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**Tree growth increases through opposing above- and belowground resource strategies**

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**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

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26 roots trait effects on growth is scarce and it remains poorly understood how these traits *together*  
27 determine tree growth. Here, we tested how leaf and root trait combinations explain tree growth.

28 2. We collected data on leaf and root traits of ten common tree species, and on soil carbon (C) and  
29 nitrogen (N) concentrations in a temperate forest in Michigan, US. Tree growth was calculated as  
30 the stem diameter increment between three censuses measured across 13000 trees and modelled  
31 as a function of different combinations of leaf and root traits and soil properties.

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

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

45  
46 **Key words:** ForestGEO network; functional traits; leaves; resource economics; roots; soil gradient;  
47 temperate forest; tree growth

## 48 49 **Introduction**

50 Studying the variation in functional traits has helped plant ecologists to explain the mechanisms that drive  
51 plant community structure (Grime, 1977). One of the processes through which traits structure forest  
52 communities is through their relationship with tree growth and survival, and resource availability. For  
53 example, forests where plant resources are readily available are often dominated by tree species with a  
54 high specific leaf area (SLA) and leaf nitrogen (N) concentration that allow efficient light interception  
55 and high photosynthetic rates and, therefore, fast tree growth (Aerts & Chapin, 2000; Reich, Tjoelker,  
56 Walters, Vanderklein, & Buschena, 1998). However, despite these established relationships, functional  
57 traits often explain only a small or moderate proportion of the variation in tree growth, potentially  
58 because studies often focus on either root but mostly on leaf traits when studying tree growth (Paine et al.,  
59 2015; Poorter et al., 2008). Since tree growth depends on simultaneous above- (light, CO<sub>2</sub>) and

60 belowground (water, nutrients) resource acquisition, we examined which (combinations of) leaf and root  
61 traits involved in resource uptake best explained variation in growth rates across more than 13000 trees  
62 from ten common deciduous tree species in a temperate forest.

63 Leaf trait effects on plant growth are mostly studied and interpreted from a resource economics  
64 perspective. The leaf economics spectrum demonstrates that at a global scale, species' leaf traits are  
65 correlated in trait syndromes that either facilitate fast resource (light) acquisition and, hence, high growth  
66 rates, or allow long-term resource conservation and, consequently, high survival rates (Reich et al., 2003;  
67 Wright et al., 2004). Tree root traits in contrast, do not generally covary along a parallel *root* economics  
68 spectrum (Weemstra et al., 2016). For example, root trait expressions typically characterized as  
69 acquisitive, such as a high specific root length (SRL, root length / root dry mass), do not necessarily trade  
70 off against conservative root traits, like high root tissue density (root mass / root volume) (Bergmann et  
71 al., 2020; Kramer-Walter et al., 2016; Ma et al., 2018), nor do they always positively correlate with other  
72 presumably acquisitive traits, like root N concentration (Bergmann et al., 2020; Ma et al., 2018;  
73 Weemstra et al., 2016). Also, the classification of root diameter as an acquisitive or conservative trait is  
74 unclear. Traditionally, thick roots are categorized as a conservative trait (Mommer & Weemstra, 2012;  
75 Reich, 2014), because they presumably have low acquisition capacities owing to their relatively small  
76 surface area and slow growth and proliferation rates (Eissenstat, 1991, 1992), and high resource  
77 conservation rates due to their long lifespans (Adams et al., 2013; Gu et al., 2011; Hansson et al., 2013;  
78 McCormack et al., 2012). In contrast, Withington et al., (2006) show that tree root diameter does not  
79 necessarily correlate with root lifespan, and recent studies suggest that a high root diameter can also be  
80 considered as an acquisitive trait (Bergmann et al., 2020; McCormack & Iversen, 2019), because thick  
81 roots provide more colonization space for mycorrhizal fungi, through which trees enhance resource  
82 uptake (Brundrett, 2002; Comas et al., 2012). In addition, the concept of a root economics spectrum  
83 assumes that having acquisitive root traits corresponds to fast tree growth. In line with this, SRL  
84 positively correlated with the growth rate of seedlings of nine temperate tree species (Reich et al., 1998),  
85 and mature trees and seedlings of inherently fast-growing species had higher SRL than trees of closely  
86 related slow-growing species (Comas, Bouma, & Eissenstat, 2002; Comas & Eissenstat, 2004). In  
87 contrast, McCormack et al. (2012) found no correlations between tree growth (*i.e.*, the diameter of a tree  
88 at ten years of age) and several root traits, with the exception of root lifespan. Direct relationships  
89 between root traits and actual growth rates of mature trees have thus not been firmly established.

