Soil nutrients rather than leaves affect biomass allocation to absorptive fine roots at individual tree level in Populus deltoides

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Soil nutrients rather than leaves affect biomass allocation to absorptive fine roots at individual tree level in *Populus deltoides*

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Abstract

Aims How soil nutrients affect absolute and relative production of major organs and the internal relationships between two resource-acquiring organs (absorptive fine roots (AFR) and leaves) at tree level remain unclear.

Methods To address these questions, we assessed soil nutrients, leaf, stem and branch (Stem-Br), coarse root (CR), transport fine root (TFR) and AFR biomass and production, leaf litterfall and AFR and TFR mortality of 12 trees in a young *Populus deltoides* plantation.

Results Biomass, production and mortality of AFRs were significantly related to those of TFRs but were independent of those of leaves, CRs and Stem-Brs. Total production had significant relationships with relative production of AFRs and TFRs. Spatial variations in soil nutrient gradients significantly altered the production of leaves, Stem-Brs and CRs but did not affect AFR and TFR production. By contrast, the relative production of AFRs and TFRs were significantly related to soil nutrients.

Conclusions AFR and TFR growth and death are tightly coupled at individual tree level. AFRs do not interact with leaves in a complimentary or inverse fashion in terms of biomass, production and mortality. Lower soil nutrients made *Populus deltoides* allocate proportionately more biomass to AFRs at the cost of leaf and Stem-Br production. Such a change significantly reduced whole-tree production. The significant relationships between AFRs and TFRs have great potential to accurately estimate C cycling through fine roots.

Keywords: biomass allocation · soil nutrients · tree organs · production · fine roots

Introduction

How trees partition biomass among leaves, stems and roots has long been a focus of ecological research. Due to great differences in lifespan and decomposition rates among these organs, changes in biomass allocation patterns could have a dramatic sequence for forest carbon (C) storage and C cycling (Fatichi et al. 2019; Rafique et al. 2016). Changes in soil nutrients can significantly affect tree growth and biomass allocation pattern (e.g. relative production of each organ), particularly the biomass allocated to fine roots (Kleczewski et al. 2012; Kobe et al. 2010). However, most studies testing soil nutrients effects are usually based on pot or field fertilization experiments (Kobe et al. 2010; Viera et al. 2017). The use of pots limits the soil volume that roots explore and the supplies of water and nutrients may not keep up with a plant's demand, thereby resulting in a strong nutrient or water limitation (Kobe et al. 2010). Fertilization could exaggerate tree responses to change in soil nutrients as fertilized plots have much greater soil nutrient load than natural plots (Kleczewski et al. 2012; Viera et al. 2017). Soil nutrients show great spatial variation in natural and plantation forests (Dai et al. 2018), but how such a spatial variation affects tree production and biomass allocation at individual tree level remains unclear. The individual trees are the basic unit of forest ecosystem, assessing intraspecies variation in production and biomass allocation pattern in response to changes in soil nutrients in the field is key to advancing our understanding of the interaction between soil and plants.

Tree biomass allocation pattern is usually estimated using measurements of organ biomass (Dybzinski et al. 2011; Poorter et al. 2012, 2015; Jevon and Lang 2022). Despite the standing biomass of coarse roots (CRs) and stems can generally reflect biomass allocation to these organs, the standing biomass of foliage and fine roots (diameter < 2mm) does not represent the amount of biomass allocated to them. Most trees shed leaves in growing season, and foliar litterfall in the growing season has been found to account for up to 30% of annual foliar production (Li et al.

2005). Fine roots experience multiple growth flushes and are short-lived (King et al. 2002, McCormack et al. 2014). As a result, fine root biomass shows great temporal variation and is not much smaller than fine root production (Li et al. 2020a, b). Further, fine roots have been treated as a single pool in biomass allocation studies (McMurtrie and Dewar 2013, Dong et al. 2016, Guo et al. 2023). The hierarchical fine root system is morphologically, chemically and functionally heterogeneous and can be further partitioned into absorptive fine roots (AFRs) and transport fine roots (TFRs) (McCormack et al. 2015; Kou et al. 2018). AFRs represent the most distal ones and function in the absorption of soil resources, while TFRs occur higher in the branching hierarchy and are involved in resource transportation and storage (McCormack et al. 2015). Field experiments showed that AFRs had more plastic responses to soil nutrients and water availability than TFRs did (Kou et al. 2018; Li et al. 2020b). Thus, separating fine roots by functional groups can not only improve estimation accuracy of biomass allocation to the root system, but can also enhance our understanding of the scaling rules governing biomass allocation among tree organs.

As the primary photosynthesis organ of trees, leaves play a dominant role in regulating the growth and biomass accumulation. Greater foliar biomass often leads to higher photosynthesis rate and therefore greater whole-tree production (Enquist and Niklas 2002, Fayolle et al. 2013, Rutishauser et al. 2013). AFRs are analogous to leaves because both are located at the terminal parts of plant vascular network and have similar structure and functions related to resource acquisition (e.g. low content of secondary woody tissue, short lifespan and physiologically more active) (Chen et al. 2019). The seasonal growth rates of loblolly pine fine roots and needles have been found to be synchronized (King et al. 2002), but this study did not include measurements of

85 fine root and needle biomass, production and mortality. So far, it is still unclear whether leaves
86 are tightly coordinated with AFRs in terms of biomass, production and mortality.

87 *Populus* species are fast growing and have been identified by the US Department of Energy as
88 a promising biofuel feedstock (Dou et al. 2017). A comprehensive study of *Populus* species,
89 production, biomass allocation pattern and litter input at individual tree level is crucial to
90 evaluating their bioenergy production and C sequestration capacity. In this study, we assessed
91 leaf, stem, CR, TFR, and AFR biomass and production, leaf litterfall, and AFR and TFR
92 mortality of 12 trees with the same age in a pure *Populus deltoides* plantation to answer the
93 following questions: 1) do greater leaf biomass, production and litterfall result in greater AFR
94 biomass, production and mortality at individual tree level? 2) how do variations in soil nutrients
95 affect absolute and relative production of major organs? 3) does change in biomass allocation to
96 certain organs significantly alter whole-tree production?

97

98 **Materials and methods**

99 Site description

100 The experiment was conducted at the research farm of University of Maryland Eastern Shore,
101 Somerset County, Maryland, USA (38° 10′ 47″ N, 75° 41′ 55″ W). Annual precipitation averages
102 1138 mm, while annual temperature averages 13℃. Relief on this farmland is flat, with a field
103 slope < 5º. Soil texture is classified as sandy loam. Total C and N contents in the 0-20 cm soil
104 layer are 1.1% and 0.08%, respectively. In the growing season of 2021, seedlings of *Populus*
105 *deltoides* were planted with a spacing of 1.0 m × 1.5 m. The seedlings were developed from
106 woody cuttings cultivated in plastic pots filled with crust humus, fiber and clay.

