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The role of fine-root mass, specific root length and life span in tree performance: A whole-tree exploration

Monique Weemstra^{1,2} | Natasa Kiorapostolou^{1,3} | Jasper van Ruijven² |
Liesje Mommer² | Jorad de Vries⁴ | Frank Sterck¹

¹Forest Ecology and Forest Management Group, Wageningen University, Wageningen, the Netherlands

²Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, the Netherlands

³Department Territorio e Sistemi Agro-Forestali, University of Padova, Legnaro, Italy

⁴Centre for Crop System Analysis, Wageningen University, Wageningen, the Netherlands

Correspondence

Monique Weemstra

Email: moniqueweemstra@hotmail.com

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Abstract

1. The root economics spectrum (RES) hypothesis predicts that fast-growing tree species have short-lived roots with high specific root length (SRL) to allow rapid resource uptake, and opposite trait expressions for slow-growing species. Yet, the mixed support for this hypothesis suggests that trees can adopt alternative strategies to increase resource uptake, besides an increase in SRL.
2. We combined a novel mechanistic whole-tree model and empirical fine-root data of 10 tree species to test the effects of one of these alternative strategies, notably increasing fine-root mass, on the tree's net C gain (used here as a proxy for tree performance), and to assess how fine-root life span influences the relative importance of SRL and fine-root mass for the C balance of trees.
3. Our results indicate that accounting for the short life span of high-SRL roots has important implications for explaining tree performance and the role of roots herein. Without considering their faster turnover, high-SRL roots and low fine-root mass resulted in the highest performance as predicted from the RES. Yet, when their higher turnover rates were accounted for, a high fine-root mass and low SRL lead to the highest performance. Both our model outcomes and field data further show a negative relationship between SRL and fine-root mass through which species aim to realize a similar root length density. This trade-off further indicates how high a SRL and low fine-root mass as well as opposite trait values can both lead to a positive C balance in a similar environment.
4. Our study may explain why high-SRL roots do not necessarily lead to the fastest tree growth as often hypothesized and demonstrates the importance of fine-root mass in combination with fine-root life span for explaining interspecific differences in tree performance. More generally, our work demonstrates the value of identifying and investigating different below-ground strategies across species from a whole-plant modelling perspective, and identifies the relationship between SRL, fine-root biomass and life span as an important functional dimension to variation in species' performance.

KEYWORDS

carbon balance, fine roots, functional traits, root economics spectrum, tree performance, whole-plant model

1 | INTRODUCTION

Plant ecologists seek to explain why and how species vary in their performance, that is plant growth, survival and reproduction, in different environments. Leaf functional traits have proven valuable predictors of plant performance (Poorter & Bongers, 2006; Reich, Walters, Tjoelker, Vanderklein, & Buschena, 1998): by measuring several key leaf traits, species can be arranged along a leaf economics spectrum (LES) that ranges from species with acquisitive leaves that grow fast when resources are readily available, to species with conservative leaves that allow high survival rates in resource-poor environments (Reich, Walters, & Ellsworth, 1992; Sterck, Poorter, & Schieving, 2006; Wright et al., 2004). Similar to leaves, fine roots acquire essential resources to plant performance. Yet unlike leaves, the fine-root functional traits that are generally measured are not clearly related to species' growth and survival rates in a root economics spectrum (RES; Ma et al., 2018; Wang et al., 2018; Weemstra et al., 2016), so that the role of fine roots in plant performance remains poorly understood.

A notable difference between the LES and the RES includes the inconsistent role of specific root length (SRL) in the RES. While SLA is a main driver of the LES and correlates strongly with other leaf traits, light interception and plant performance (Wright et al., 2004), correlations between SRL and other fine-root traits, soil resource uptake and tree growth are inconsistent (Weemstra et al., 2016), with the exception of the generally negative relationship between SRL and fine-root life span (McCormack, Adams, Smithwick, & Eissenstat, 2012; Weemstra et al., 2016). The different roles of SLA and SRL in resource economics may partly result from the multiple environmental constraints that act on fine roots, but not on leaves that are predominantly optimized to capture light in a given light environment (Weemstra et al., 2016). For instance, fine roots of high SRL may be most efficient to enhance fine-root surface area and acquire soil resources at relatively low biomass investments (Eissenstat & Yanai, 1997), but such thin fine roots may not be able to penetrate compact soils (Clark, Whalley, & Barraclough, 2003; Hodge, Berta, Doussan, Merchan, & Crespi, 2009). Consequently, trees may depend on other root strategies to enhance their performance that are not included in a RES across tree species.