90 Although relationships between traits and tree growth are more consistent for leaves than roots,  
91 leaf traits often only explain a small proportion of the variation in tree growth; for instance, globally, SLA  
92 explained 3% of the variation in growth rate (Paine et al., 2015). The low predictive power of traits may  
93 result from examining the effects of only a single leaf trait (*e.g.*, Gibert et al., 2016; Paine et al., 2015) or

94 root trait (Comas et al., 2002; Comas & Eissenstat, 2004), because such univariate or single-organ trait  
95 relationships with growth do not account for the relationships *among* traits that may strongly influence  
96 plant growth or survival (Laughlin & Messier, 2015) and may be too simplistic to represent the functional  
97 integration of multiple traits at the whole-tree level (Marks & Lechowicz, 2006; Umaña et al., in press;  
98 Weemstra et al., 2020). Alternately, relationships between leaf and/or root traits individually may be  
99 contingent on specific environmental conditions and may not be useful for predicting growth in varying  
100 environmental conditions. For example, when water availability limits growth, trees can enhance their  
101 root biomass (Weemstra et al., 2017), and/or their SRL to enhance water uptake (Freschet & Roumet,  
102 2017), and/or decrease their SLA to reduce water loss through evapotranspiration (Greenwood et al.,  
103 2017; Poorter et al., 2009). In this case, the tree water balance can be modulated by the synergistic effects  
104 of root and leaf traits, so that different trait combinations may be adaptive in the same environment. These  
105 simultaneous trait adjustments should ultimately be reflected in the performance of trees, such that  
106 combinations of leaf and root traits better explain tree growth than the traits of single organs.

107         The combined effects of leaf and root traits on tree growth should be particularly relevant across  
108 soil nutrient gradients. In the first place, nutrient availability directly drives variation in leaf and root  
109 traits; for example, both SLA and SRL have been found to increase with soil fertility (Ordoñez et al.,  
110 2009; Ostonen, Lohmus, Helmisaari, Truu, & Meel, 2007). Secondly, the effect of trait variation on tree  
111 growth depends on the resource environment: species with conservative traits perform better (*i.e.*, have  
112 higher survival rates) in low-resource environments where they are not outcompeted by acquisitive, fast-  
113 growing species, while having acquisitive traits is beneficial to growth only when resources are readily  
114 available (Aerts & Chapin, 2000). Quantifying trait variation and how this influences tree growth,  
115 therefore, requires consideration of soil nutrient availability.

116         The objective of this study is to improve our understanding of tree growth from underlying  
117 variation in leaf and root functional traits which ultimately enhances our knowledge of the functional  
118 processes that structure forest communities. To this end, we determine which, how and to what degree  
119 (combinations of) leaf and root traits influence growth rates across ten temperate tree species along a soil  
120 carbon (C) and N gradient. We expect that single leaf and/or root traits typically defined as ‘acquisitive’  
121 (*e.g.*, high SRL, SLA, leaf, and root N%) do not consistently lead to faster growth, because resource  
122 acquisition and tree growth can be enhanced through different synergistic trait combinations. We tested  
123 our expectation using growth data collected for more than 13000 trees of ten common deciduous,  
124 broadleaved species (Table 1) in a temperate forest in central Michigan, US, in three censuses between  
125 2003 and 2014. Growth data were combined with species’ leaf and root trait data and with data on soil N  
126 and C % collected on our study site to test which (combination) of these variables best explained the  
127 variation in growth rates across these trees.

128

## 129 **Methods**

### 130 *Study site and species*

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

142 During the 2014 census, 45 woody species were counted at the Big Woods plot. Here, we focused  
143 on ten deciduous tree species (Table 1) common in the eastern USA and at Big Woods and that covered  
144 44 % of the total number of stems, and 71 % of the basal area of all woody vegetation censused in 2014 at  
145 the Big Woods plot. Their basal area and abundance in this forest at the time of each census are presented  
146 in Supplementary Table S1.