Tree mass measurement

In spring 2022, 6 trees were randomly selected for biomass measurements. Stem and branch biomass were assessed by directly harvesting aboveground woody components. Root mass was determined using the soil core method. For each tree, 5 soil cores (5.5 cm diameter × 40 cm length) were sampled. One soil core centered on the stump enclosed the whole stump and the surrounding area, while the rest soil cores were 20 cm, 30 cm, 40 cm, and 50 cm away from the stump, respectively. The collected soil cores were rinsed with clean tap water and then passed through a series of sieves (openings 2 mm to 1.0 mm) to isolate the roots. The roots were sorted into live absorptive roots (first to second order roots) (AFRs), live transport roots (third order to roots with a diameter ≤ 2 mm) (TFRs), live CRs (diameter > 2 mm) and dead AFRs and TFRs according to the protocols described in Li et al. (2013) and Li et al. (2020b). In the growing season of 2022, 12 communities, which were around 8 m to 50 m apart from each other and had quite different mean basal diameters and heights, were selected. Trees within each community had similar basal diameter and height and the one living in the center of the small community was chosen for the biomass and necromass measurements. The chosen trees were all enclosed with nylon nets (mesh size 4 cm × 4 cm) and fallen leaves in the nets were collected periodically until all leaves had dropped. The measurements were conducted when tree growth completely stopped. The chosen trees were cut down at the surface of the ground. The basal diameter and height of each tree were measured. Stem and branch were regarded as a whole and termed as Stem-Br. Root mass was measured using the same method as mentioned above except that the small trunk-centered soil core was replaced by a larger soil core (40 cm diameter and 40 cm length) to collect roots growing right around the stump and the basal stump as well. All biomass

compartments and dead AFRs and TFRs were air-dried to constant weight and then weighed. Subsamples were taken to determine air-dry to oven- dry (50 ℃) factor.

Root decomposition experiment

Fine root decomposition dynamics was measured using the litter bag method. The live AFRs and TFRs collected in spring 2022 were used as decomposing materials. Approximately 0.10 g of AFRs or TFRs were mixed with 50 g of soil and then put into a 0.1-mm polyethylene bag, 5 cm ×15 cm in size. In June, 5 AFR bags and 5 TFR bags were inserted at 15 cm depth in the soil in each community. The bags were retrieved 35, 65 and 110 days after the start of the experiment. On each sampling day, 1 to 2 bags were collected in each community per bag type. Soil particles adhering to the roots were carefully removed with clean water. Fine roots were oven-dried at 50 ℃ to constant weight and weighed.

Production and litter input calculation

For each chosen tree, CR and Stem-Br production was estimated as the difference in biomass measured between spring and winter of 2022, while leaf production equaled the accumulative leaf litterfall. We did not detect any dead stem and CRs. Therefore, the litter inputs through stem and CRs were assumed to be zero. AFR and TFR production and mortality were estimated using the improved soil coring model developed by Li and Lange (2015). The minirhizotron-based model was not employed because it requires sampling fine roots multiple times during growing season and installing minirhizotron tubes right beneath the seedlings (Li et al. 2020, 2023). Both affect the whole tree growth, particularly for the seedlings (Hendricks et al. 2006, Addo-Danso et al. 2016). The improved soil coring method could underestimate AFR estimates but cause minimal disturbance to the rooting environment and reflect root growth and death responses to

soil spatial heterogeneity (Li et al. 2023). This is a compromise as there is no way to optimize both.

AFR and TFR production and mortality are calculated using the following equations.

$$Pr = Br - Br0 + Mr \quad (1)$$

$$Mr = U\,T \quad (2)$$

$$U = K(Nr - N0)\frac{e^{-\frac{\lambda}{k}e^{-kT}}}{E_1\left(\frac{\lambda}{k}e^{-kT}\right) - E_1\left(\frac{\lambda}{k}\right)} \quad (3)$$

$$E_1(z) = \int_z^{\infty}\frac{e^{-x}}{x}dx \quad (4)$$

where Pr and Mr are fine root production and mortality from the start to the end of the growing season, respectively, B0 and N0 represent fine root biomass ($g \cdot m^{-1}$) and necromass ($g \cdot m^{-1}$) at the start of growing season, respectively, Br and Nr represent fine root biomass ($g \cdot m^{-1}$) and necromass ($g \cdot m^{-1}$) at the end of growing season, respectively, U is fine root morality rate ($g \cdot m^{-1} \cdot day^{-1}$), T is the length of the growing season (day) and K and λ are parameters.

K and λ can be calculated through Eq. 5.

$$y(t) = y0\, e^{\frac{\lambda}{k}(1 - e^{-kt})} \quad (5)$$

where y(t) is the mass remaining of fine roots in litterbags at time t (day) and y0 is the initial mass of fine roots in litterbags.

Soil nutrients

Five soil cores (5 cm diameter, 15 cm length) were collected around each sampled tree. Soils were passed through a 2 mm sieve to remove gravels and plant materials. Soils collected from

170 the same tree were mixed up and air dried to constant. Soil pH values, Cation Exchange Capacity
171 (CEC), base saturation, and C, N, P and K concentrations were assessed at Agricultural and
172 Environmental Service Lab, University of Georgia (http://aesl.ces.uga.edu) (SI Table 1).

173 **Data analysis**

174 The individual trees were treated as replicates (n = 12). One-way ANOVA analysis was used to
175 assess the differences in means of measured AFR, TFR, CR, Stem-Br and leaf parameters. Post-
176 hoc testing of means was conducted using Tukey's HSD. Pearson's correlation analysis (n = 12)
177 was used to determine the relationships among biomass, production and mortality of organs and
178 soil nutrient parameters. Natural log transformation was conducted before making regression
179 models. In all cases, significant effects were determined at 0.05 probability level. All data were
180 analyzed using the SPSS statistical software (version 17.0; IBM Corporation, Somers, NY 10,
181 589, USA).
182

183 **Results**

184 Biomass and production of different organs

185 CRs had the greatest standing biomass and therefore the biggest relative biomass to the total,
186 followed by Stem-Brs, leaves, TFRs, and AFRs (Fig. 1, 2). CRs had the biggest production and
187 consequently the highest relative production to the total, followed by Stem-Brs, leaves, AFRs
188 and TFRs (Fig. 1, 2).

189 The biomass allocation pattern differed greatly among individuals. The CVs (coefficient of
190 variance) of absolute and relative biomass and production varied over two folds among the five
191 organs (Fig. 3). CVs of absolute AFR and TFR biomass and production were twofold lower than

192 those of CRs, leaves and Stem-Brs, while CVs of relative AFR and TFR biomass and production
193 were two-fold higher than those of CRs, leaves and Stem-Brs (Fig. 3).

194 Intercorrelations between biomass and production of various organs and the total

195 Leaf, Stem-Br and CR biomass measurements were significantly correlated with each other;
196 the same pattern was found among leaf, Stem-Br and CR production measurements (Fig. 4).
197 Leaf, Stem-Br and CR biomass and production were independent of AFR and TFR biomass and
198 production, respectively, while AFR biomass and production were significantly related to TFR
199 biomass and production, respectively (Fig. 4). Total biomass was significantly related to leaf,
200 Stem-Br and CR biomass, but had no relationship with AFR and TFR biomass (Fig. 5). Similarly,
201 total production was significantly related to leaf, Stem-Br and CR production, but was
202 independent of AFR and TFR production (Fig. 5). Belowground litter input through AFR and
203 TFR mortality was significantly lower than aboveground leaf litterfall (Fig. 6). AFR mortality
204 was significantly higher than TFR mortality (Fig. 6). Leaf litterfall was not related to AFR and
205 TFR mortality and the sum of AFR and TFR mortality (Fig. 7), while there was a significant
206 positive relationship between AFR mortality and TFR mortality (Fig. 7). Total production was
207 significantly and negatively related to relative production of AFRs and TFRs, but was
208 independent of relative production of CRs, Stem-Brs and leaves (Fig. 8). Relative production of
209 AFRs had significant negative relationships with production of leaf and Stem-Brs (Fig. 9).

