Characterizing Above- and Belowground Carbon Partitioning in Forest Trees along an Altitudinal Gradient using Area-Based Indicators

Source: Arctic, Antarctic, and Alpine Research, 47(1):59-69.
Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado
DOI: http://dx.doi.org/10.1657/AAAR0014-014
URL: http://www.bioone.org/doi/full/10.1657/AAAR0014-014

Arctic, Antarctic, and Alpine Research, Vol. 47, No. 1, 2015, pp. 59–69

Characterizing above- and belowground carbon partitioning in forest trees along an altitudinal gradient using area-based indicators

Zhun Mao[1,2,7]
Yan Wang[3]
Christophe Jourdan[4]
Lauric Cécillon[1,2]
Jérôme Nespoulous[3]
Hervé Rey[5]
Laurent Saint-André[4,6] *and*
Alexia Stokes[3]

[1]Institut national de Recherche en Sciences et Technologies pour l'Environnement et l'Agriculture (IRSTEA), UR EMGR, 2 Rue de la Papeterie, BP 76, 38402 Saint-Martin-d'Hères Cedex, France
[2]Université Grenoble Alpes (UGA), 38402 Saint-Martin-d'Hères Cedex, France
[3]Institut National de la Recherche Agronomique (INRA), UMR AMAP, Boulevard de la Lironde, 34398 Montpellier Cedex 5, France
[4]Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), UMR Eco&Sols–Ecologie Fonctionnelle & Biogéochimie des Sols & Agroécosystèmes (Montpellier SupAgro-CIRAD-INRA-IRD), 2 Place Viala, 34060 Montpellier, France
[5]CIRAD, UMR AMAP, Boulevard de la Lironde, 34398 Montpellier Cedex 5, France
[6]INRA, UR BEF–Biogéochimie des Ecosystèmes Forestiers, 54280 Champenoux, France
[7]Corresponding author: maozhun04@126.com

Abstract

Characterizing the above- and belowground carbon stocks of ecosystems is vital for a better understanding of the role of vegetation in carbon cycling. Yet studies on forest ecosystems at high altitudes remain scarce. We examined above- and belowground carbon partitioning in trees growing in mixed montane/upper montane forest ecosystems in the French Alps. Field work was performed in three forests along a gradient of both altitude (1400 m, 1700 m, and 2000 m) and altitude-induced species composition (from lower altitude *Abies alba* and *Fagus sylvatica* to higher altitude *Picea abies* and *Pinus uncinata*). We performed forest inventories and root sampling along soil wall profiles, so that the stand basal area (SBA, in m^2 ha^{-1}) and root cross-sectional area (RCSA, in m^2 ha^{-1}) were estimated at each altitude. To characterize the carbon allocation trend between the above- and belowground compartments, the ratio of RCSA to SBA was then calculated. We found that both SBA and RCSA of coarse roots (diameter > 2 mm) were significantly different among the three altitudes. No significant difference in RCSA of fine roots (diameter ≤ 2 mm) was found among altitudes. The ratio of RCSA of fine roots to SBA augmented with increasing elevation, suggesting that forest ecosystems at higher altitudes allocate more carbon from above- to belowground organs. This increased allocation to fine roots would allow trees to scavenge nutrients more efficiently throughout the short growing season. Furthermore, this work highlighted the interest of using easy to measure area-based indicators as proxies of root and stem biomass when investigating carbon partitioning in highly heterogeneous montane/upper montane forests.

DOI: http://dx.doi.org/10.1657/AAAR0014-014

Introduction

Increasing elevation can lead to significant changes in numerous environmental factors, for example, decreasing air and soil temperatures (Shreve, 1924; Körner and Paulsen, 2004), increased radiation (Körner and Renhardt, 1987; Körner, 2007), increasing precipitation (Graefe et al., 2010) or snow depth (Groffman et al., 2009), and declining soil quantity and quality (Sveinbjörnsson et al., 1995; Leuschner et al., 2007). Changes in abiotic factors due to altitude can have an important influence on plant growth, community structure, and ecosystem processes (Sundqvist et al., 2013).

It has been well documented that aboveground growth of plants is more restricted at higher altitudes (Hertel and Schöling, 2011a). Above/belowground biomass ratios, signifying the extent of carbon allocation between shoots and roots, are equally highly sensitive to altitudinal gradients, and since 1979 plant growth theory (Grime, 1979) proposes that in stress-dominated, cold habitats, a higher proportion of dry matter is allocated to root systems. This increase in belowground dry matter would act as a sink for reserves, which could then be mobilized during seasonal growth periods. However, the carbon assimilation capacity of plants does not necessarily change with altitude because photosynthesis in high altitude plants is very efficient (Körner, 1982; Oleksyn et al., 1998; Körner and Paulsen, 2004). Therefore, extra storage of reserves in root systems at high altitudes may be superfluous, especially in trees, where high concentrations of non-structural carbohydrates are usually found located at the stem base (Mialet-Serra et al., 2005, 2008; Legros et al., 2009). We suggest that above/belowground partitioning does occur in trees along an altitudinal gradient (Hertel and Schöling, 2011a, 2011b), but that root size must also be considered, because fine and coarse roots do not possess the same functional role within a root system.

Tree fine roots are most commonly defined as ≤2 mm in diameter (see Finér et al., 2007; Helmisaari et al., 2007; Mao, 2012). The role of

1523-0430/06 $7.00

fine roots is to absorb nutrients and water, unlike thicker roots, which serve as a structure to bear the foraging fine roots and to anchor the tree (Pregitzer, 2002; Stokes et al., 2009). In temperate forests, Hertel and Schöling (2011b) argued that the increased investment in fine root biomass of *Picea abies* at higher elevations was due to reduced nutrient availability. An augmentation in fine root absorptive area would thus aid mineral uptake (Oleksyn et al., 1998). In mountain forests, it is still not clear how carbon is allocated between fine and coarse roots and this aspect has been neglected by most studies on carbon allocation. Although Soethe et al. (2006) showed that in tropical montane forests situated along an altitudinal gradient, the density and vertical distribution of large roots (15–20 mm in diameter) changed within the soil profile, similar data for thinner and fine roots were not shown. Hertel and Schöling (2011b) reviewed studies on above- and belowground carbon partitioning in European forests and showed that in the European Alps, data on root biomass in mountain forests above an altitude of 1500 m were extremely scanty. This lack of belowground carbon data is probably due to the difficulty in sampling root biomass in these areas, as forests are spatially heterogeneous and soil is often too stony to be sampled using cores. This knowledge gap highlights the necessity for finding new indicators as proxies for estimating above/belowground carbon allocation.

We investigated tree above/belowground carbon partitioning in heterogeneous mixed forest ecosystems in the French Alps. Three montane/upper montane forests (see Körner, 2012) were located at three altitudes: 1400 m, 1700 m, and 2000 m (the climatic tree line, i.e., the altitudinal limit of tree growth, see Körner, 1998). We hypothesized that an altitudinal gradient would alter: (1) above/belowground partitioning, with a greater investment in the belowground carbon sink, and (2) partitioning between fine and coarse roots, with a non-linear correlation between both root types because of the specific role of coarse and fine roots each in tree function. To investigate carbon partitioning at the ecosystem level, we used area-based proxies instead of biomass-based indicators, which are usually employed. The advantages and drawbacks of both sorts of indicators are discussed.

Materials and Methods

STUDY SITES, SOIL, AND VEGETATION CHARACTERISTICS

Our study sites are all situated near the village of Chamrousse, Isère, France (45°07′N, 5°52′E, elevation 1766 m). They 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) in Isère, French Alps. All sites were south- or southwest-facing, and dominant species changed with altitude (see the section "*STEM DENSITY*" in "Results" for more details).

