Estimates and relationships between aboveground and belowground resource exchange surface areas in a Sitka spruce managed forest

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Summary Our knowledge of the nature of belowground competition for moisture and nutrients is limited. In this study, we used an earth impedance method to determine the root absorbing area of Sitka spruce (Picea sitchensis (Bong.) Carr.) trees, making measurements in stands of differing density (2-, 4- and 6-m inter-tree spacing). We compared absorbing root area index (RAI absorbing; based on the impedance measure) with fine root area index (RAI fine; based on estimates of total surface area of fine roots) and related these results to investment in conductive roots. Root absorbing area was a near-linear function of tree stem diameter at 1.3 m height. At the stand level, RAI absorbing, which is analogous to and scaled with transpiring leaf area index (maximum stomatal pore area per unit ground area; LAI transpiring), increased proportionally with basal area across the three stands. In contrast, RAI fine was inversely proportional to basal area. The ratio of RAI absorbing to LAI transpiring ranged from 7.7 to 17.1, giving an estimate of the relative aboveground versus belowground resource exchange areas. RAI absorbing provides a way of characterizing ecosystem functioning as a physiologically meaningful index of belowground absorbing area.

Keywords: absorbing root surfaces, earth impedance, fine roots, plant allometry/scaling, RAI: LAI ratio, root area index.

Introduction

Plants acquire carbon and nutrients from the environment, which are then allocated to new tissue growth or maintenance of existing tissue (or storage). This partitioning of resources influences the efficiency of future acquisition rates of carbon and soil resources. For example, increased allocation to photosynthetically active leaf area must be supported by an increase in water supply from the soil through the absorbing root surface (Shipley and Meziane 2002). Therefore, the ratio of absorbing root area to transpiring leaf area is of fundamental importance to plant survival (Sperry et al. 1998).

The pipe model theory predicts that a given unit of leaf area is supported by a continuation of conducting tissue of constant cross-sectional area, analogous to a pipe system (Shinozaki et al. 1964). More recent research suggests that plants adapt to hydrological pressures by differentially adjusting the cross-sectional area of xylem conducting tissue relative to their leaves (Magnani et al. 2000). However, this theory has never been extended to the belowground absorbing surface area of the roots. It has been estimated that the radial conductivity through the absorbing roots is eight orders of magnitude lower than that of the saturated conductivity of the xylem and soil (Steudle and Peterson 1998). This may suggest that the supply of water to the leaves is predominantly controlled by the hydraulic properties of the absorbing roots (Sperry et al. 2002). Consequently, the absorbing root to leaf area ratio may provide useful insights into the way plants adapt to their environment.

Plant root systems perform a range of functions including structural support, storage, transport and absorption (Schulze et al. 1983, Körner 1994). Conventionally, the functional components of the root system have often been differentiated according to soil depth and diameter. Coarse roots (>2 mm in diameter) are generally woody and provide mechanical support and conductive capacity to the tree (Jackson et al. 1996, Nicoll and Ray 1996, Čermák et al. 2008, Tatarinov et al. 2008). In contrast, fine roots (often defined as ≤2 mm in diameter) have been distinguished as the primary exchange surface for water and nutrients between the soil and plant, analogous to the role played by leaves for carbon and energy uptake (Hendrick and Pregitzer 1992, Pregitzer et al. 1993, Jackson et al. 1997, Gill and Jackson 2000, Pregitzer 2002). However, unlike leaves and branches, it is difficult to distin-
guish between absorbing and conducting (non-absorbing) roots. A recently established earth impedance (EI) method allows us to isolate the absorbing root surface area of individual trees (Aubrecht et al. 2006, Čermák et al. 2006), which has the potential to improve our understanding of water and nutrient uptake at the soil–root interface.

The EI method is based on the physical principle of electrical current continuity (Aubrecht et al. 2006). A large field trial has shown absorbing root surface area to be proportional to the cross-sectional area of aboveground conducting tissue (Čermák et al. 2006). Additionally, lab-based studies have found electrical resistance to be correlated with geometric root surface areas (Cao et al. 2010). However, it is important to establish how this method relates to the more conventional measure of fine root area at the stand level. Therefore, the main objective of this study is to further evaluate the EI method within a Sitka spruce managed forest, making comparisons between stands of different tree densities. We will do this by establishing allometric relationships with aboveground biometric parameters and making comparisons with the geometric surface area of fine roots across different stand densities. An additional core objective is to use the EI method to evaluate the role of plantation density on ecophysiological allocation patterns of leaves and roots.

