

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

The root economics spectrum: divergence of absorptive root strategies with root diameter

D. Kong^{1,2}, J. Wang³, P. Kardol⁴, H. Wu⁵, H. Zeng⁶, X. Deng¹, and Y. Deng¹

¹Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China

²College of Biosciences and Biotechnology, Shenyang Agricultural University, Shenyang, China

³Belle W. Baruch Institute of Coastal Ecology & Forest Science, Clemson University, Georgetown, South Carolina, USA

⁴Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

⁵School of Life Sciences, Henan University, Kaifeng, China

⁶Key Laboratory for Urban Habitat Environmental Science and Technology, Peking University Shenzhen Graduate School, Shenzhen, China

Received: 22 July 2015 – Accepted: 28 July 2015 – Published: 13 August 2015

Correspondence to: D. Kong (deliangkong1999@126.com)

Published by Copernicus Publications on behalf of the European Geosciences Union.

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Plant roots usually vary along a dominant ecological axis, the root economics spectrum (RES), depicting a tradeoff between resource acquisition and conservation. For absorptive roots, which are mainly responsible for resource acquisition, we hypothesized that root strategies as predicted from the RES shift with increasing root diameter. To test this hypothesis, we used seven contrasting plant species for which we separated absorptive roots into two categories: thin roots (< 247 μm diameter) and thick roots. For each category, we analyzed a range of root traits closely related to resource acquisition and conservation, including root tissue density, carbon (C) and nitrogen (N) fractions as well as root anatomical traits. The results showed that trait relationships for thin absorptive roots followed the expectations from the RES while no clear trait relationships were found in support of the RES for thick absorptive roots. Our results suggest divergence of absorptive root strategies in relation to root diameter, which runs against a single economics spectrum for absorptive roots.

1 Introduction

Plant traits reflecting a tradeoff between resource acquisition and conservation represents an essential ecological axis for plant strategies that is important for our understanding of how plants drive ecosystem processes and ecosystem responses to environmental change (Cornwell et al., 2008; Freschet et al., 2010; Reich, 2014; Westoby et al., 2002). On the one end of this ecological axis, there are species with an acquisitive strategy, i.e., fast acquisition of resources (CO_2 for leaves and nutrients for roots) accompanied with a short lifespan. On the other end of the axis, there are species with a conservative strategy, i.e., slow acquisition accompanied with a long lifespan. Originally, such an ecological axis has been demonstrated for leaves, which is widely known as the leaf economics spectrum (Diaz et al., 2004; Osnas et al., 2013; Wright et al., 2004). More recently, similar trait spectra have been demonstrated across

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



plant organs from leaves to stems and roots, thus forming a whole “plant economics spectrum” (Freschet et al., 2010; Laughlin et al., 2010; Prieto et al., 2015; Reich, 2014).

Resource acquisition in plant roots is performed by absorptive roots, i.e., the first two or three orders of a root branch with primarily-developed tissues which are only a part of the commonly used “fine roots” (< 2 mm in diameter) (Guo et al., 2008; Long et al., 2013; Pregitzer et al., 2002). For absorptive roots, the tissue density, i.e., root dry mass per unit root volume, is a key trait of the root economics spectrum (RES) as tissue density is closely linked to the acquisition-conservation tradeoff (Birouste et al., 2014; Craine et al., 2005; Espeleta et al., 2009; Mommer and Weemstra, 2012). In general, absorptive roots with higher tissue density are slower in nutrient acquisition and longer in lifespan whereas absorptive roots with lower tissue density may enable faster acquisition but maintain a shorter lifespan (Ryser, 1996; Wahl and Ryser, 2000; Withington et al., 2006). Recently, tissue density for absorptive roots was found to negatively correlate with root diameter. This could be because root cortex is less dense than root stele and because in thicker roots a larger proportion of the root cross-sectional area is accounted for by the cortex (Chen et al., 2013; Kong et al., 2014; Kong and Ma, 2014). On the other hand, compared with thinner absorptive roots, thicker absorptive roots may acquire resources faster because of their greater dependence on mycorrhizal fungi (Kong et al., 2014; Kong and Ma, 2014; St John, 1980), and may also have a longer lifespan due to the larger diameter (Adams et al., 2013; Eissenstat and Yanai, 1997; Wells and Eissenstat, 2001). As such, the trait syndrome for thicker absorptive roots would differ from the predictions of faster acquisition and shorter lifespan. This highlights the importance of discriminating the thicker from the thinner absorptive roots when exploring root strategies. However, we are unaware of any previous studies that have tested for effects root diameter in driving root trait spectra.

