RESEARCH ARTICLE

Tree growth increases through opposing above-ground and below-ground resource strategies

Monique Weemstra[1] (iD) | Jenny Zambrano[2] (iD) | David Allen[3] (iD) | María Natalia Umaña[1] (iD)

[1]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

[2]The School of Biological Sciences, Washington State University, Pullman, WA, USA

[3]Department of Biology, Middlebury College, Middlebury, VT, USA

Correspondence
Monique Weemstra
Email: moniqueweemstra@hotmail.com

Funding information
ForestGEO Early Career Research Grant

Handling Editor: Deepak Barua

Abstract

1. Studying functional traits and their relationships with tree growth has proved a powerful approach for understanding forest structure. These relationships are often expected to follow the classical resource economics perspective, where acquisitive leaves combined with acquisitive roots are expected to enhance resource uptake and tree growth. However, evidence for coordinated leaf and roots trait effects on growth is scarce and it remains poorly understood how these traits *together* determine tree growth. Here, we tested how leaf and root trait combinations explain tree growth.

2. We collected data on leaf and root traits of 10 common tree species, and on soil carbon (C) and nitrogen (N) concentrations in a temperate forest in Michigan, US. Tree growth was calculated as the stem diameter increment between three censuses measured across 13,000 trees and modelled as a function of different combinations of leaf and root traits and soil properties.

3. The two best models explaining tree growth included both specific leaf area (SLA), root diameter and soil C or N concentration, but their effects on growth were contingent on each other: thick roots were associated with high growth rates but *only* for trees with low SLA, and high SLA was related to fast growth but *only* for trees with thin roots. Soil C and N% negatively impacted the growth of trees with high SLA or high root diameter.

4. *Synthesis*. In this study, resource economics did not explain the relationships between leaf and root traits and tree growth rates. First, for trees with low or intermediate SLA, thick roots may be considered as acquisitive, as they were associated with faster tree growth. Second, trees did not coordinate their leaf and root traits according to plant resource economics but enhanced their growth rates by combining thick (acquisitive) roots with conservative (low SLA) leaves or *vice versa*. Our study indicates the need to re-evaluate the combined role of leaves and roots to unveil the interacting drivers of tree growth and, ultimately, of forest structure and suggests that different adaptive whole-tree phenotypes coexist.

KEYWORDS
ForestGEO network, functional traits, leaves, resource economics, roots, soil gradient, temperate forest, tree growth

1 | INTRODUCTION

Studying the variation in functional traits has helped plant ecologists to explain the mechanisms that drive plant community structure (Grime, 1977). One of the processes through which traits structure forest communities is through their relationship with tree growth and survival, and resource availability. For example, forests where plant resources are readily available are often dominated by tree species with a high specific leaf area (SLA) and leaf nitrogen (N) concentration that allow efficient light interception and high photosynthetic rates and, therefore, fast tree growth (Aerts & Chapin, 2000; Reich et al., 1998). However, despite these established relationships, functional traits often explain only a small or moderate proportion of the variation in tree growth, potentially because studies often focus on either root but mostly on leaf traits when studying tree growth (Paine et al., 2015; Poorter et al., 2008). Since tree growth depends on simultaneous above-ground (light and CO_2) and below-ground (water and nutrients) resource acquisition, we examined which (combinations of) leaf and root traits involved in resource uptake best explained variation in growth rates across more than 13,000 trees from 10 common deciduous tree species in a temperate forest.

Leaf trait effects on plant growth are mostly studied and interpreted from a resource economics perspective. The leaf economics spectrum demonstrates that at a global scale, species' leaf traits are correlated in trait syndromes that either facilitate fast resource (light) acquisition and, hence, high growth rates, or allow long-term resource conservation and, consequently, high survival rates (Reich et al., 2003; Wright et al., 2004). Tree root traits, in contrast, do not generally covary along a parallel *root* economics spectrum (Weemstra et al., 2016). For example, root trait expressions typically characterized as acquisitive, such as a high specific root length (SRL, root length/root dry mass), do not necessarily trade-off against conservative root traits, like high root tissue density (root mass/root volume; Bergmann et al., 2020; Kramer-Walter et al., 2016; Ma et al., 2018), nor do they always positively correlate with other presumably acquisitive traits, like root N concentration (Bergmann et al., 2020; Ma et al., 2018; Weemstra et al., 2016). Also, the classification of root diameter as an acquisitive or conservative trait is unclear. Traditionally, thick roots are categorized as a conservative trait (Mommer & Weemstra, 2012; Reich, 2014) because they presumably have low acquisition capacities owing to their relatively small surface area and slow growth and proliferation rates (Eissenstat, 1991, 1992), and high resource conservation rates due to their long life spans (Adams et al., 2013; Gu et al., 2011; Hansson et al., 2013; McCormack et al., 2012). In contrast, Withington et al. (2006) show that tree root diameter does not necessarily correlate with root life span, and recent studies suggest that a high root diameter can also be considered as an acquisitive trait (Bergmann et al., 2020; McCormack & Iversen, 2019) because thick roots provide more colonization space for mycorrhizal fungi, through which trees enhance resource uptake (Brundrett, 2002; Comas et al., 2012). In addition, the concept of a root economics spectrum assumes that having acquisitive root traits corresponds to fast tree growth. In line with

this, SRL positively correlated with the growth rate of seedlings of nine temperate tree species (Reich et al., 1998), and mature trees and seedlings of inherently fast-growing species had higher SRL than trees of closely related slow-growing species (Comas et al., 2002; Comas & Eissenstat, 2004). In contrast, McCormack et al. (2012) found no correlations between tree growth (i.e. the diameter of a tree at 10 years of age) and several root traits, with the exception of root life span. Direct relationships between root traits and actual growth rates of mature trees have thus not been firmly established.