147

### 148 *Growth data*

149 Each individual tree was tagged and identified to the species level in three censuses: 2003, 2007 – 2010,  
150 and 2014. The vast majority of trees measured between 2007 and 2010 were measured in 2008 so this  
151 census will here be referred to as the 2008 census (Allen et al., 2020). All dead and living tree and shrub  
152 stems  $\geq 3.2$  cm diameter at breast height (DBH) were recorded at each census and the DBH was measured  
153 for living trees. The 2003 and 2008 censuses were carried out in a 12-ha part of the current plot. Between  
154 2008 and 2010, 11 ha of adjacent forest were added to Big Woods, and the resultant 23-ha plot was  
155 censused in 2014 (Allen et al., 2020). Trees within 20 m distance from the forest edge or main roads were  
156 excluded from the analyses to avoid edge effects on tree growth. The DBH of multiple stems of the same  
157 individual was summed so that each tree is represented once per census in our dataset. Ultimately, this  
158 resulted in a dataset consisting of 19736 observations for 13368 different individuals (the same trees were  
159 measured at different censuses) of our ten study species across the three censuses. Relative growth rate  
160 (RGR) was then determined for each census interval and for each living tree as the DBH increment  
161 divided by the number of days between two consecutive censuses.

162

163 *Soil data*

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

172

173 *Leaf and root trait data*

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

184 Roots were collected from three to four individual trees per species. Roots were dug up from the  
185 top 15 – 20 cm of the soil and traced back to the base of the stem for species identification. Roots were  
186 cleaned and, immediately after collection, first- to third-order roots were scanned (EPSON STD 4800,  
187 US). Root scans were analysed with WinRhizo (version: Regular 2019; Regent Instruments, Canada),  
188 providing data on total root length, mean root diameter and total root volume assuming a cylindrical  
189 shape. Scanned roots were oven-dried (48 h at 64° C), to obtain dry weight, and ground to determine their  
190 C and N concentrations using dry combustion (Stable Isotope Core Laboratory, Washington State  
191 University). We calculated SRL (total root length / root dry mass) and root tissue density (root dry mass /  
192 root volume); root mean diameter values were directly retrieved from WinRhizo.

193 Plant growth rates may depend on the mycorrhizal association of species, and species associating  
194 with arbuscular mycorrhizal fungi may have higher growth rates than species associating with  
195 ectomycorrhizal fungi (Cornelissen et al., 2001). To account for these potential effects, we obtained

196 information on species' mycorrhizal associations (Table 1) from Brundrett, Murase, & Kendrick (1990),  
197 and the Fine-Root Ecology Database (Iversen et al., 2018).

198

### 199 *Statistical analyses*

200 To test which traits and trait combinations influenced tree growth rates, we selected the following leaf and  
201 root traits based on their role in leaf and root resource strategies (Wright et al., 2004, Bergmann et al.,  
202 2020): SLA, leaf dry matter content, leaf N %, SRL, root diameter, root tissue density, root N %. We also  
203 tested interspecific correlations among traits, and whether traits differed between arbuscular and  
204 ectomycorrhizal tree species (Pearson's  $r$ ).

205 We determined the drivers of tree growth using mixed-effects models with RGR as response  
206 variable. We included combinations of species' root and leaf traits (with a maximum of two traits to avoid  
207 overly complicated trait interactions that are difficult to interpret), soil C %, N % and C:N ratio, and their  
208 interactions as fixed explanatory variables. Tree DBH and census year at the time of measurement were  
209 included as fixed covariates to account for tree size-dependent variation and temporal variation,  
210 respectively, in RGR. Species' identity nested in species' mycorrhizal association (arbuscular or  
211 ectomycorrhizal) were included as intercept-specific random effects to account for inherent differences  
212 between species and mycorrhizal associations in RGR, and the 1-ha subplot was included as a random  
213 intercept to account for spatial autocorrelation. All variables were scaled by subtracting the overall mean  
214 from the individual observations and dividing this value by the overall standard deviation for each  
215 variable. Mixed-effect models were fitted using the 'lmer' function in the 'lme4' package (Bates et al.,  
216 2015) in R Statistical Software (R Core Team, 2021).

217 Growth models were run across 13368 unique individuals that were measured at two or three  
218 censuses. Full models were defined as:

219

$$220 \quad y_{tsp} = \beta_0 + \beta_1 \text{trait variable}_1 \times \beta_2 \text{trait variable}_2 \times \beta_3 \text{soil} + \beta_4 \text{DBH} + \beta_5 \text{Census} + \tau_{mf/s} + \tau_p$$

221 equation (1)

222

223 where  $y_{tsp}$  is the predicted growth rates (*i.e.*,  $\log(\text{RGR}+1)$ ) of each individual tree  $t$  of species  $s$  in subplot  
224  $p$ ; *trait variable* represents a given leaf or root trait; *soil* refers to a soil variable (*i.e.*, soil C %, soil N %,  
225 or soil C:N); *DBH* refers to log-transformed DBH of  $t$  and *Census* to the census year in which  $t$  was  
226 measured,  $\tau_{mf/s}$  represents the species nested in mycorrhizal type, and  $\tau_p$  the subplot of  $t$  as random  
227 intercepts;  $\beta_0$  indicates the intercept;  $\beta_1 - \beta_5$  indicate the slope associated with a respective explanatory  
228 variable. In addition to the full models, we ran reduced models that included subsets of these fixed effects,  
229 as well as a null model that included only the fixed covariates and random intercepts.