In addition to structural traits such as density, the chemical composition of absorptive roots may constitute another important aspect of testing root strategies in relation root diameter (Hidaka and Kitayama, 2011; Meier and Bowman, 2008; Poorter and Bergkotte, 1992; Poorter et al., 2009). For example, carbon (C) and nitrogen (N), the

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



two most abundant elements in plants, are usually bound to organic compounds which may contain labile (e.g., soluble sugars and proteins in living cells) and recalcitrant fractions (e.g., cellulose and lignin in structural tissues) (Atkinson et al., 2012; Berg and McClaugherty, 2008; Feng et al., 2009; Poorter et al., 2009; Shipley et al., 2006).

5 Generally, absorptive roots with less labile C and more labile N indicate an acquisitive strategy. This is because high root activity may be accompanied by an increased production of metabolism-related proteins with a high labile N content; such roots may be palatable for herbivores and have a relative short lifespan. On the other hand, conservative roots have less labile C and N fractions as more of these chemicals are used for
10 construction of structural tissues resulting in lower root activity and a longer lifespan. However, compared with thinner absorptive roots, thicker absorptive roots may have higher labile C and N fractions as these labile fractions can be stored in their thick root cortex (Chapin III, 1980; Long et al., 2013; Lux et al., 2004; Withington et al., 2006). As such, the chemical traits of thicker absorptive roots integrate “opposing” effects of root
15 metabolism and storage suggesting them having neither a true acquisitive nor a true conservative strategy. Therefore, to evaluate the impact of thickness on root strategies it is necessary to examine C and N fractions in relation to root diameter.

Here, we selected a variety of plant species common to tropical and subtropical forests in south China with contrasting phylogeny and root structure. The aim of our
20 study was two-fold. First, we examined the influence of root diameter on the root economics spectrum (RES). We hypothesized that root strategies diverge between thinner and thicker absorptive roots, with a trade-off between acquisitive and conservative traits for thinner roots but not for thicker roots. The hypothesis was tested using a series of trait relationships involving both structural and chemical traits. Second, root C and N
25 fraction, have been suggested to vary in predictive ways across branch orders (Fan and Guo, 2010; Goebel et al., 2011). However, we hypothesized that patterns of root C and N fractions across branch orders differ in species varying in absorptive root diameter.

MD, USA). The determination of absorptive roots in a root branch was based on Long's study (Long et al., 2013).

2.5 Chemical analyses

Root C and N concentrations were determined using an element analyzer (VarioEl, Elemental Analysen-systeme GmbH, Germany). Root C fractions (extractive; acid-soluble fraction; acid-insoluble fraction) were determined by a sulfuric acid digestion method. First, we separated the extractive and labile C fraction from other C fractions. A milled powder sample of c. 100 mg (m_0) was extracted with 15 mL of cetyl trimethylammonium bromide (CTAB) solution for 3 h, filtered, repeatedly washed with de-ionized water until pH was 7.0, and then oven-dried at 60 °C to a constant weight, m_1 . Second, the filtered residue was digested with 30 mL of sulfuric acid (72 %) at 22 °C for 3 h, filtered, repeatedly washed (until pH was 7.0), dried and weighed, m_2 . After the acid-digestion step, the ash content, m_3 , was determined by combusting 15–30 mg of sample at 550 °C for 4 h. Finally, the extractive, acid-soluble fraction, and acid-insoluble fraction were calculated as $100\% \times (m_0 - m_1)/(m_0 - m_3)$, $100\% \times (m_1 - m_2)/(m_0 - m_3)$, $100\% \times (m_2 - m_3)/(m_0 - m_3)$, respectively.