Although relationships between traits and tree growth are more consistent for leaves than roots, leaf traits often only explain a small proportion of the variation in tree growth; for instance, globally, SLA explained 3% of the variation in growth rate (Paine et al., 2015). The low predictive power of traits may result from examining the effects of only a single leaf trait (e.g. Gibert et al., 2016; Paine et al., 2015) or root trait (Comas et al., 2002; Comas & Eissenstat, 2004) because such univariate or single-organ trait relationships with growth do not account for the relationships *among* traits that may strongly influence plant growth or survival (Laughlin & Messier, 2015) and may be too simplistic to represent the functional integration of multiple traits at the whole-tree level (Marks & Lechowicz, 2006; Umaña et al., in press; Weemstra et al., 2020). Alternately, relationships between leaf and/or root traits individually may be contingent on specific environmental conditions and may not be useful for predicting growth in varying environmental conditions. For example, when water availability limits growth, trees can enhance their root biomass (Weemstra et al., 2017), and/or their SRL to enhance water uptake (Freschet & Roumet, 2017), and/or decrease their SLA to reduce water loss through evapotranspiration (Greenwood et al., 2017; Poorter et al., 2009). In this case, the tree water balance can be modulated by the synergistic effects of root and leaf traits so that different trait combinations may be adaptive in the same environment. These simultaneous trait adjustments should ultimately be reflected in the performance of trees such that combinations of leaf and root traits better explain tree growth than the traits of single organs.

The combined effects of leaf and root traits on tree growth should be particularly relevant across soil nutrient gradients. In the first place, nutrient availability directly drives variation in leaf and root traits; for example, both SLA and SRL have been found to increase with soil fertility (Ordoñez et al., 2009; Ostonen et al., 2007). Second, the effect of trait variation on tree growth depends on the resource environment: species with conservative traits perform better (i.e. have higher survival rates) in low-resource environments where they are not outcompeted by acquisitive, fast-growing species while having acquisitive traits is beneficial to growth only when resources are readily available (Aerts & Chapin, 2000). Quantifying trait variation and how this influences tree growth, therefore, requires consideration of soil nutrient availability.

The objective of this study is to improve our understanding of tree growth from underlying variation in leaf and root functional traits which ultimately enhances our knowledge of the functional processes that structure forest communities. To this end, we determine which, how and to what degree (combinations of) leaf and root

traits influence growth rates across 10 temperate tree species along a soil carbon (C) and N gradient. We expect that single leaf and/or root traits typically defined as 'acquisitive' (e.g. high SRL, SLA, leaf and root N%) do not consistently lead to faster growth because resource acquisition and tree growth can be enhanced through different synergistic trait combinations. We tested our expectation using growth data collected for more than 13,000 trees of 10 common deciduous, broadleaved species (Table 1) in a temperate forest in central Michigan, US, in three censuses between 2003 and 2014. Growth data were combined with species' leaf and root trait data and with data on soil N and C% collected on our study site to test which (combination) of these variables best explained the variation in growth rates across these trees.

2 | MATERIALS AND METHODS

2.1 | Study site and species

This study was carried out at the Big Woods Forest Dynamics Plot (hereafter, Big Woods) at the Edwin S. George Reserve (Pickney: 42°27′46.5″N, 84°00′21.9″W) which is part of the ForestGEO network. The studied forest is subjected to a warm-summer humid continental climate with monthly average temperatures ranging from −5.3℃ (January) to 21.4℃ (July), and a mean annual precipitation of 857 mm, measured between 1981 and 2010 (Arguez et al., 2010). The plot is hilly due to glacial scouring with moraine and basin topography and an esker running through the plot; its elevation ranges between 270 and 305 m above sea level (Allen et al., 2018). Soils at Big Woods are generally sandy loam, shallow and mineral (Allen et al., 2020). The dominant vegetation is black oak–white oak–hickory, where the canopy is dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.), and the sub- and mid-canopy strata are dominated by red maple (*Acer rubrum* L.), black cherry (*Prunus serotina* Ehrh.) and witch-hazel (*Hamamelis virginiana* L.; Allen et al., 2018, 2020).

During the 2014 census, 45 woody species were counted at the Big Woods plot. Here, we focused on 10 deciduous tree species (Table 1) common in the eastern USA and at Big Woods and that covered 44% of the total number of stems, and 71% of the basal area of all woody vegetation censused in 2014 at the Big Woods plot. Their basal area and abundance in this forest at the time of each census are presented in Table S1.

2.2 | Growth data

Each individual tree was tagged and identified to the species level in three censuses: 2003, 2007–2010 and 2014. The vast majority of trees measured between 2007 and 2010 were measured in 2008 so this census will here be referred to as the 2008 census (Allen et al., 2020). All dead and living tree and shrub stems ≥3.2 cm diameter at breast height (DBH) were recorded at each census and the DBH was measured for living trees. The 2003 and 2008 censuses were carried out in a 12-ha part of the current plot. Between 2008 and 2010, 11 ha of adjacent forest was added to Big Woods, and the resultant 23-ha plot was censused in 2014 (Allen et al., 2020). Trees within 20 m distance from the forest edge or main roads were excluded from the analyses to avoid edge effects on tree growth. The DBH of multiple stems of the same individual was summed so that each tree is represented once per census in our dataset. Ultimately, this resulted in a dataset consisting of 19,736 observations for 13,368 different individuals (the same trees were measured at different censuses) of our 10 study species across the three censuses. Relative growth rate (RGR) was then determined for each census interval and for each living tree as the DBH increment divided by the number of days between two consecutive censuses.

2.3 | Soil data

Soil data were collected in June 2019. In each of 23 subplots of 1 ha that covered Big Woods (Figure S1), four soil samples were collected from the top 10 cm of the soil at their northern, eastern, southern and western edges. Adjacent soil samples from two subplots (e.g. the eastern sample of one plot and the western sample of the adjacent plot on its right) were pooled as they could not be considered spatially independent. The resultant 92 soil samples were air-dried and sieved, and soil C and total N concentrations were determined using dry combustion (Stable Isotope Core Laboratory, Washington State University). We assigned the soil C and N concentration and soil C:N ratio values of the nearest soil sample to each tree in the census dataset based on the tree's coordinates in the plot.

2.4 | Leaf and root trait data

In June 2019, three fully expanded and sun-exposed leaves were collected for between 7 and 11 mature individual trees per species (Table 1); the number of individuals sampled per species depended on the abundance of trees per species. Since healthy, mature *Fraxinus americana* trees were scarce at Big Woods, we collected leaves for only four trees of this species. Leaves were scanned with a portable leaf area meter (LI-3100C; LICOR) and leaf area determined. Scanned leaves were weighed to determine their fresh weight and leaf dry weight was measured after oven-drying (48 hr at 64℃). From these leaf measurements, we calculated SLA (fresh leaf area/leaf dry weight) and leaf dry matter content (leaf dry weight/leaf fresh weight). Leaves were then ground, and their C and N concentrations were determined using elemental combustion (Stable Isotope Core Laboratory, Washington State University) and expressed as a percentage of the total mass.