230 We selected the best growth model based on the Akaike Information Criteria (AIC; Akaike,  
231 1974) using maximum likelihood, and models whose AIC differed  $< 2$  were considered equally good. We  
232 determined the goodness-of-fit of the models by computing marginal  $R^2$  ( $R^2_m$ ) and conditional  $R^2$  ( $R^2_c$ )  
233 using the 'r.squaredGLMM' function in the 'MuMIn' package (Barton, 2019) in R Statistical Software (R  
234 Core Team, 2021). Marginal  $R^2$  indicates the variance explained by all fixed factors in the model relative  
235 to the total variance explained by the model as a whole (*i.e.*, the sum of the variance of the fixed factors,  
236 random factors and error term) (Nakagawa & Schielzeth, 2013). Conditional  $R^2$  is calculated as the sum  
237 of the variance of the fixed and both random factors divided by the total variance of the model (Nakagawa  
238 & Schielzeth, 2013). Mixed-model probability ( $P$ ) values were obtained with the 'lmerTest' package  
239 (Kuznetsova et al., 2017). Confidence intervals around the predicted growth rates were estimated with  
240 parametric bootstrapping (1000 iterations) using the 'bootpredictlme4' package (Duursma, 2021).

241

## 242 **Results**

### 243 *Soil properties*

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

248

### 249 *Trait – growth relationships*

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

255 Relative growth rate among trees ranged from 0 to 1.98 mm mm<sup>-1</sup> y<sup>-1</sup> and was on average 0.23  
256 mm mm<sup>-1</sup> y<sup>-1</sup>. Based on the AIC of all models, there were two best models explaining tree growth  
257 (Supplementary Table S4). The fixed variables in *Model 1* (Table 2) included root diameter, SLA, soil C  
258 %, tree DBH and census year and explained 22 % of the variation in tree growth ( $R^2_m$ ); the fixed factors  
259 and random intercepts together explained 30 % of the growth variation ( $R^2_c$ ). *Model 2* (Table 2) included  
260 root diameter, SLA, soil N %, tree DBH and census year which explained 21 % of the variation in tree  
261 growth ( $R^2_m$ ), and fixed and random factors together explained 29 % of the variation in growth ( $R^2_c$ ).

262 *Model 1* showed a significant positive effect of SLA but not of root diameter on growth (Table 2).  
263 However, the significant, negative two-way interaction between root diameter and SLA indicates that this



264 effect of SLA depended on and differed from the effects of root diameter (Fig. 1a): for trees with thin  
265 roots, trees with high SLA had faster growth rates than trees with low SLA (compare *e.g.*, the RGR of  
266 high-SLA trees to the RGR of low SLA-trees at the same low root diameter), but for trees with thick  
267 roots, growth was similar regardless of variation in SLA (the RGR of high-SLA trees and of low SLA-  
268 trees is similar at high root diameter). Furthermore, this interaction implies that root diameter has an  
269 increasingly positive effect on growth as SLA decreases (Fig. 1a: compare the slopes of the regression  
270 lines associated with variation in SLA). Soil C % had an overall negative impact on tree growth which  
271 also influenced trait effects on growth, as reflected by the significant, negative interactions between soil C  
272 % and root diameter, and between soil C % and SLA (Table 2). These interactions indicated that an  
273 increase in soil C % had a negative effect on the growth of trees with thick roots (Fig. 1b) or with a high  
274 SLA (Fig. 1c) but no or a marginal effect on the growth of trees with thin roots (Fig. 1b) or with low SLA  
275 (Fig. 1c).