Our study plot at 1700 m was situated on a slope of 10°–15°, but at 1400 m and 2000 m, the slope angle might reach 25°. The maximum depth of rooted soil layer at 1400 m and 1700 m attained approximately 1.0 m, but only 0.5 m at 2000 m. Soils were acidic at all sites, ranging from (*a*) "Cambisols (Hyperdystric)" according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2007), above green schist and with an abundant water supply at 1400 m (Joud, 2006; Mao et al., 2012), to (*b*) "Cambisols (Humic, Hyperdystric)" according to the WRB (IUSS Working Group WRB, 2007), above the crystalline formation at 1700 m (Joud, 2006; Mao et al., 2012), and to (*c*) "Epileptic Umbrisols (Hyperdystric)" according to the WRB (IUSS Working Group WRB, 2007), above the crystalline formation at 2000 m. A high presence of coarse elements (rocks and stones) throughout the soil profile was found at all sites. Soil carbon (C) and nitrogen (N) contents were measured using a carbon nitrogen elemental analyzer (CHN: NCS2500, ThermoQuest) and samples were taken within a soil depth of]0.0, 0.3] m[1] via excavation of mini-monoliths in which roots were simultaneously sampled (see the section "*ESTIMATION OF TREE ROOT DENSITY*" for more details): 12 sampling spots at 1400 m, 13 sampling spots at 1700 m, and 2 sampling spots at 2000 m. In each sampling spot (i.e., mini-monoliths), soils were sampled in one upper humus layer and one or two lower layers of 0.1 m. The thickness of humus was generally ≤0.1 m for all the three altitudes with the thickest at 1700 m (~>0.06 m) and the thinnest at 1400 m (~>0.03 m). No significant differences were found between altitude (using analysis of variance, ANOVA) and the mean C and N contents were 13.18% ± 8.95% (mean ± standard deviation) and 0.71% ± 0.38% (mean ± standard deviation), respectively.

In these forests, trees are naturally grouped into clusters, or "tree islands," with a closed canopy above the cluster. Between the tree islands are gaps, which often form after, for example, tree failure during a storm or tree mortality. In gaps, the canopy is open and vegetation is composed of herbaceous and shrubby species (Mao et al., 2012). At 1400 m, dominant herbaceous species included *Gallium rotundifolium* L., *Lysimachia nemorum* L., *Viola* sp., *Luzula sylvatica* (Huds.) Gaudin., and *Stellaria media* (L.) Vill. subsp. Media., whereas at 1700 m, dominant understory species included *Rhododendron ferrugineum* L. and *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L. subsp. *vitis-idaea*, *Melampyrum sylvaticum* L., and *Hieracium* sp. At 2000 m, we found *Cupressus* sp. and *Rhododendron ferrugineum* L. as the dominant dwarf shrub and *Gentiana lutea* L., *Platanthera bifolia* Rich., *Viola tricolor* L., *Primula hirsuta* All., and *Soldanella alpina* L. as common herbaceous species.

CLIMATE DATA

Mean monthly air temperature was lowest in January or February (–2.3 °C at 1400 m, –3.6 °C at 1700 m, –5.2 °C at 2000 m) and highest in July (13.7 °C at 1400 m, 12.0 °C at 1700 m, 10.2 °C at 2000 m). Mean monthly solar radiation ranged from 200 MJ m^{-2} in the winter to 800 MJ m^{-2} in the summer. Average annual precipitation is 1530 mm at 1400 m, 1710 mm at 1700 m, and 1900 mm at 2000 m. Precipitation also showed seasonal variation with the lowest quantity in July and August and highest quantity (in the form of snow) in December. All the above data were obtained from an enhanced version of *AURELHY* model of Météo-France (1961–1990; Benichou an Le Breton, 1987), *HELIOS* model, and their couplings since 2011 (Piedallu and Gegout, 2007, 2008). Factors such as altitude, topography, exposition, and radiation were considered when modeling air temperature and precipitation. All above meteorological models performed computations at a scale of 1 km (except the solar radiation, which was computed at a scale of 50 m) with satisfactory validations using observed data in France.

ABOVEGROUND FOREST STRUCTURE

We performed forest inventories at 1400 m and 1700 m in 2009 (Mao et al., 2012). During these forest inventories, at each

---

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

of the two lower altitudes, two 25 m × 25 m (except for one plot at 1400 m that was 25 m × 30 m) plots were set up (Mao et al., 2012). With regard to 2000 m, these inventories were performed in summer 2010. Three plots (two were 20 m × 20 m and one was 25 m × 25 m) were identified. In order to sample forest heterogeneity, within each plot at least two tree islands and two gaps were present for 1400 m and 1700 m. Because the forest at 2000 m was less dense, each plot enveloped at least one tree island and one gap. All tree islands were comparable in size, that is, with a radius of 3–5 m, while gap size increased with increasing altitude due to the sparser tree density. At 2000 m, smaller study plots (20 m × 20 m) were used to avoid an over-large surface of tree-free zones within plots. At each plot, species, height, and diameter at breast height per tree were recorded. Young trees <1.3 m in height were not measured. The stand basal area (SBA, in m² ha^{-1}) for each altitude was then calculated using the sum of basal area of each tree individual divided by the surface of the plot. In order to demonstrate any spatial heterogeneity, we calculated the SBA for each plot per altitude.

MEASUREMENT OF ROOT DENSITY

To measure root distribution, we selected sites within the plots used for forest inventories at 1400 m and 1700 m. At each plot we chose one of the two tree islands and one of the two gaps, and in the middle of each, a trench 1.0 m (length) × 0.6 m (width) × 1.0 m (depth, i.e., the maximum rooting depth) was dug. Therefore, four trenches were dug at both 1400 m and 1700 m. For each trench, root distribution was measured along each soil profile wall, therefore $n = 4$ (number of trenches) × 4 (number of profile walls per trench) = 16 for each altitude (Mao et al., 2012). Because the site at 2000 m was popular with tourists (skiing in the winter and mountain biking in summer), our access was limited and we measured only eight soil profiles (0.5–0.8) m (width) × 0.5 m (depth, i.e., the maximum rooting depth). Three profiles were dug in summer 2010 and five in summer 2012 (therefore $n = 8$). These soil profiles were distributed among eight plots used for forest inventories: three in gaps, two close to tree islands, and three in transition zones between gaps and islands.

All roots (regardless of species) were counted and classed into six different diameter classes:]0, 1] mm,]1, 2] mm,]2, 5] mm,]5, 10] mm,]10, 20] mm, and]20, 50] mm. Root diameter was noted once a root was superior or equal to 5 mm in diameter. The threshold chosen between fine (2 mm included) and coarse roots (2 mm excluded) was 2 mm. It was difficult to identify live versus dead roots using Böhm's trench profile method (Böhm, 1979). We assumed that the counted roots contained mostly live roots, as decomposed or dead roots usually dropped from the soil profile surface during excavation. Root density was expressed as the stand root cross-sectional area (RCSA, in m² ha^{-1}), which can also be called "Root Area Ratio" and has been a widely measured root indicator measured via the soil profile method (Smit et al., 2000). Here RCSA is calculated using the following equation:

$$RCSA = \frac{10000}{A}\sum_{i=B}^{E}\sum_{n=1}^{N_i}\frac{\pi}{4}\left(10^{-3}d_{i,n}\right)^2 \qquad (1)$$

where, N_i is number of root counts on the soil profile of surface A (in m²) in the diameter class i, $i \in [B, E]$; B and E are the beginning and end number of root diameter class, $B, E \in [1, 6]$ and $B \le E$. In the present study, $B = 1$, $E = 2$ for RCSA of fine roots and $B = 3$, $E = 6$ for RCSA of coarse roots. $d_{i,n}$ and $\frac{\pi}{4}\left(10^{-3}d_{i,n}\right)^2$ are diameter (in mm) and CSA (in m²) of the n^{th} root in diameter class i, respectively; 10,000 allows standardizing RCSA to a surface of 10,000 m² analogous to SBA. In case of $i \le 3$ (i.e., root diameter ≤ 5 mm), Equation 1 is simplified to

$$RCSA = \frac{10000}{A}\sum_{i=B}^{E}\frac{\pi}{4}\left(10^{-3}\overline{d_i}\right)^2 N_i \qquad (2)$$

where, $\overline{d_i}$ is mean diameter of roots of diameter class i.

For the root profiles at 1400 m and 1700 m, $A = 1.0$ m² (i.e., 1.0 m × 1.0 m) or 0.6 m² (i.e., 0.6 m × 1.0 m). For the root profiles at 2000 m, the measured root density was standardized at a soil width of 1.0 m and a soil depth of 1.0 m in order to facilitate comparison with the other altitudes.

