 30 min using Hobo® logging sensors (HOBO Pendant® Event Data Logger UA-003-64, Onset, USA) at a height of 1.5 m above each rhizotron; readings were missing during several periods at the end of the experiment (0.2 % of data were missing at 1700 m and 39 % of data were missing at 2000 m) when certain sensors malfunctioned. In order to



FIG. 1. Tree islands (closed forest) and gaps in a montane forest in the French Alps (1400 m). The green circle shows a typical tree island, comprising one or two dominant trees and smaller trees of the same species. The blue circle shows a gap situated between tree islands.

predict the missing climate data, we performed correlations between the mean daily air temperatures measured by our Hobo® logging sensors and the data from the ROMMA station at 1800 m, which was situated on the same hillside and close to our study site at 1700 m (Supplementary Data Table S2; Mao *et al.*, 2013b). Soil water potential (ψ) was measured using electrical resistance blocks (WaterMark, IRROMETER Company, Inc., USA) installed in one gap and one tree island at 1400 and 1700 m (equipment was frequently stolen at 2000 m so we were unable to monitor this site continuously). Six sensors were installed every 10 cm along a soil profile ranging from 10 to 70 cm in both gaps and islands. Mean values of ψ were calculated for depths of 0–30 and 30–70 cm. Data were logged every 30 min from July 2012 to November 2013 (Kim *et al.*, 2017).

A full description of soil type can be found in Mao *et al.* (2015). To measure soil organic carbon (SOC) and total nitrogen (N), samples ($n = 3$ at each sampling point) were taken from tree islands and gaps at depths of 5, 20 and 40 cm at all sites, and also at depths of 70 cm at elevations of 1400 and 1700 m. Soil was finely ground in a ball mill, and SOC and total N were measured by dry combustion using an elemental analyser (Thermo-Finnigan EA1112, Milan, Italy). The mean value of each set of three samples was calculated and used for subsequent statistical analysis.

Installation of rhizotrons

Tree root dynamics were measured using vertical rhizotrons (Bohm, 1979; Huck and Taylor, 1982; Mao *et al.*, 2013a, b; Wang *et al.*, 2018). In 2009, two plots of 25×25 m (except for one plot at 1400 m which was 25×30 m) were set up at each study site (Supplementary Data Fig. S1). Plots were located on the same topographical unit at a distance of approx. 100 m. Within each plot at 1400 and 1700 m, two trenches of 1.0 m (length) \times 0.6 m (width) \times 1.0 m (depth) were dug. At 2000 m, the soil was shallower, and the depth of the trench was only 0.5 m and width was 0.5 m. One trench was dug in a tree island and the other in a gap between trees; therefore, $n = 4$ rhizotrons per altitude (Supplementary Data Fig. S1). As the soil was removed during the digging of the trench, it was kept aside and then sieved through a 5 mm size sieve, before air drying for 6 h. Before installing the Plexiglas® pane, roots crossing the soil profile were cut with secateurs. Inside each trench, a 0.005 m thick Plexiglas® pane was placed against the uphill face of the trench at an angle of 15° (sloping from top to bottom) with regard to the vertical. This angle would permit roots to grow downwards due to positive geotropism (Huck and Taylor, 1982). The sieved and air-dried soil from the same trench was then gently poured into the space (approx. 0.05 m) and slowly compacted using a wooden plank. To protect roots from light and variations in temperature, each Plexiglas® pane was covered with foil-backed felt insulation and black plastic sheeting. Trenches were then covered with wooden boards and corrugated iron, to prevent direct rainfall onto rhizotrons and to avoid damage from passing animals. During the winter months, we removed and replaced snow (to its original thickness) before and after measurements. The entire installation took place in May 2009 at 1400 m, in July 2009 at 1700 m and in July 2010 in 2000 m. One rhizotron at a tree island of 1400 m and one at a gap of 2000 m was overhauled in 2012 July due to the appearance of an air gap between the Plexiglas® face and soil surface. More details on rhizotron installation are available in Mao *et al.* (2013b) and Mohamed *et al.* (2017).

Measurements of root dynamics

Root elongation was traced onto a transparent sheet which was placed over the Plexiglas® pane. We used permanent colour pens, and changed the colour every month (for the method, see Mohamed *et al.*, 2017); the date of the observation was noted. Root diameter was highly variable (Supplementary Data Fig. S2a); therefore, we classified roots into the following categories: 2–5, 1–2 and 0–1 mm (Mao *et al.*, 2013a). We did not classify roots into topological order, because it is not easy to determine root order in rhizotrons, as part of the root is often hidden in the soil (Supplementary Data Fig. S2b). We measured tree root growth only. It was possible to distinguish tree roots from herbaceous roots by their colour and thickness, although it was not possible to distinguish between different tree species, apart from roots of *F. sylvatica*, that are light in colour, and were not found in rhizotrons. To quantify root dynamics, the plastic sheets with root tracings were digitized in the laboratory using a 0.61×0.91 m Summagrid V digitizer (GTCO

Calcomp, Inc., Columbia, MD, USA) which was operated by the RhizoDigit[®] software (CIRAD, Montpellier, France). This software permits the acquisition of spatial co-ordinates and the length of each segment of growth, as well as the date on which it was measured (more details are shown in [Mao et al., 2013a, b](#)). We classed soil into shallow (0–0.3 m) and deep soil (>0.3 m) using root density distribution ([Schenk and Jackson, 2002; Mao et al., 2012](#)). Rhizotron angle was taken into account when determining the soil depth to which a root belonged. The root elongation rate (RER) was calculated for different coloured segments; therefore, one root possessed several RER values belonging to different growth periods. To avoid errors due to human visual judgement, only root segments that elongated >1.0 mm between two observation dates were measured. The occurrence of growing segments (number of growing roots) per day and mean RER were calculated within each layer of soil, and also over the whole rhizotron. Between the period September 2009 and November 2013, a total of 8990 roots emerged from the 12 rhizotrons.

We measured the RER and mortality 1 year after roots had first emerged, i.e. July 2010 at 1400 m, January 2011 at 1700 m and January 2012 at 2000 m, because the initial flush of roots caused by rhizotron installation results in an overestimation of root activity ([Majdi, 1996; Joslin and Wolfe, 1998; Strand et al., 2008](#)). Therefore, only 5905 roots out of the 8990 that had initiated in the 4 years after rhizotron installation were analysed.

Monthly based root growing degree days

We used growing degree days (GDDs) to estimate if relative root growth was similar at each field site. GDDs are defined as the sum of the average temperature in one plot minus a base temperature, where the base temperature equals a threshold that supports adequate plant growth, over a specified period of time ([Zalesny et al., 2004](#)). Therefore, to determine if the number of GDDs influenced average root elongation, the number of growing roots or dormancy, we calculated GDDs as a function of monthly mean soil temperature, using eqn (1) ([Romo and Eddleman, 1995](#)):

$$\left\{ \begin{aligned} \text{GDD}_m &= \sum \text{GDD} = \sum \left[\left(\frac{T_{\max} + T_{\min}}{2} \right) - T_{\text{base}} \right] \\ &= (T_{\text{soil}} - T_{\text{base}}) \times d \end{aligned} \right. \quad (1)$$

where GDD_m is monthly cumulated GDDs; T_{soil} is monthly soil temperature (°C); T_{\max} is daily maximum soil temperature; T_{\min} is daily minimum soil temperature; T_{base} is the mean base temperature when roots began growth (°C); and d is days between two observation dates. When T_{soil} is below T_{base} , GDD_m is not accumulated.