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

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

## 285 286 **Discussion**

287 Since tree growth depends on the simultaneous use and uptake of above- and belowground resources,  
288 combining above- and belowground traits to predict growth is needed to advance our knowledge of the  
289 underlying processes that drive forest community structure and composition. We studied variation in tree  
290 growth by testing the interacting effects of multiple leaf and root traits and soil properties on growth. Root  
291 diameter, SLA and soil C % or N % were found to be the best predictors of variation in tree growth. In  
292 contrast to the classical plant resource economics framework, our study identified high root diameter as  
293 an acquisitive trait for trees with conservative (low- or intermediate-SLA) leaves as it had a positive effect  
294 on the growth of these trees. In turn, high SLA was associated with fast tree growth, which is in line with  
295 plant resource economics, but mostly for trees with thin roots. These results imply that trait expressions  
296 (such as high root diameter and high SLA) can be acquisitive for some trees, but not for others, as their  
297 effects on tree growth depend on the expression of other traits. Furthermore, the growth of trees with

298 acquisitive leaves or roots was more sensitive to changes in soil C and N concentrations across the Big  
299 Woods plot than of trees with conservative traits. Our study provides new insights on how tree growth is  
300 the outcome of above- and belowground trait combinations and interactions as well as soil properties, that  
301 are not necessarily coordinated along the resource acquisitive – conservative trait spectrum.

302

### 303 *Interactions between leaf and root traits relate to tree growth rates*

304 Together, the fixed factors of our best models – *i.e.*, root diameter, SLA, and soil C % (*Model 1*) or soil N  
305 % (*Model 2*) – and the covariates (DBH and census year) explained just over 20 % of the variation in  
306 growth rates across more than 13000 trees. This is comparable to, or lower than observed in other models  
307 in forests. Martínez-Vilalta and collaborators (2010) found that single traits explained 17 % (leaf N %) to  
308 46 % (maximum plant height) of the variation in growth across up to 70000 trees of 44 species across  
309 Spain. However, in the same study, incorporating trait combinations and climatic data further increased  
310 the percentage of growth variation explained to 67 %. Similarly, across 40 – 120 tropical tree species,  
311 models that included combinations of traits (*i.e.*, wood density, seed mass and adult size) explained three  
312 times more of the variation in tree growth than models including single traits only (20 – 60 % depending  
313 on the traits versus on average 8% of single-trait models (Visser et al., 2016). In our study, traits (SLA  
314 and root diameter) and soil properties (C % or N %) explained a moderate part of the variation in growth  
315 compared to the aforementioned studies. It is likely that other traits – for example, wood density, which is  
316 an important predictor of tree growth variation (Poorter et al., 2008) – and other environmental variables  
317 – for instance, light and water availability – would further enhance the predictive power of our model.  
318 Still, our work and that of others stress the importance of using a multi-trait approach and incorporating  
319 environmental variables to better explain tree growth.

320 For leaves, the positive effect of SLA on growth (especially for thin-rooted trees; Fig. 1a) is  
321 concordant with the concept of resource economics – with high-SLA leaves being more efficient at light  
322 interception which enhances tree growth (Cornelissen et al., 1996; Poorter et al., 2009). For roots,  
323 however, the positive effect of root diameter on growth observed on trees with low SLA contrasts  
324 expectations of the classical resource economics framework, which assumes that thick roots are  
325 ‘conservative’ (Mommer & Weemstra, 2012; Reich, 2014) owing to their relatively small surface area,  
326 slow growth rates (Eissenstat, 1991, 1992), and long lifespans (Adams et al., 2013; Gu et al., 2011;  
327 Hansson et al., 2013; McCormack et al., 2012). Other studies, however, indicate that thick roots may also  
328 be acquisitive, since they provide a larger colonization space for (arbuscular) mycorrhizal fungi  
329 (Brundrett, 2002; Comas et al., 2012), and are associated with higher mycorrhizal hyphal length for both  
330 ectomycorrhizal (Chen et al., 2018) and arbuscular mycorrhizal tree species (Eissenstat et al., 2015),  
331 through which trees can enhance soil resource uptake, and hence, their growth rates. Mycorrhizal

332 associations may thus partly explain why at Big Woods, thick roots were associated with faster tree  
333 growth, but it remains unclear why they presumably contribute to the growth of trees with low- or  
334 intermediate SLA, but not with high SLA. Our study indicates that linking root traits to actual measures  
335 of tree growth can further reveal their actual functionality in terms of plant performance, but also suggests  
336 that not only root and leaf traits should be combined, but the traits of their fungal partners as well.