ESTIMATION OF TREE ROOT DENSITY

Tree species to which roots belonged were not distinguished during the root counting performed in 2009 and 2010. In order to estimate the proportion of roots from trees compared to that of roots from shrubby and herbaceous plants, we used a set of unpublished root data sampled at 1400 m and 1700 m in 2010 (see Mao, 2012). The data were collected within the same plots as those in this study. Roots were measured using mini-monoliths of 0.2 m (length) × 0.2 m (width) × (0.2–0.3) m (depth) with total $n = 25$ (12 at 1400 m and 13 at 1700 m). For each mini-monolith, soil within the area of 0.2 m × 0.2 m was carefully excavated per soil layer of 0.1 m in thickness (except the first layer, i.e., the humus layer that may vary in thickness between mini-monoliths). During excavation, we avoided damaging roots from the lateral soil profiles. Then, root intercepts on lateral soil walls were counted using the same protocol as in this study, except that different plant functional groups (trees, shrubby, and herbaceous species) were distinguished when roots were >1 mm in diameter. For root intercepts of]0, 1] mm in diameter, the plant functional group was difficult to identify in situ due to the presence of a variety of understory species at 1400 m and 1700 m. Therefore, we estimated the root length density of roots that were collected from the mini-monoliths, washed in the laboratory, sorted according to functional group, scanned, and analyzed using the software WINRHIZO (Regent Inc., Canada). It was relatively easy to separate roots from different functional groups using this method because of differences in color, texture, and smell. At the 2000 m site, the plant functional group was identified in the five profiles sampled in 2012, even for roots]0, 1] mm, as understory species were much less variable. The mean proportion (r, in %) of roots from tree species per altitude was then calculated.

The r values were then applied to root distribution data in which the functional group was not identified and RCSA of tree species were estimated. We multiplied the term r to the RCSA of]0, 1] mm,]1, 2] mm, and]2, 5] mm diameter classes to estimate the root density of tree species. As we only had r to a depth of 0.3 m, that is, the maximum depth of the mini-monoliths, we supposed that roots below 0.3 m were from both tree and non-tree species and thus applied the term r down to the lowest soil layer. Simultaneously, we compared the estimated RCSA of tree species by applying r down to the lowest soil layer and r to 0.3 m in depth.

ESTIMATION OF SENSITIVITY OF AREA-BASED INDICATORS TO BIOMASS

To investigate the altitudinal evolution of carbon allocation from stem to underground organs, Hertel and Schöling (2011a, 2011b) used a ratio of root biomass (in g m^{-2}) and stem biomass (in g m^{-2}). In their study, root and stem biomass were estimated using soil coring and allometric regression models (Hertel and Schöling, 2011a, 2011b). In our study, we characterized the altitudinal evolution using the ratio of the stand RCSA and stand SBA.

To determine if tree SBA is sensitive enough to the tree stem biomass (SBM, in t ha^{-1}), we estimated the SBM using allometric equations for European species. For each species, the choice of equation is conducted by the following order of priority: (1) equations developed at the same region (Alps Mountain); (2) equations developed at a region in Europe. We chose the equations calibrated in Czech and Germany for *P. abies*, the equation calibrated in Germany for *F. sylvatica* (see Zianis et al., 2005), and that calibrated in Spain for *A. alba* (see Ruiz-Peinado et al., 2011). We used the equation of *Pinus sylvestris* L. for Finnish boreal forests (Zianis et al., 2005) to estimate the biomass of *P. uncinata*, for which no equation was found.

Likewise, in order to explore and estimate if tree RCSA is sensitive enough to root biomass, we explored the correlation between tree RCSA and root biomass, which were measured via mini-monolith to a soil depth of 0.3 m. Nevertheless, this evaluation was limited to the sites at 1400 m and 1700 m, as no mini-monolith data were available at 2000 m.

The above comparisons allowed us to discuss the advantages and disadvantages of the “area-based” indicator compared to the “mass-based” indicator.

STATISTICAL ANALYSES

We used ANOVA to test the significance of altitude and root diameter, as well as their possible interaction on the RCSA/SBA ratio. Before each ANOVA, we tested the normality of data using a Shapiro-Wilk test. A logarithmic transformation was applied if the data did not follow a normal distribution. We then used a Tukey’s honestly significant difference test (Tukey HSD) for comparison of different levels within a factor. All mean data shown are ± standard deviation. Statistical analyses were performed using the R 2.13.0 (R Development Core Team, 2011).

Results

MEAN PROPORTION OF ROOTS FROM TREE SPECIES

The value of r increased as a function of root diameter and attained >70%–98% at]2, 5] mm (Table 1), and r was almost 100% in classes of bigger diameter (data not shown). The disparity of r between tree islands and gaps was greatest at 1400 m and 1700 m, especially for roots]0, 1] mm and]1, 2] mm. At 2000 m, the difference between tree islands and gaps disappeared, probably due to the low stand density at this altitude (Table 1).

The estimated RCSA of tree species by applying r down to the lowest soil layer and that by applying r to 0.3 m in depth showed that values were highly similar (Fig. 1). Therefore, we assume that the choice of soil depth for r has a limited influence on the estimation of RCSA. Hereafter, we present only those results estimated by applying r down to the deepest soil layer.

STEM DENSITY

The stand basal area (SBA) decreased significantly with increasing altitude from 48.5 m^2 ha^{-1} at 1400 m to 30.5 m^2 ha^{-1} at 1700 m and 18.1 m^2 ha^{-1} at 2000 m (Fig. 2, part a). Likewise, both the dominant height and tree number decreased from 1400 m to 2000 m (Fig. 2, part b). Trees >20.0 m in height constituted 24.1% of the total stem number at 1400 m but only 4.8% at 1700 m. Maximum tree height at 2000 m was less than 10.0 m. The number of small trees ([1.3, 5.0] m in height) was comparable between three altitudes (356 trees ha^{-1} at 1400 m, 288 trees ha^{-1} at 1700 m and 316 trees ha^{-1} at 2000 m). For the second class of small trees (]5.0, 10.0] m in height), the highest and lowest tree number were found at 2000 m (288 trees ha^{-1}) and 1700 m (64 trees ha^{-1}), respectively (Fig. 2, part b).

Species composition shifted significantly from 1400 m to 2000 m. Broad-leaved species that were 16.0% of SBA at 1400 m were almost absent at 1700 m. In particular, at 1700 m, *F. sylvatica*, the most dominant broad-leaved species at 1400 m disappeared completely, whereas *P. uncinata* could occasionally be found. *A. alba*, *P. abies,* and *P. uncinata* were the most dominant species at 1400 m, 1700 m, and 2000 m, respectively. *P. abies* was the only species present at all altitudes, implying a wider ecological range at higher elevations (>1400 m in altitude) than *A. alba* and *P. uncinata*, which were absent at 2000 m and 1400 m, respectively (Fig. 2, part a). At 2000 m, forests tended to be less diverse than those at lower altitudes due to a high dominance of *P. uncinata* (96.0% of SBA) against *P. abies* (4.0% of SBA).

ROOT DENSITY AND RCSA/SBA RATIO

Total RCSA was significantly higher at 1700 m, and lowest at 2000 m (ANOVA, F = 5.1, $p < 0.05$, Fig. 3). Mean total RCSA at 1400 m, 1700 m, and 2000 m were 16.8 ± 12.1 m^2 ha^{-1} (mean ± standard deviation), 39.5 ± 32.0 m^2 ha^{-1}, and 26.1 ± 39.4 m^2 ha^{-1}, respectively. The highly significant differences in total RCSA were mainly due to the presence of RCSA of coarse roots (ANOVA, F = 5.4, $p < 0.01$). At all altitudes, fine roots constituted less than 15% of the total RCSA (Fig. 3). RCSA of fine roots at 1700 m (2.6 m^2 ha^{-1}) comprised only 6.6% of the total RCSA, that is, the least among the three altitudes, due to the presence of a large amount of coarse roots. Unlike coarse roots, no significant difference in RCSA of fine roots was found between altitudes (ANOVA, F = 1.2, $p > 0.1$, Fig. 3).

The correlation between RCSA of fine and coarse roots was significant, but exhibited a non-linear trend because of scattered data points (Fig. 4). If the data were fitted using a monomial equation $RCSA_{fine\ root} = a \times RCSA_{coarse\ root}{}^{b}$, the coefficients a and b were significantly altitude-dependent. For the same value of RCSA of coarse roots, a higher altitude tended to have a lower RCSA of fine roots (Fig. 4). At a low root density of coarse roots (<~25 m^2 ha^{-1}), the RCSA of fine roots augmented rapidly with increasing RCSA of coarse roots. The speed of increase in RCSA of fine roots became more attenuated at higher RCSA of coarse roots (Fig. 4).