The cumulative GDD (CGDD) at a given month i was calculated by the formula:

$$\text{CGDD}_i = \sum_{\text{February}}^i \text{GDD}_m \quad (2)$$

where, CGDD_i is the CGDD at a given month i ; CGDD of the year was cumulated from February to the following January, as

the lowest temperature was often found in February; GDD_m is monthly cumulated GDD.

The parameter t_{base} was calculated for each root diameter class at each field site by regressing RER data (y) and monthly soil temperature (x) in order to obtain a linear relationship $y = ax + b$. When y was zero, x was considered as t_{base} ($-b/a$). Nine regressions were performed for each root category at all three altitudes to determine t_{base} . The parameter T_{base} was then calculated as the mean of all t_{base} values at each altitude [eqn (3)]. We only regressed RER data and soil temperature <8 °C, because these regressions were highly linear (data shown in the Results). Above 8 °C, data were more dispersed, leading to non-linearity, thus affecting the point at which the regression line crossed the x -axis (see the Results for details and results of statistical analyses). t_{base} of all altitudes and all root diameter classes ranged from 0.74 to 1.34 °C ($P < 0.001$), except for 1–2 mm roots at 1400 m (where t_{base} was -0.01 °C). We excluded outliers when calculating T_{base} :

$$T_{\text{base}} = \frac{\sum t_{\text{base}}}{n} = 1.07 \pm 0.08 \quad (3)$$

where $n = 8$.

Root growing span

In our study, we found that it was almost impossible to determine whether roots had died, or whether they had entered a dormant period for several months. Therefore, we used ‘root growing span’ to represent the life span of a root. When root growth was no longer detected (after a period of 6 months), we assumed that a root had ‘stopped’ growing (had died or entered a long dormancy phase), and we terminated observations.

Statistical analysis

An analysis of covariance (ANCOVA) for general linear mixed model fits was used to analyse the effects of root diameter, soil depth and vegetation structure on the RER and number of growing roots, with soil/air temperature or ψ as a covariable. Data were transformed to meet a normal distribution when needed. We ran different models whereby we: (1) considered each rhizotron as a random effect; and (2) considered each rhizotron as a random factor nested under temperature. The Akaike information criterion (AIC) was calculated to choose the best fitted model. A post-hoc Tukey’s honest significance test (HSD) was performed when ANCOVA was significant.

Paired t -tests were used to determine differences in soil temperature during the growing and non-growing seasons and differences in snow depth between tree islands and gaps. Data from the three elevations were pooled.

Spearman’s rank correlations were performed to determine the relationship between the mean daily air temperature, monthly soil temperature and the number of growing roots or RER.

A Cox proportional hazard model was used to analyse the effects of root diameter class on root mortality risk. Different

Cox hazard models were performed for three root classes separately to test the effect of patch type and elevation (R package ‘Survival’ by Therneau, 2013).

Analysis of variance (ANOVA) was used to analyse the influence of patch (tree island or gap), root diameter, altitude and year on mean monthly cumulated root length in the upper (0–30 cm) soil layer in individual rhizotrons during the growing season for each year separately. A Tukey’s HSD test was performed when the ANOVA result was significant.

Data shown are means \pm s.e. All data were analysed using R software 3.0.2 (R Development Core Team, 2011). Tukey’s test was performed using the package ‘multcomp’ (Hothorn et al., 2016) and mixed general linear model analysis on ANCOVA was conducted using the packages ‘lme4’ (Bates et al., 2015) and ‘car’ (Fox and Weisberg, 2011).

RESULTS

Climatic, meteorological and soil data

The mean monthly air temperature for all field sites combined was lowest in January or February (-3.8 °C) and highest in August (15.1 °C), with a mean annual temperature of 5.8 °C (Fig. 2A). Average annual precipitation is 1116 mm (Fig. 2A). During the growing season, soil temperature in gaps was significantly higher than that in tree islands for all soil depths (Fig. 2B; Supplementary Data Table S3). However, during the dormant season, significant differences were only found in soil temperatures at 90 cm deep, where soil was warmer than near the surface. Both total SOC and total soil N decreased significantly with increasing soil depth (Supplementary Data Table S4). SOC was significantly lower in gaps than in tree islands (Supplementary Data Table S5). However, there were no significant differences in total soil N between gaps or tree islands (Supplementary Data Table S5).

At a depth of 0 – 30 cm, mean ψ differed little between gaps and tree islands at 1700 m (Supplementary Data Table S4; Fig. S3). At 1400 m, differences between gaps and tree islands were more pronounced, with tree islands being drier than gaps near the soil surface (Supplementary Data Table S4; Fig. S3). At both altitudes, ψ was lower (wetter) at a depth of 30 – 100 cm compared with that nearer the surface (Supplementary Data Table S4; Fig. S3).

Snow cover generally commenced in November and snow usually remained in place until the months of April at both 1400 and 1700 m and May at 2000 m (Fig. 2). The maximum snow depth was in January or February from 2010 to 2012, and in April 2013. The deepest snow occurred at 2000 m (0.6 m in 2010–2011, 1.7 m in 2011–2012 and 3.0 m in 2012–2013). Snow cover was much less at 1400 m. Snow depths were significantly deeper in gaps than in tree islands (Supplementary Data Table S3).

Number of growing roots

The mean number of growing roots for all diameter classes and altitudes was highest in May 2011, June 2012 and July 2013, which in 2013 was just before bud break (Fig. 3). In 2011 (at 1400 and

1700 m) and 2012 (at all altitudes), the mean number of growing roots in all diameter classes reached a peak just before the highest soil temperature occurred and then started to decrease (Fig. 3).

The number of growing roots was positively correlated with both mean daily air temperature in all root diameter classes and monthly soil temperature in 0 – 1 mm diameter class roots, but R was very low (Fig. 4). When air temperature was considered as a covariate and root diameter classes, soil depth and vegetation type were factors, root diameter class had the strongest impact on root number compared with other factors (Table 1). The number of growing roots in the 2 – 5 mm diameter class was significantly less than in the 1 – 2 mm class ($P < 0.001$), which in turn was significantly less than in the 0 – 1 mm class ($P < 0.001$). When air temperature was considered as a covariable, the number of growing roots in gaps was significantly higher compared with that in tree islands at 1400 and 1700 m (in 2010 and 2011 at 1400 m and in all years at 1700 m; Fig. 4; Supplementary Data Table S6), while no significant differences were found at 2000 m.