210 Relationships between soil nutrients and relative and absolute production of various organs

211 Leaf, Stem-Br, CR and total production showed significant positive relationships with soil
212 CEC, while AFR and TFR production was not related to any of these soil parameters studied
213 (Table 1). Relative production of AFRs and TFRs had significant negative relationships with soil

214 N concentration and CEC, but significant positive relationships with soil P concentration (Table
215 2). Relative production of Stem-Brs was significantly related to soil CEC and P concentration
216 (Table 2).

217 **DISCUSSION**

218 Biomass-based vs production-based allocation pattern

219 Most studies on biomass allocation pattern at various scales do not measure AFR, TFR and leaf
220 production, leading to great uncertainties (Kobe et al. 2010; Poorter and Sack 2012; Poorter et al.
221 2015; Drake et al. 2019; Liu et al. 2021; Jevon and Lang, 2022). In this poplar plantation, 11% of
222 leaves was lost, and around 100% of AFRs and 35% of TFRs died during the growing season,
223 highlighting the need for using production estimates to assess tree biomass allocation pattern. As
224 expected, quantifying the standing biomass alone significantly underestimated the amount of
225 biomass allocated to AFRs and TFRs, resulting in a different allocation pattern from that based
226 on the production measurements (Fig. 1), but it did not affect the estimate of relative leaf
227 contribution to the total, even though 11% of leaves was not taken into account in the biomass-
228 based allocation estimation. The reason was that AFR and TFR production values were greater
229 than their standing biomass values, which led to a greater total production estimate and therefore
230 reduced percent leaf production contribution. The disparity between the biomass-based and
231 production-based allocation pattern could widen over time because of the effects of ontogeny and
232 tree size (Mensah et al. 2016). Adult trees tend to invest more biomass to stems than seedlings
233 (Peichl and Arain 2007) and the increment in tree size decreases the ratio of annual AFR, TFR
234 and leaf production to total biomass.

235 Interaction between AFRs and leaves

The relationship between fine root and leaf biomass has been examined in many forests, but the results were not consistent, varying from a linear relationship between fine root and leaf biomass to no relationship (Santantonio et al. 1989, Vanninen and Mäkela 1999, Jha et al. 2010). Unfortunately, these studies were conducted at the stand level and therefore cannot be generalized to the individual tree level. As resource-acquiring organs, AFRs and leaves depend on each other for resources. Greater leaf production helps to produce more photosynthate for roots to grow. Similarly, higher AFR biomass or production enables a tree to obtain more soil nutrients for leaf growth. For this reason, a positive relationship between AFR and leaf biomass or production is expected. However, AFR biomass, production and mortality were not related to leaf biomass, production and litterfall, respectively (Fig. 4), indicating that the two resource-acquiring organs do not interact in a complementary or inverse fashion in terms of biomass, production and litter return. By contrast, AFR biomass, production and mortality were significantly related to TFR biomass, production and mortality, respectively, even though AFRs and TFRs are physically and functionally different (Fig. 4). Field observations on a loblolly pine plantation, a slash pine plantation and a forested wetland also showed that the growth and death dynamics of AFRs were closely related to those of TFRs (Kou et al. 2018; Li et al. 2020b; Li et al. 2023), suggesting that AFR and TFR growth and death are tightly coordinated at both individual tree and ecosystem levels.

Effects of soil nutrients on production and biomass allocation pattern

In this study, the difference in biomass allocation pattern among individuals could be mainly ascribed to soil nutrients rather than age or light availability because the seedlings grown in this plantation were developed by individuals of the same age and each sampled tree was in the center of the community. Previous reports showed that high soil nutrients promoted tree growth

(Kobe et al. 2010; Kleczewski et al. 2012; Viera et al. 2017). Consistent with these reports, production of CRs, Stem-brs and leaves were significantly and positively related to soil CEC in our study. By contrast, spatial variations in soil nutrients did not affect AFR and TFR production but their relative production (Table 1). Relative production of AFRs and TFRs had significant and negative relationships with soil N content and CEC (Table 2). This generally aligns with the prediction of optimal partitioning theory (OPT), in which plants allocate relatively more biomass to the organ that acquires the most limiting resources to optimize growth (Gedroc et al. 1996). Further analysis did not fully support OPT because relative production of AFRs was significantly and negatively related to total, leaf and Stem-Br production. The negative relationships indicate that tree growth is greatly constrained rather than optimized if poplar trees invest more biomass in AFRs to absorb limiting soil resources and the increase in relative production of AFRs is at the cost of production of leaves and Stem-Brs (e.g. production trade-off between AFRs and leaves and Stem-Brs). For these reasons, trees adjust biomass allocation patterns just to maximize their survival rather than to optimize wood or whole-tree production. Moreover, different soil nutrients had different and even contrasting effects on biomass allocation to the same organ and the effect of the same kind of soil nutrients on biomass allocation differed greatly among organs (Table 2). The change in biomass allocation pattern was not caused by single soil nutrient parameter but by the interaction of several soil nutrient parameters and the production trade-off between AFRs and leaves and Stem-Brs. Experimental manipulations of one or two soil nutrients could exaggerate their effects on biomass allocation and therefore reduce the counteractive effects of other soil nutrients (Kobe et al. 2010). The negative relationships between relative production of AFRs and TFRs and total production supports a statement that biomass allocation and whole-tree growth are interdependent (Robinson 2023). Further, our study showed that the interrelationship driven

by variation in soil nutrients was limited to AFRs and TFRs, while changes in biomass allocation to CRs, leaves and Stem-Brs did not alter whole-tree growth.

Relationships among main organs

The significant positive relationships between leaf biomass and biomass of CRs, Stem-Brs and the total were consistent with the previous reports that CR, Stem-Br and whole-tree growth was driven by leaf biomass (Fig. 2, Basuki et al. 2009; Xiang et al. 2011). Further, our study showed that greater leaf production also resulted in higher CR, Stem-Br and total production. AFR and TFR biomass were independent of not only leaf biomass but also biomass of CRs, Stem-Brs and the total. Such results did not provide full support for allometric partitioning theory, which states that biomass of all plant organs should scale predictably with overall plant size and be independent of environmental variation (Enquist and Niklas 2002). In Enquist and Niklas (2002), roots were regarded as a whole rather than divided into different functional groups. AFR and TFR biomass account for less than 15% of total biomass (Dong et al. 2016, Drake et al. 2019). Their effect on the correlations between biomass of roots and other organs are thus not evident. Since AFRs, TFRs and CRs are functionally different (McCormack et al. 2015) and AFR and TFR production represents over 30% of the total, they should be investigated separately in biomass allocation studies.