Roots were collected from three to four individual trees per species. Roots were dug up from the top 15–20 cm of the soil and traced back to the base of the stem for species identification. Roots

TABLE 1 Study species, mycorrhizal association, and mean root and leaf traits (standard deviation between parentheses). MF, mycorrhizal fungal association: AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; N Growth, number of observations included in growth models (total = 19,736 observations across 10 species and three censuses), number of individuals between parentheses (total = 13,368 different trees measured repeatedly at different censuses); N Leaf, N Root, number of trees sampled per species for leaf trait and root trait measurements, respectively. SLA, specific leaf area (g/cm^2); LN, leaf nitrogen concentration (%); LDMC, leaf dry matter content (g/g); SRL, specific root length (m/g); RN, root nitrogen concentration (%); RD, root diameter (mm); RTD, root tissue density (g/cm^3)

Latin name	Common name	Family	MF	N growth	N leaf	N root	SLA	LN	LDMC	SRL	RN	RD	RTD
Acer rubrum L.	Red maple	Sapindaceae	AM[a]	7,231 (4,318)	9	3	81.17 (10.47)	1.97 (0.22)	0.41 (0.04)	12.86 (5.56)	0.79 (0.1)	0.45 (0.08)	0.54 (0.1)
Fraxinus americana L.	White ash	Oleaceae	AM[a]	17 (11)	4	4	129.04 (16.22)	2.78 (0.29)	0.31 (0.04)	22.19 (8.44)	1.13 (0.25)	0.43 (0.05)	0.34 (0.06)
Ostrya virginiana (Mill.) Koch	American hophornbeam	Betulaceae	EcM[a]	421 (231)	10	4	110.9 (17.75)	2.02 (0.13)	0.47 (0.03)	14.57 (5.07)	1.04 (0.08)	0.3 (0.05)	1.08 (0.25)
Prunus serotina Ehrh.	Black cherry	Rosaceae	AM[a]	8,025 (6,014)	10	3	85.09 (8.74)	2.06 (0.44)	0.4 (0.03)	12.03 (5.83)	1.04 (0.04)	0.39 (0.07)	0.79 (0.11)
Quercus alba L.	White oak	Fagaceae	EcM[a]	1,301 (866)	9	3	85.98 (7.54)	2.72 (0.29)	0.35 (0.02)	16.61 (3.48)	0.99 (0.08)	0.31 (0.04)	0.82 (0.1)
Quercus rubra L.	Red oak	Fagaceae	EcM[a]	161 (90)	11	3	83.35 (9.7)	2.28 (0.19)	0.37 (0.02)	8.99 (1.37)	0.8 (0.11)	0.37 (0.02)	1.04 (0.04)
Quercus velutina Lam.	Black oak	Fagaceae	EcM[a]	1,097 (785)	9	4	57.68 (5.93)	2.45 (0.2)	0.37 (0.03)	24.45 (8.9)	0.99 (0.08)	0.35 (0.04)	0.49 (0.25)
Sassafras albidum (Nutt.) Nees	Sassafras	Lauraceae	AM[b]	828 (529)	7	3	109.44 (16.12)	3.24 (0.28)	0.26 (0.01)	16.85 (3.67)	1.04 (0.36)	0.38 (0.03)	0.56 (0.2)
Tilia americana L.	American basswood	Malvaceae	EcM[a]	73 (40)	10	3	115.68 (16.98)	2.92 (0.2)	0.34 (0.03)	14.14 (4.67)	0.93 (0.14)	0.34 (0.05)	0.83 (0.07)
Ulmus americana L.	American elm	Ulmaceae	AM[a]	582 (484)	10	3	83.23 (13.46)	2.18 (0.33)	0.34 (0.05)	8.81 (0.86)	0.85 (0.06)	0.46 (0.03)	0.68 (0.07)

[a]Brundrett et al. (1990).

[b]Fine-Root Ecological Database (Iversen et al., 2018).

were cleaned and, immediately after collection, first- to third-order roots were scanned (EPSON STD 4800). Root scans were analysed with WinRhizo (version: Regular 2019; Regent Instruments), providing data on total root length, mean root diameter and total root volume assuming a cylindrical shape. Scanned roots were oven-dried (48 hr at 64℃), to obtain dry weight, and ground to determine their C and N concentrations using dry combustion (Stable Isotope Core Laboratory, Washington State University). We calculated SRL (total root length/root dry mass) and root tissue density (root dry mass/root volume); root mean diameter values were directly retrieved from WinRhizo.

Plant growth rates may depend on the mycorrhizal association of species, and species associating with arbuscular mycorrhizal fungi may have higher growth rates than species associating with ectomycorrhizal fungi (Cornelissen et al., 2001). To account for these potential effects, we obtained information on species' mycorrhizal associations (Table 1) from Brundrett et al. (1990), and the Fine-Root Ecology Database (Iversen et al., 2018).

2.5 | Statistical analyses

To test which traits and trait combinations influenced tree growth rates, we selected the following leaf and root traits based on their role in leaf and root resource strategies (Wright et al., 2004, Bergmann et al., 2020): SLA, leaf dry matter content, leaf N%, SRL, root diameter, root tissue density and root N%. We also tested interspecific correlations among traits, and whether traits differed between arbuscular and ectomycorrhizal tree species (Pearson's r).

We determined the drivers of tree growth using mixed-effects models with RGR as response variable. We included combinations of species' root and leaf traits (with a maximum of two traits to avoid overly complicated trait interactions that are difficult to interpret), soil C%, N% and C:N ratio, and their interactions as fixed explanatory variables. Tree DBH and census year at the time of measurement were included as fixed covariates to account for tree size-dependent variation and temporal variation, respectively, in RGR. Species' identity nested in species' mycorrhizal association (arbuscular or ectomycorrhizal) were included as intercept-specific random effects to account for inherent differences between species and mycorrhizal associations in RGR, and the 1-ha subplot was included as a random intercept to account for spatial autocorrelation. All variables were scaled by subtracting the overall mean from the individual observations and dividing this value by the overall standard deviation for each variable. Mixed-effect models were fitted using the 'lmer' function in the LME4 package (Bates et al., 2015) in R Statistical Software (R Core Team, 2021).