Root elongation rate (RER)

At 1400 m, the RER in all diameter classes and for all years increased rapidly in May, reached a peak in July 2011 and then decreased (Fig. 2C–E). At 1700 and 2000 m, the RER of all diameter classes and for all years was highest in June and lowest in December (Fig. 2C–E). The dynamics of the RER followed a similar pattern to those of soil and air temperatures (Fig. 2A, B). The RER was positively and significantly correlated with both monthly soil and daily air temperatures (Spearman test: 2 – 5 mm, $\rho = 0.71$; 1 – 2 mm, $\rho = 0.71$; 0 – 1 mm, $\rho = 0.73$, $P < -0.01$). No significant relationship was found between RER and ψ at any elevation or patch type.

Root diameter size class had a much greater influence on RER than soil depth and forest patch type (Table 1). The RER in gaps was significantly higher than in tree islands, and RER in the deeper soil layer was significantly higher than that in the shallow layer (Table 1; Supplementary Data Fig. S4).

When mean air temperature was used as a covariable and all soil depths were combined, the RER in gaps was significantly higher compared with that in tree islands at 1400 and 1700 m (in 2010 and 2011 at 1400 m and in all years at 1700 m, Supplementary Data Table S6; Fig. S4), but no significant differences were found at 2000 m (Supplementary Data Table S6). However, for the same soil temperature, RER was significantly higher in gaps than in tree islands ($P = 0.04$) in 2010 at 1400 m only.

Mean cumulated root length and growing degree days (CGDDs)

Total cumulated length (in the 0 – 0.3 m soil layer) was significantly correlated with CGDDs in all root diameter classes (Fig. 5) and root length in the 2 – 5 mm class accumulated faster than in the other two diameter classes ($P < 0.001$, Fig. 5). When CGDD data for all years were combined, roots (all diameter classes combined) at 2000 m required significantly more CGDDs before growth was initiated, compared with roots at 1400 and 1700 m ($P = 0.020$, Table 2). At the end of the growing season, the CGDD was significantly greater at 1400 m compared with the other two altitudes ($P = 0.010$, Table 2).

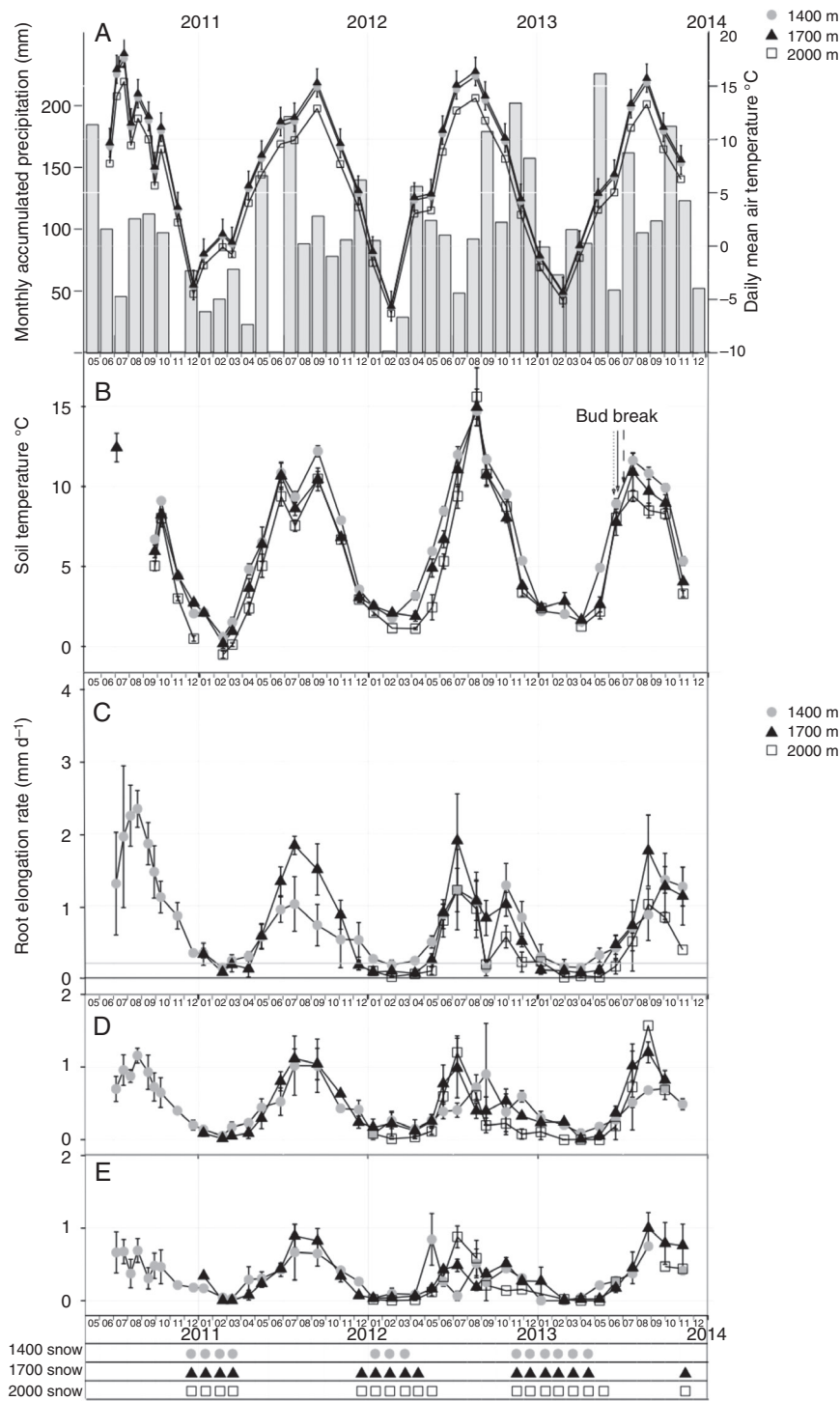


FIG. 2. Mean daily root elongation rate (RER, m d^{-1}) from May 2011 to November 2013 at three altitudes. The RER was not measured at all altitudes until 2012. (A) Mean daily air temperature and accumulated precipitation of each month; (B) mean monthly soil temperature at each altitude and (C) 2–5 mm roots compared with (D) 1–2 mm roots and (E) 0–1 mm roots. Snow cover is indicated as the number of months over which the soil surface was covered by snow at each altitude. Aerial bud burst in 2013 is shown with a dotted arrow (1400 m), a solid arrow (1700 m) and a dashed arrow (2000 m) (data from Wang et al., 2018). Data are means \pm s.e. ($n = 4$). In (A), the asterisk denotes that some precipitation data are missing for November 2010 and June 2011. Note that the scale of root elongation rate for the three diameter classes is different.