Materials and methods

Study site

The study was carried out during July–August 2007 at Cloich, which is part of the Forestry Commission’s Glentress Forest, ~32 km outside of Edinburgh, UK at 55°42′ N, 03°16′ W. The site was originally planted in 1970 with Sitka spruce (Picea sitchensis (Bong.) Carr.) at an average tree density of ~3000 stems per hectare (equivalent to approximately a 2-m inter-tree spacing). In early 1986, three plots of differing tree density were established by selectively thinning the existing forest to 625 and 278 stems per hectare, which corresponds to inter-tree spacings of ~4 and 6 m, respectively (Greens et al. 1995). This management intervention has resulted in trees with widely varying trunk diameters. These distinctive aboveground characteristics may be supported by correspondingly distinctive belowground root distributions. At the time of planting, the soil was prepared by ploughing the topsoil to excavate drainage trenches. The trees were planted on parallel-mounded ridges (also known as ribbons) separated by the drainage trenches. The soil on the ridges was ~15 cm deeper than the furrows. The trees in all three stands are sustained by a shallow peat (~30 cm deep in the furrows) overlaying Silurian Ordovician greywacke (Sheppard et al. 1995). There was no significant understorey in any of the plots.

Root absorbing area

Root absorbing area was evaluated using the electrical impedance method (Aubrecht et al. 2006). If a simple electrical circuit is established between a tree and the soil, the current will only enter (or exit) the tree through the same porous surface area used in water and nutrient uptake. From the difference in conductivity of tree tissue and the soil, we estimated the soil–root exchange surface area based on the equation:

\[ S = \rho I \frac{U}{U} \]

where \( S \) is the total root absorption surface (in square metres), \( \rho \) is the resistivity of the water conducting tissue (in ohm metres), \( I \) is the distance from the stem (in metres), \( l \) is the current flowing through the wood stem, root system and soil to auxiliary metal electrodes from an external power supply (in amperes) and \( U \) is the potential difference between the stem boundary and a potential electrode in the soil (in volts).

We inserted six electrodes into the stem of the tree and eight soil electrodes in a 60° arc around the stem and connected them to an alternating current generator. The soil electrodes were 10 mm in diameter and inserted 20 cm into the soil to ensure a sufficient conducting surface. An auxiliary potential electrode was inserted at the base of the trunk and another in the soil at a defined distance, \( l \), from the stem. The distance from the stem to both the current and potential soil electrodes was determined by the course of potential (volts). The amount of current flowing from the tree stem to the surrounding soil, via the root segment, decreases with increasing distance from the tree. This drop in voltage was mapped by progressively moving the soil potential electrode away from the stem in a radial direction. The point at which the drop in voltage plateaus is considered to be \( l \), which corresponds to the mean distance of all the absorbing root segments of the tree.

Resistivity of the water conducting tissue (\( \rho_{\text{wood}} \)) of the roots was calculated using the four-point Wenner method where \( \rho_{\text{wood}} = 2l\pi R \) (Aubrecht et al. 2006). The four electrodes were inserted into the sapwood at an equal distance, \( a \), apart. The electrical impedance, \( R \), was measured with the electrodes 2, 4 and 6 cm apart and the mean was taken. Current was generated and the impedance measurements were made using a four-pole AVO/Megger DET5/4D Earth/Ground Tester.

In each stand (2-, 4- and 6-m spaced trees), six trees were measured using the electrical impedance method. The target trees in each stand were chosen based on the quantiles of total method (Čermák et al. 2004), such that the whole range of tree sizes was covered and each tree represented approximately the same fraction of stand basal area. The measurement was repeated for four 60° segments, each of which was multiplied by 1.5 and summed to estimate the whole tree root surface (360°). Two segments were measured in opposite directions along rows where trees were planted, and two others were measured along perpendicular segments (across trenches), as there is reason to believe that roots preferentially grow within the ridges (Savill 1976).
Fine root area