337         At the same time, we stress that the positive effects of root diameter on tree growth were  
338 contingent on SLA. Specifically, tree growth rates were enhanced through combinations of conservative  
339 (low-SLA) leaves and potentially acquisitive (thick) roots, *or* of acquisitive (high-SLA) leaves and less  
340 acquisitive (thin) roots, rather than through coordinated leaf and root traits. This is further underwritten by  
341 the lack of leaf and root trait correlations across species. If similar leaf and root traits were associated  
342 with above- and belowground resource uptake and would be coordinated at the whole-plant level, then  
343 leaf and root N %, SLA and SRL, or leaf dry matter content and root tissue density would correlate  
344 among species; however, we found no significant relationships between any leaf and root traits  
345 (Supplementary Table S2). The uncoupling of leaf and root traits that contributed to tree growth rates in  
346 this study, points towards the existence of multiple adaptive (*i.e.*, improving growth) phenotypic designs  
347 (*cf.* Marks & Lechowicz, 2006). Our study however covers a relatively small number of temperate  
348 broadleaved tree species growing in the same forest plot, so it remains to be tested whether the same  
349 above- and belowground trait combinations also enhance the growth of trees in other systems or for other  
350 species. Still, our results suggest that different whole-plant phenotypes coexist at a small spatial scale, and  
351 that at least locally, leaf and root traits have no coordinated effects on tree growth as assumed by  
352 traditional resource economics.

#### 353 354 *Trait effects on growth are contingent on soil properties*

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

362         We found that increases in soil C and N % reduced the growth of species with high SLA or with  
363 thick roots but had only minor effects on the growth of trees with low SLA or low root diameter (Fig. 1b,  
364 c). According to plant resource economics, a high SLA is beneficial to growth only when resources are  
365 readily available (Aerts & Chapin, 2000), because fast C gain requires rapid resource supply. As resource

366 availability decreases, acquisitive leaves may become a disadvantage because their short lifespans incur  
367 high plant resource losses while resource-uptake rates remain low. Concordant with our results, trees with  
368 high SLA may thus be more sensitive to increases in soil C %, and corresponding decreases in nutrient  
369 availability, than trees with low SLA (Grime, 1977; Reich et al., 2003). Like aboveground patterns, trees  
370 with thick, long-lived roots are expected to be less susceptible to adverse environmental variation than  
371 trees with thin, short-lived roots, but here, we observed the reverse. The mechanisms behind the  
372 relationships between traits, soil fertility and tree growth are less evident for roots than leaves, potentially  
373 because the trade-off between resource acquisition and conservation is less straightforward for root  
374 diameter than for SLA. Thick, mycorrhized and long-lived roots may be simultaneously more acquisitive  
375 and more conservative than thin roots as also hypothesized by Kong et al. (2017), so that their impacts on  
376 tree growth along environmental gradients become less predictable. Additional information on  
377 mycorrhizal colonization rates or hyphal traits (as proxies for the resource uptake capacity of thick versus  
378 thin roots) and root lifespan (as a proxy of resource conservation), is needed for a more mechanistic test  
379 of how trade-offs between these (mycorrhizal) root properties determine the growth of trees.

380

#### 381 *Consequences of considering root and leaf trait interactions for understanding tree growth*

382 Our study first highlights that root traits, like root diameter, may not fit the resource economics spectrum  
383 as leaf traits do. First, thick, low-SLA leaves are generally considered to be conservative (Reich et al.,  
384 1997), whereas thick roots were here associated with fast growth and may thus be acquisitive, at least for  
385 trees with low to intermediate SLA, and potentially in interaction with mycorrhizal fungi. Second, the  
386 trade-off between resource acquisition and conservation of root traits did not explain tree growth  
387 responses to soil nutrient availability. Recent studies have called for a new, multidimensional trait space  
388 that accommodates these different belowground strategies (Bergmann et al., 2020; Kramer-Walter et al.,  
389 2016; Weemstra et al., 2016); this study shows the consequences of such a new framework in the context  
390 of tree growth, and as such, provides new insights in the functionality of (mycorrhizal) root traits.

391 Second, this work demonstrates that tree growth is not necessarily enhanced by root and leaf trait  
392 coordination along the resource acquisition – conservation continuum. These above-belowground trait  
393 modulations of growth imply that growth rates cannot necessarily be deduced from a single trait:  
394 additional traits may alter the relationships among traits, between a single trait and growth rates, and  
395 between traits, tree growth and soil fertility (Arnold, 1983; Laughlin & Messier, 2015; Marks &  
396 Lechowicz, 2006). This argument contradicts the resource economics theory which postulates that leaf  
397 and root traits tightly covary in trait syndromes (Reich, 2014; Wright et al., 2004) that in turn, correlate  
398 with plant demographic rates (Janse-Ten Klooster et al., 2007; Poorter et al., 2008). Instead, different leaf  
399 and root trait combinations – that do not necessarily covary unidirectionally in trait syndromes –

400 reflecting different adaptive phenotypes can lead to enhanced individual plant growth and ultimately  
401 fitness (this study; Marks & Lechowicz, 2006), may predict species' distributions along environmental  
402 gradients (Chapin et al., 1987; Laughlin & Messier, 2015), and can explain species' responses to  
403 environmental change (Kleyer & Minden, 2015). Understanding how these interacting above- and  
404 belowground traits affect tree growth contributes to grasping the mechanisms shaping forest structure.