Root mortality risk based on root growing span

When roots from all diameter classes, sites and forest patch type were pooled together, Cox proportional hazards regression showed that root diameter class had a more important effect on

the risk of mortality (when a root stopped growing) compared with other factors. Roots in the 1–2 mm diameter class had 0.82 times more risk of mortality than roots in the 2–5 mm diameter class. Roots in the 0–1 mm diameter class had 1.84 times

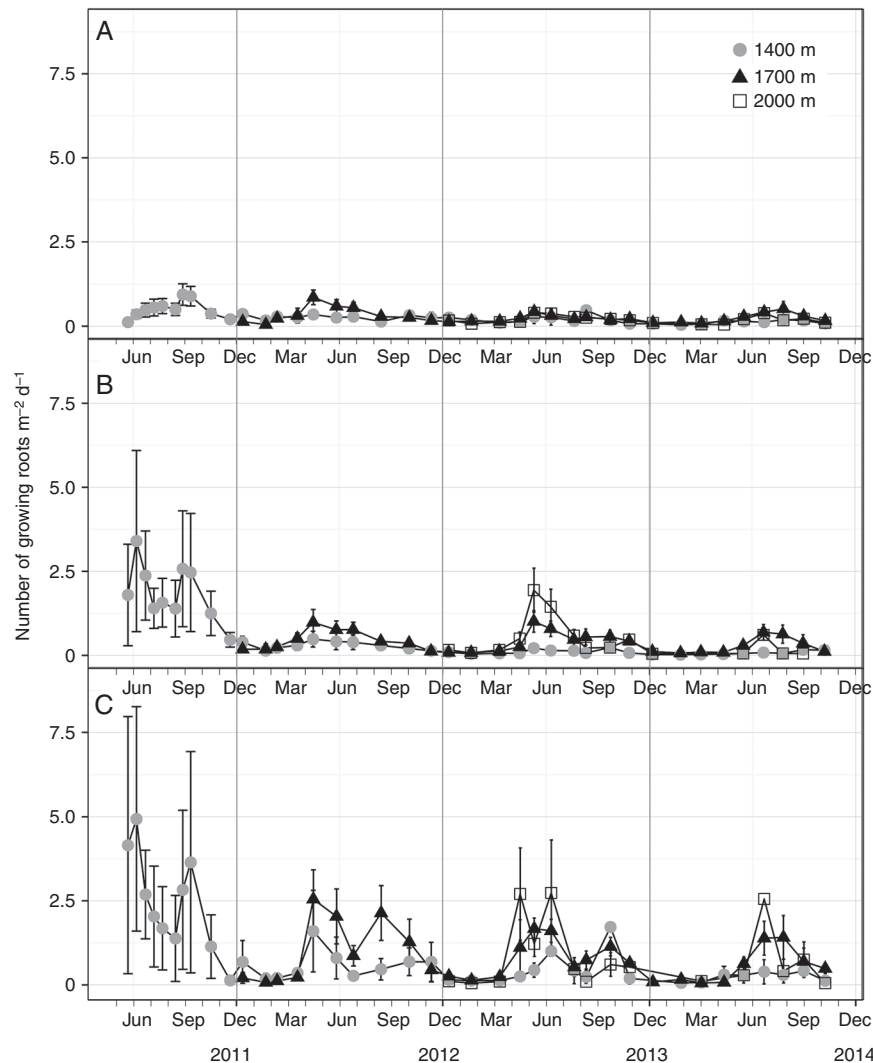


FIG. 3. Mean daily number of growing roots per square metre at different altitudes and in different root diameter classes. (A) Initiation of 2–5 mm diameter class roots was lowest, compared with (B) 1–2 mm diameter class roots and (C) 0–1 mm diameter class roots.

more risk of mortality compared with roots in the 2–5 mm class ($P < 0.001$, Table 3). For roots in the 2–5 mm diameter class, roots at 1700 m had 0.3 times less risk of mortality than at 1400 m (Table 3; Supplementary Data Fig. S5); no significant differences in mortality risk were found between roots in different patch types (Table 3; Supplementary Data Fig. S5). For roots in 1–2 and 0–1 mm diameter classes, roots at 1700 m had a significantly lower risk of mortality than at 1400 m, and roots at 2000 m had significantly greater mortality risk (Table 3; Supplementary Data Fig. S5). Roots in tree islands had 0.15 times less risk of mortality than roots in gaps for 1–2 mm diameter classes and 0.13 times less risk for roots in 0–1 mm diameter classes ($P = 0.008$, $P < 0.01$, Table 3; Supplementary Data Fig. S5). No significant differences in mortality risk were found between roots at different depths in the soil.

DISCUSSION

Differences in root growth between gaps and tree islands

The number of growing roots and the RER of fine roots at the same mean daily air temperature were higher in gaps than in

tree islands at 1400 and 1700 m; however, at the same monthly soil temperature, these differences disappeared. Soil temperature is a major driver of root growth in temperate forests (Mao *et al.*, 2013a), but, as soil is buffered from the atmosphere, temperature variations in soil are less variable than highly fluctuating air temperatures (Barton *et al.*, 1989). In our study, we measured mean monthly soil temperature only, possibly masking the effects of any more rapid changes in soil temperature between gaps and tree islands, especially during snowmelt and the summer. At 2000 m altitude, no differences in the number of growing roots and RER were observed between gaps and tree islands. As this elevation was approaching the thermal limit of forest growth (Körner, 2003), trees were more scattered and stem density was lower than at the other altitudes (Mao *et al.*, 2015). Therefore, biophysical differences between open and closed forest were less marked. Several processes may be occurring to explain the differences in root demography between gaps and tree islands: (1) gaps were warmer than tree islands, and temperature is a driver of root meristem activity (Barlow and Rathfelder, 1985; Wang *et al.*, 2018); (2) although we found no direct relationship between RER and ψ , wetter soil may increase micro-organism activity with positive effects on