Besides an increase in SRL, trees can also enlarge their below-ground surface area by increasing their fine-root mass. It is considered a less efficient strategy than an increase in SRL because it requires carbon (C) for the production and maintenance of fine roots. At the same time, high-SRL roots may present substantial C losses to the tree due to their short life span (McCormack et al., 2012; Weemstra et al., 2016). In terms of a tree's C balance, an increase in fine-root mass may thus also represent a viable strategy to enhance below-ground surface area, soil resource uptake and plant performance. In fact, *within* species, changing fine-root mass proves an important response to soil resource availability: on poor soils, trees increase their fine-root mass rather than their SRL to enhance resource uptake (Espeleta & Donovan, 2002; Hertel, Strecker, Mueller-Haubold, & Leuschner, 2013; Weemstra et al., 2017).

Across species, it has been suggested that fine-root biomass may be an important factor in soil resource uptake (Valverde-Barrantes, Freschet, Roumet, & Blackwood, 2017) and hence species' performance. Yet variation in fine-root mass has only rarely been quantified across tree species, and is difficult to compare as it can be strongly influenced by plant size (Poorter et al., 2012) and environmental variables (Ostonen et al., 2017). For instance, Hansson, Helmisaari, Sah, and Lange (2013) found that *Picea abies* trees had a larger fine-root biomass than *Betula pendula* and *Pinus sylvestris* trees (700 vs. 200 and 230 g/m² soil respectively). Yet because *P. abies* trees were also larger, these differences in fine-root mass may merely reflect ontogenetic effects rather than species-specific uptake strategies. In contrast, Ostonen, Lohmus, Helmisaari, Truu, and Meel (2007) corrected for plant size and found more fine-root mass per unit basal area for *P. abies* and *P. sylvestris* than *B. pendula*. Valverde-Barrantes, Raich, and Russell (2007) compared fine-root mass between six tropical tree species of similar size and concluded that species' identity is an important factor explaining fine-root biomass differences, and Withington, Reich, Oleksyn, and Eissenstat (2006) reported 2.5 times variation in fine-root mass across 11 temperate tree species in a common garden. Yet, the implications of such interspecific variation in fine-root mass for the RES and associated differences in species' performance remain largely unexplored.

This study assesses the importance of below-ground strategies beyond the RES for the performance of trees, focusing on fine-root mass in relation to SRL and fine-root life span. More specifically, we examine the contributions of fine-root mass and life span to variation in tree performance that may be insufficiently explained by the common RES traits alone. To this end, we (a) explore adaptive fine-root strategies using a whole-tree model that simulates tree net C gain (used here as a proxy for tree performance) based on the expected trade-offs between fine-root mass, SRL and fine-root life span and (b) test the empirical evidence of such strategies by comparing fine-root traits and biomass across 10 tree species growing in a common garden.

2 | MATERIALS AND METHODS

2.1 | Fine-root data collection

Fine-root data were collected from 10 temperate broad-leaved tree species (Table 1) growing in a common garden forest at the Hollandse Hout, the Netherlands (52°28'N, 5°26'E), established in the 1960s and 1970s. The forest is subjected to a temperate marine climate with mild winters and summers and an annual rainfall of c. 800 mm (KNMI, 2020). The soil is described as a calcareous and nutrient-rich clay soil with a homogeneous texture throughout the forest, and the groundwater table ranges between 1.6 and 1.2 m below the soil surface (Weemstra, Eilmann, Sass-Klaassen, & Sterck, 2013).

Fine-root mass and morphology were measured in three mono-specific forest plots per species. Per plot, three soil samples up to 1 m depth and randomly distributed over the plot were collected using a 42 mm diameter root auger, the roots washed out, separated

TABLE 1 Species' fine-root mass, length density (calculated from fine-root mass and specific root length) and morphological traits (means and standard errors) and species' preference for moist environments (Ellenberg value; species with higher values prefer wetter sites)

Species	Observed fine-root traits					Ellenberg moisture ^a value
	Biomass (kg/m ³)	Specific root length (m/g)	Length density (m/m ³)	Tissue density (g/cm ³)	Mean diameter (mm)	
<i>Alnus glutinosa</i> (L.) Gaertn.	0.09 (0.02)	40.1 (7.1)	3,870	0.18 (0.02)	0.40 (0.02)	9
<i>Acer pseudoplatanus</i> (L.)	0.29 (0.04)	34.2 (3.3)	9,860	0.25 (0.02)	0.34 (0.01)	6
<i>Betula pendula</i> (Roth)	0.28 (0.07)	25.3 (2.1)	7,000	0.38 (0.04)	0.35 (0.02)	NA
<i>Fraxinus excelsior</i> (L.)	0.25 (0.06)	54.4 (13.8)	13,500	0.20 (0.01)	0.37 (0.02)	NA
<i>Fagus sylvatica</i> (L.)	0.24 (0.02)	34.5 (2.4)	8,400	0.33 (0.02)	0.26 (0.01)	5
<i>Populus trichocarpa</i> (Torr. & Gray)	0.12 (0.02)	59.1 (10.8)	7,440	0.24 (0.02)	0.32 (0.03)	7
<i>Prunus avium</i> (L.)	0.37 (0.06)	27.0 (2.7)	9,990	0.29 (0.03)	0.37 (0.02)	5
<i>Quercus robur</i> (L.)	0.23 (0.03)	32.0 (1.5)	7,590	0.32 (0.01)	0.31 (0.01)	NA
<i>Salix alba</i> (L.)	0.17 (0.03)	69.2 (6.6)	11,730	0.17 (0.02)	0.29 (0.01)	8
<i>Tilia cordata</i> (Mill.)	0.23 (0.03)	23.4 (1.8)	5,290	0.28 (0.02)	0.39 (0.01)	5