After acid-digestion, a 5 mg subsample of residue after acid-digestion was taken to measure N concentration and N allocation in the acid-insoluble C fraction. The N in the extractive fraction was too low to measure. Thus, estimates of N in the acid-soluble fraction were calculated as the difference between total N and N in the acid-insoluble fraction.

2.6 Statistical analyses

Relationships between root tissue density and root N concentration and each of the three C fractions were assessed by linear regressions. Here, we introduced a new term for root tissue, "root EC" which referred to tissues outside the stele including the epidermis plus cortex. Root EC was used for two reasons. First, the thickness of

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



root EC can be a proxy of the size of root diameter ($R^2 = 0.91$ and $R^2 = 0.99$ for linear regressions in this study and in Kong's study (Kong et al., 2014), respectively). Second, root EC can be an indicator of root chemical compounds as the storage of labile C and most of root N are found in root EC (Chen et al., 2013). The relationships between the thickness of root EC and root tissue density and root chemicals were also investigated with linear regressions.

To explore the effect of root diameter on root ecological strategies, the above analyses were repeated for thin and thick absorptive roots, respectively. We used a mean thickness of 247 μm for root EC as the cut-off point between thin and thick absorptive roots. The mean thickness of root EC was used because the thickness of root EC for absorptive roots followed a normal distribution (Fig. S1a). To avoid the influence of biological N fixation on relationships between root N and root tissue density and root EC, a legume species, *A. auriculiformis*, was excluded in these analyses. In addition, for the thin absorptive roots, relationships between the extractive C fraction and root tissue density were further explored by a quadratic polynomial regression using moving average analysis. Moving average analyses were used as it improved the goodness of fit. No polynomial regression relationships were found for the other two C fractions.

We acknowledge that the seven species we used represent a relative small species pool. To validate the results of our study, we further used the data of 96 woody species from one of our previous studies where only the first-order roots were included (Kong et al., 2014). For the 96 species, they followed a skewed normal distribution with abundant species having thinner root EC (Fig. S1b), and hence lower mycorrhizal colonization (Kong et al., 2014). Here, we used a thickness of 182.8 μm for root EC as a cut-off between thin and thick absorptive roots (Kong et al., 2014) which is thinner than in our current study. The thickness of 182.8 μm for root EC corresponded to a transition of mycorrhizal colonization with increasing root diameter (Kong et al., 2014). This may also indicate a divergence of strategy between thin and thick absorptive roots (Baylis, 1975; St John, 1980). In this dataset, relationships between root tissue density and

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



root N concentration and thickness of root EC were examined for both the thin and thick absorptive roots.

To test interspecific differences of root chemical fractions among root orders, two-way ANOVAs were used with plant species and root order as fixed factors. Tukey's HSD test was conducted to evaluate differences in chemical fractions among root branch orders within species (Long et al., 2013). All statistical analyses were carried out in SPSS (version 13.0; SPSS Inc. Chicago, USA) with significant level at $p = 0.05$.

3 Results

3.1 Root strategies for thin and thick absorptive roots

Root tissue density was negatively correlated with root N concentration for total and thin but not for thick absorptive roots (Fig. 1). Similarly, using a larger species pool, negative relationships between root tissue density and root N concentration were found for total and thin but not for thick absorptive roots (Fig. S2).

For the thin absorptive roots, the extractive C fraction peaked at medium root tissue density (Fig. 2a). Moving average analysis showed a quadratic regression relationship of the extractive C fraction with root tissue density in these thin absorptive roots (Fig. S3), while no relationships were found between acid-soluble and acid-insoluble fractions and root tissue density. It was also noted that in the thin absorptive roots, the acid-soluble and -insoluble fractions were relative higher in the higher and lower range of root tissue density, respectively (Fig. 2b, c). For thick absorptive roots, none of the three C fractions were correlated with root tissue density.