Causes for the independence of AFR production

The independence of AFR production to soil nutrients, CR, leaf, Stem-Br and total production may be caused by the following facts. First, the influences of mycorrhizal fungi have not been considered in biomass allocation pattern studies (Hartmann et al. 2020). Mycorrhizal fungi could consume up to 30% of total photosynthate (Allen and Kitajima 2010; Ekblad et al. 2016). In

return, they improve the uptake of water and nutrients by host trees. Trees may preferentially allocate carbohydrate to mycorrhizal fungi instead of AFRs when soil nutrients are scarce as mycorrhizal hyphae can forage over longer distances than AFRs in nutrient-void spaces and explore locations which are hard for AFRs to reach. In addition, mycorrhizal association increases the lifespan of AFRs (King et al. 2002). The influences exerted by mycorrhizal fungi could make AFR response to soil micro-environmental changes more specific and therefore greatly undermine the correlations of AFR production to soil nutrients and production of other organs. Second, plant roots release exudate into the rhizosphere to enhance microbial activity, thereby increasing soil nutrient availability (Cheng et al. 2014). Root exudates account for 5-10% of plant photosynthate (Farrar et al. 2003) and are regulated by soil environments (Zhang et al. 2016). The great spatial variations in soil nutrients lead to an evident difference in exudate production among individual trees and therefore may weaken the relationships among AFRs and other organs. Third, competition among trees has the potential to change biomass allocation to AFRs. Roots could respond to competitor-induced decreased resource availability by increasing specific root length and area or by growing new roots into unexplored zones (Schenk 2006). Due to the heterogeneous distribution of soil nutrients, the competition intensity differs greatly among individuals. AFRs are more sensitive to soil environment changes than CRs (McCormack et al. 2015; Kou et al. 2018). As a result, AFR production may not be proportional to the growth of other organs and soil nutrient gradients.

Conclusions

AFRs, TFRs and leaves are ephemeral. Thus, assessing standing biomass alone cannot give reliable estimates of biomass allocation to these organs, potentially resulting in misleading results. By measuring biomass and production of AFRs, TFRs, CRs, Stem-Brs and leaves of

individual trees, our study overcame this inherent weakness associated with previous biomass allocation studies. Spatial variations in soil nutrients at tree level significantly altered biomass allocation pattern and production of main organs in this poplar plantation, but different organs showed various responses. Soil nutrients did not affect AFR and TFR production but significantly altered their relative production. The whole-tree growth could be suppressed when relatively more biomass is allocated to AFRs. The change in biomass allocation to AFRs should not be considered as a strategic decision to optimize growth but the outcome of tree adaptive or acclimatory responses to changes in soil nutrients. AFRs and leaves do not interact in a complementary or inverse way in terms of biomass, production and mortality. The significant relationships between AFRs and TFRs in terms of biomass, production and mortality have a great implication for accurately quantifying fine root C cycling.

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Author contributions

Dr. Cumming and Xuefeng Li planned the project. Xuefeng Li and Nahom Ftwi conducted the tree biomass harvesting with the help from other undergraduates. Xuefeng Li analyzed the data and interpreted the results. Xuefeng Liwrote the manuscript, with feedback and approval from Janna Kleinsasser and Theophilus O. Isimikalu.

Conflict of interest statement

The authors declare no interest conflicts.

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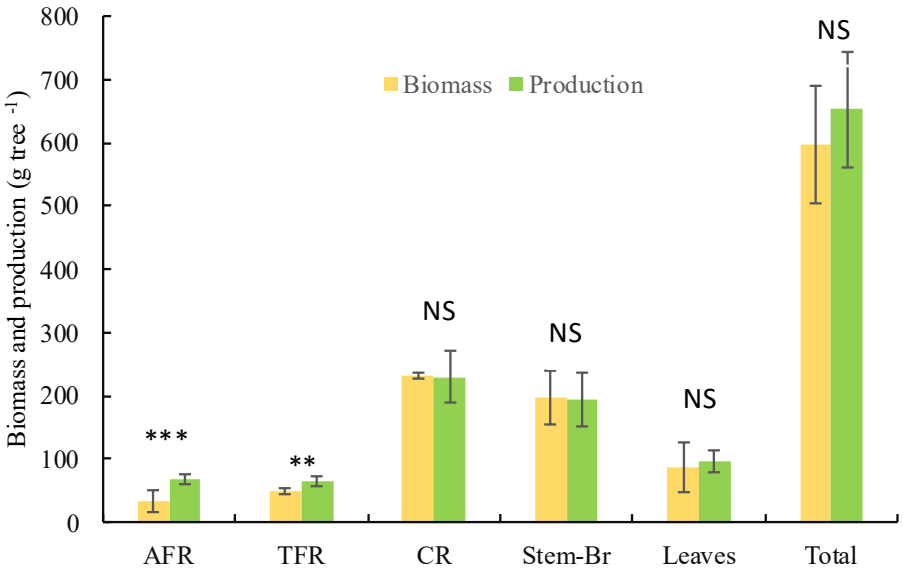


Fig. 1 Biomass and production of absorptive fine roots (AFR), transport fine roots (TFR), coarse roots (CR), combination of stems and branches (Stem-Br), leaves and the total (n = 12, ± SE; NS stands for not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ in mean values for each organ).

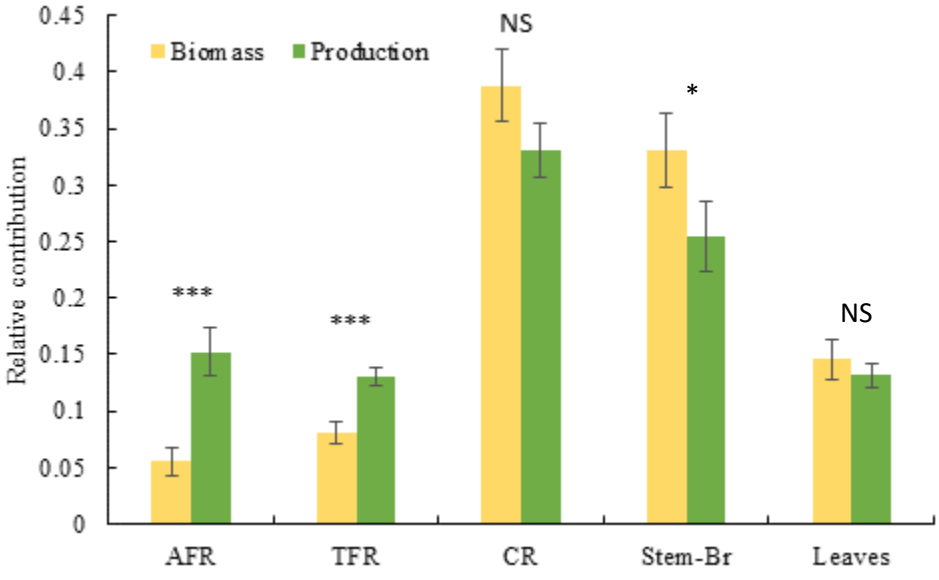
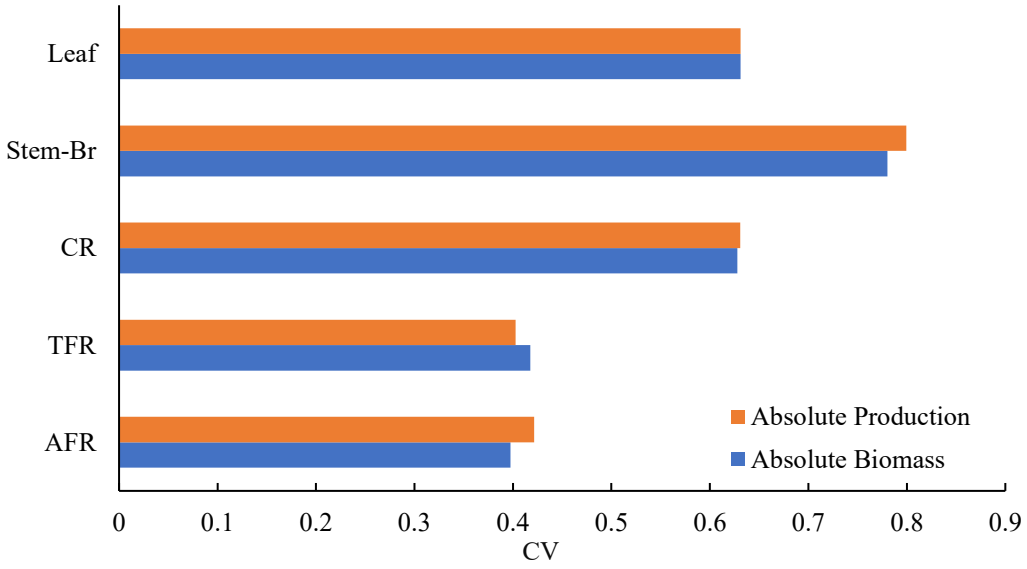
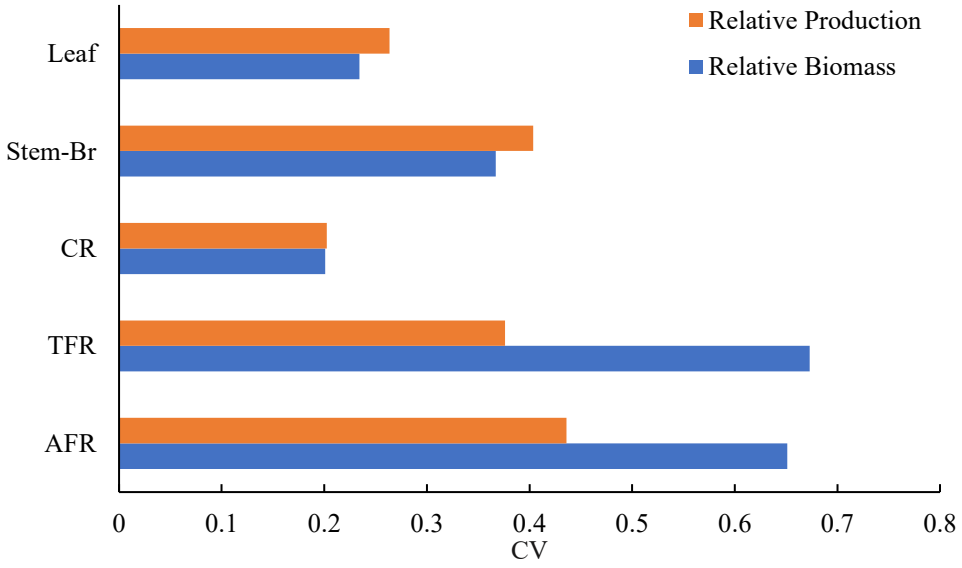