Growth models were run across 13,368 unique individuals that were measured at two or three censuses. Full models were defined as:

$$y_{tsp} = \beta_0 + \beta_1 \text{trait variable}_1 \times \beta_2 \text{trait variable}_2$$
$$\times \beta_3 \text{soil} + \beta_4 \text{DBH} + \beta_5 \text{Census} + \tau_{mf/s} + \tau_p, (1)$$

where y_{tsp} is the predicted growth rates (i.e. log(RGR + 1)) of each individual tree t of species s in subplot p; trait variable represents a given leaf or root trait; soil refers to a soil variable (i.e. soil C%, soil N% or soil C:N); DBH refers to log-transformed DBH of t and Census to the census year in which t was measured, $\tau_{mf/s}$ represents the species nested in mycorrhizal type, and τ_p the subplot of t as random intercepts; β_0 indicates the intercept; β_1–β_5 indicate the slope associated with a respective explanatory variable. In addition to the full models, we ran reduced models that included subsets of these fixed effects, as well as a null model that included only the fixed covariates and random intercepts.

We selected the best growth model based on the Akaike Information Criteria (AIC; Akaike, 1974) using maximum likelihood, and models whose AIC differed <2 were considered equally good. We determined the goodness-of-fit of the models by computing marginal R^2 (R_m^2) and conditional R^2 (R_c^2) using the 'r.squaredGLMM' function in the MuMIn package (Barton, 2019) in R Statistical Software (R Core Team, 2021). Marginal R^2 indicates the variance explained by all fixed factors in the model relative to the total variance explained by the model as a whole (i.e. the sum of the variance of the fixed factors, random factors and error term; Nakagawa & Schielzeth, 2013). Conditional R^2 is calculated as the sum of the variance of the fixed and both random factors divided by the total variance of the model (Nakagawa & Schielzeth, 2013). Mixed-model probability (p) values were obtained with the LMERTEST package (Kuznetsova et al., 2017). Confidence intervals around the predicted growth rates were estimated with parametric bootstrapping (1,000 iterations) using the BOOTPREDICTLME4 package (Duursma, 2021).

3 | RESULTS

3.1 | Soil properties

Throughout the Big Woods plot, soil C% and N% varied five times (soil C range: 1%–5%, mean: 1.9%; soil N range: 0.06%–0.29%, mean: 0.12%), and soil C:N ratio varied two times (range: 12–25, mean: 16; Figure S1a–c). Soil C and N% were positively correlated across soil samples collected throughout the forest plot (Figure S1d).

3.2 | Trait–growth relationships

Leaf and root trait expressions varied across species (Table 1; Figure S2). Among the 10 study species, significant correlations were observed between root N% and SRL (positive), and between leaf dry matter content and leaf N% (negative; Table S2). Traits did not differ significantly between arbuscular and ectomycorrhizal tree species, except for root diameter which was higher for the former than for the latter group (Table S3).

Relative growth rate among trees ranged from 0 to 1.98 mm mm^{-1} y^{-1} and was on average 0.23 mm mm^{-1} y^{-1}. Based on the AIC of all models, there were two best models explaining tree

growth (Table S4). The fixed variables in Model 1 (Table 2) included root diameter, SLA, soil C%, tree DBH and census year and explained 22% of the variation in tree growth (R^2_m); the fixed factors and random intercepts together explained 30% of the growth variation (R^2_c). Model 2 (Table 2) included root diameter, SLA, soil N%, tree DBH and census year which explained 21% of the variation in tree growth (R^2_m), and fixed and random factors together explained 29% of the variation in growth (R^2_c).

Model 1 showed a significant positive effect of SLA but not of root diameter on growth (Table 2). However, the significant, negative two-way interaction between root diameter and SLA indicates that this effect of SLA depended on and differed from the effects of root diameter (Figure 1a): for trees with thin roots, trees with high SLA had faster growth rates than trees with low SLA (compare e.g. the RGR of high-SLA trees to the RGR of low-SLA trees at the same low root diameter), but for trees with thick roots, growth was similar regardless of variation in SLA (the RGR of high-SLA trees and

of low-SLA trees is similar at high root diameter). Furthermore, this interaction implies that root diameter has an increasingly positive effect on growth as SLA decreases (Figure 1a: compare the slopes of the regression lines associated with variation in SLA). Soil C% had an overall negative impact on tree growth which also influenced trait effects on growth, as reflected by the significant, negative interactions between soil C% and root diameter, and between soil C% and SLA (Table 2). These interactions indicated that an increase in soil C% had a negative effect on the growth of trees with thick roots (Figure 1b) or with a high SLA (Figure 1c) but no or a marginal effect on the growth of trees with thin roots (Figure 1b) or with low SLA (Figure 1c).

Outcomes of Model 2 were partly similar to those of Model 1 (Table 2), due to the high correlations between soil N% and soil C% (Figure S1d). Model 2 showed a significant positive effect of SLA on tree growth, with a similar effect size (i.e. estimates) as Model 1 (Table 2). It also showed significant two-way interactions, with a negative interaction between root diameter and SLA (Figure S3a), a positive interaction between root diameter and soil N% (Figure S3b) and a negative interaction between SLA and soil N% (Figure S3c).

In both Model 1 and Model 2, RGR did not vary with tree size (DBH), but it was significantly higher in the first census interval (2003–2008) compared to the second census interval (2008–2014; Table 2).

TABLE 2 Model statistics for the two best growth models (i.e. with the lowest AIC; Table S4). RGR, relative growth rate; SLA, specific leaf area; Soil C, Soil N, soil carbon, soil nitrogen concentration, respectively; DBH, tree diameter at breast height; Estimate, fixed-variable estimate; p, probability value. Significant variables and corresponding estimates and p values are in bold ($\alpha = 0.05$). Negative interaction estimates indicate that the effects of the different variables on growth differ in direction. The full model is described in the Materials and Methods section

Fixed variable	Estimate	p
Model 1: RGR ~ Root diameter × SLA × Soil C + DBH + Census year		
Intercept	0.20	0.375
Root diameter	0.05	0.267
SLA	**0.02**	**0.007**
Soil C	**−0.01**	**0.048**
DBH	0.00	0.314
Year	**−0.03**	**0.000**
Root diameter × SLA	**−0.01**	**0.014**
Root diameter × Soil C	**−0.00**	**0.004**
SLA × Soil C	**−0.00**	**0.004**
Root diameter × SLA × Soil C	0.00	0.510
Model 2: RGR ~ Root diameter × SLA × Soil N + DBH + Census year		
Intercept	0.20	0.378
Root diameter	0.05	0.287
SLA	**0.02**	**0.007**
Soil N	−0.01	0.169
DBH	0.00	0.323
Year	**−0.03**	**0.000**
Root diameter × SLA	**−0.01**	**0.013**
Root diameter × Soil N	**−0.00**	**0.002**
SLA × Soil N	**−0.01**	**0.001**
Root diameter × SLA × Soil N	−0.00	0.236