405

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421

#### 422 **Conflict of Interest**

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

426

#### 427 **Data availability**

428 Census and trait data are archived with the University of Michigan Library Repository:  
429 <https://doi.org/10.7302/wx55-kt18> (Allen et al., 2019).

430

#### 431 **Author contributions**

432 MNU and JZ conceived the ideas and designed methodology; DA, MNU and JZ collected the data; MW  
433 analysed the data; MW led the writing of the manuscript. All authors contributed critically to the drafts  
434 and gave final approval for publication.

435

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436 **Tables and Figures**

437

438 **Table 1.** Study species, mycorrhizal association, and mean root and leaf traits (standard deviation between parentheses). *MF*, mycorrhizal fungal association:  
 439 *AM*, arbuscular mycorrhizal; *EcM*, ectomycorrhizal; *N Growth*, number of observations included in growth models (total = 19736 observations across ten species  
 440 and three censuses), number of individuals between parentheses (total = 13368 different trees measured repeatedly at different censuses); *N Leaf*, *N Root*, number  
 441 of trees sampled per species for leaf trait and root trait measurements, respectively. *SLA*, specific leaf area ( $\text{g cm}^{-2}$ ); *LN*, leaf nitrogen concentration (%); *LDMC*,  
 442 leaf dry matter content ( $\text{g g}^{-1}$ ); *SRL*, specific root length ( $\text{m g}^{-1}$ ); *RN*, root nitrogen concentration (%); *RD*, root diameter (mm); *RTD*, root tissue density ( $\text{g cm}^{-3}$ ).

443

Latin name	Common name	Family	MF	N Growth	N Leaf	N Root	SLA	LN	LDMC	SRL	RN	RD	RTD
<i>Acer rubrum</i> L.	Red maple	Sapindaceae	AM <sup>1</sup>	7231 (4318)	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)
<i>Fraxinus americana</i> L.	White ash	Oleaceae	AM <sup>1</sup>	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)
<i>Ostrya virginiana</i> (Mill.) Koch	American hophornbeam	Betulaceae	EcM <sup>1</sup>	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)
<i>Prunus serotina</i> Ehrh.	Black cherry	Rosaceae	AM <sup>1</sup>	8025 (6014)	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)
<i>Quercus alba</i> L.	White oak	Fagaceae	EcM <sup>1</sup>	1301 (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)
<i>Quercus rubra</i> L.	Red oak	Fagaceae	EcM <sup>1</sup>	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)
<i>Quercus velutina</i> Lam.	Black oak	Fagaceae	EcM <sup>1</sup>	1097 (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)
<i>Sassafras albidum</i> (Nutt.) Nees	Sassafras	Lauraceae	AM <sup>2</sup>	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)

<i>Tilia americana</i> L.	American basswood	Malvaceae	EcM <sup>1</sup>	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)
<i>Ulmus americana</i> L.	American elm	Ulmaceae	AM <sup>1</sup>	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)

444 <sup>1</sup> Brundrett, Murase, & Kendrick (1990); <sup>2</sup> Fine-Root Ecological Database (Iversen et al. 2018)



445 **Table 2.** Model statistics for the two best growth models (*i.e.*, with the lowest AIC; Supplementary Table S4). *RGR*,  
 446 relative growth rate; *SLA*, specific leaf area; *Soil C*, *Soil N*, soil carbon, soil nitrogen concentration, respectively;  
 447 *DBH*, tree diameter at breast height; *Estimate*, fixed-variable estimate; *P*, probability value. Significant variables and  
 448 corresponding estimates and *P* values are in bold ( $\alpha = 0.05$ ). Negative interaction estimates indicates that the effects  
 449 of the different variables on growth differ in direction. The full model is described in the Methods section.  
 450