The effect of altitude on RCSA/SBA was significant for both coarse roots (ANOVA, F = 9.8, $p < 0.001$, Fig. 5, part a) and fine roots (ANOVA, F = 7.7, $p < 0.01$, Fig. 5, part b). The minimum RCSA/SBA of both coarse and fine roots was found at 1400 m (Fig. 5, parts a and b). The maximum RCSA/SBA of coarse roots occurred at 1700 m (1.25 ± 1.15, Fig. 5, part a), which was significantly greater than that at 1400 m (0.31 ± 0.21) but was not significantly different when compared to that at 2000 m (1.15 ± 1.27, Tukey HSD). With regard to fine roots, RCSA/SBA increased almost linearly from 0.05 ± 0.03 at 1400 m to 0.08 ± 0.04 at 1700

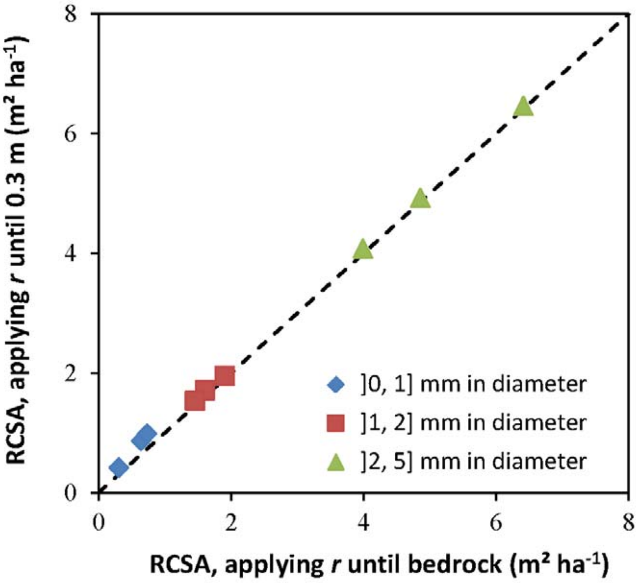

FIGURE 1. The estimated root cross-sectional area (RCSA) of all tree species was determined by applying *r* to a depth of 0.3 m (*y*-axis) and then plotted against *r* to the bedrock depth (x-axis).

m and reached 0.12 ± 0.07 at 2000 m (Fig. 5, part b). For RCSA/SBA of fine roots, no significant differences were found either between 1700 m and 2000 m. However, RCSA/SBA of fine roots at 1400 m was significantly lower than that at 1700 m and at 2000 m.

SENSITIVITY OF AREA-BASED INDICATORS TO BIOMASS

Stem basal area (SBA) was positively and linearly correlated with stem biomass (SBM), which was estimated using allometric equations (Fig. 6, part a). The sensitivity of SBA to SBM, expressed as the variation of SBA per variation of SBM (i.e., d*SBA* / d*SBM*) was dependent on altitude and tended to be greater at higher altitudes (Fig. 6, part b). In particular, for the forest at 2000 m, a modification of 1.0 t ha of stem biomass could result in a change of almost 0.5 m^2 ha in SBA (Fig. 6, part b).

In the first top 0.3 m of soil, RCSA correlated positively with tree root biomass for both 1400 m and 1700 m (Fig. 6, part c). At 1400 m, the slope of tree root biomass and RCSA of all the root diameters were slightly lower than that at 1700 m (Fig. 6, part c).

Discussion

ALTITUDINAL EVOLUTION OF TREE SPECIES AND ABOVE- AND BELOWGROUND CARBON ALLOCATION

Although the three altitudes were only 300 m from each other, the vertical evolution of species composition was significant. The continuous altitudinal shift in species composition can be described as follows: (1) *P. abies* was omnipresent at all sites with more individuals at 1700 m; and (2) *A. alba* was present at 1400 m and 1700 m and *P. uncinata at* 1700 m and 2000 m.Therefore, 1700 m could be considered a transitional site, as *A. alba* and *P. uncinata,* which are both dominant at 1400 m and 2000 m, respectively, become secondary species here. These results confirmed that our choice of sites was appropriate for studying altitudinal effects in mixed montane/upper montane forests. In terms of carbon stock at the ecosystem level, unsurprisingly, our results showed that at higher altitudes, aboveground tree growth in terms of both number and stand basal area was significantly lower, as also shown by Graefe et al. (2008) and Hertel and Schöling (2011b).

Fine roots are the most active tree organs, not only accounting for carbon flux from plant to soil (Norby and Jackson, 2000), but also influencing heavily carbon allocation from above- to belowground (Hertel and Schöling, 2011a, 2011b). We showed that no statistical differences in mean RCSA of fine roots occurred between the three altitudes. This result was similar to that found in a meta-analysis on *P. abies* carried out by Hertel and Schöling (2011b), who showed that altitude had no significant effect on tree fine root biomass density in the European Alps. Nevertheless, Hertel and Schöling (2011a, 2011b) found a significant increase in the biomass of fine roots of *P. abies* stands with increasing altitude (390–1100 m) in studies in the Harz mountain range, northern Germany. When the ratio of fine root biomass density and stem biomass density was calculated in the same stands, they found that this ratio augmented drastically with increasing elevation. Al-

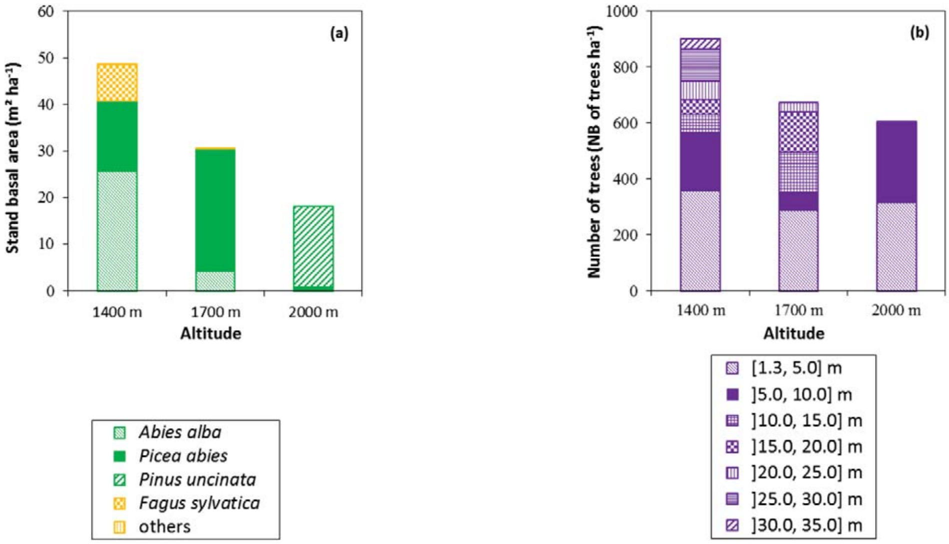

FIGURE 2. Aboveground dendrometric data. (a) Stand basal area (SBA, in m^2 ha^{-1}, y-axis) according to altitude (x-axis) and species (legend); (b) number of trees (in NB of trees, ha^{-1}, y-axis) according to altitude (x-axis) and class of tree height (m, legend). In (a), "others" include *Sorbus aucuparia* L. and *Acer pseudoplatanus* L., which accounted for less than 1% of species composition. Colors in (a): green denotes evergreen conifers and orange denotes broadleaved species; in (b): purple indicates that all species are mixed.

TABLE 1

Proportion of roots from tree species (*r*, in %). *r* was estimated using data from mini-monoliths and new root data sampled in summer of 2012 (for 2000 m). Only a maximum soil depth of 0.3 m was referred to. SD denotes standard deviation. The zone in gray denotes that the root diameter of]0, 1] mm, *r* was estimated using root WINRHIZO (which allows measuring of root length density for each type of functional group), as it was impossible to identify to which functional group a root tip belonged.