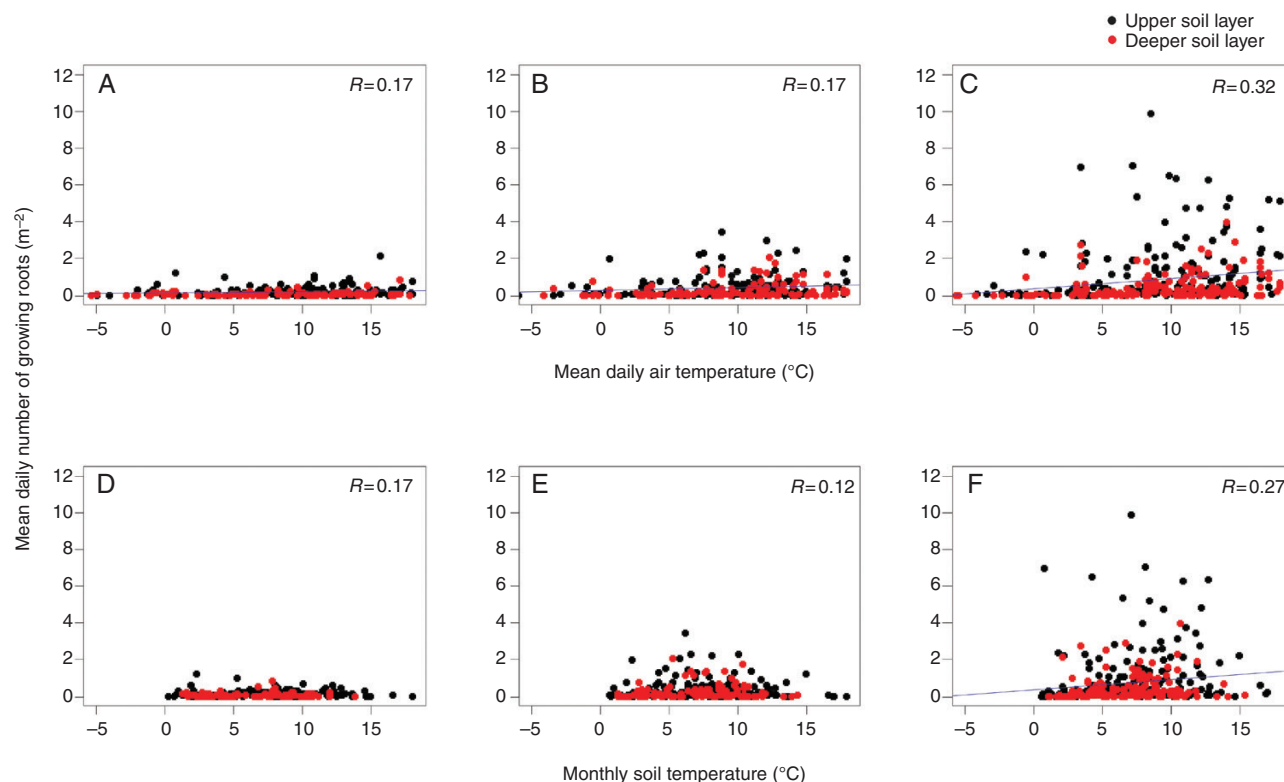


FIG. 4. Numbers of growing roots in (A) 2–5 mm, (B) 1–2 mm and (C) 0–1 mm diameter classes were significantly but poorly correlated with mean daily air temperature. Numbers of growing roots in (D) 2–5 mm, (E) 1–2 mm and (F) 0–1 mm diameter classes were significantly correlated with monthly soil temperature in the same soil layer. R from Spearman's correlations is shown on each graph (for both soil layers combined). Regression lines are shown when $P < 0.05$.

root growth; (3) snowmelt under trees may increase the formation of frost in soil compared with gaps, because melted water from the thinner snow layer infiltrates into soil around trunks before freezing in the soil (Stadler *et al.*, 1996); and (4) a much thinner layer of thermally protective snow under trees may also result in greater variations in daily or weekly soil temperatures

not measured in our study, which could result in colder soil hindering root growth (Tierney *et al.*, 2001).

Modifications in the risk of root mortality

We showed that the risk of mortality of 0–1 mm diameter roots was higher in gaps than in tree islands. As higher temperatures are known to increase the turnover rate of roots (McCormack and Guo, 2014; Kitajima *et al.*, 2010), the higher temperatures we observed, especially in the early growing season, probably explain the greater risk of root mortality observed in gaps. According to Gill and Jackson (2000), increased maintenance respiration, nutrient mineralization and soil micro-organism activity explain why survivorship is lower at higher temperatures. Although we found no differences in root mortality risk at different depths, Kitajima *et al.* (2010) suggest that root turnover rate can be explained by soil temperature alone, which is a more accurate predictor than soil depth. As tree fine roots in gaps were further from trees than the proximal roots in tree islands, carbohydrate resources may be less available for maintaining fine root longevity. However, Wang *et al.* (2018) showed that carbohydrate levels remained high in fine roots all year round. A plausible hypothesis for explaining the increased mortality of distal roots is that these roots are naturally 'shed' from the tree, in the same way that foliage is shed and renewed (Mainiero and Kazda, 2006). However, at 2000 m, we found a higher mortality risk for roots in the 0–1 and 1–2 mm diameter classes in both gaps and tree islands. At this elevation, trees might produce ephemeral,

TABLE 1. Results of ANCOVA tests on the relationships between root diameter, soil depth and patch type (tree island/gap) on the number of growing roots and root elongation rate (RER), with daily mean air temperature or monthly soil temperature as covariates

	d.f.	χ^2	$P (>\chi^2)$
Number of growing roots			
Air temperature	1	6.64	0.009
Root diameter	2	137.01	<0.001
Gap/tree island	1	4.57	0.03
Soil depth	1	51.15	<0.001
RER			
Air temperature	1	137.93	<0.001
Root diameter	2	175.96	<0.001
Gap/tree island	1	4.64	0.03
Soil depth	1	19.64	<0.001
Soil temperature			
Air temperature	1	106.3	<0.001
Root diameter	2	76.66	<0.001
Gap/tree island	1	0.04	0.84
Soil depth	1	30.09	<0.001

Type II Wald χ^2 tests are shown, along with degrees of freedom (d.f.) and probability (P).

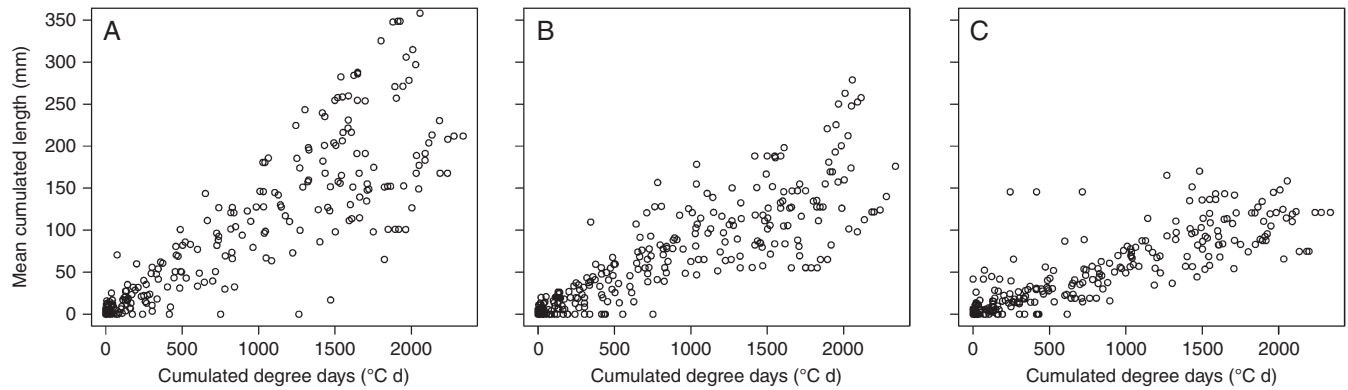


FIG. 5. Cumulated root length and degree days in the upper soil layer (0–30 cm), with all patch type (tree island/gap) and altitudes combined, for roots in (A) 2–5 mm ($r^2 = 0.48$, $P < 0.001$), (B) 1–2 mm ($r^2 = 0.43$, $P < 0.001$) and (C) 0–1 mm ($r^2 = 0.40$, $P < 0.001$) diameter classes.

short-lived fine roots when it is warm, to cope with the significantly shorter growing season. Increased root mortality risk at 2000 m may equally be due to the shift in species composition with altitude, which is partly the result of lower temperatures and a shorter growing season. A study to disentangle the rate of root mortality of individual species with that at the community level is therefore necessary to investigate further how forest structure impacts fine root dynamics.