We sampled for fine root area by taking intact soil cores in each of the plots. Sampled soil cores had a diameter of 8 cm and a depth of 30 cm. Random stratified core samples were taken on the planting ridges \((n = 15)\) and in the furrows \((n = 15)\) in the 2-m spaced plot. In the 4-m spaced plot, an additional 15 core samples were taken on ridges devoid of trees. Finally, in the 6-m spaced plot, a further 15 additional cores were taken in trenches surrounded by ridges with no trees. This sampling regime was applied to explore possible differences in fine root area both between treatments and within plots, which will allow us to accurately scale to the stand level. Samples were taken at 0–15 and 15–30 cm below the soil surface by splitting each core into two. We carefully washed all the roots out of the soil and separated the live and dead roots based on a visual distinction in colour and resilience. Live roots ≤ 2 mm in diameter were then scanned, dried and weighed. As there was no significant understorey, we are confident that the vast majority of fine roots were produced by the large Sitka spruce trees. The roots were scanned at 600 dpi on an Epson GT 10000 A3 flat bed scanner and the images were analysed using the WinRhizo™ software to calculate the surface area of fine roots (in square centimetres). We scaled root area to the plot level by multiplying the mean fine root area per unit ground area by the total area occupied by each of the sampling locations.

Coarse root volume

Roots of the target trees were also excavated using an air spade (Soil Pick; MBW, Slinger, WI). Roots were exposed along two 30° horizontal angular sectors down to a depth of 30 cm. The centre of each sector corresponded to those measured by the electrical impedance method. The coarse root architecture of each of the target trees was modelled by measuring the root diameters \((D_{\text{root}_i}, \text{diameter of individual root} ~ i ~ \text{from tree} ~ t, \text{sector} ~ s \text{and distance} ~ x)\) at defined distances from the stem \((50, 75, 125, 175, 250 \text{ and} 325 \text{ cm})\) using a calliper and a measuring tape anchored near the trunk. The cross-sectional area \((A_{\text{root}_i}, \text{square metres of individual root} \ i \text{from tree} \ t, \text{sector} \ s \text{and distance} \ x)\) of all the individual roots was calculated and summed at each distance for each angular sector:

\[
A_{\text{root}_i} = \sum x A_{\text{real}_i}.
\]  

(2)

For each sector, a 2° or 3° polynomial function \(f(x)\) was used to link \(A_{\text{root}_i}\) (in square metres) with distance \(x\) (in metres). Root volume \((V_{\text{root}}, \text{cubic metres})\) was calculated for each tree and sector, via the bounded integral of function \(f(x)\):

\[
V_{\text{root}} = \int_{a}^{b} f(x)dx
\]  

(3)

where \(a\) was defined as 50 cm from the stem due to the presence of small buttresses and \(b\) was the maximum radial distance of root growth from the stem. The total root volume for each tree was calculated by multiplying the two measured sectors of 30° by 6 to account for the full 360° of root extension.

Tree social area

We used a measure of social area \((A_{\text{social}}, \text{in square metres})\) to estimate the apparent competitive environment surrounding a tree (Figure 5). Social area is a share of the stand area associated with a particular sample tree according to its size and the available surrounding space. \(A_{\text{social}}\) was calculated from Eq. (4) where \(d_i\) (in metres) is a series of distances to the nearest neighbouring trees which are weighted by the corresponding basal area of the sample tree \((A_{\text{bas}_i}, \text{in square metres})\) and that of each neighbouring tree \((A_{\text{bas}_j}, \text{in square metres})\) as a circular area (Čermák et al. 2006):

\[
A_{\text{social}} = \pi \left( \sum_{i=1}^{n} d_i \left( \frac{A_{\text{bas}_i}}{A_{\text{bas}_j} + A_{\text{bas}_i}} \right)^2 \right). 
\]  

(4)

In addition, projected tree crown area was calculated from field measurements and analysed using an irregular octagon approach.

Leaf area index

Leaf area index (LAI) was estimated from a published allometric relationship between diameter at breast height (DBH) and foliar biomass based on data from a Sitka spruce stand growing in similar conditions (Tobin et al. 2006). We applied this equation to all the trees in each of the treatment plots and summed the values to estimate the total foliar biomass in each stand. We calculated the foliar biomass per unit ground area and used a half-surface specific leaf area value of 4.48 m² kg⁻¹ to convert from foliar biomass to LAI (Tobin et al. 2006).