Fig. 2 Relative contributions of leaf, absorptive fine root (AFR), transport fine root (TFR), coarse root (CR), and stem and branch combination (Stem-Br) biomass and production to total biomass and production, respectively. (n = 12, ± SE; NS stands for not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ in mean values for each organ)





509 Fig. 3 Coefficients of variation (CV) of absolute and relative leaf, stem and branch combination (Stem-

510 Br), coarse root (CR), transport fine root (TFR), absorptive fine root (AFR) biomass and production

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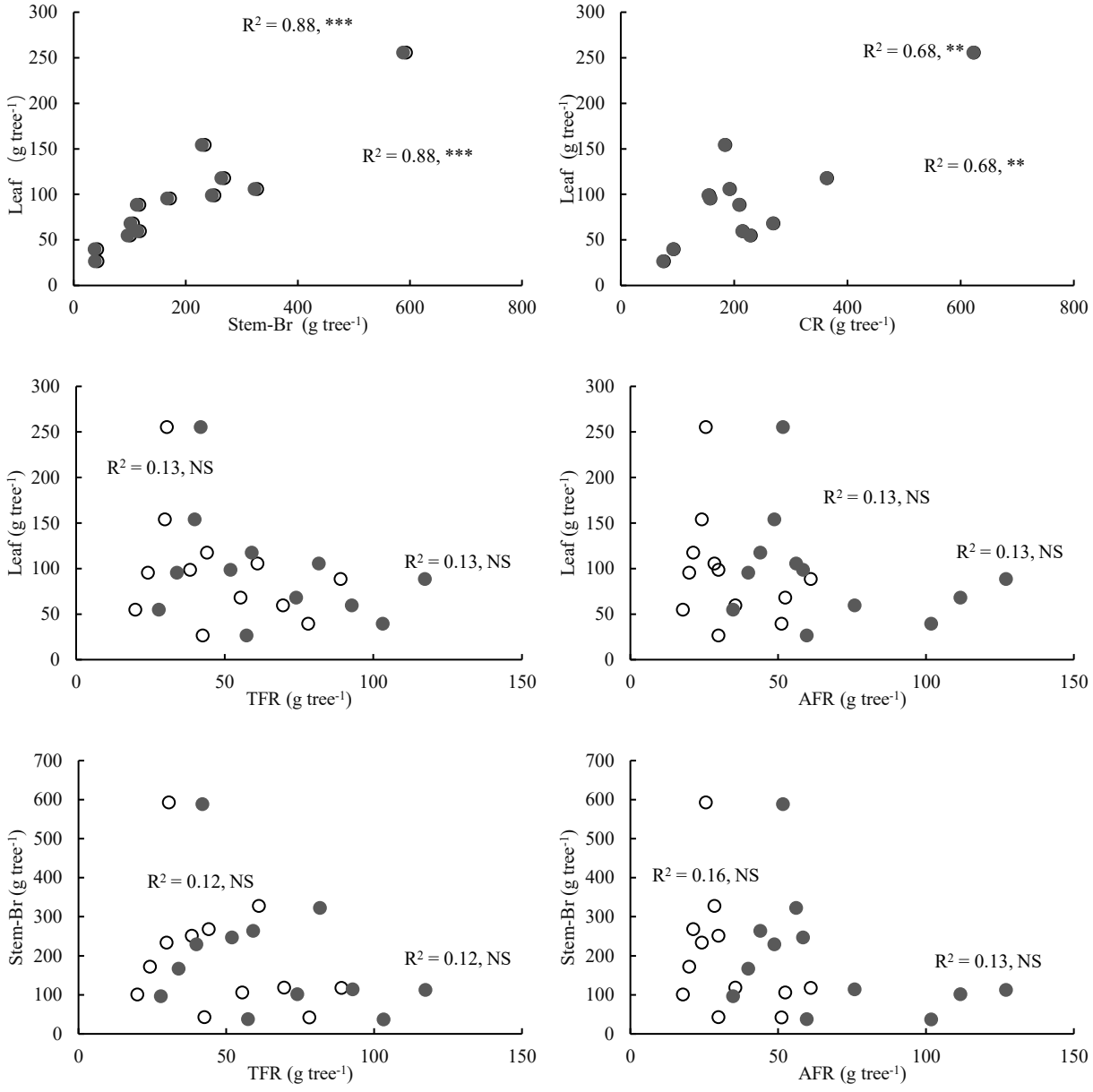