In general, thicker roots possessed a longer growing span compared with fine roots, as also found by, for example, Wells and Eissenstat (2001) and Baddeley and Watson (2005). However, as diameter is usually well correlated to root order, and hence root function, root order may be the driving factor behind survivorship and longevity, as suggested by Kitajima *et al.* (2010). Valenzuela-Estrada *et al.* (2008), working on *Vaccinium corymbosum*, showed that higher order proximal roots with thicker diameters had more epidermal cells and larger vessel diameters than lower order distal fine roots. It was suggested that thicker roots are more expensive to construct in terms of carbon; therefore, if more investment has taken place in constructing thicker roots, more return on the investment will be gained if these roots live longer. We assume that root life span should maximize the lifetime root efficiency or the lifetime benefits relative to the lifetime costs (Eissenstat and Yanai, 1997). Fine roots in a cold environment, for example at higher

elevations and during the winter months, have a low assimilation ability, but remain alive (Schindlbacher *et al.*, 2007; Ruehr and Buchmann, 2010), and can recover quickly after a period of cold weather (Barlow and Rathfelder, 1985). These roots provide a transport pathway to allow for the provision of resources for a rapid production of fine roots as soon as the root growing season starts the following year.

Root growing season

The growing season of roots decreased significantly at higher altitudes, as also shown by Moser *et al.* (2010). We showed that roots at 1400 m elongated for a longer period (7–10 months) compared with those at 1700 m (6–7 months) and 2000 m (5–8 months). However, we found that the number of growing roots was lower at 1400 m for the same mean daily air temperature. Our results show that roots at higher elevations are more responsive to increases in air or soil temperature, to compensate for the shorter growing season, as also suggested by Mao *et al.* (2015), who found that at the same field sites, the ratio of fine root cross-sectional area to stand basal area increased with increasing elevation.

Due to an exceptionally long and severe winter in 2013, the growing season started considerably later at 2000 m, resulting

TABLE 2. Growing season for roots in all three altitudes from 2011 to November 2013

Altitude (m)	Start date	Stop date	Start CGDD (°C d)	End CGDD (°C d)	CGDD during growing season (°C d)	No. of growing months
1400	19 April 2011	12 January 2012	135.43 (12.97)	1957.80 (66.18)	1822.37 (113.46)	10
1700	17 May 2011	3 November 2011	231.07 (47.65)	1601.42 (133.46)	2090.13 (102.21)	7
2000	27 June 2011	12 December 2011	469.68 (49.02)	1481.40 (91.17)	1487.90 (86.35)	7
1400	11 April 2012	7 January 2013	145.03 (13.78)	2235.16 (72.76)	1370.35 (172.06)	10
1700	17 May 2012	27 November 2012	220.58 (33.82)	1832.28 (139.67)	1611.70 (227.39)	7
2000	11 June 2012	7 January 2013	192.83 (11.79)	1589.82 (130.43)	1049.57 (170.34)	8
1400	13 May 2013	8 November 2013	221.78 (17.64)	1709.68 (57.88)	1011.72 (84.66)	7*
1700	17 Jun 2013	8 November 2013	360.21 (29.06)	1409.78 (104.19)	1396.99 (210.54)	6*
2000	23 July 2013	8 November 2013	558.02 (61.55)	1191.93 (105.87)	633.91 (77.04)	5*

Growing season was decided when the RER in 2–5 mm diameter classes was $>0.2 \text{ mm d}^{-1}$.

‘Start CGDD’ is the CGDD that is needed for roots to start growing. ‘End CGDD’ is the CGDD at the end of the growing season. ‘CGDD during the growing season’ is the CGDD between the start and stop dates. The ‘start date’ and ‘stop date’ are when observations were commenced and terminated, respectively. Data shown are means (s.e.)

*The observation stopped in November 2013.

TABLE 3. Results of Cox proportional hazard regressions on root growing span examined in relation to root diameter and patch type [tree island (closed forest)/gap]

Covariable	Cox regression	Hazard ratio	Standard error	95 % CI		z	P
				Lower	Upper		
All roots							
ref: 2–5 mm root							
1–2 mm root	0.60	1.83	0.06	1.63	2.04	10.52	<0.001
0–1 mm root	1.04	2.84	0.05	2.56	3.15	19.81	<0.001
2–5 mm root							
Ref: 1400 m							
1700 m	–0.36	0.7	0.1	0.57	0.85	–3.48	<0.001
2000 m	–0.28	0.75	0.21	0.49	1.14	–1.33	0.18
ref: Gap							
Tree island	–0.1	0.91	0.1	0.75	1.1	–0.97	0.33
1–2 mm root							
Ref: 1400 m							
1700 m	–0.44	0.65	0.06	0.57	0.73	–6.73	<0.001
2000 m	0.4	1.49	0.1	1.22	1.81	3.9	<0.001
ref: Gap							
Tree island	–0.16	0.85	0.06	0.76	0.96	–2.64	0.008
0–1 mm root							
Ref: 1400 m							
1700 m	–0.34	0.71	0.03	0.66	0.77	–9.36	<0.001
2000 m	0.17	1.18	0.06	1.05	1.33	2.78	0.005
ref: Gap							
Tree island	–0.13	0.87	0.03	0.81	0.93	–3.95	<0.001

Hazard ratios for categorical covariates are the risk of stopping growth relative to a reference (ref) level (Cox, 1972), given for each covariate in the covariate column. A ratio >1 indicates that roots from that level of the covariable have a greater risk of mortality than roots from the reference level, while the opposite is true if the ratio is <1. The values for 95 % confidence intervals (CIs) are upper and lower limits and are not symmetrical about the hazard ratio. The z-value is the power of the test.

in a total of only 5 months growing season compared with 7 months at 1400 m and 6 months at 1700 m. At 2000 m, snow cover was prevalent until the month of June, and root growth started in July, after 558 CGDDs, compared with 360 and 222 CGDDs at 1400 and 1700 m, respectively. The effect of the long winter resulted in a very low number of growing roots at 2000 m in 2013. Therefore, we suggest that if a root starts to grow after a certain number of CGDDs (approx. 500 CGDDs), a normal rate of root growth may not occur in the ensuing growing season. Calculating CGDDs for root activity has rarely been performed (Zalesny *et al.*, 2004), and we show that it can provide useful information with regard to root system dynamics.

Links between root diameter and elongation

As long as soil temperature remained above freezing, and even when the mean daily air temperature was <0 °C, 2–5 mm class roots continued elongating, as also found by Mao *et al.* (2012), but the RER of 0–1 mm class roots only started to increase when air temperatures reached 2 or 3 °C (Fig. 2). In a controlled growth chamber, where 1-year-old seedlings of *P. abies* were grown at different soil temperatures, it was found that roots only started growing when soil temperatures were between 4 and 5 °C (Alvarez-Uria and Körner, 2007). We

suggest that the threshold of temperature required to initiate growth probably differs between roots of different diameters. Fine roots, regardless of tree age [in the study of Alvarez-Uria and Körner (2007), all roots were <1 mm in diameter], may need higher temperatures for growth to initiate, compared with coarser roots.