4 | DISCUSSION

Since tree growth depends on the simultaneous use and uptake of above-ground and below-ground resources, combining above-ground and below-ground traits to predict growth is needed to advance our knowledge of the underlying processes that drive forest community structure and composition. We studied variation in tree growth by testing the interacting effects of multiple leaf and root traits and soil properties on growth. Root diameter, SLA and soil C% or N% were found to be the best predictors of variation in tree growth. In contrast to the classical plant resource economics framework, our study identified high root diameter as an acquisitive trait for trees with conservative (low- or intermediate-SLA) leaves as it had a positive effect on the growth of these trees. In turn, high SLA was associated with fast tree growth, which is in line with plant resource economics, but mostly for trees with thin roots. These results imply that trait expressions (such as high root diameter and high SLA) can be acquisitive for some trees, but not for others, as their effects on tree growth depend on the expression of other traits. Furthermore, the growth of trees with acquisitive leaves or roots was more sensitive to changes in soil C and N concentrations across the Big Woods plot than of trees with conservative traits. Our study provides new insights on how tree growth is the outcome of above-ground and below-ground trait combinations and interactions as well as soil properties that are not necessarily coordinated along the resource acquisitive–conservative trait spectrum.
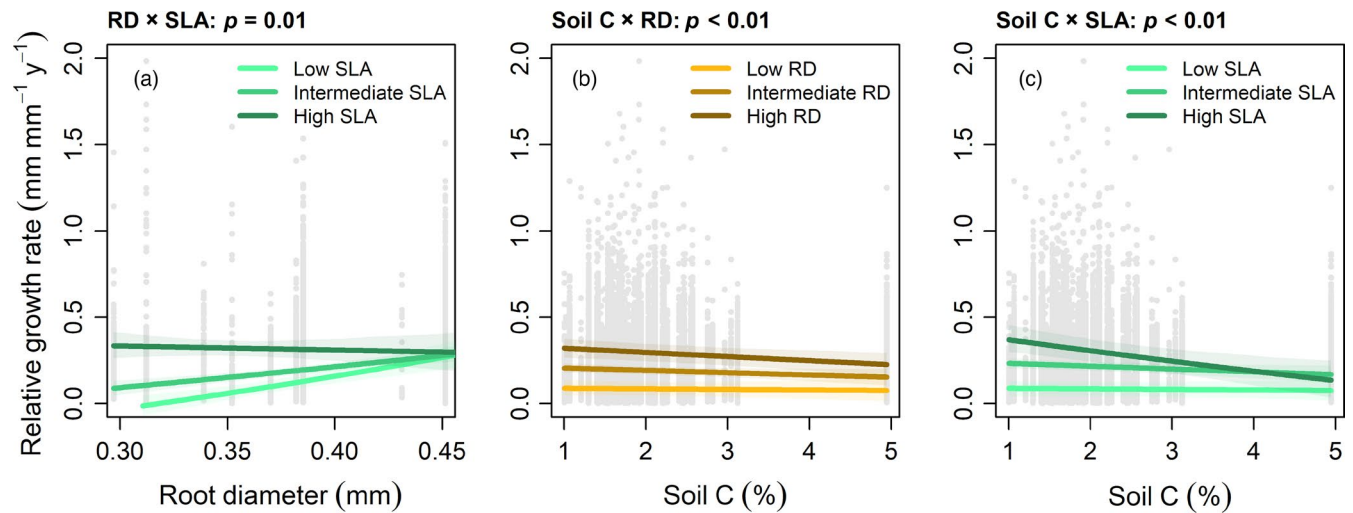
FIGURE 1 Observed (grey data points) and predicted (regression lines) tree growth by Model 1 (Table 2) for different values of (a) root diameter (RD) and specific leaf area (SLA), (b) root diameter and soil C% and (c) SLA and soil C%. Coloured regression lines mark model predictions under (a, c) low, intermediate, and high SLA (60, 85, 130 cm^2/g, respectively) and (b) low, intermediate and high root diameter (0.30, 0.38, 0.46 mm, respectively). *p* values represent the significance of the interaction between model variables obtained from Table 2. Regression line for low-SLA trees in (a) is truncated, because the combination of low SLA and root diameter values <0.31 mm was not observed in our dataset

4.1 | Interactions between leaf and root traits relate to tree growth rates

Together, the fixed factors of our best models—that is, root diameter, SLA and soil C% (Model 1) or soil N% (Model 2)—and the covariates (DBH and census year) explained just over 20% of the variation in growth rates across more than 13,000 trees. This is comparable to, or lower than observed in other models in forests. Martínez-Vilalta et al. (2010) found that single traits explained 17% (leaf N%) to 46% (maximum plant height) of the variation in growth across up to 70,000 trees of 44 species across Spain. However, in the same study, incorporating trait combinations and climatic data further increased the percentage of growth variation explained to 67%. Similarly, across 40–120 tropical tree species, models that included combinations of traits (i.e. wood density, seed mass and adult size) explained three times more of the variation in tree growth than models including single traits only (20%–60% depending on the traits versus on average 8% of single-trait models; Visser et al., 2016). In our study, traits (SLA and root diameter) and soil properties (C% or N%) explained a moderate part of the variation in growth compared to the aforementioned studies. It is likely that other traits—for example, wood density, which is an important predictor of tree growth variation (Poorter et al., 2008)—and other environmental variables—for instance, light and water availability—would further enhance the predictive power of our model. Still, our work and that of others stress the importance of using a multi-trait approach and incorporating environmental variables to better explain tree growth.