^aEllenberg (1974).

into fine and coarse roots based on their diameter (fine roots being <2 mm diameter) and weighed. As roots were sampled with a root auger and cut into smaller fragments, we were unable to accurately sort roots based on their order. Fine roots were scanned, the scans were analysed with WinRhizo (Regent Instruments) to determine total fine-root length, mean diameter and mean root volume, and the fine roots were oven-dried at 60°C for 48 hr to determine dry mass. Fine-root SRL was calculated by dividing fine-root length by dry wt; fine-root tissue density was calculated by dividing fine-root dry wt by fine-root volume; and fine-root length density (fine-root length per soil volume) was calculated by multiplying SRL and fine-root mass.

2.2 | Whole-tree model description

The model simulates the whole-tree net C gain—used here as a proxy for performance—as the C gained in the crown through photosynthesis minus the C lost by the respiration and turnover of above- and below-ground plant tissue. It is based on an existing tree growth model that calculates net daily C gain based on above-ground (crown and stem) structure and physiology (Sterck, Markesteijn, Schieving, & Poorter, 2011; Sterck & Schieving, 2011; Supplementary File: Model Description). This above-ground model calculates photosynthetic C gain in the crown based on a three-dimensional tree structure consisting of a cylindrical crown of given dimensions in which leaves are homogeneously distributed and their photosynthetic capacities characterized by an average SLA and leaf nitrogen (N) content, and a stem running from the soil surface to the leaves. Here, we focus on the new incorporation of a below-ground component that is linked to above-ground functioning, and which together determine whole-tree performance

(see Supplementary File: Model Description and Figure S1 for more detailed explanations).

Analogous to the leaves and the stem, the root system is characterized by a below-ground cylindrical shape that contains the coarse and fine roots (Supplementary File: Model Description, Figure S1). Within this cylinder, fine roots are evenly distributed and acquire water and nutrients from the soil. In reality, fine roots are heterogeneously distributed over the soil (Canadell et al., 1996), but our simplified, uniform fine-root distribution allows an explicit study of the impacts of fine-root mass, SRL and life span on resource uptake and the C balance of trees. The coarse-root system is a below-ground extension of the stem and functions similarly; it has a given length and sapwood area and transports water and nutrients from the fine roots to the stem and then to the crown. Fine and coarse roots are thus defined by their function (uptake and transport of soil resources respectively) and characterized by different respiration and turnover rates (Table 2).

The supply of water and nutrients from the soil to the model tree is fixed in our model; we assume simple boundary conditions for soil water and soil nutrients by setting constant values for soil water potentials and soil nutrient concentrations (Table S4). This implies that our simulations cannot include soil dynamics in nutrient and water availability, which was beyond the scope of this study. We used N as the model nutrient that is a key component in tree functional processes, for example leaf photosynthetic capacity and tissue respiration.

The uptake of nutrients from the soil by the model tree, that is the solute flux from soil into the fine root, is defined by an adjusted Michaelis-Menten equation (see also Supplementary File: Model Description). It is determined by the fine-root area (A_{fr} , m²), the root uptake capacity (I_{max} , mol m⁻² s⁻¹), the solute concentration in the soil (S_b , mol/m³) and the Michaelis constant

	Value	Source
Turnover rate		
Leaves	0.005 day ⁻¹	Sterck and Schieving (2011)
Wood/coarse roots	0.0003 day ⁻¹	Sterck and Schieving (2011)
Fine roots	0.005 day ⁻¹	Weemstra et al. (2016)
Respiration rate		
Leaves	1,000 µmol CO ₂ kg ⁻¹ N s ⁻¹	Lambers, Chapin, and Pons (1998); Sterck and Schieving (2011)
Wood/coarse roots	0.4 µmol CO ₂ kg ⁻¹ s ⁻¹	Sterck and Schieving (2011)
Fine roots	100 µmol CO ₂ kg ⁻¹ N s ⁻¹	Reich et al. (2008) ^a

^aFine-root respiration rates were based on Reich et al. (2008), but were lower in our model simulations to arrive at realistic C balance predictions.