LAI accounts for the entire surface area of the leaf organ and is thus much larger than the water conducting surface area, which is determined by stomatal diameter and density (stomatal pore area). In order to make a direct comparison with our measure of root absorbing area, we calculated stomatal pore area index (SPI), a dimensionless index of stomatal pore area per unit lamina area (Sack et al. 2003). Jeffree et al. (1971) measured the maximum possible surface area of an individual stomatal pore in Sitka spruce to be 127 × 10⁻⁷ cm² with 6000 pores per square centimetre across the needle lamina. Based on these measurements, we calculate the SPI to be 7.62 × 10⁻³ cm² cm⁻², which we multiplied by our estimate of LAI to obtain the transpiring leaf area index (LAItranspiring).

Data analysis

Relationships between root absorbing surface area and DBH; stem resistivity and DBH; and stem/root volume and social area were determined using ordinary least squares regression analysis. Differences in the estimated parameters of the power functions for root absorbing area (EI method) fitted between
soil segments that run parallel or perpendicular to the drainage trenches were determined using an analysis of covariance on linearized data (log–log transformation). Plot differences between fine root surface area were determined using a hierarchical nested analysis of variance with location (i.e., ridge or furrow with or without trees) nested within-plot to test for the effect of tree density on RAI\textit{lin}. Statistical tests were done in R (R Development Core Team 2008).

Plot level coarse root volume was calculated by generating eight random neighbours for each of the sample trees from a population of 50 trees. The distances between neighbours were based on the assumption of systematically distributed grid tree spacing within each of the three plots. Equation (4) was applied to each of the 50 trees and the coarse root volume was calculated from the log-linear relationship between social area and coarse root volume (the intercept was set at the origin to avoid negative root volumes; Figure 6A).

**Results**

The management intervention of selective thinning resulted in distinctive tree metrics within the three treatment plots. Generally, the biometric parameters, such as tree diameter and crown projected area, were smallest in the 2-m plot and reached a maximum in the 6-m plot. In contrast, the basal and crown projected area, were smallest in the 2-m plot and reached a maximum in the 6-m plot. In contrast, the basal area was highest in the 2-m plot and lowest in the 6-m plot. Generally, the biometric parameters, such as tree diameter and crown projected area, were smallest in the 2-m plot and reached a maximum in the 6-m plot. In contrast, the basal area was highest in the 2-m plot and lowest in the 6-m plot.

Using the EI method, we found that trees with diameters in the range 15–50 cm had absorbing root surface areas in the range 4–10 m² (Figure 1). Within the range of trees that we measured, the relationship between DBH and absorbing root surface area was linear. However, a fitted non-linear power function (Figure 1) allowed the predicted values of the model to approach the origin. Given the high variance in absorbing root surface area, the effect of the curvature is small. In contrast, a linear model has a y-intercept of 2.6 m², thus overestimating the root absorbing area for small trees. Consequently, we applied the power function to our tree inventory data in order to extrapolate the total root absorbing area to the stand level. We used this measure of root area to estimate the absorbing root area index (RAI\textit{absorbing}). RAI\textit{absorbing} ranged from 0.28 m² m⁻² in the 6-m spaced plot to ∼1.11 m² m⁻² in the 2-m spaced plot (Table 1). These values are substantially lower in magnitude than the range in LAI (4.8–8.5 m² m⁻²).

However, RAI\textit{absorbing} is more closely analogous to and scales with LAI\textit{transpiring}, which represents 0.8% of the total estimated LAI (Table 1). LAI\textit{transpiring} ranged from 6.5 × 10⁻² in the 2-m spaced plot to ∼3.7 × 10⁻² in the 6-m spaced plot. The resulting RAI\textit{absorbing}:LAI\textit{transpiring} ratios fall in the range 7.7–17.1, which is a functionally descriptive estimate of the relative aboveground versus belowground resource-capturing ability. The values are an order of magnitude greater than those for the RAI\textit{lin}:LAI ratio (0.7–1.6).