For leaves, the positive effect of SLA on growth (especially for thin-rooted trees; Figure 1a) is concordant with the concept of resource economics—with high-SLA leaves being more efficient at light interception which enhances tree growth (Cornelissen

et al., 1996; Poorter et al., 2009). For roots, however, the positive effect of root diameter on growth observed on trees with low SLA contrasts expectations of the classical resource economics framework, which assumes that thick roots are 'conservative' (Mommer & Weemstra, 2012; Reich, 2014) owing to their relatively small surface area, slow growth rates (Eissenstat, 1991, 1992) and long life spans (Adams et al., 2013; Gu et al., 2011; Hansson et al., 2013; McCormack et al., 2012). Other studies, however, indicate that thick roots may also be acquisitive, since they provide a larger colonization space for (arbuscular) mycorrhizal fungi (Brundrett, 2002; Comas et al., 2012), and are associated with higher mycorrhizal hyphal length for both ectomycorrhizal (Chen et al., 2018) and arbuscular mycorrhizal tree species (Eissenstat et al., 2015), through which trees can enhance soil resource uptake, and hence, their growth rates. Mycorrhizal associations may thus partly explain why at Big Woods, thick roots were associated with faster tree growth, but it remains unclear why they presumably contribute to the growth of trees with low or intermediate SLA, but not with high SLA. Our study indicates that linking root traits to actual measures of tree growth can further reveal their actual functionality in terms of plant performance but also suggests that not only root and leaf traits should be combined but also the traits of their fungal partners as well.

At the same time, we stress that the positive effects of root diameter on tree growth were contingent on SLA. Specifically, tree growth rates were enhanced through combinations of conservative (low-SLA) leaves and potentially acquisitive (thick) roots, *or* of acquisitive (high-SLA) leaves and less acquisitive (thin) roots, rather than through coordinated leaf and root traits. This is further underwritten by the lack of leaf and root trait correlations across species. If similar leaf and root traits were associated with above-ground and below-ground resource uptake and would be coordinated at

the whole-plant level, then leaf and root N%, SLA and SRL, or leaf dry matter content and root tissue density would correlate among species; however, we found no significant relationships between any leaf and root traits (Table S2). The uncoupling of leaf and root traits that contributed to tree growth rates in this study points towards the existence of multiple adaptive (i.e. improving growth) phenotypic designs (*cf*. Marks & Lechowicz, 2006). Our study however covers a relatively small number of temperate broadleaved tree species growing in the same forest plot, so it remains to be tested whether the same above-ground and below-ground trait combinations also enhance the growth of trees in other systems or for other species. Still, our results suggest that different whole-plant phenotypes coexist at a small spatial scale, and that at least locally, leaf and root traits have no coordinated effects on tree growth as assumed by traditional resource economics.

4.2 | Trait effects on growth are contingent on soil properties

Overall, soil C% had a negative effect on tree growth. This is in line with the assumption that soils with higher C% have greater accumulation of organic matter, reflecting slower litter decomposition and lower nutrient availability, which could, in turn, contribute to slower growth rates. Across the Big Woods plot, soil C% was positively correlated to soil N% which contrasts the assumption of lower nutrient availability; however, since we measured total and not available N, it is possible that the higher N levels that we observed on soils with higher C% were stored inside soil organic matter that is not readily available to plants.

We found that increases in soil C and N% reduced the growth of species with high SLA or with thick roots but had only minor effects on the growth of trees with low SLA or low root diameter (Figure 1b, c). According to plant resource economics, a high SLA is beneficial to growth only when resources are readily available (Aerts & Chapin, 2000) because fast C gain requires rapid resource supply. As resource availability decreases, acquisitive leaves may become a disadvantage because their short life spans incur high plant resource losses while resource-uptake rates remain low. Concordant with our results, trees with high SLA may thus be more sensitive to increases in soil C%, and corresponding decreases in nutrient availability than trees with low SLA (Grime, 1977; Reich et al., 2003). Like above-ground patterns, trees with thick, long-lived roots are expected to be less susceptible to adverse environmental variation than trees with thin, short-lived roots, but here, we observed the reverse. The mechanisms behind the relationships between traits, soil fertility and tree growth are less evident for roots than leaves, potentially because the trade-off between resource acquisition and conservation is less straightforward for root diameter than for SLA. Thick, mycorrhized and long-lived roots may be simultaneously more acquisitive and more conservative than thin roots as also hypothesized by Kong et al. (2017) so that their impacts on tree growth along environmental gradients become less predictable. Additional information

on mycorrhizal colonization rates or hyphal traits (as proxies for the resource uptake capacity of thick vs. thin roots) and root life span (as a proxy of resource conservation) is needed for a more mechanistic test of how trade-offs between these (mycorrhizal) root properties determine the growth of trees.

4.3 | Consequences of considering root and leaf trait interactions for understanding tree growth

Our study first highlights that root traits, like root diameter, may not fit the resource economics spectrum as leaf traits do. First, thick, low-SLA leaves are generally considered to be conservative (Reich et al., 1997), whereas thick roots were here associated with fast growth and may thus be acquisitive, at least for trees with low to intermediate SLA, and potentially in interaction with mycorrhizal fungi. Second, the trade-off between resource acquisition and conservation of root traits did not explain tree growth responses to soil nutrient availability. Recent studies have called for a new, multidimensional trait space that accommodates these different belowground strategies (Bergmann et al., 2020; Kramer-Walter et al., 2016; Weemstra et al., 2016); this study shows the consequences of such a new framework in the context of tree growth, and, as such, provides new insights in the functionality of (mycorrhizal) root traits.

Second, this work demonstrates that tree growth is not necessarily enhanced by root and leaf trait coordination along the resource acquisition–conservation continuum. These above-ground–below-ground trait modulations of growth imply that growth rates cannot necessarily be deduced from a single trait: additional traits may alter the relationships among traits, between a single trait and growth rates, and between traits, tree growth and soil fertility (Arnold, 1983; Laughlin & Messier, 2015; Marks & Lechowicz, 2006). This argument contradicts the resource economics theory which postulates that leaf and root traits tightly covary in trait syndromes (Reich, 2014; Wright et al., 2004) that, in turn, correlate with plant demographic rates (Janse-Ten Klooster et al., 2007; Poorter et al., 2008). Instead, different leaf and root trait combinations—that do not necessarily covary unidirectionally in trait syndromes—reflecting different adaptive phenotypes can lead to enhanced individual plant growth and ultimately fitness (this study; Marks & Lechowicz, 2006) may predict species' distributions along environmental gradients (Chapin et al., 1987; Laughlin & Messier, 2015) and can explain species' responses to environmental change (Kleyer & Minden, 2015). Understanding how these interacting above-ground and below-ground traits affect tree growth contributes to grasping the mechanisms shaping forest structure.

CONFLICT OF INTEREST

Jenny Zambrano and María Natalia Umaña are both Associate Editors for Journal of Ecology, but took no part in the peer review and decision-making processes for this paper. The other authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.N.U. and J.Z. conceived the ideas and designed the methodology; D.A., M.N.U. and J.Z. collected the data; M.W. analysed the data; M.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13729.