TABLE 2 Carbon cost model parameters for different plant organs and literature sources

(K_{mfr} , i.e. the substrate concentration required to achieve 50% of I_{max} , mol/m³; nutrient uptake parameters are presented in Tables S2 and S4). The fine-root absorptive area in this equation is determined by fine-root mass and SRL. Fine-root uptake is thus calculated as:

$$\text{Uptake} = A_{fr} \frac{I_{max} * S_b}{S_b + K_{mfr}} \quad (1)$$

More water and nutrient uptake allows a higher leaf area index (LAI), with implications for the net C gain of the whole tree.

Together, fine-root traits and LAI drive the three key processes of the whole-tree C budget, that is photosynthesis, respiration and tissue turnover (Figure 1; Supplementary File: Model Description). First, photosynthesis is directly constrained by LAI; a larger LAI allows greater photosynthetic C gain as more light is intercepted in the crown. In turn, the LAI is limited by nutrient uptake as leaves require relatively high nutrient levels to maintain photosynthetic capacity. Second, whole-tree respiration is driven by the respiration costs of sapwood, leaves and fine roots. Sapwood respiration is based on a constant mass-based respiration rate; fine-root and leaf respiration rates are determined by their respective nutrient contents, which are supposed parts of active proteins involved in nutrient uptake and photosynthesis respectively. Third, whole-tree tissue turnover represents the total C loss per day via shedding of leaves, sapwood and fine roots. It is directly simulated from the mass and life span of these different organs (as illustrated for fine roots in Figure 1). From these integrated C processes, the whole-tree net C gain (kg C/day) is calculated (photosynthetic C gain minus respiration C loss minus turnover C loss); a higher net C gain represents better tree performance.

2.3 | Model parameterization

Above-ground trait values were parameterized as described in Sterck, Anten, Schieving, and Zuidema (2016; Table S1). The below-ground structure is defined by the root system radius that is set

equal to that of the crown, that is 5 m, and a rooting depth fixed at 2 m (Table S2) approximately corresponding to the groundwater levels on our forest site (Weemstra et al., 2013). Within this fine-root system cylinder, we modelled a range of fine-root mass (i.e. 0–0.5 kg fine-root mass/m³ soil) and SRL (i.e. 0–150 m/g) values based on previous work (Weemstra et al., 2016, 2017).

The below-ground processes that directly contribute to the whole-tree C balance are fine-root respiration and turnover (Figure 1). Their respiration and turnover parameters (and those of other plant organs) were obtained from the literature (Table 2) and whole-tree measures of respiration and turnover were then summed for all plant organs (Supplementary File: Model Description). Fine-root respiration rates were based on Reich et al. (2008), but were lower in our model simulations and used to balance the C budget and arrive at more realistic C balance predictions in our model. Fine-root uptake parameters are obtained from the literature but were not completely available for tree species specifically (Table S2).

2.4 | Model simulations

We simulated tree performance with a steady state in tree water and nutrient status. This implies that water loss rates from the crown through transpiration equals the water flow through the coarse roots and stem, and water uptake rates by the fine roots, so that the water fluxes in the tree's leaf, sapwood and fine-root tissue remain constant. Water uptake is regulated by the LAI that represents the evaporative pull, and by the leaf water potential, as stomata are closed when insufficient water is available to maintain transpiration rates (Supplementary File: Model Description). The steady state in tree nutrient status implies that nutrient uptake rates by the fine roots are assumed equal to the nutrient losses via whole-tree tissue turnover, leading to a constant nutrient status of the model tree (Supplementary File: Model Description). Nutrient uptake by fine roots constrains the LAI, as leaves require nutrients and need to be replaced. We related fine-root nutrient

FIGURE 1 Conceptual whole-tree performance model. The whole-tree net carbon (C) gain (upper box) is used as a proxy for plant performance. It is calculated based on three underlying whole-tree C processes as the C gained by photosynthesis minus C lost by tissue turnover and respiration (grey boxes). These three C processes are in turn determined by interacting crown (i.e. leaf area index (LAI); green box) and fine-root properties (i.e. fine-root mass, specific root length (SRL) and life span, brown boxes) and the uptake of water and nutrients (blue boxes). Carbon loss (through respiration and turnover) depends on the mass and the turnover and respiration rates of the different organs (Table 2). Carbon is gained through photosynthesis, which is determined by the LAI. LAI is in turn constrained by water and nutrient uptake which is determined by the fine-root surface area (reflected by fine-root mass and SRL). In our first scenario, fine-root life span is fixed at 200 days. In the second scenario, fine-root life span varies with SRL (Equation 2), so that an increase in SRL leads to greater C losses due to faster turnover (dashed blue lines). Note that in the model, the shapes of the crown and root system are considered to be cylinders in which leaves and fine roots, respectively, are uniformly distributed (Figure S1). Solid lines indicate positive relationships; dashed arrows represent negative relationships

uptake to the LAI of a tree, representing its crown photosynthesis, and not to its photosynthetic capacity at the individual leaf (mass or area) level. Fine-root mass and SRL determine water and nutrient uptake as a large root-absorptive area allows more rapid resource uptake.