A greater number of finer roots elongated, compared with roots from thicker diameter classes, but the daily mean RER was higher in thicker roots, as also found by Mao *et al.* (2013a) at the same field site, and in other species, e.g. *Libocedrus decurrens* Torr (Wilcox, 1962). This phenomenon was reflected in the amount of total root length cumulated after 2000 CGDDs, with twice as much root length cumulated in the 2–5 mm diameter class compared with the 0–1 mm diameter class (Fig. 5). Fine roots are necessary for water and nutrient uptake, thus a higher number of elongating fine roots will permit a better scavenging of soil resources. Thicker roots anchor these foraging fine roots in the soil matrix (Barlow, 1989; Pregitzer *et al.*, 2002; Stokes *et al.*, 2009). Therefore, roots of different diameters possess different roles, reflected in their growth strategy. Thicker roots are more expensive for the tree to construct than fine roots as the C/N ratio is lower and specific root length (the ratio between root length and dry weight) is higher in fine roots (Pregitzer *et al.*, 1997). Therefore, although less numerous, once initiated, these roots grow faster and act as a transport pathway and structural support for the more numerous absorbing fine roots.

CONCLUSIONS

The RER was primarily driven by soil temperature (between 0 and 8 °C), not soil water potential, and so was less when soil was colder, e.g. in tree islands and at higher elevations. Roots at higher elevations were more responsive to the increase in temperature at the beginning of the growing season, probably to compensate for the shorter growing season. Compared with thicker roots, thinner roots were more numerous and required higher temperatures to initiate growth although they possessed a shorter life span. The difference between tree islands and gaps was less marked at 2000 m, probably due to the decrease in tree density near the treeline, resulting in fewer differences in the biophysical environment. Root turnover rates were lower in colder soils (tree islands), especially for the finest roots. However, finer roots at 2000 m had a greater risk of mortality: producing ephemeral, short-lived fine roots could also be a strategy to cope with the shorter growing season at a higher elevation. Therefore, heterogeneous forest structure and situation play a significant role in determining root demography in temperate forests, mostly because of modifications to local soil temperatures.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Figure S1: map showing the position of the 12 rhizotrons. Figure S2: images of elongating roots in rhizotrons at 2000 m. Figure S3: water potential (ψ in –kPa) of (a) 0–30 cm soil and (b) 30–70 cm soil in tree islands and gaps at 1400 and 1700 m altitude. Figure S4: root elongation rate. Figure S5: survival probability. Table

S1: site information. Table S2: regression relationships. Table S3: paired *t*-tests on soil temperature and snow depth between gaps and tree islands. Table S4: soil total organic carbon, total nitrogen content and water potential (ψ) in tree islands and gaps at different soil depths and elevations. Table S5: results of ANOVA tests.

ACKNOWLEDGEMENTS

Funding was received from the China Scholarship Council (Y.W.) and the INRA metaprogram AAFCC (Adaptation of Agriculture and Forests to Climate Change). We thank L. Selli (University of Bologna, Italy) and Y. Monnier (INRA, France) for technical assistance. Thanks are due to two anonymous reviewers for their rapid and helpful reviews.

LITERATURE CITED

- Abramoff RZ, Finzi AC. 2015. Are above- and below-ground phenology in sync? *New Phytologist* **205**: 1054–1061.
- Alvarez-Uria P, Körner C. 2007. Low temperature limits of root growth in deciduous and evergreen temperate tree species. *Functional Ecology* **21**: 211–218.
- Ares A, Neill AR, Puettmann KJ. 2010. Understory abundance, species diversity and functional attribute response to thinning in coniferous stands. *Forest Ecology and Management* **260**: 1104–1113.
- Baddeley JA, Watson CA. 2005. Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. *Plant and Soil* **276**: 15–22.
- Barlow PW. 1989. Metamers and nodules and the development of shoot and root systems. *Botanical Journal of the Linnean Society* **100**: 255–279.
- Barlow PW, Rathfelder EL. 1985. Cell division and regeneration in primary root meristems of *Zea mays* recovering from cold treatment. *Environmental and Experimental Botany* **25**: 303–314.
- Barton AM, Fletcher N, Redhead S. 1989. The relationship between treefall gap size and light flux in a Neotropical rain forest in Costa Rica. *Journal of Tropical Ecology* **5**: 437–439.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**: 1–48.
- Bauhus J, Bartsch N. 1996. Fine-root growth in beech (*Fagus sylvatica*) forest gaps. *Canadian Journal of Forest Research* **26**: 2153–2159.
- Bohm W. 1979. *Methods of studying root systems*. Berlin: Springer-Verlag.
- Brunner I, Bakker MR, Björk RG, et al. 2013. Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. *Plant and Soil* **362**: 357–372.
- Cox DR. 1972. Regression models and life tables (with discussion). *Journal of the Royal Statistical Society, Series B* **34**: 187–220.
- Denslow JS, Ellison AM, Sanford RE. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology* **86**: 597–609.
- Eissenstat D, Yanai R. 1997. The ecology of root lifespan. *Advances in Ecological Research* **27**: 1–60.
- Eissenstat D, Bauerle T, Comas L, et al. 2005. Seasonal patterns of root growth in relation to shoot phenology in grape and apple. *Acta Horticulturae* **721**: 21–26.
- Fox J, Weisberg S. 2011. *An R companion to applied regression*, 2nd edn. Thousand Oaks CA: Sage.
- Geng Y, Wang L, Jin D, Liu H, He J-S. 2014. Alpine climate alters the relationships between leaf and root morphological traits but not chemical traits. *Oecologia* **175**: 445–455.
- Gill RA, Jackson RB. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**: 13–31.
- Graefe S, Hertel D, Leuschner C. 2008. Fine root dynamics along a 2,000-m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil* **313**: 155–166.
- Griffiths RP, Gray AN, Spies TA. 2010. Soil properties in old-growth Douglas-fir forest gaps in the western Cascade Mountains of Oregon. *Northwest Science* **84**: 33–45.
- Heithecker TD, Halpern CB. 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *Forest Ecology and Management* **248**: 163–173.
- Hothorn T, Bretz F, Westfall P, et al. 2016. Package 'multcomp'. <http://cran.stat.sfu.ca/web/packages/multcomp/multcomp.pdf>.
- Huck MG, Taylor HM. 1982. The rhizotron as a tool for root research. *Advances in Agronomy* **35**: 1–35.
- Joslin JD, Wolfe MH. 1998. Impacts of water input manipulations on fine root production and mortality in a mature hardwood forest. *Plant and Soil* **204**: 165–174.
- Kim JH, Fourcaud T, Jourdan C, et al. 2017. Vegetation as a driver of temporal variations in slope stability: the impact of hydrological processes. *Geophysical Research Letters* **44**: 4897–4907.
- Kitajima K, Anderson KE, Allen MF. 2010. Effect of soil temperature and soil water content on fine root turnover rate in a California mixed conifer ecosystem. *Journal of Geophysical Research* **115**: G04032. doi:10.1029/2009JG001210.
- Körner C. 2003. *Alpine plant life. Functional plant ecology of high mountain ecosystems*. Berlin: Springer.
- Kubisch P, Leuschner C, Coners H, Gruber A, Hertel D. 2017. Fine root abundance and dynamics of stone pine (*Pinus cembra*) at the alpine treeline is not impaired by self-shading. *Frontiers in Plant Science* **8**: 602. doi:10.3389/fpls.2017.00602.
- Lahti M, Aphalo P, Finér L, Ryyppö A, Lehto T, Mannerkoski H. 2005. Effects of soil temperature on shoot and root growth and nutrient uptake of 5-year-old Norway spruce seedlings. *Tree Physiology* **25**: 115–122.
- Lopushinsky W, Max T. 1990. Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. *New Forests* **4**: 107–124.
- Lyr H. 1996. Effect of the root temperature on growth parameters of various European tree species. *Annales des Sciences Forestières* **53**: 317–323.
- Mainiero R, Kazda M. 2006. Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. *Forest Ecology and Management* **237**: 135–142.
- Majdi H. 1996. Root sampling methods – applications and limitations of the minirhizotron technique. *Plant and Soil*, **185**: 255–258.
- Mao Z, Saint-André L, Genet M, et al. 2012. Engineering ecological protection against landslides in diverse mountain forests: choosing cohesion models. *Ecological Engineering* **45**: 55–69.
- Mao Z, Bonis M-L, Rey H, Saint-André L, Stokes A, Jourdan C. 2013a. Which processes drive fine root elongation in a natural mountain forest ecosystem? *Plant Ecology and Diversity* **6**: 231–243.
- Mao Z, Jourdan C, Bonis M-L, et al. 2013b. Modelling root demography in heterogeneous mountain forests and applications for slope stability analysis. *Plant and Soil* **363**: 357–382.
- Mao Z, Wang Y, Jourdan C, et al. 2015. Characterizing above- and below-ground carbon partitioning in forest trees along an altitudinal gradient using area-based indicators. *Arctic, Antarctic, and Alpine Research* **47**: 59–69.
- McCormack ML, Guo D. 2014. Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science* **5**: 205.
- Mohamed A, Monnier Y, Mao Z, et al. 2017. An evaluation of methods for root image acquisition when using rhizotrons. *Plant Method*, **13**: 11. doi:10.1186/s13007-017-0160z.
- Moser L, Fonti P, Büntgen U, et al. 2010. Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. *Tree Physiology* **30**: 225–233.
- Müller K, Wagner S. 2003. Fine root dynamics in gaps of Norway spruce stands in the German Ore Mountains. *Forestry* **76**: 149–158.
- Nagelmüller S, Hiltbrunner E, Körner C. 2016. Critically low soil temperatures for root growth and root morphology in three alpine plant species. *Alpine Botany* **126**: 11–21.
- Norby RJ, Jackson RB. 2000. Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist* **147**: 3–12.
- Phillips RP, Meier IC, Bernhardt ES, Grandy AS, Wickings K, Finzi AC. 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO₂. *Ecology Letters* **15**: 1042–1049.
- Pregitzer KS, Kubiske ME, Yu CK, Hendrick RL. 1997. Relationships among root branch order, carbon, and nitrogen in four temperate species. *Oecologia* **111**: 302–308.
- Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL. 2002. Fine root architecture of nine North American trees. *Ecological Monographs* **72**: 293–309.