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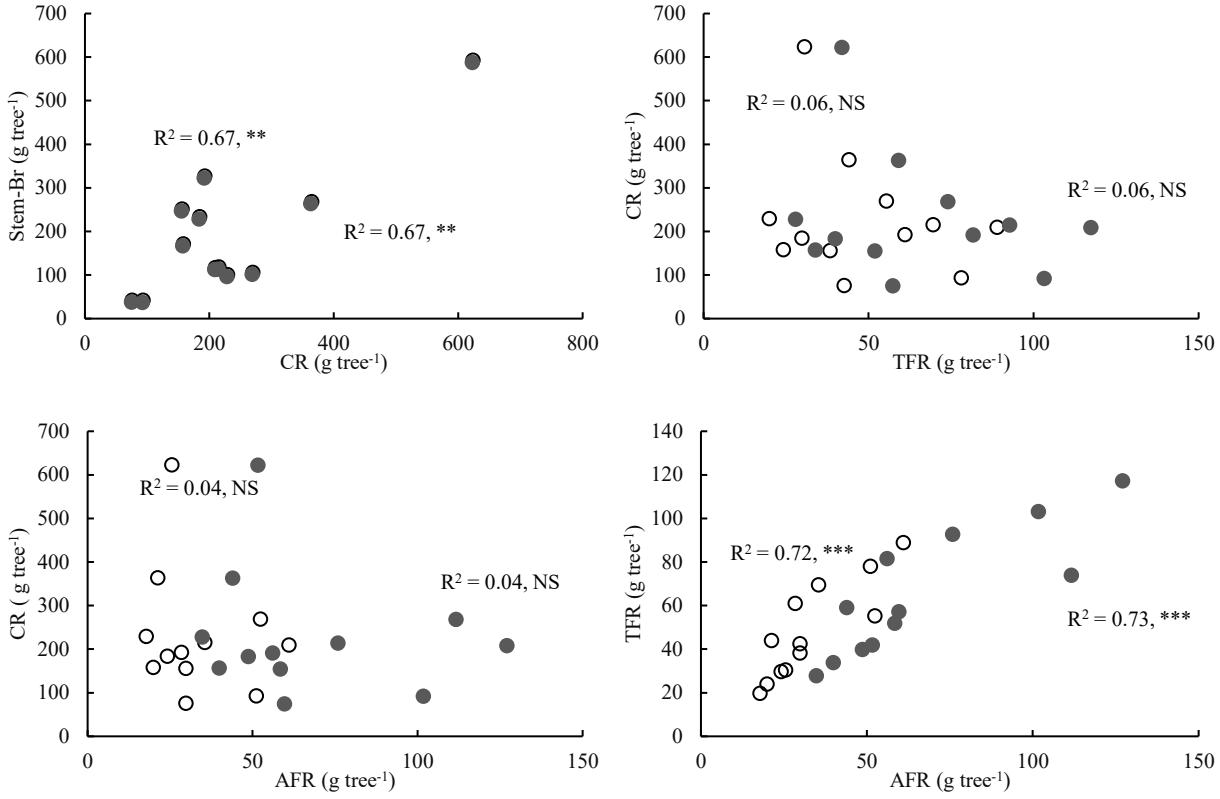
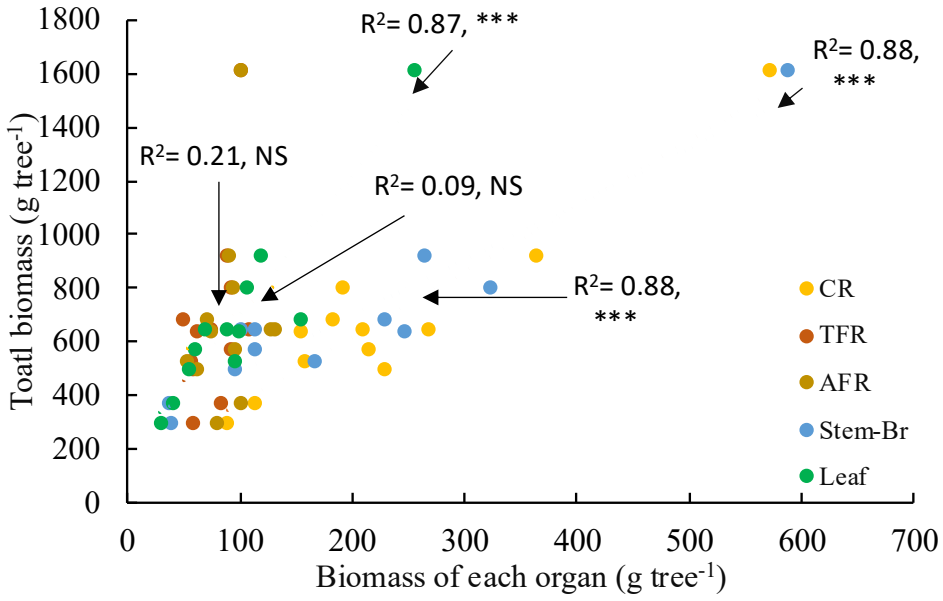


Fig. 4 Correlations among leaf, absorptive fine root (AFR), transport fine root (TFR), coarse root (CR), and stem and branch combination (Stem-Br) biomass and production. Hollow circles and filled circles stand for biomass and production, respectively. (n = 12; NS stands for not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)



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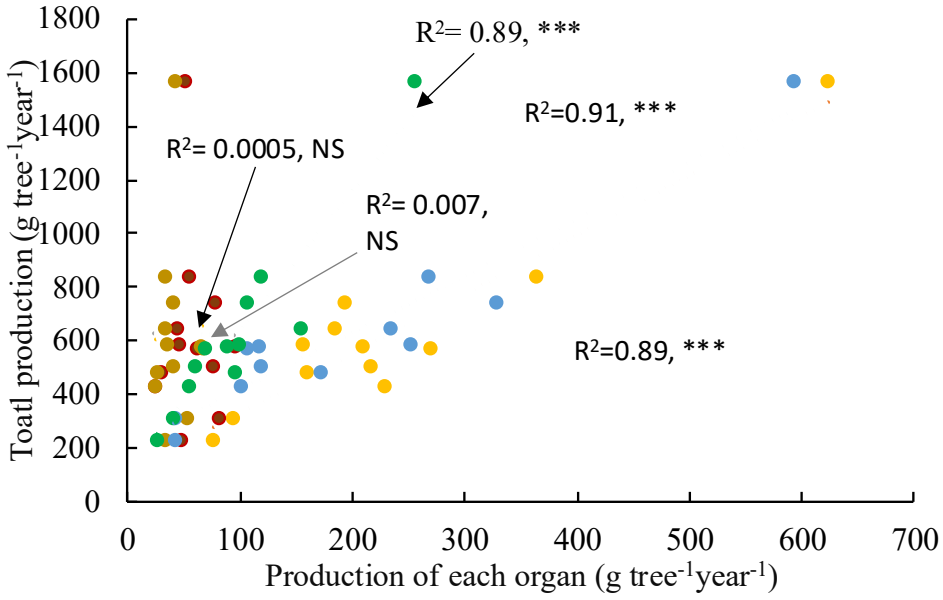