DATA AVAILABILITY STATEMENT

Data are archived with the University of Michigan Library Repository. Census data: https://doi.org/10.7302/wx55-kt18 (Allen et al., 2019). Tree (leaf and root) trait and soil data: https://doi.org/10.7302/mn5x-7s97.

ORCID

Monique Weemstra (iD) https://orcid.org/0000-0002-6994-2501
Jenny Zambrano (iD) https://orcid.org/0000-0002-0122-9937
David Allen (iD) https://orcid.org/0000-0002-0712-9603
María Natalia Umaña (iD) https://orcid.org/0000-0001-5876-7720

REFERENCES

Adams, T. S., McCormack, M. L., & Eissenstat, D. M. (2013). Foraging strategies in trees of different root morphology: The role of root lifespan. *Tree Physiology*, *33*(9), 940–948. https://doi.org/10.1093/treephys/tpt067

Aerts, R., & Chapin III, F. S. (2000). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research*, *30*, 1–67. https://doi.org/10.1016/S0065-2504(08)60016-1

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723. https://doi.org/10.1109/TAC.1974.1100705

Allen, D., Dick, C. W., Burnham, R. J., Perfecto, I., & Vandermeer, J. (2020). *The Michigan Big Woods research plot at the Edwin S. George Reserve, Pickney, MI, USA* (No. 207; Miscellaneous Publications). Museum of Zoology, University of Michigan. http://hdl.handle.net/2027.42/156251.

Allen, D., Dick, C. W., Strayer, E., Perfecto, I., & Vandermeer, J. (2018). Scale and strength of oak–mesophyte interactions in a transitional oak–hickory forest. *Canadian Journal of Forest Research*, *48*(11), 1366–1372. https://doi.org/10.1139/cjfr-2018-0131

Allen, D., Vandermeer, J., Dick, C., Perfecto, I., & Burnham, R. J. (2019). *Michigan Big Woods research plot data [Data set]*. University of Michigan - Deep Blue. https://doi.org/10.7302/wx55-kt18

Arguez, A., Durre, I., Applequist, S., Squires, M., Vose, R., Yin, X., & Bilotta, R. (2010). *NOAA's U.S. climate normals (1981–2010)*. NOAA National Centers for Environmental Information. https://doi.org/10.7289/V5PN93JP

Arnold, S. J. (1983). Morphology, performance and fitness. *American Zoologist*, *23*(2), 347–361. https://doi.org/10.1093/icb/23.2.347

Barton, K. (2019). *MuMIn: Multi-model inference* (R package version 1.43.6) [Computer software]. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., York, L. M., & Mommer, L. (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, *6*(27). https://doi.org/10.1126/sciadv.aba3756

Brundrett, M. C. (2002). Coevolution of roots and mycorrhizas of land plants. *New Phytologist*, *154*(2), 275–304. https://doi.org/10.1046/j.1469-8137.2002.00397.x

Brundrett, M., Murase, G., & Kendrick, B. (1990). Comparative anatomy of roots and mycorrhizae of common Ontario trees. *Canadian Journal of Botany*, *68*(3), 551–578. https://doi.org/10.1139/b90-076

Chapin, F. S., Bloom, A. J., Field, C. B., & Waring, R. H. (1987). Plant responses to multiple environmental factors. *BioScience*, *37*(1), 49–57. https://doi.org/10.2307/1310177

Chen, W., Eissenstat, D. M., & Koide, R. T. (2018). Root diameter predicts the extramatrical hyphal exploration distance of the ectomycorrhizal fungal community. *Ecosphere*, *9*(4). https://doi.org/10.1002/ecs2.2202

Comas, L., Bouma, T., & Eissenstat, D. (2002). Linking root traits to potential growth rate in six temperate tree species. *Oecologia*, *132*(1), 34–43. https://doi.org/10.1007/s00442-002-0922-8

Comas, L. H., & Eissenstat, D. M. (2004). Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology*, *18*(3), 388–397. https://doi.org/10.1111/j.0269-8463.2004.00835.x

Comas, L. H., Mueller, K. E., Taylor, L. L., Midford, P. E., Callahan, H. S., & Beerling, D. J. (2012). Evolutionary patterns and biogeochemical significance of angiosperm root traits. *International Journal of Plant Sciences*, *173*(6), 584–595. https://doi.org/10.1086/665823

Cornelissen, J., Aerts, R., Cerabolini, B., Werger, M., & van der Heijden, M. (2001). Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, *129*(4), 611–619. https://doi.org/10.1007/s004420100752

Cornelissen, J. H. C., Diez, P. C., & Hunt, R. (1996). Seedling growth, allocation and leaf attributes in a wide range of woody plant

species and types. *The Journal of Ecology*, *84*(5), 755. https://doi.org/10.2307/2261337

Duursma, R. (2021). *bootpredictlme4: Predict method for lme4 with bootstrap*. https://github.com/RemkoDuursma/bootpredictlme4

Eissenstat, D. M. (1991). On the relationship between specific root length and the rate of root proliferation: A field study using citrus rootstocks. *New Phytologist*, *118*(1), 63–68. https://doi.org/10.1111/j.1469-8137.1991.tb00565.x

Eissenstat, D. M. (1992). Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition*, *15*(6–7), 763–782. https://doi.org/10.1080/01904169209364361

Eissenstat, D. M., Kucharski, J. M., Zadworny, M., Adams, T. S., & Koide, R. T. (2015). Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist*, *208*(1), 114–124. https://doi.org/10.1111/nph.13451

Freschet, G. T., & Roumet, C. (2017). Sampling roots to capture plant and soil functions. *Functional Ecology*, *31*(8), 1506–1518. https://doi.org/10.1111/1365-2435.12883

Gibert, A., Gray, E. F., Westoby, M., Wright, I. J., & Falster, D. S. (2016). On the link between functional traits and growth rate: Meta-analysis shows effects change with plant size, as predicted. *Journal of Ecology*, *104*(5), 1488–1503. https://doi.org/10.1111/1365-2745.12594

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., Fensham, R., Laughlin, D. C., Kattge, J., Bönisch, G., Kraft, N. J. B., & Jump, A. S. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, *20*(4), 539–553. https://doi.org/10.1111/ele.12748

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, *111*(982), 1169–1194. https://doi.org/10.1086/283244

Gu, J., Yu, S., Sun, Y., Wang, Z., & Guo, D. (2011). Influence of root structure on root survivorship: An analysis of 18 tree species using a minirhizotron method. *Ecological Research*, *26*(4), 755–762. https://doi.org/10.1007/s11284-011-0833-4