			Proportion of roots from tree species (*r*, in %)					
			]0, 1] mm		]1, 2] mm		]2, 5] mm	
Altitude	Patch	Number of sampling location	Mean	SD	Mean	SD	Mean	SD
2000 m	Gap	3	14.4	0.8	67.9	6.1	88.7	12.7
	Tree island	2	23.6	8.5	65.1	14.1	69.6	7.6
1700 m	Gap	5	24.5	9.2	72.7	19.8	85.4	22.6
	Tree island	4	60.0	17.4	95.2	9.5	98.4	3.2
1400 m	Gap	5	13.6	13.9	76.9	22.1	86.7	18.9
	Tree island	5	78.5	19.7	86.0	19.4	96.6	4.9

though we also showed that RCSA/SBA of fine roots increased at higher altitudes, differences were less pronounced due to an increasing spatial heterogeneity. The absolute value of RCSA of fine roots was almost unchanged at the highest altitude, suggesting that RCSA/SBA increased at higher elevations at the detriment of aboveground growth. This result differs from but is complementary to the observations by Hertel and Schöling (2011a, 2011b), who found a significant increase in fine roots of *P. abies* stands with increasing altitude but at a lower elevation range (390–1100 m). The increase in carbon allocation to fine roots at high altitudes was also found at species scale, for example, Johnston and Pickering (2004) studying the herbaceous species *Achillea millefolium*, and Oleksyn et al. (1998) and Ran et al. (2013) studying seedlings and saplings of *P. abies* and *Abies faxoniana* Rehd. et Wils, respectively. This phenomenon was also demonstrated at the community scale where species was not taken into account, for example, Pérez and Frangi (2000) on grasslands and Luo et al. (2005) on all the types of functional group.

One possible reason for the augmentation in fine root proportion is that at higher altitudes, soils were shallower; therefore, the actual volume of soil, and hence available nutrients, was limited (Sundqvist et al., 2013). Although we have no data to quantify soil mineral resources at the three altitudes, an increase in carbon allocation resulting in a higher absorptive area

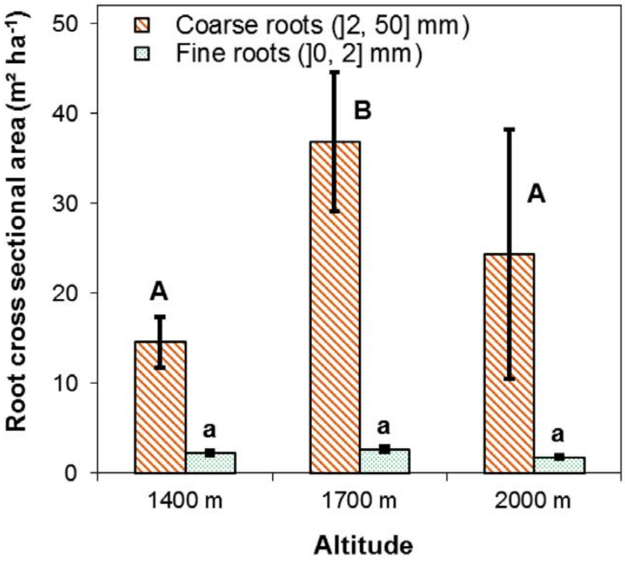

FIGURE 3. **Mean root cross sectional area (RCSA) of coarse and fine roots as a function of altitude. Error bars denote standard error. Different letters indicate significant differences between the altitudes according to Tukey's HSD test; capitals and small letters are used for coarse and fine roots, respectively.**

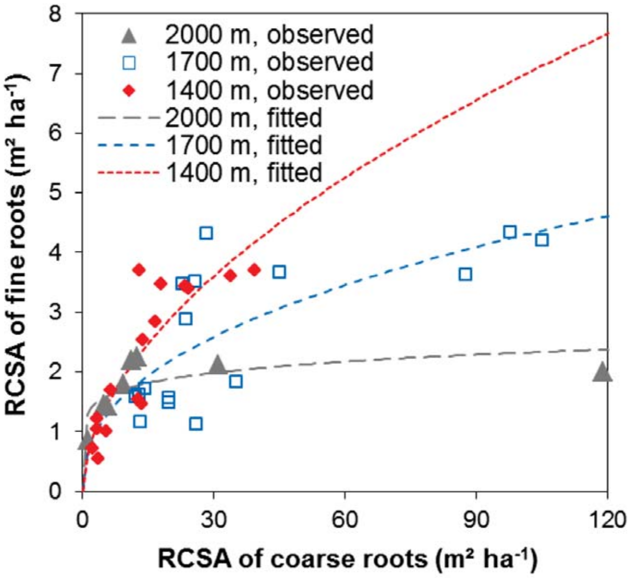

FIGURE 4. **Correlation between root cross sectional area (RCSA) of fine roots and that of coarse roots. Data points denote observed values and lines denote fitted values. The formula for fitted curves was $RCSA_{fine\ root} = a \times RCSA_{coarse\ root}^{b}$, where the calibrated a and b were as follows: $a = 0.57$ and $b = 0.54$ for 1400 m; $a = 0.62$ and $b = 0.41$ for 1700 m; $a = 1.28$ and $b = 0.13$ for 2000 m.**

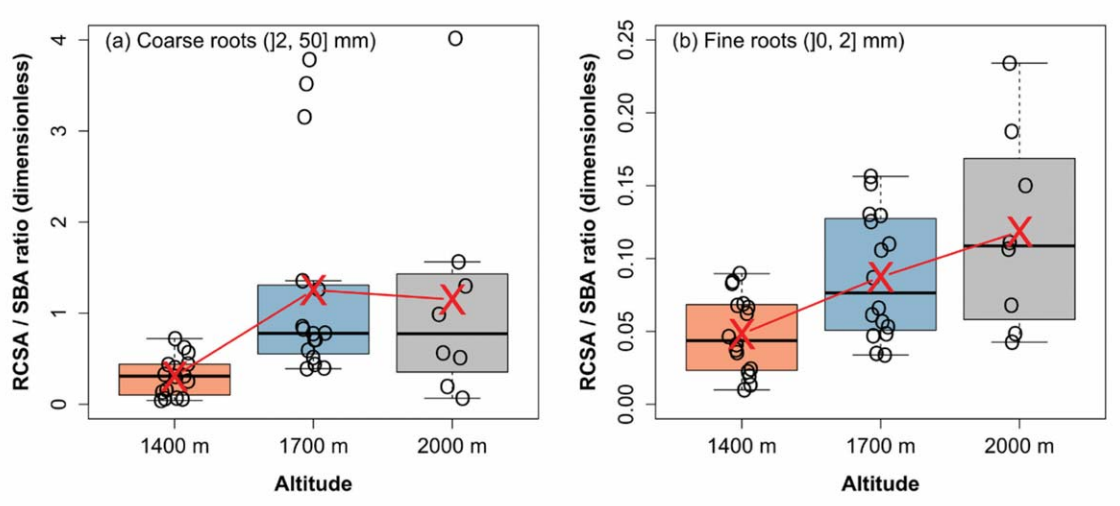

FIGURE 5. The ratio of root cross sectional area (RCSA) and with stem basal area (SBA) (y-axis) as a function of altitude (x-axis) for coarse roots (a) and fine roots (b). In scatter points, each hollow point denotes one ratio calculated using a sampled soil profile. Attention should be paid to the different graduations in y-axes. In boxplots, each box represents the quantile distribution of the cloud of points: the bottom, top, and bands near the middle of each box were the Q1 (25th percentile), Q3 (75th percentile), and Q2 (median); the vertical dashed line through the box shows the limit between the 10th percentile and the 90th percentile; in (a), hollow circles outside the boxplot are outliers. "X" symbols and solid curve represents the mean values and their altitudinal tendency, respectively.