To address our first objective, we ran two model scenarios with different uptake benefits and associated C costs of fine-root mass, SRL and life span. The first scenario includes the combined effects of changes in fine-root mass and SRL on resource uptake and LAI, and ultimately on the whole-tree net C gain from its underlying C processes (photosynthesis, respiration and turnover). Here, fine-root life span is *fixed* at 200 days (based on values from Weemstra et al., 2016) to assess whether an increase in SRL is more beneficial to plant performance than an increase in fine-root mass because

the C costs per absorptive root area are lower. The second scenario tests how the trade-off between SRL and fine-root life span affects tree performance by running the model with a *variable* fine-root life span (year) as a function of SRL (m/g; blue dashed lines in Figure 1) derived from the linear regression between SRL and root life span data measured across 25 tree species (Weemstra et al., 2016):

$$\log(\text{fine-root life span}) = 7.074 - 0.382 \log(\text{SRL}) \quad (2)$$

Comparing the outcomes of the first and second scenarios reveals the impact of the trade-off between fine-root SRL and life span on whole-tree performance and shows whether an increase in fine-root mass and SRL can both be adaptive in terms of uptake benefits and C costs.

2.5 | Statistical analyses

To assess our second objective, we used our model to predict the net C gain of our study trees based on their observed SRL and fine-root mass, and tested the (linear and nonlinear) relationships between SRL and fine-root mass and the predicted net C gain of species to determine which trait correlated most with the modelled C balance of species. We further tested Pearson correlations among fine-root mass and morphological traits (i.e. SRL, fine-root tissue density and fine-root diameter) across our 10 study species. We also correlated fine-root traits and Ellenberg values for moisture to test whether species' variation in root traits was related to their environmental preferences. All analyses were carried out with R statistical software (R Core Team, 2019).

3 | RESULTS

3.1 | Different fine-root strategies and tree performance: model outcomes

The first model scenario predicts whole-tree performance (i.e. net C gain) based on variation in fine-root mass and SRL independent from fine-root life span (Figure 2a). Under these conditions, trees maintained a positive C balance by having a fine-root mass between 0.10 and 0.25–0.45 kg/m³ depending on variation in SRL. Within this range of fine-root mass values, the net C gain increased by reducing fine-root mass while increasing SRL. The highest net C gain (i.e. 0.38 kg C/day) was achieved by relatively high SRL (150 m/g) and low fine-root mass (0.16 kg/m³). Fine-root mass values higher than c. 0.45 kg/m³ always resulted in a negative C balance regardless of changes in SRL. Compared to the first

scenario, in the second scenario (where high-SRL roots had shorter life span), similar root trait values resulted in a positive C balance, but the C gain optimum shifted; the highest net C gain (0.39 kg C/day) was achieved by having a relatively low SRL (lower than c. 30 m/g) and high fine-root mass (between 0.25 and 0.35 kg/m³; Figure 2b).

3.2 | Different fine-root strategies and tree performance: a field test

Fine-root mass across our 10 species measured in the field varied between 0.09 kg/m³ soil for *Alnus glutinosa* and 0.37 kg/m³ for *Prunus avium*, SRL ranged from 23 m/g for *Tilia cordata* to 69 m/g for *Salix alba* and the corresponding root length density between 3,900 (*A. glutinosa*) and 13,500 m/m³ (*Fraxinus excelsior*; Table 1). Variation in SRL was mainly driven by variation in fine-root tissue density (Pearson $r = -.74$, $df = 8$, $p = .01$) rather than in fine-root diameter (Pearson $r = -.31$, $df = 8$, $p = .38$). Species with a high fine-root mass tended to have a low SRL and vice versa (Figure 2b; Pearson $r = -.61$, $df = 8$, $p = .06$).

Based on their observed fine-root mass and SRL (Table 1), the model (scenario 2) predicted a positive C balance for all 10 tree species (Figure 2b) after model calibration for a single soil nutrient concentration (parameter S_b , Table S4). For two species, however (*A. glutinosa* and *P. avium*), the net C gain approached zero (0.01 and 0.03 kg C/day respectively). The highest net C gain (0.38 kg C/day) was simulated for *Fagus sylvatica* and *Quercus robur* and approached the optimum. The relationship between species' predicted net C gain and SRL was not significant ($F_{1,8} = 0.09$, $p = .77$, $N = 10$); the relationship between fine-root mass and net C gain was nonlinear (bell-shaped) and significant ($F_{2,7} = 101.5$, $p < .001$, $N = 10$).