There was significantly more root absorbing surface area in segments that ran along ridges created by the drainage furrows (P < 0.01). This distinction is the expression of a significantly different estimate of the power or allometric parameter b in the power law function, \( y = ax^b \) (P < 0.01). That is, the proportional change in absorbing root surface area associated with DBH is distinct between segments that were oriented parallel to the drainage channels and those perpendicular to the drainage trenches (Figure 2). The observed difference is more pronounced for larger trees, indicating that there is continual preferential growth along ridges or ribbons as the trees mature. Additionally, we found the resistivity of the water-conducting tissue (\( \rho \) in Eq. (1)) to be a negative power function of DBH (Figure 3) within the range of data (P < 0.01, \( R^2 = 0.64 \)).

Calculations of mean RAI\textit{lin} from core samples ranged from 5.56 m² m⁻² in the 2-m spaced plot to 7.55 m² m⁻² in the 6-m spaced plot. The range in RAI\textit{absorbing} was 0.07–0.64 m² m⁻², which is an order of magnitude greater than the range in RAI\textit{lin} (0.05–0.37 m² m⁻²) (Table 1).

**Table 1.** A comparison of aboveground and belowground resource-capturing areas of three Sitka spruce (\textit{P. sitchensis}) stands of differing tree densities. Measurements of stand structure (including coarse root volume) show distinct biomass allocation patterns. Belowground resource-capturing area is expressed as root area index, RAI (root area per unit ground area). RAI\textit{lin} is estimated from fine root excavation and geometric calculation, RAI\textit{absorbing} is estimated from the EI method. Where applicable, we report the standard errors.

|                      | 2-m plot | 4-m plot | 6-m plot |
|----------------------|----------|----------|----------|
| Tree density [stems per hectare] | 3000     | 625      | 278      |
| Basal area (\( A_{\text{basal}} \)) [m² ha⁻¹] | 71.43    | 55.56    | 50.69    |
| Mean DBH [cm]        | 19.9 (±0.69) | 29.0 (±0.99) | 42.3 (±1.06) |
| Mean crown projected area [m²] | 6.2 (±0.47) | 15.9 (±1.16) | 39.0 (±2.28) |
| RAI\textit{lin} [m² m⁻²] | 5.56 (±0.44) | 7.13 (±0.57) | 7.55 (±0.54) |
| RAI\textit{absorbing} [m² m⁻²] | 1.11      | 0.50     | 0.28     |
| LAI [m² m⁻²]         | 8.5       | 5.8      | 4.8      |
| LAI\textit{transpiring} | 6.5 × 10⁻² | 4.4 × 10⁻² | 3.7 × 10⁻² |
| RAI\textit{lin}:LAI ratio | 0.7       | 1.2      | 1.6      |
| RAI\textit{absorbing}:LAI\textit{transpiring} ratio | 17.1      | 11.3     | 7.7      |
| Social area (\( A_{\text{social}} \)) [m²] | 4.84 (±0.21) | 19.51 (±0.43) | 43.99 (±0.55) |
| Coarse root volume [m² ha⁻¹] | 33.67     | 38.44    | 22.11    |
| Absorbing root area per unit coarse root volume [m² m⁻³] | 331.22    | 129.65   | 124.48   |

The letters a and b indicate statistical distinction at the 5% level (where applicable).
in the 6-m spaced plot (Table 1). There was a significant difference between the 2-m plot and both the 4- and 6-m plots. Though there appears to be a slight negative trend with basal area, there was no significant difference between the 4- and 6-m spaced plots (Table 1). Including the location where each core sample was taken (i.e., ridge or furrow with or without trees present), nested within each individual plot, significantly increased the explanatory power of the model ($P < 0.01$, $R^2 = 0.13$; Figure 4). We used social area as a measure of the competitive environment of individual trees, which can be compared with projected crown area (Figure 5). Our mean estimates for social area for a sample of 50 trees within each plot were 4.8, 19.5 and 45 m² for the 2-, 4- and 6-m plots, respectively (Table 1).
Figure 5. Spatial representation of six individual sample trees and their nearest neighbours from three differentially spaced Sitka spruce plots (2, 4 and 6 m). Tree location and basal area are represented by a circle with a dot in the centre. Social area of target trees is calculated according to Eq. (4) (Čermák et al. 2006) and represented by broken lines. Crown area is represented by the solid line.
This shows that the trees in the 6-m plot experience less competitive pressure despite the presence of larger neighbours.