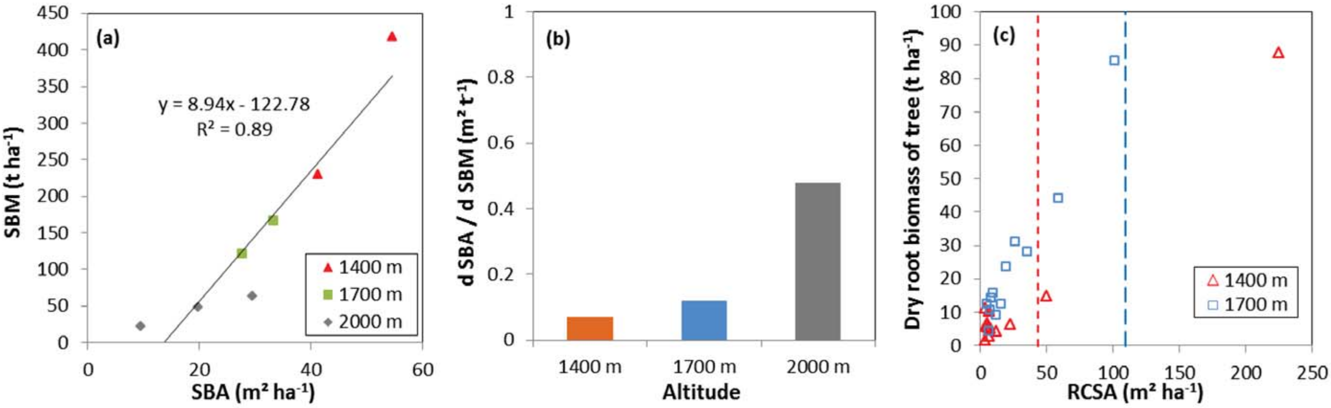

FIGURE 6. (a) Allometric equations estimated stem biomass (SBM, in t ha^{-1}) against stem basal area (SBA, in m^2 ha^{-1}); (b) the changed SBA once SBM changes 1 t; (c) measured dry root biomass of tree species against measured root cross sectional area (RCSA, in m^2 ha^{-1}) of all diameters, based on the mini-monolith database. In (a), each point represents a sample plot of an altitude; in (c) each point represents an estimated indicator of a monolith (0.3 m in soil depth). The short and long dashed lines in (c) denote the maximum RCSA found in used soil profiles for this present study at 1400 m and 1700 m, respectively.

of fine roots would allow trees to scavenge more efficiently if soils were nutrient poor.

At higher elevations, the growing season is also considerably shorter (Mao et al., 2013), and therefore a tree's physiological activity needs to be condensed over a reduced period. Based on experiments on seedlings, Alvarez-Uria and Körner (2007) and Schenker et al. (2014) observed very limited root growth and production in common European tree seedlings at soil temperatures below 6 °C. Despite the constraints to growth, root mortality remains low as long as soil temperatures do not drop below freezing (Hendrick and Pregitzer, 1993). Roots might thus continue to grow and proliferate once soil temperature becomes more favorable. Moreover, at our study sites, tree root growth is driven by soil temperature and can even continue in winter months when the aerial organs are dormant (Mao et al., 2013). These phenomena could thus impact the relative proportions of shoot and fine root biomass, which would be more pronounced at high elevations.

Alternatively, Körner and Renhardt (1987) suggested that in herbaceous species growing at high altitudes, an increase in fine root length would compensate for a possible lack of mycorrhizas. Several studies observed a decrease in fungal richness, biomass, or colonization on roots with increasing altitude, for example, Weir (1918), Haselwandter and Read (1980), Väre et al. (1997), Uchida et al. (2008), Lugo et al. (2008), Ruotsalainen et al. (2009), and Bahram et al. (2012). Nevertheless, studies have also shown an absence of altitudinal effects (Ruotsalainen et al., 2004), or even an inverse effect (van Maanena et al., 2000) or a complex altitudinal tendency (Read and Haselwandter, 1981). Altitudinal variation of the levels of root infection could also be significantly different depending on fungal species (Väre et al., 1997; Ruotsalainen et al., 2004), the host species, and the studied scale (Granath et al., 2007). In our study, the majority of tree species are from the Pinaceae family, the roots of which are mainly colonized by ectomycorrhizal (ECM) fungi (Smith and Read, 2010). According to Gardes and Dahlberg (1996), some ECM fungi can be very dependent on certain tree species growing along an altitudinal gradient, suggesting that ECM fungi might be more abundant at higher altitudes at our field site. Therefore, we cannot say with any certainty whether the increase in carbon allocation to fine roots at 2000 m is due to changes in fungal associations. In future studies, the altitudinal evolution of ECM fungal communities needs to be characterized in order to better elucidate this issue.

CARBON ALLOCATION BETWEEN COARSE AND FINE ROOTS

The total RCSA was mostly contributed by coarse roots. The significantly lower proportion of fine root density to that of coarse roots has been reported in previous studies, either with regard to biomass (Keyes and Grier, 1981; Vogt et al., 1996; Helmisaari et al., 2002) or CSA (Mao et al., 2012). However, both RCSA and RCSA/SBA of coarse roots responded differently to altitude compared to those of fine roots. RCSA of coarse roots at 1700 m was higher than that at 1400 m and 2000 m. This phenomenon could be attributed to the root system architecture of *P. abies,* which produces many superficial and thick lateral roots in this area (Drexhage and Gruber, 1999; Stokes et al., 2007). Therefore, coarse roots might be more directly influenced by altitude-induced species composition than by altitude itself. When the quantity of coarse roots was low (<~25 m² ha), RCSA of fine roots was positively correlated with that of coarse roots (Fig. 4). A positive correlation between coarse and fine roots was found by Ruess et al. (1996). Likewise, a meta-analysis in Chen et al. (2004) showed that the biomass of fine roots was positively correlated with that of coarse roots. This phenomenon could be explained by the fact that coarse roots possessing higher topological orders are mother roots, thus highlighting the importance of taking into account the quantity of coarse roots when studying and modeling fine root dynamics. However, as RCSA of coarse roots increased, the increasing speed of the curve of RCSA of fine roots decreased significantly and even tended to reach a plateau (Fig. 4). This result suggests that there are factors restricting fine root development when the density of coarse roots is high. The photosynthetic capacity of trees is not reduced at higher altitudes (Körner, 1982; Oleksyn et al., 1998), suggesting that carbon stocks are theoretically sufficient for substantial fine root development. Here, the non-linear relationship between RCSA of coarse and fine roots tends to support sink-driven growth rather than that driven by source activity (Fourcaud et al., 2008). Sink-driven growth and development will be governed by environmental (e.g., temperature, nutrition supply) or developmental constraints rather than by photosynthetically produced resources.

CHOOSING INDICATORS TO EVALUATE CARBON ALLOCATION: "AREA BASED" OR "MASS BASED"?

We used "area-based" indicators, that is, RCSA and SBA as proxies to characterize the above- and belowground carbon stock as well as the pattern of carbon allocation between them. Both indicators are also biologically meaningful and have been widely used when characterizing stand productivity. Their ratio, which is dimensionless, can be used for comparison between stands and between studies. Compared to the "mass-based" indicators, that is, stem and root biomass, the use of area-based proxies had several advantages:

1. Area-based proxies are more easily measured than estimations or direct measurements of biomass, which are costly (e.g., tree felling), or time-consuming laboratory work such as root washing and drying.
2. Area-based proxies may be more precisely estimated than biomass. Stem biomass has usually been determined via allometric equations (Janssens et al., 1999; Kitayama and Aiba, 2002) calibrated from other sites. This approach can lead to bias when applied to either, for example, mixed stands with less common tree species, or to stands along an environmental gradient, where the same species might exhibit quite different characteristics.
3. Area-based proxies diminish sampling constraints due to soil depth. It is difficult to sample the biomass of coarse roots in situ, especially in stony soil on mountain slopes. Although fine roots may be easier to sample via coring, Chen et al. (2004) suggested that an artifact of the coring method was that the most common maximum sampling depth used for fine roots was 0.30 m. Using data from such a shallow soil depth may significantly underestimate the total root biomass and underground carbon stock of a given ecosystem (Chen et al., 2004). In mixed montane/upper montane forests, a non-negligible quantity of fine roots can be found at deeper soil layers that are far away from the soil organic layer (Mao et al., 2012). Estimation of RCSA based on root counting in soil profiles can, in contrast, avoid or attenuate the above problems when determining biomass.

The use of area-based indicators is based on the hypothesis that the variation of RCSA and SBA corresponds to and correlates with that of root and stem biomass, respectively. In the present study, the satisfactory correlation between area-based and mass-based indicators supports the use of area-based indicators. Nevertheless, these proxies for biomass can be potentially risky when studying carbon partitioning for the following reasons:

1. Area-based proxies are either hyper-sensitive or under-sensitive to spatial and temporal variations in biomass. We showed that SBA was more sensitive at higher altitudes (Fig. 6, part b) particularly at 2000 m, where tree morphology and growth were very heterogeneous. As a result, in future studies, we suggest using area-based proxies for less heterogeneous forest stands only.
2. For underground organs, the relationship between RCSA and root biomass is species and site dependent. We observed a slightly lower slope in data distribution at 1400 m compared to 1700 m (Fig. 6, part c) and that results may be biased by the root architecture of trees present on the site. Therefore, if root sampling depth was greater, the slope at 1400 m should approach that of 1700 m, so the effect of site would diminish. In future studies, we suggest sampling roots down to the maximum rooting depth if area-based proxies are to be used.