Hansson, K., Helmisaari, H.-S., Sah, S. P., & Lange, H. (2013). Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. *Forest Ecology and Management*, *309*, 58–65. https://doi.org/10.1016/j.foreco.2013.01.022

Iversen, C. M., Powell, A. S., McCormack, M. L., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O., van Bodegom, P. M., & Violle, C. (2018). *Fine-Root Ecology Database (FRED): A global collection of root trait data with coincident site, vegetation, edaphic, and climatic data* (version 2) [Computer software]. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy. https://roots.ornl.gov/

Janse-Ten Klooster, S. H., Thomas, E. J. P., & Sterck*, F. J. (2007). Explaining interspecific differences in sapling growth and shade tolerance in temperate forests. *Journal of Ecology*, *95*(6), 1250–1260. https://doi.org/10.1111/j.1365-2745.2007.01299.x

Kleyer, M., & Minden, V. (2015). Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic and Applied Ecology*, *16*(1), 1–9. https://doi.org/10.1016/j.baae.2014.11.002

Kong, D., Wang, J., Zeng, H., Liu, M., Miao, Y., Wu, H., & Kardol, P. (2017). The nutrient absorption–transportation hypothesis: Optimizing structural traits in absorptive roots. *New Phytologist*, *213*(4), 1569–1572. https://doi.org/10.1111/nph.14344

Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., & Laughlin, D. C. (2016). Root traits are multidimensional: Specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, *104*(5), 1299–1310. https://doi.org/10.1111/1365-2745.12562

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest PACKAGE: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13). https://doi.org/10.18637/jss.v082.i13

Laughlin, D. C., & Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution*, *30*(8), 10. https://doi.org/10.1016/j.tree.2015.06.003

Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R. D., Eissenstat, D. M., McCormack, M. L., & Hedin, L. O. (2018). Evolutionary history resolves global organization of root functional traits. *Nature*, *555*(7694), 94–97. https://doi.org/10.1038/nature25783

Marks, C. O., & Lechowicz, M. J. (2006). Alternative designs and the evolution of functional diversity. *The American Naturalist*, *167*(1), 55–66. https://doi.org/10.1086/498276

Martínez-Vilalta, J., Mencuccini, M., Vayreda, J., & Retana, J. (2010). Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species: Determinants of demographic rates across species. *Journal of Ecology*, *98*(6), 1462–1475. https://doi.org/10.1111/j.1365-2745.2010.01718.x

McCormack, M. L., Adams, T. S., Smithwick, E. A. H., & Eissenstat, D. M. (2012). Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist*, *195*(4), 823–831. https://doi.org/10.1111/j.1469-8137.2012.04198.x

McCormack, M. L., & Iversen, C. M. (2019). Physical and functional constraints on viable belowground acquisition strategies. *Frontiers in Plant Science*, *10*, 1215. https://doi.org/10.3389/fpls.2019.01215

Mommer, L., & Weemstra, M. (2012). The role of roots in the resource economics spectrum: Commentary. *New Phytologist*, *195*(4), 725–727. https://doi.org/10.1111/j.1469-8137.2012.04247.x

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Ordoñez, J. C., van Bodegom, P. M., Witte, J.-P.-M., Wright, I. J., Reich, P. B., & Aerts, R. (2009). A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, *18*(2), 137–149. https://doi.org/10.1111/j.1466-8238.2008.00441.x

Ostonen, I., Lohmus, K., Helmisaari, H.-S., Truu, J., & Meel, S. (2007). Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. *Tree Physiology*, *27*(11), 1627–1634. https://doi.org/10.1093/treephys/27.11.1627

Paine, C. E. T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H., Daïnou, K., de Gouvenain, R. C., Doucet, J.-L., Doust, S., Fine, P. V. A., Fortunel, C., Haase, J., Holl, K. D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., … Hector, A. (2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology*, *103*(4), 978–989. https://doi.org/10.1111/1365-2745.12401

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*(3), 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., Harms, K. E., Licona, J. C., Martínez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Peña-Claros, M., Webb, C. O., & Wright, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, *89*(7), 1908–1920. https://doi.org/10.1890/07-0207.1

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P. B., Tjoelker, M. G., Walters, M. B., Vanderklein, D. W., & Buschena, C. (1998). Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology*, *12*(3), 327–338. https://doi.org/10.1046/j.1365-2435.1998.00208.x

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(25), 13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*, *164*(S3), S143–S164. https://doi.org/10.1086/374368

Umaña, M., Swenson, N. G., Marchand, P., Cao, M., & Zhang, C. (in press). Relating leaf traits to seedling performance in a tropical forest: Building a hierarchical functional framework. *Ecology*. https://doi.org/10.1002/ecy.3385

Visser, M. D., Bruijning, M., Wright, S. J., Muller-Landau, H. C., Jongejans, E., Comita, L. S., & Kroon, H. (2016). Functional traits as predictors of vital rates across the life cycle of tropical trees. *Functional Ecology*, *30*(2), 168–180. https://doi.org/10.1111/1365-2435.12621

Weemstra, M., Kiorapostolou, N., Ruijven, J., Mommer, L., Vries, J., & Sterck, F. (2020). The role of fine-root mass, specific root length and life span in tree performance: A whole-tree exploration. *Functional Ecology*, *34*(3), 575–585. https://doi.org/10.1111/1365-2435.13520

Weemstra, M., Mommer, L., Visser, E. J. W., Ruijven, J., Kuyper, T. W., Mohren, G. M. J., & Sterck, F. J. (2016). Towards a multidimensional root trait framework: A tree root review. *New Phytologist*, *211*(4), 1159–1169. https://doi.org/10.1111/nph.14003

Weemstra, M., Sterck, F. J., Visser, E. J. W., Kuyper, T. W., Goudzwaard, L., & Mommer, L. (2017). Fine-root trait plasticity of beech (*Fagus sylvatica*) and spruce (*Picea abies*) forests on two contrasting soils. *Plant and Soil*, *415*(1–2), 175–188. https://doi.org/10.1007/s11104-016-3148-y

Withington, J. M., Reich, P. B., Oleksyn, J., & Eissenstat, D. M. (2006). Comparisons of structure and life span in roots and leaves among temperate trees. *Ecological Monographs*, *76*(3), 381–397. https://doi.org/10.1890/0012-9615(2006)076[0381:COSALS]2.0.CO;2

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

SUPPORTING INFORMATION

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