**Model 1:  $RGR \sim \text{Root diameter} * SLA * \text{Soil C} + DBH + \text{Census year}$**

Fixed variable	Estimate	<i>P</i>
Intercept	0.20	0.375
Root diameter	0.05	0.267
<b>SLA</b>	<b>0.02</b>	<b>0.007</b>
<b>Soil C</b>	<b>-0.01</b>	<b>0.048</b>
DBH	0.00	0.314
<b>Year</b>	<b>-0.03</b>	<b>0.000</b>
<b>Root diameter * SLA</b>	<b>-0.01</b>	<b>0.014</b>
<b>Root diameter * Soil C</b>	<b>-0.00</b>	<b>0.004</b>
<b>SLA * Soil C</b>	<b>-0.00</b>	<b>0.004</b>
Root diameter * SLA * Soil C	0.00	0.510

**Model 2:  $RGR \sim \text{Root diameter} * SLA * \text{Soil N} + DBH + \text{Census year}$**

Fixed variable	Estimate	<i>P</i>
Intercept	0.20	0.378
Root diameter	0.05	0.287
<b>SLA</b>	<b>0.02</b>	<b>0.007</b>
Soil N	-0.01	0.169
DBH	0.00	0.323
<b>Year</b>	<b>-0.03</b>	<b>0.000</b>
<b>Root diameter * SLA</b>	<b>-0.01</b>	<b>0.013</b>
<b>Root diameter * Soil N</b>	<b>-0.00</b>	<b>0.002</b>
<b>SLA * Soil N</b>	<b>-0.01</b>	<b>0.001</b>
Root diameter * SLA * Soil N	-0.00	0.236

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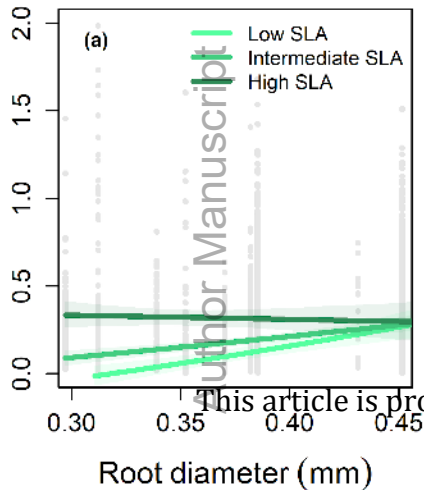
636

### 637 **Figure legend**

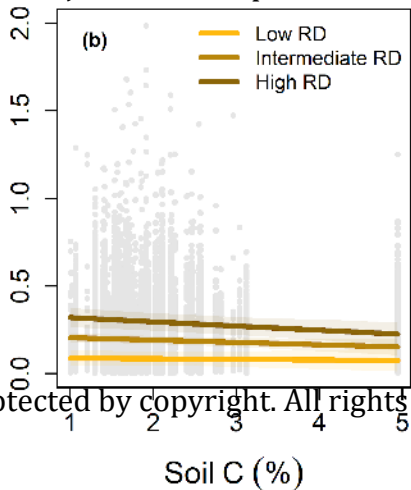
638 **Figure 1.** Observed (grey data points) and predicted (regression lines) tree growth by Model 1 (Table 2)  
639 for different values of (a) root diameter (RD) and specific leaf area (SLA), (b) root diameter and soil C %,  
640 and (c) SLA and soil C %. Coloured regression lines mark model predictions under (a, c) low,  
641 intermediate, and high SLA (60, 85, 130 cm<sup>2</sup>.g<sup>-1</sup>, respectively), and (b) low, intermediate, and high root  
642 diameter (0.30, 0.38, 0.46 mm, respectively). *P* values represent the significance of the interaction  
643 between model variables obtained from Table 2. Regression line for low-SLA trees in (a) is truncated,  
644 because the combination of low SLA and root diameter values < 0.31 mm was not observed in our data  
645 set.

Relative growth rate ( $\text{mm mm}^{-1} \text{y}^{-1}$ )

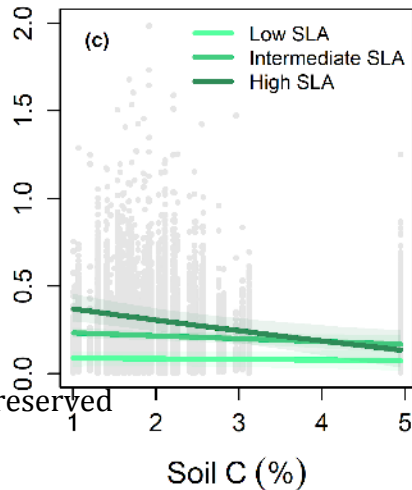
RD x SLA:  $P = 0.01$



Soil C x RD:  $P = 0.001$



Soil C x SLA:  $P < 0.01$



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