The coarse root network was evaluated as each individual plant’s investment in the total volume of coarse roots (for practical purposes, defined as roots ≥5 mm in diameter). The coefficients of determination for the polynomial fits $f(x)$ used to link radial root area ($A_r$, in square metres) with distance ($x$, in metres) within Eq. (3) were fairly high (mean $R^2 = 0.85$). Social area accounts for ~71% of the variation in root volume investment (Figure 6A). This relationship appears to plateau as social area increases above ~30 m$^2$.

The aboveground stem volume shows a similar relationship (Figure 6B), indicating a proportional investment in aboveground and belowground tissue. At the stand level, the proportion of absorbing root area per unit coarse root volume declines with reduced tree density (Table 1).

Discussion

For the most part, field studies of root systems have failed to address their resource-capturing ability. Here, we use an EI method to measure the absorbing root surface area. The results from our study show a strong correlation between absorbing root surface area and DBH (Figure 1) and also show good agreement with measurements made on Norway spruce ($P. abies$) (Cermák et al. 2006). The observed trend is in accordance with conventional hydraulic theory where a given unit of sapwood area would be expected to be supported by a proportional amount of absorbing root surface area (Sperry et al. 1998).

We observed a distinct asymmetry in the development of the root system around individual trees. The method of spaced-furrow ploughing is known to restrict root development, with roots preferentially proliferating along the lines of the ploughed ridges (Savill 1976). This differential development of the root system is expressed in the amount of root absorbing surface area that was measured in segments along ridges and those across ridges. This disparity was more pronounced in the larger trees with a maximum discrepancy of ~3 m$^2$ of absorbing root surface area in the largest trees (Figure 2).

Conventionally, it has been assumed that fine roots are the functional equivalent of leaves in their ability to capture resources. This idea is complicated by the ambiguous definitions used for fine roots, having been classified by various authors anywhere in the range <1 mm to as much as <5 mm in diameter (Persson et al. 1995, Pregitzer et al. 1998, Vanninen and Makela 1999). Here, we quantified a measure of root area index (in square metres of root area per unit ground area) based on fine root excavation (RAI$_\text{fine}$) and our estimates across the three plots (Table 1) correspond well to global estimates in temperate coniferous forests and boreal forests of 11 and 4.6 m$^2$ m$^{-2}$, respectively (Jackson et al. 1997). These estimates are comparable in magnitude to LAI, with the ratio of RAI$_\text{fine}$:LAI ranging from 0.7 to 1.6 (Table 1). RAI$_\text{fine}$ was significantly lower in the 2-m plot relative to the other two study plots, despite having the largest basal area, which conflicts with the requirement for a correlation between the hydraulic conducting surface areas of the roots and stem. The traditional approach of inferring root physiological function based on arbitrary size classification has been questioned before (Pregitzer 2002). The widely held
assumption that all roots of a given size class (fine roots) function in the same way in terms of water and nutrient uptake may not be true and, consequently, measurements of RAIabsorbing may be misleading in this context. Furthermore, there is evidence to suggest that the absorbing surface area of roots is only represented by a short zone (~100–200 mm) behind the root tip (Steudle 1994). Consequently, any inconsistency in the ratio of fine root biomass to number of root tips will introduce error into the measurements and interpretation of fine root surface area.

In contrast, RAIabsorbing (based on the EI method) was proportional to basal area across the three stands, ranging from 0.28 m² m⁻² in the 6-m spaced plot to ~1.11 m² m⁻² in the 2-m spaced plot (Table 1). Interestingly, RAIabsorbing was not directly proportional to RAIbasal, with the absorbing component accounting for between 3.7 and 19.6% of the total fine root area (Table 1). This outcome probably reveals differences in the proportion of total fine root surface area that is used for nutrient and water uptake, although independent measures of the absorbing zone of the fine roots of each tree would be needed to explore this further.

Our measure of RAIabsorbing is analogous to LAItranspiring, which is the proportion of the total LAI accounted for by the SPI. Functionally, SPI has been shown to correlate well with the hydraulic conductance of the leaf lamina (Sack et al. 2003). The ratios of RAIabsorbing:LAItranspiring observed here may indicate a comparatively higher root absorbing surface area with respect to stomatal pore area, possibly to compensate for dry non-conductive zones that may develop in the rhizosphere (Newman 1969, Bristow et al. 1984, Sperry et al. 1998).