FIGURE 2 Tree performance landscapes under different fine-root trait combinations. Net daily carbon (C) gain simulated based on variation in specific root length (SRL) and fine-root biomass for (a) our first model scenario (fixed fine-root life span) and (b) the second model scenario (fine-root life span varying with SRL; Equation 2). White areas indicate a negative C balance (i.e. net C gain <0 kg/d), grey areas indicate a positive C balance with darker grey indicating higher net C gain. Thin black lines indicate the isoclines that mark the highest net C gain. Coloured lines represent the root length for a given fine-root mass and specific root length; yellow: 2,500; green: 5,000; red: 10,000; blue: 25,000 m/m³. Symbols in (b) represent 10 tree species positioned in the performance landscape based on their observed fine-root mass and SRL in the field (Table 1). Thick black regression line (b) describes the relationship between fine-root mass and SRL across the 10 species

4 | DISCUSSION

This study combines a modelling approach and empirical data to test the relative importance of a combination of fine-root traits (i.e. fine-root mass, SRL and life span) for the whole-tree C balance. Our model simulations imply that assuming a fixed fine-root life span, a high SRL in combination with low fine-root mass leads to the highest carbon gain; yet taking the faster turnover rates of high-SRL roots into account reveals that having a high fine-root mass and long-lived, low-SRL roots results in a higher net C gain. Moreover, accounting for the fast turnover of roots with high SRL reveals a trade-off between fine-root mass and SRL, where a low SRL and high fine-root mass lead to the highest net C gain, but opposite trait values also yield a positive C balance; this trade-off was also observed across the 10 tree species measured in the field. Our results may explain why high tree growth rates not necessarily correspond to high SRL and indicate how the resource uptake of trees can be enhanced through other trait adjustments, such as a high fine-root mass in combination with low fine-root life span. In ecology, fine-root mass and length density are rarely considered when comparing species' variation in plant performance, but our work indicates that together with root life span, they may serve as important functional dimensions to fine-root trait variation and improve our understanding of its role in species' performance.

4.1 | Trees can increase their C balance through different below-ground strategies

According to our model simulations the fast turnover rates of high-SRL roots have a pronounced impact on the C balance of trees. Assuming a fixed root life span of 200 days (scenario 1), the highest net C gain is realized through a combination of relatively low fine-root mass and high SRL corresponding to a root length density of c. 22,000 m/m³. Under these conditions, trees have a large fine-root surface area and hence fast resource uptake below-ground, leading to higher photosynthetic C gain above-ground, while keeping C losses due to root respiration and turnover low. This positive relationship between SRL and tree growth is predicted by classical plant root theory (Eissenstat, 1992), expected from the RES (Reich, 2014) and observed across tree species (Comas & Eissenstat, 2004). In contrast, accounting for their faster turnover in the second scenario reduces the benefits of a high SRL for tree performance; consequently, the highest net C gain is obtained by having long-lived, low-SRL roots to reduce C losses due to root turnover, and a relatively large fine-root mass to maintain sufficient resource acquisition. The interplay between SRL, fine-root mass and life span may explain why SRL and tree growth rates were neither correlated in previous work (McCormack et al., 2012), nor across our 10 study species. Instead, fine-root mass did nonlinearly correlate with the predicted net C gain, with species with relatively low and high fine-root mass having a low net C gain. Fine-root mass and life span together may prove relevant below-ground traits to understand and explain species' growth differences where SRL alone does not.

The second scenario also suggests a trade-off between fine-root mass and SRL, that is trees can obtain a relatively high net C gain through high SRL and low fine-root mass (leading to the highest net C gain), as well as by producing low-SRL roots and high fine-root mass. Our field data support this trade-off predicted by the model—species with high fine-root mass tended to have a low SRL and vice versa. Withington et al. (2006) measured fine-root mass and SRL of 11 temperate tree species in a common garden forest; reanalysing their data also yielded a negative relationship between fine-root mass and SRL (Pearson $r = -.65$, $df = 9$, $p = .03$), pointing towards a potential general trade-off between the two strategies to enhance root surface area. Our empirical data and model outcomes and those of others (Marks & Lechowicz, 2006; Withington et al., 2006) imply that different fine-root trait expressions may lead to similar performance in a shared environment that may be partly driven by species' identity.

Our study species seem to steer their fine-root mass and SRL towards a rather similar root length density but realized this through either an increase in SRL or fine-root mass (Figure 2b: the regression line runs in-between the green and red root length density lines). Withington et al. (2006) found c. 10-fold higher values for root length density across partly overlapping temperate tree species. This difference results from the 1.5 to 2.5 times lower SRL values we observed for the same species, and from the low fine-root biomass on our resource-rich study site (Cornelissen et al., 2012) compared to other temperate forests (Finér, Ohashi, Noguchi, & Hirano, 2011; Weemstra et al., 2017). Although not explicitly tested or shown here, additional model simulations demonstrate that on less fertile soils (i.e. lower values for S_b than in the current model) the maximum net C gain indeed corresponds to higher root length density. Although root length density is a more direct proxy of root surface area and therefore a main driver of nutrient uptake (Ros, de Deyn, Koopmans, Oenema, & van Groenigen, 2018; Ryser & Lambers, 1995), we found that the optimal C gain is achieved by a fourfold lower root length density in the second compared to the first scenario. For our model tree, this relatively low root length density may reduce resource uptake and hence C gain in the crown, but due to the low turnover rates of its fine roots, it can still achieve the highest C balance.