- Prieto I, Roumet C, Cardinael R, *et al.* 2015. Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *Journal of Ecology* **103**: 361–373.
- Prieto I, Stokes A, Roumet C. 2016. Root functional parameters predict fine root decomposability at the community level. *Journal of Ecology* **104**: 725–733.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Radville L, McCormack ML, Post E, Eissenstat DM. 2016. Root phenology in a changing climate. *Journal of Experimental Botany* **67**: 3617–3628.
- Romo J, Eddleman L. 1995. Use of degree-days in multiple-temperature experiments. *Journal of Range Management* **48**: 410–416.
- Ruehr NK, Buchmann N. 2010. Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities differ among microbial and root–rhizosphere respiration. *Tree Physiology* **30**: 165–176.
- Sanford RL Jr. 1990. Fine root biomass under light gap openings in an Amazon rain forest. *Oecologia* **83**: 541–545.
- Scharenbroch B, Bockheim J. 2007. Impacts of forest gaps on soil properties and processes in old growth northern hardwood–hemlock forests. *Plant and Soil* **294**: 219–233.
- Schenk HJ, Jackson RB. 2002. The global biogeography of roots. *Ecological Monographs* **72**: 311–328.
- Schindlbacher A, Zechmeister-Boltenstern S, Glatzel G, Jandl R. 2007. Winter soil respiration from an Austrian mountain forest. *Agricultural and Forest Meteorology* **146**: 205–215.
- Siira-Pietikäinen A, Pietikäinen J, Fritze H, Haimi J. 2001. Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. *Canadian Journal of Forest Research* **31**: 88–99.
- Stadler D, Wunderli H, Auckenthaler A, Flüeler H, Bründl M. 1996. Measurement of frost-induced snowmelt runoff in a forest soil. *Hydrology Process* **10**: 1293–1304.
- Stokes A, Atger C, Bengough AG, Fourcaud T, Sidle RC. 2009. Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant and Soil* **324**: 1–30.
- Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R. 2008. Irreconcilable differences: fine-root life spans and soil carbon persistence. *Science* **319**: 456–458.
- Therneau T. 2013. *A package for survival analysis in S*. R package version 2.37-4. <http://CRAN.R-project.org/package=survival>. Box, 980032: 23298–0032.
- Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT. 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* **56**: 175–190.
- Tomlinson P. 1980. *The biology of trees native to tropical Florida*. Harvard University Press: Cambridge, MA.
- Valenzuela-Estrada LR, Vera-Caraballo V, Ruth LE, Eissenstat DM. 2008. Root anatomy, morphology, and longevity among root orders in *Vaccinium corymbosum* (Ericaceae). *American Journal of Botany* **95**: 1506–1514.
- Wang Y, Mao Z, Bakker MR, *et al.* 2018. Linking tree root growth and production to soil temperature and carbon supply in temperate forests. *Plant and Soil* (in press). <https://doi.org/10.1007/s11104-018-3596-7>
- Wells CE, Eissenstat DM. 2001. Marked differences in survivorship among apple roots of different diameters. *Ecology* **82**: 882–892.
- Whitmore T. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* **70**: 536–538.
- Wilcox H. 1962. Growth studies of the root of incense cedar, *Libocedrus decurrens*. II. Morphological features of the root system and growth behavior. *American Journal of Botany* **49**: 237–245.
- Wilczynski C, Pickett S. 1993. Fine root biomass within experimental canopy gaps: evidence for a below-ground gap. *Journal of Vegetation Science* **4**: 571–574.
- Yang B, Pang X, Hu B, Bao W, Tian G. 2017. Does thinning-induced gap size result in altered soil microbial community in pine plantation in eastern Tibetan Plateau? *Ecology and Evolution* **7**: 2986–2993.
- Zalesny R Jr, Bauer E, Riemenschneider D. 2004. Use of belowground growing degree days to predict rooting of dormant hardwood cuttings of *Populus*. *Silvae Genetica* **53**: 154–160.