Conclusions and Perspectives

Studying above- and belowground carbon partitioning in montane/upper montane forest stands is sometimes challenged by the major environmental heterogeneity in soils. Roots from tree, shrubby, and herbaceous species are mixed and the presence of stones in soil hinders root coring to deep soil layers. In our study, we examined above- and belowground carbon partitioning in mixed montane/upper montane coniferous forest ecosystems in the French Alps. To limit the effect of shrubby and herbaceous species, we estimated the proportion of roots from tree species among total roots as a function of tree spacing (gap versus tree island). Then, to circumvent the sampling difficulty using cores, we introduced area-based indicators, that is, stem basal area (SBA), root cross-sectional area (RCSA), and their ratio (SBA/RCSA) as proxies that are easy to measure and estimate via forest inventories and soil profile excavation. Compared to the standard estimations of biomass, the use of area-based proxies demonstrated a promising potential for studying carbon partitioning, although some risks exist. This case study provided an original and promising approach to characterize the carbon partitioning in trees for future studies in heterogeneous forests.

Simultaneously, as one of the rare studies on carbon partitioning along the highest altitudinal transect in the European Alps (from 1400 m to 2000 m), we found that, for fine roots, RCSA/SBA increased with increasing altitude. This phenomenon supported the hypothesis that ecosystems at higher altitudes tended to allocate more carbon to belowground organs. This relative increase in fine root area would allow trees to scavenge more efficiently in shallower or nutrient poor soils throughout the shorter growing season. For fine roots, higher RCSA/SBA at higher altitudes was mainly caused by a severe decline of aboveground tree growth, and the differences in RCSA/SBA were less pronounced due to an increasing spatial heterogeneity at higher elevations. These findings can thus contribute to the scarcity of information about carbon partitioning at high altitudes.

To estimate carbon stocks more accurately, future studies should focus on the dynamic aspects of shoot and fine root demography along environmental gradients. For this objective, long-term studies are required for determining if, for example, carbon partitioning is related to local environmental conditions and seasonality.

Acknowledgments

This study was financed by an AXA Ph.D. bursary (Mao), an INRA Jeune Equipe and a French-funded Agence Nationale de la Recherche (ANR) project ECOSFIX (Ecosystem Services of Roots–Hydraulic Redistribution, Carbon Sequestration and Soil Fixation, ANR-2010-STRA-003-01). The UR BEF, one of the research units contributing to the present study, is supported by the French National Research Agency through the Laboratory of Excellence ARBRE (ANR-12-LABXARBRE-01). We thank V. Perez (AgroParisTech, Nancy, France) and Météo-Chamrousse (http://www.meteo-chamrousse.com/) for climate data. We thank the Office National des Forêts and the Mairie de Chamrousse for their kind help with site selection and work permits. Dr. B. Courbaud (IRSTEA, France) is gratefully acknowledged for his help with site selection and plot installation. Finally, we are thankful to Dr. M. Genet, F. Pailler, F-X. Mine (ISARA, France), M. Foulonneau (Université de Savoie, France), C. Gadenne (AgroParisTech, France), Dr. H. Vogt-Schilb (CNRS and Biotope, France), M-L. Bonis (Université Paris VI, France), and Auberge du Virage, Chamrousse, for their help with field work and logistics.

References Cited

Alvarez-Uria, P., and Körner, C., 2007: Low temperature limits of root growth in deciduous and evergreen temperate tree species. *Functional Ecology,* 21: 211–218.

Bahram, M., Põlme, S., Kõljalg, U., Zarre, S., and Tedersoo, L., 2012: Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. *New Phytologist,* 193: 465–473.

Benichou, P., and Le Breton, O., 1987: Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *La Météorologie*, 7: 23–34.

Böhm, W., 1979: *Methods of Studying Root Systems.* Berlin: Springer.

Chen, W. J., Zhang, Q. F., Cihlar, J., Bauhus J., and Price, D. T., 2004: Estimating fine-root biomass and production of boreal and cool temperate forests using aboveground measurements: A new approach. *Plant and Soil,* 265: 31–46.

Drexhage, M., and Gruber, F., 1999: Above- and below-stump relationships for *Picea abies*: estimating root system biomass from breast-height diameters. *Scandinavian Journal of Forest Research,* 14: 328–333.

Finér, L., Helmisaari, H. S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., Eldhuset, T., Godbold, D., Grebenc, T., Konôpka, B., Kraigher, H., Möttönen, M. R., Ohashi, M., Oleksyn, J., Ostonen, I., Uri, V., and Vanguelova, E., 2007: Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.). *Plant Biosystems,* 141(3): 394–405.

Fourcaud, T., Zhang, X. P., Stokes, A., Lambers, H., and Körner, C., 2008: Plant growth modelling and applications: the increasing importance of plant architecture in growth models. *Annals of Botany,* 101: 1053–1063.

Gardes, M., and Dahlberg, A., 1996: Mycorrhizal diversity in arctic and alpine tundra: an open question. *New Phytologist,* 133: 147–157.

Graefe, S., Hertel, D., and Leuschner, C., 2008: Fine root dynamics along a 2000-m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil,* 313: 155–166.

Graefe, S., Hertel, D., and Leuschner, C., 2010: N, P and K limitation of fine root growth along an elevation transect in tropical mountain forests. *Acta Oecologica,* 36: 537–542.

Granath, G., Vicari, M., Bazely, D. R., Ball, J. P., Puentes, A., and Rakocevic T., 2007: Variation in the abundance of fungal endophytes in fescue grasses along altitudinal and grazing gradients. *Ecography,* 30: 422–430.

Grime, J. P., 1979: *Plant Strategies and Vegetation Processes*. Chichester, U.K.: Wiley.

Groffman, P. M., Hardy, J. P., Fisk, M. C., Fahey, T. J., and Driscoll, C.T., 2009: Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest. *Ecosystems,* 12: 927–943.

Haselwandter, K., and Read, D. J., 1980: Fungal associations of roots of dominant and sub-dominant plants in high-alpine vegetation systems with special reference to mycorrhiza. *Oecologia,* 45: 57–62.

Helmisaari, H. S., Makkonen, K., Kellomäki, S., Valtonen, E., and Mälkönen, E., 2002: Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *Forest and Ecology Management,* 165: 317–326.

Helmisaari, H. S., Derome, J., Nöjd, P., and Kukkola, M., 2007: Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. *Tree Physiology,* 27: 1493–1504.

Hendrick, R. L., and Pregitzer, K. S., 1993: Patterns of fine root mortality in two sugar maple forests. *Nature,* 361: 59–61.

Hertel, D., and Schöling, D., 2011a: Norway spruce shows contrasting changes in below- versus above-ground carbon partitioning towards the alpine treeline: evidence from a central European case study. *Arctic, Antarctic, and Alpine Research,* 43(1): 46–55.

Hertel, D., and Schöling, D., 2011b: Below-ground response of Norway spruce to climate conditions at Mt. Brocken (Germany)—a re-assessment of Central Europe's northernmost treeline. *Flora,* 206: 127–135.

IUSS Working Group WRB, 2007: *World Reference Base for Soil Resources 2006, First Update 2007*. Rome: FAO, World Soil Resources Reports No. 103.

Janssens, I. A., Sampson, D. A., Cermak, J., Meiresonne, L., Riguzzi, F., Overloop, S., and Ceulemans, R., 1999: Above- and belowground phytomass and carbon storage in a Belgian Scots pine stand. *Annals of Forest Science*, 56(2): 81–90.

Johnston, F. M., and Pickering, C.M., 2004: Effect of altitude on resource allocation in the weed *Achillea millefolium* (yarrow, Asteraceae) in the Australian Alps. *Australian Journal of Botany,* 52(5): 639–646.

Joud, D., 2006: *Guide pour identifier les stations forestières de Rhône-Alpes—Synthèse pour les Alpes du Nord et les montagnes de l'Ain.* CRPF Rhône-Alpes, 132 pp.

Keyes, M. R., and Grier, C. C., 1981: Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research, 11:* 599–605.

Kitayama, K., and Aiba, S. I., 2002: Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology,* 90: 37–51.

Körner, C., 1982: CO_2 exchange in the alpine sedge *Carex curvula* as influenced by canopy structure, light and temperature. *Oecologia,* 53: 98–104.

Körner, C., 1998: A re-assessment of high elevation treeline positions and their explanation. *Oecologia,* 115: 445–459.