While for some species the simulated C gain nearly equalled C loss, tree-ring analyses on the same species and the same site suggest that the trees on this productive forest soil grow fast compared to trees of the same species on less fertile soils (Weemstra et al., 2013). The discrepancies between modelled and observed growth rates may be caused by the absence of data, for instance on species-specific root uptake parameters in our model. Furthermore, our study species generally vary in their leaf traits, such as SLA and leaf N content (Janse-Ten Klooster, Thomas, & Sterck, 2007; Withington et al., 2006), which further determine C gain and tree growth. As we aimed to specifically assess root trait effects on tree performance, this interspecific variation in above-ground traits was not accounted for in our model, but would affect the net C gain of our study species.

The trade-off between SRL and fine-root mass may not only be driven by the higher C costs of high-SRL roots, but also by forest soil

properties. For example, trees need thick, low-SRL roots to penetrate compact soils (Materechera, Dexter, & Alston, 1991) and may maintain sufficient root surface area by increased root biomass, or by increasing root diameter and reducing SRL to allow higher mycorrhizal colonization rates (Eissenstat, Kucharski, Zadworny, Adams, & Koide, 2015; Horan, Chilvers, & Lapeyrie, 1988). The soil biotic and abiotic environment plays, however, no explicit role in our model simulations; mycorrhizal fungi were not included and soil water and nutrients were set at constant values and never limiting for our model trees, while in reality, soil resource supply often varies strongly over time and space (Ettema & Wardle, 2002). Because incorporating more realistic, dynamic soil models adds complexity that was beyond the scope of our study, plant properties—predominantly root surface area (Equation 1), but also LAI as a driver of water uptake—are the key determinants of resource uptake in our model. In addition, we used N as our model nutrient but other resources may be limiting too that may influence the relative importance of SRL and fine-root mass for performance. For example, SRL may increase more strongly in response to phosphorus (P) compared to N limitations (Hill, Simpson, Moore, & Chapman, 2006). Our work thus highlights the importance of increasing fine-root mass and life span for tree growth when increases in SRL are constrained by biotic or abiotic environmental properties, although the relative importance of these traits for tree performance likely varies across (soil) environments.

4.2 | Underlying drivers of the trade-off between specific root length and fine-root mass

The observed trade-off between SRL and fine-root mass across our species may be related to their environmental preferences. Species that typically prefer moist sites (based on their Ellenberg moisture values, Table 1) had less fine-root mass (Pearson $r = -.81$, $df = 5$, $p = .03$) and tended to have higher SRL (Pearson $r = .70$, $df = 5$, $p = .08$) than species that prefer drier sites. These species—*A. glutinosa*, *F. excelsior* and *S. alba*—have been found to produce aerenchyma tissue in their roots (Kuzovkina, Knee, & Quigley, 2004; Rusch & Rennenberg, 1998; Thomas, 2016) to maintain soil resource uptake in waterlogged anaerobic or hypoxic conditions (Hodge et al., 2009), which would reduce their fine-root tissue density and increase their SRL. Although we did not measure anatomical root properties, nor hypoxia on our study site, such adaptations to wet sites may have driven these tree species to reduce their fine-root mass and associated C costs, while still maintaining sufficient fine-root surface area through a high SRL.

In fact, fine-root tissue density may have played a pivotal role in our species' expression of these two below-ground strategies. A high tissue density could explain both a low SRL (due to the large mass per unit root volume) and a high fine-root biomass for a given fine-root length; indeed, fine-root tissue density was negatively correlated with SRL (Pearson $r = -.74$, $df = 8$, $p = .01$) and positively (although not significantly) correlated with fine-root mass (Pearson $r = .54$, $df = 8$, $p = .11$) across our 10 species. Producing dense roots

would induce higher C costs but could also improve the tree's C balance, because a high tissue density may be associated with longer life span (Wahl & Ryser, 2000). It was beyond the scope of our study to identify the underlying drivers of variation in SRL; to explicitly test the effects of SRL and fine-root mass on tree performance, we kept root tissue density constant in our model simulations. Nonetheless, our field results underline the importance of further examining root tissue density and anatomy to better understand the role of fine-root mass in relation to fine-root morphology in species' resource strategies, performance and environmental preferences.