The electrical resistance (R, in ohms) of an object (such as a tree stem) is dependent on tree height (h), stem cross-sectional area (A), and the nature of the water-conducting tissue or resistivity (ρ, in ohm metres) (Eq. (5)):

\[ R = \frac{\rho h}{A} \tag{5} \]

Resistivity is a material-specific constant at a given temperature. Therefore, we would expect the observed differences in resistivity to be attributed to differences in the xylem structure, assuming constant temperature. The smaller trees have the highest electrical resistivity of the water-conducting tissue (Figure 3). This is likely to be associated with differences in stem density. It is well understood that the space available for the growth of a tree will affect the characteristics of its woody tissue, with high stand densities yielding more dense wood (Brazier 1970, Petty et al. 1990). Furthermore, the basic density of Sitka spruce wood depends primarily on tracheid diameter relative to wall thickness (Mitchell and Denne 1997). This suggests that the trees in the 2-m plot will generally have thinner tracheids, which are associated with lower cavitation risk, and, consequently, low hydraulic conductivity. Accordingly, the higher RAIabsorbing:LAItranspiring ratio observed in the 2-m plot may correspond to lower plant hydraulic conductivity. This relationship is supported by modelled predictions of root to leaf area ratios, with higher ratios corresponding to low soil and xylem conductivity (Sperry et al. 1998).

The conducting root system functions to mobilize soil resources across the soil profile because, unlike the atmosphere, the soil experiences little mixing (Carvalheiro and Nepstad 1996). The network of coarse conducting roots of individual trees, measured as root volume, varies in accordance with the competitive environment (social area) (Figure 6A). It is well established that both competition and resource availability influence biomass allocation during tree growth (Gersani and Sachs 1992, Reynolds and Pacala 1993, Belcher et al. 1995, Maliakal et al. 1999). As tree density decreases, each individual tree will have more resources (both light and soil resources) available. Therefore, as social area increases, individual plants are more productive both aboveground and belowground. However, at large separation (large social areas), both these relationships plateau (Figure 6).

Hydraulic constraints associated with increasing tree height may account for a reduced investment in stem tissue (Schafer et al. 2000, Koch et al. 2004, Niklas and Spatz 2004). In contrast, root proliferation may be constrained by diminishing marginal returns (Bloom et al. 1985), assuming that a benefit is accrued by maximizing leaf area and stomatal conductance while minimizing root biomass (Sperry et al. 1998, Shipley and Meziane 2002). Mechanical constraints (e.g., increased wind loading) on trees with reduced density and increased crown dimensions may also contribute to additional investment in structural root architecture (Nicolle and Ray 1996, Greens et al. 1995). Furthermore, root efficiency can be determined by the differences between an individual’s nutrient and water uptake and the cost of growth and maintenance of servicing roots (Gersani et al. 2001). Consistent with these ideas, the efficiency of belowground investment can be illustrated in our data by the amount of absorbing root area per unit coarse root volume (Table 1). Our results demonstrate that, as the tree density decreases across the plots, every additional unit of absorbing root area is supported by a proportionally greater investment in coarse conducting roots (Table 1), rendering further investment progressively less efficient.

Conclusions

Conventionally, fine roots (commonly defined as being ≤2 mm in diameter) have been thought to function as the pathway for water and nutrient uptake by plants, analogous to the role that leaves play for carbon and energy uptake (Jackson et al. 1997, Pregitzer 2002). Consequently, an accurate and physiologically meaningful measure of root area index is of fundamental importance in establishing a functional understanding of energy exchange and nutrient cycling. Despite the fundamental role that roots play in global biogeochemical cycles, they are poorly represented in global models.
relative to their foliar counterparts (Woodward and Osborne 2000). Leaf area facilitates accurate simulation of carbon and energy gain in terrestrial models. In a similar way, root area, measured using the electrical impedance method, may provide physiologically meaningful data for simulating soil resource acquisition.

The inherent difficulties in conducting studies with an integrated approach to the plant–soil continuum have dramatically hindered our understanding of this functional association (Högberg and Read 2006). Here, we express a physiologically relevant estimate of RAI (RAI_{absorbing}), which is fundamental to our understanding of roots as functional plant organs. This variable has considerable potential to improve our efforts of modelling water and nutrient uptake. Additionally, comparison between leaf and root areas as resource-capturing organs will improve our understanding of the functionally important exchange surfaces between plants and their environment.

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