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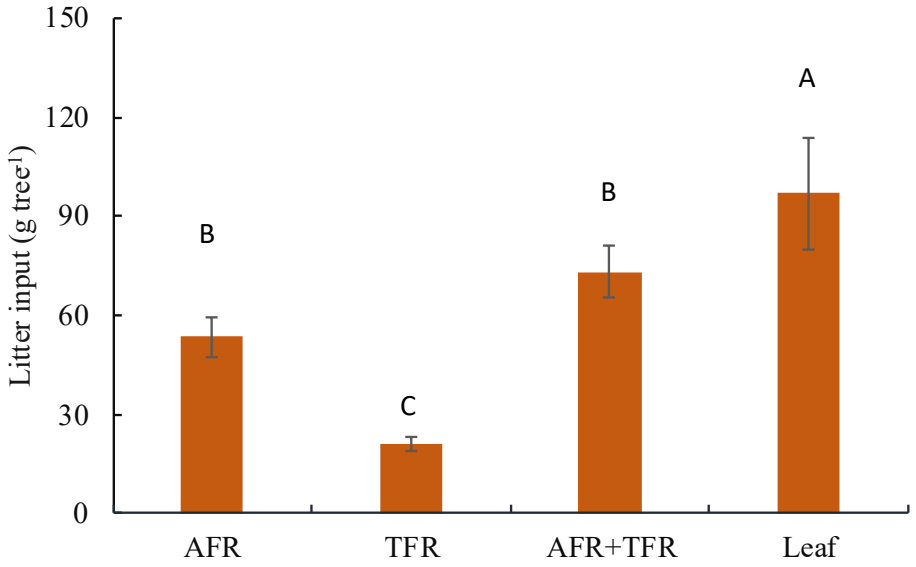
525 Fig. 5 Relationships between total biomass and leaf, absorptive fine root (AFR), transport fine root (TFR),
526 coarse root (CFR), and stem and branch combination (Stem-Br) biomass and between total production
527 and leaf, absorptive fine root (AFR), transport fine root (TFR), constructive root (CFR), and stem and
528 branch combination (Stem-Br) production. (n = 12; NS stands for not significant, * $P < 0.05$, ** $P < 0.01$,
529 *** $P < 0.001$)



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531 Fig. 6 Absorptive fine root (AFR) and transport fine root (TFR) mortality and leaf litterfall

532 (n = 8, ± SE; Different letters stands for significant difference in mean values)

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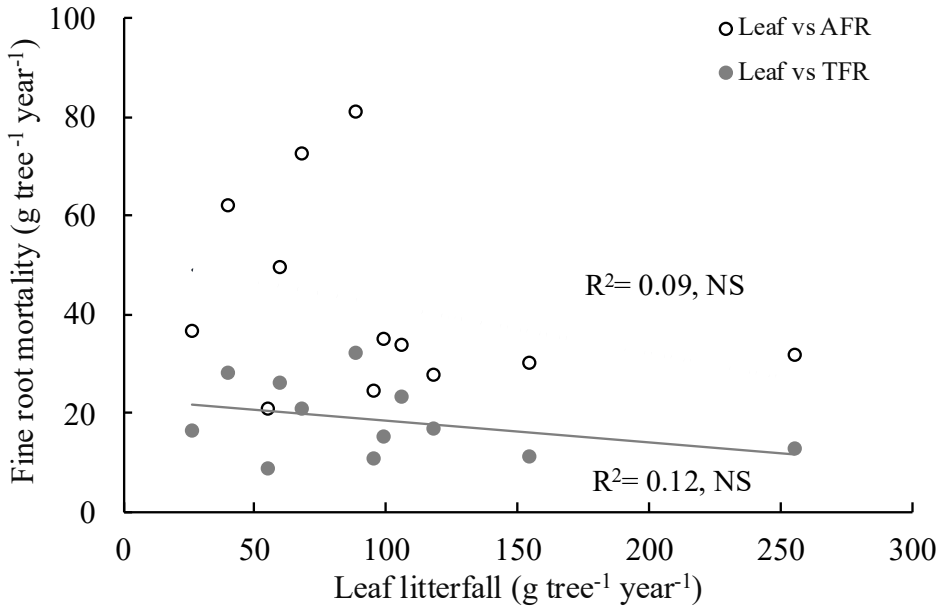

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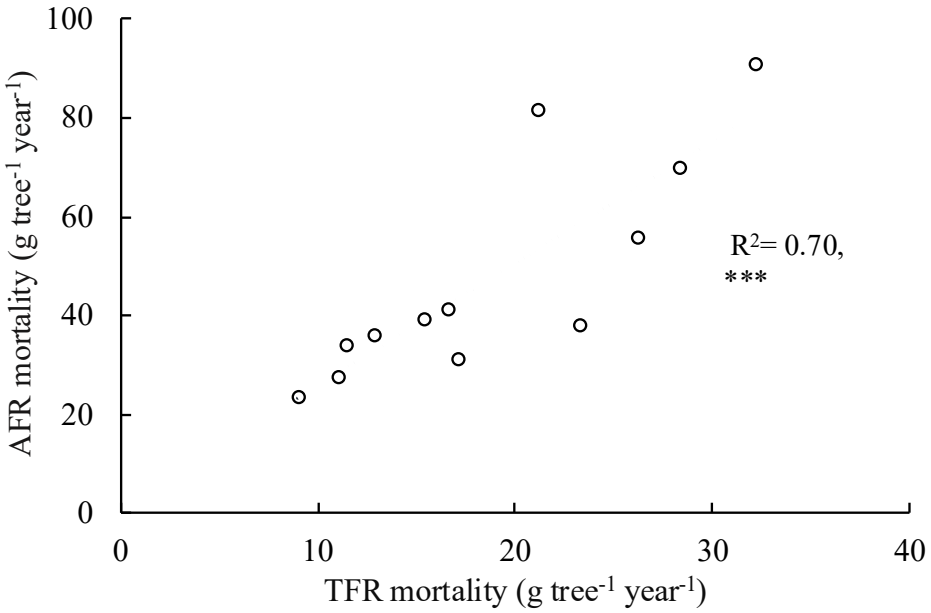

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537 Fig. 7 Correlations among absorptive fine root (AFR) mortality, transport fine root (TFR) mortality and

538 leaf litterfall (n = 12; NS stands for not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