4.3 | Additional dimensions of a root economics spectrum

This study highlights the relevance of increasing fine-root mass for tree net C gain, but its relative importance only became apparent when considering the shorter life span of high-SRL roots. In a recent study, Li et al. (2019) also pointed to fine-root biomass as a potentially important additional dimension to the RES. Across an environmental gradient in a subalpine Chinese forest, they observed two orthogonal axes of tree-root variation. The first was associated with a trade-off between SRL and root N content and correlated mostly with soil fertility, but the second axis represented root system size, including fine-root mass and length density, which was associated with stem density. They argued that in a more developed forest with larger trees and more stems, trees invest in enhancing their root system (e.g. higher fine-root mass or length density) rather than in the production of acquisitive (e.g. high SRL) fine roots.

The observed and simulated trade-off between fine-root mass and SRL may explain why interspecific variation in SRL does not necessarily explain plant performance. To interpret interspecific variation in fine-root mass or fine-root length (density) in the context of plant performance, the plasticity of, and ontogenetic effects on these root traits need to be controlled for. This can be particularly challenging for forest trees, for which above- and below-ground biomass may be difficult to estimate and that can be subjected to highly heterogeneous (soil) environments. Here, we specifically selected our study site and trees (i.e. homogenous soils and even-aged trees) to minimize these confounding effects, and our model tests the effects of fine-root mass and SRL on plant performance while keeping other variables constant. Only few field studies have quantified fine-root mass (Valverde-Barrantes et al., 2007) and morphology (Withington et al., 2006) across species in similar environments, but did not measure tree growth, so that the relative contributions of species identity, plant size and site conditions to fine-root mass are still largely unknown. Our results suggest that understanding the role of fine roots in species' performance requires more information on interspecific variation in fine-root biomass and length density, and fine-root life span.

Mycorrhizal symbiosis presents a third and essential strategy to enhance below-ground surface area and soil resource uptake.

The absence of mycorrhizal fungi in our model could imply that our model underestimated the net C gain of our study species. Although mycorrhizal fungi can take up 10%–20% of the net primary productivity of trees (Hobbie & Hobbie, 2008; Smith & Read, 2008), they may strongly contribute to tree resource acquisition and improve tree performance. Conceptually, our model would allow the implementation of mycorrhizal hyphae in an analogous manner as the fine roots, that is with a certain mass density, specific hyphal length, respiration, uptake and turnover rate, but currently, there are many uncertainties regarding data on such traits and on their nutrient uptake benefits and C costs which complicates obtaining reliable estimates of their impacts on the whole-tree C balance. For instance, exchange rates of C and nutrients between tree and fungus are largely unknown and vary with soil nutrient availability (Näsholm et al., 2013). The construction costs of hyphae are assumed to be higher than those of roots (Eissenstat, 1992), but are hardly quantified, and differ between fungal species; species that produce long hyphae and rhizomorphs may require more C than species that produce no extraradical hyphae (Agerer, 2001; Bidartondo, Ek, Wallander, & Söderström, 2001). Addressing these uncertainties and implementing them into whole-tree performance models present a crucial next step as they likely represent a highly important dimension in explaining plant performance from root trait variation (Laliberté, 2016).

Currently, plant ecologists seek to identify the multiple dimensions of fine-root trait variation related to plant performance (Laliberté, 2016; Liese, Alings, & Meier, 2017; Valverde-Barrantes & Blackwood, 2016; Wang et al., 2018; Weemstra et al., 2016). This study demonstrates that fine-root mass and length density—in combination with fine-root life span—can represent an additional below-ground dimension to capture species' variation in performance. Identifying the roles of mycorrhizal symbiosis, the drivers of SRL and fine-root mass (e.g. the role of fine-root tissue density and anatomy), root life span and fine-root traits not generally included in the RES (e.g. fine-root branching, exudation) are important next steps. The resulting multidimensional root trait space may contribute to explaining the relationships between below-ground functioning and plant performance across species that cannot be explained by a single RES. The development of large-scale fine-root databases that include a larger variety of root traits (Iversen et al., 2017) parallel to the inclusion of roots in mechanistic tree models offers promising prospects.

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AUTHORS' CONTRIBUTIONS

M.W., F.S., L.M. and J.v.R. conceived the ideas and designed methodology; N.K. and M.W. collected the field data; F.S. and J.d.V. developed the model; M.W., N.K. and F.S. analysed the data; M.W., F.S. and J.v.R. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.931zcrjg3> (Weemstra et al., 2019) and to the fine-root ecological database (FRED; Iversen et al., 2017).

ORCID

Monique Weemstra <https://orcid.org/0000-0002-6994-2501>
 Natasa Kiorapostolou <https://orcid.org/0000-0001-9235-951X>
 Jasper van Ruijven <https://orcid.org/0000-0003-0003-2363>
 Liesje Mommer <https://orcid.org/0000-0002-3775-0716>
 Jorad de Vries <https://orcid.org/0000-0003-2656-2231>
 Frank Sterck <https://orcid.org/0000-0001-7559-6572>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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