Körner, C., 2007: The use of 'altitude' in ecological research. *Trends in Ecology & Evolution,* 22: 569–574.

Körner, C., 2012: *Alpine Treelines—Functional Ecology of the Global High Elevation Tree Limits*. Basel: Springer.

Körner, C., and Paulsen, J., 2004: A world-wide study of high altitude treeline temperatures. *Journal of Biogeography,* 31: 713–732.

Körner, C., and Renhardt, U., 1987: Dry matter partitioning and root length/leaf area ratios in herbaceous perennial plants with diverse altitudinal distribution. *Oecologia,* 74: 411–418.

Legros, S., Mialet-Serra, I., Caliman, J. P., Siregar, F. A., Clement-Vidal, A., Fabre, D., and Dingkuhn, M., 2009: Phenology, growth and physiological adjustments of oil palm (*Elaeis guineensis*) to sink limitation induced by fruit pruning. *Annals of Botany,* 104: 1183–1194.

Leuschner, C., Moser, G., Bertsch, C., Röderstein, M., and Hertel, D., 2007: Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology,* 8: 219–230.

Lugo, M .A., Ferrero, M., Menoyo, E., Estévez, M. C., Sineriz, F., and Anton, A., 2008: Arbuscular mycorrhizal fungi and rhizospheric bacteria diversity along an altitudinal gradient in South American Puna grassland. *Microbial Ecology*, *55*(4): 705–713.

Luo, T. X., Brown, S., Pan, Y. D., Shi, P. L., Ouyang, H., Yu, Z. L., and Zhu, H. Z., 2005: Root biomass along subtropical to alpine gradients: global implication from Tibetan transect studies. *Forest Ecology and Management,* 206: 349–363.

Mao, Z., 2012: *Temporal and Spatial Modelling of Root Reinforcement in Montane and Subalpine Forests*. Ph.D. thesis, Ecole Doctorale, SIBAGHE, University Montpellier II.

Mao, Z., Saint-André, L., Genet, M., Mine, F. X., Jourdan, C., Rey, H., Courbaud, B., and Stokes, A., 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., and Jourdan, C., 2013: Which processes drive fine root elongation in a natural mountain forest ecosystem? *Plant Ecology and Diversity,* 6(2): 231–243.

Mialet-Serra, I., Clement, A., Sonderegger, N., Roupsard, O., Jourdan, C., Labouisse, J. P., and Dingkuhn, M., 2005: Assimilate storage in vegetative organs of coconut (*Cocos nucifera*). *Experimental Agriculture,* 41: 161–174.

Mialet-Serra, I., Clement-Vidal, A., Roupsard, O., Jourdan. C., and Dingkuhn, M., 2008: Whole-plant adjustments in coconut (*Cocos nucifera*) in response to sink-source imbalance. *Tree Physiology,* 28: 1199–1209.

Norby, R. J., and Jackson, R. B., 2000: Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist,* 147: 3–12.

Oleksyn, J., Modrzyński, J., Tjoelker, M. G., Żytkowiak, R., Reich, P. B., and Karolewski, P., 1998: Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecolology,* 12: 573–590.

Pérez, C. A., and Frangi, J. L., 2000: Grassland biomass dynamics along an altitudinal gradient in the Pampa. *Journal of Range Management,* 53(5): 518–528.

Piedallu, C., and Gegout, J. C., 2007: Multiscale computation of solar radiation for predictive vegetation modelling. *Annals of Forest Science*, 64: 899–909.

Piedallu, C., and Gegout, J. C., 2008: Efficient assessment of topographic solar radiation to improve plant distribution models. *Agricultural and Forest Meteorology*, 148: 1696–1706.

Pregitzer, K. S., 2002: The fine roots of trees—a new perspective. *New Phytologist,* 156: 267–270.

R Development Core Team, 2011: *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing,. www.R-project.org.

Ran, F., Zhang, X. L., Zhang, Y. B., Korpelainen, H., and Li, C. Y., 2013: Altitudinal variation in growth, photosynthetic capacity and water use efficiency of *Abies faxoniana* Rehd. et Wils. seedlings as revealed by reciprocal transplantations. *Trees,* 27: 1405–1416.

Read, D. J., and Haselwandter, K., 1981: Observations on the mycorrhizal status of some alpine plant communities. *New Phytologist,* 88: 341–352.

Ruess, R. W., Van Cleve, K., Yarie, J., and Viereck, L. A., 1996: Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. *Canadian Journal of Forest Research,* 26: 1326–1336.

Ruiz-Peinado, R., del Rio, M., and Montero, G., 2011: New models for estimating the carbon sink capacity of Spanish softwood species. *Forest Systems,* 20(1): 176–188.

Ruotsalainen, A. L., Väre, H., Oksanen, J., and Tuomi, J., 2004: Root fungus colonization along an altitudinal gradient in north Norway. *Arctic, Antarctic, and Alpine Research,* 36: 239–243.

Ruotsalainen, A. L., Markkola, A. M., and Kozlov, M. V., 2009: Mycorrhizal colonisation of mountain birch (*Betula pubescens* ssp. czerepanovii) along three environmental gradients: Does life in harsh environments alter plant-fungal relationships? *Environmental Monitoring and Assessment,* 148: 215–232.

Schenker, G., Lenz, A., Körner, C., and Hoch, G., 2014: Physiological minimum temperatures for root growth in seven common European broad-leaved tree species. *Tree Physiology* 34: 302–313.

Shreve, F., 1924: Soil temperature as influenced by altitude and slope exposure. *Ecology,* 5: 128.

Smit, A. L., Bengough, A. G., Engels, C., van Noordwijk, M., and Pellerin, S., 2000: *Root Methods: A Handbook.* Berlin: Springer.

Smith, S. E., and Read, D. J., 2010: *Mycorrhizal Symbiosis*. Third edition. New York: Academic Press (access online via Elsevier).

Soethe, N., Lehmann, J., and Engels, C., 2006: Root morphology and anchorage of six native tree species from a tropical montane forest and an elfin forest in Ecuador. *Plant and Soil,* 279: 173–185.

Stokes, A., Abd Ghani, M., Salin, F., Danjon, F., Jeannin, H., Berthier, S., Kokutse, A. D., and Frochot, H., 2007: Root morphology and strain distribution during tree failure on mountain slopes. *In* Stokes, A., Spanos, I., Norris, J. E., and Cammeraat, L. H. (eds), *Eco- and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability.* Dordrecht: Springer Publishers, Developments in Plant and Soil Sciences Volume 103, pp. 165–173.

Stokes, A., Atger, C., Bengough, A. G., Fourcaud, T., and Sidle, R. C., 2009: Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant and Soil,* 324: 1–30.

Sundqvist, M. K., Sanders, N. J., and Wardle, D. A., 2013: Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. *Annual Review of Ecology, Evolution, and Systematics,* 44: 261–280.

Sveinbjörnsson, B., Davis, J., Abadie, W., and Butler, A., 1995: Soil carbon and nitrogen mineralization at different elevations in the Chugach Mountains of south-central Alaska, USA. *Arctic and Alpine Research,* 27(1): 29–37.

Uchida, M., Nakatsubo, T., Kasai, Y., Nakane, K., and Horikoshi, T, 2008: Altitudinal differences in organic matter mass loss and fungal biomass in a subalpine coniferous forest, Mt. Fuji, Japan. *Arctic, Antarctic, and Alpine Research,* 32(3): 262–269.

van Maanena, A., Debouzieb, D., and Gourbierea, F., 2000: Distribution of three fungi colonising fallen *Pinus sylvestris* needles along altitudinal transects. *Mycological Research,* 104: 1133–1138.

Väre, H., Vestberg, M., and Ohtonen, R., 1997: Shifts in mycorrhiza and microbial activity along an oroarctic altitudinal gradient in Northern Fennoscandia. *Arctic and Alpine Research,* 29: 93.

Vogt, K. A., Vogt, D. J., Palmiotto, P. A., Boon, P., O'Hara, J., and Asbjornsen, H., 1996: Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant and Soil,* 187: 159–219.

Weir, J. R., 1918: Notes on the altitudinal range of forest fungi. *Mycologia,* 10(1): 4–14.

Zianis, D., Muukkonen, P., Mäkipää, R., and Mencuccini, M., 2005: *Biomass and Stem Volume Equations for Tree Species in Europe.* Silva Fennica Monographs 4, 63 pp.

MS accepted October 2014