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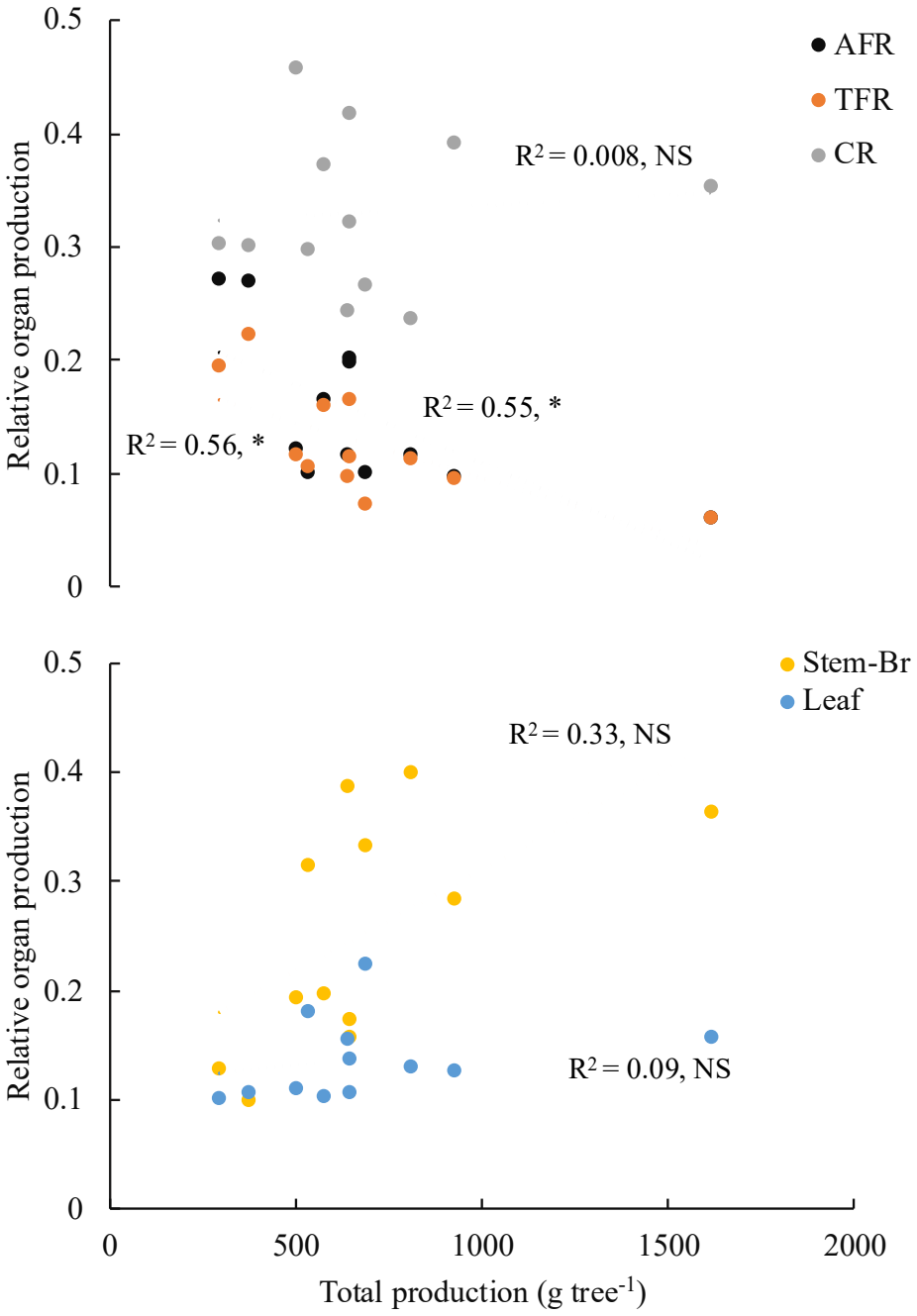

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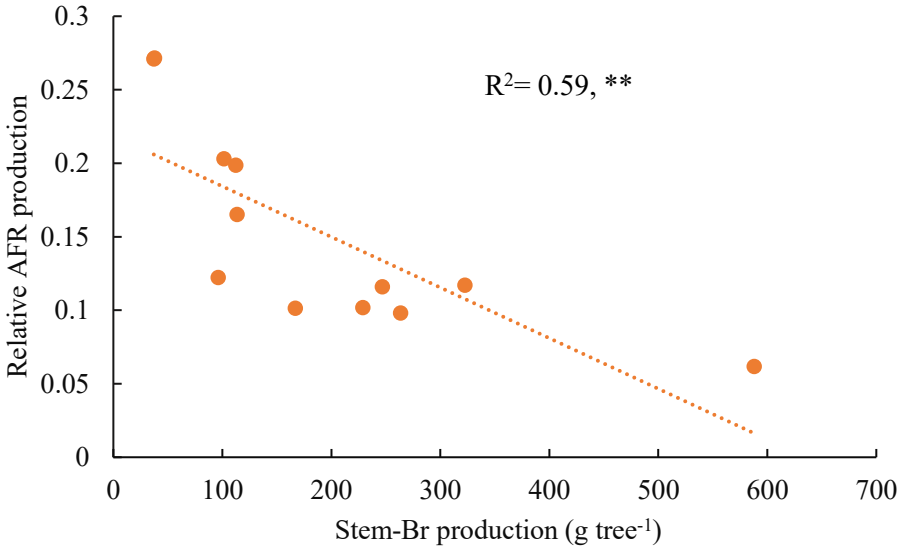
546 Fig. 8 Relationships between total production and relative production of leaves, absorptive fine roots
547 (AFR), transport fine roots (TFR), coarse roots (CR), and stem and branch combination (Stem-Br) to the
548 total. (n = 12; NS stands for not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)



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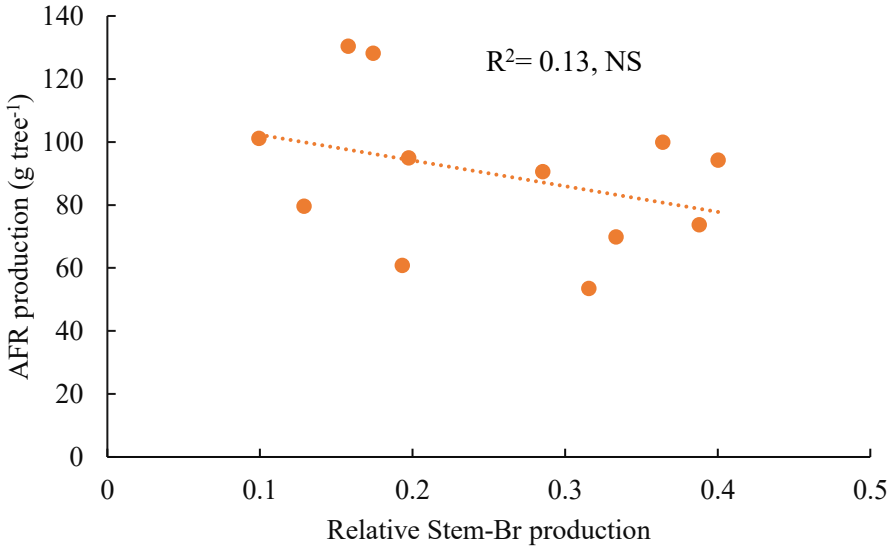

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551 Fig. 9 Relationships between Stem-Br production and relative production of absorptive fine roots (AFR)
552 and between AFR production and relative production of Stem-Brs. (n = 12; NS stands for not significant,
553 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

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Table 1 Correlations of soil properties to leaf, absorptive fine root (AFR), transport fine root (TFR), coarse root (CR), and stem and branch combination (Stem-Br) and total production

	N	C	CEC	P	K	Base saturation	pH	Bulk Density
Total	0.29	0.14	0.63*	-0.44	0.49	0.34	0.35	0.45
Leaf	0.31	0.18	0.61*	-0.45	0.34	0.16	0.19	0.38
Stem-Br	0.35	0.10	0.63*	-0.53	0.48	0.28	0.37	0.50
CR	0.19	0.03	0.60*	-0.36	0.47	0.37	0.34	0.46
TFR	0.05	0.34	0.09	0.03	0.37	0.39	0.30	0.11
AFR	-0.07	0.43	-0.08	0.27	0.12	0.30	0.22	-0.40

Note: Values are correlation coefficient; CEC is cation exchange capacity; n = 12, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 2 Correlations of soil properties to relative production of leaves, absorptive fine roots (AFR), transport fine roots (TFR), coarse roots (CR), and stem and branch combination (Stem-Br)

	N	C	CEC	P	K	Base saturation	pH	Bulk Density
Leaf	0.34	0.24	0.37	-0.39	-0.08	-0.21	-0.16	0.01
Stem-Br	0.56	0.16	0.63*	-0.74**	0.37	0.19	0.22	0.42
CR	-0.01	-0.16	0.16	-0.04	0.12	0.09	0.07	0.01
TFR	-0.61*	-0.15	-0.78**	0.80**	-0.36	-0.15	-0.19	-0.43
AFR	-0.61*	-0.1	-0.78**	0.83***	-0.4	-0.17	-0.18	-0.55

Note: Values are correlation coefficient; CEC is cation exchange capacity; n = 12, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Supplementary Files

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- 3Table.docx