Across total absorptive roots, thickness of root EC was positively correlated with total root N concentration (Fig. 3a) and negatively with root N in the acid-insoluble fraction (Fig. 3b). Thickness of root EC was also positively correlated with the extractive C fraction (Fig. 3c) and negatively with the acid-insoluble fraction (Fig. 3e). However, in

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



each of thin and thick absorptive roots, no relationships were found between thickness of root EC and each of these chemical fractions (all p values > 0.05 , Fig. 3a–e).

Thickness of root EC decreased linearly with root tissue density (Fig. 4), but no relationships were found when separated between thin and thick absorptive roots. Using a large species pool we found a very similar pattern: a significant relationship between thickness of root EC and root tissue density for total absorptive roots, a weaker relationship for thin and no relationship for thick absorptive roots (Fig. S4).

3.2 Effects of plant species and root order on root C and N fractions

All chemical fractions except the extractive fraction showed significant differences among species and root orders (p values < 0.05 , Table 1), and there were significant interactions for all chemical fractions (all p values < 0.05) indicating plant species-specific effects of root order on plant chemical traits.

The extractive C fraction tended to increase with increasing root order for species with thin absorptive roots such as *D. dichotoma* and *A. auriculiformis*, but decreased for species with thick absorptive roots, except for *C. lanceolata* (Fig. 5a). For both acid-soluble and acid-insoluble fractions, patterns were largely idiosyncratic, including both increases and decreases with root branch orders (Fig. 5b and c). For all species, root N concentration in all species decreased with increasing root order (Fig. 6a), whereas N in the acid-insoluble fraction increased with increasing root order, except for *C. chinensis* (Fig. 6b).

4 Discussion

The acquisition-conservation tradeoff in plants has been suggested to be consistent across plant organs (roots, leaves, and stems), as such constituting a key ecological axis, i.e., the “plant economics spectrum” (Freschet et al., 2010; Prieto et al., 2015; Reich, 2014). The negative relationship between root tissue density and root N con-

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



centration across total absorptive roots that we found in our study provides support for a root economics spectrum (RES). This is because absorptive roots with higher tissue density usually have longer lifespan (Eissenstat and Yanai, 1997; Ryser, 1996; Withington et al., 2006), while their lower N concentration would be associated with slow resource acquisition (Kong et al., 2010; Mommer and Weemstra, 2012; Reich et al., 2008). However, our results also showed that the negative relationship between root tissue density and root N concentration existed only in thin absorptive roots, but not in thick roots (Fig. 1). Although these results were based on a relative small number of species, reanalysis of data from a previous study using 96 species (Kong et al., 2014) revealed very similar patterns (Fig. S1). This indicates that the conventionally recognized RES may be confined to thin absorptive roots only, as such supporting our first hypothesis.

The divergence of absorptive root strategies with root diameter was further supported by the relationships between root tissue density and root C fractions. Theoretically, absorptive roots with lower tissue density would have higher activity, while higher root activity also consumes more labile C thus leaving less labile C and more recalcitrant C fractions in these roots. In contrast, for absorptive roots with higher tissue density, more C is used for structural tissues demanding recalcitrant C fractions (Fan and Guo, 2010). Therefore, we would expect an inverted U-shaped relationship for labile C fractions and a U-shaped relationship for recalcitrant C fractions when correlated with root tissue density. In fact, for thin absorptive roots we found an inverted U-shaped relationship between the labile, extractive C fraction and root tissue density (Fig. 2a, S2). As for recalcitrant C fractions in thin absorptive roots, the acid-insoluble C fraction peaked at lower but not at higher root tissue density which seems to contradict with the expected inverted U-shaped curve. However, the acid-soluble C fraction peaked at higher root tissue density (Fig. 2b). As such, it could be that thin absorptive roots with higher tissue density are constructed with more acid-soluble C compounds, such as cellulose, rather than acid-insoluble C compounds, such as lignin; production of lignin would require more energy than production of cellulose (Novaes et al., 2010). There-

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



fore, with increasing root tissue density, recalcitrant C fractions in thin absorptive roots may follow a pattern opposite to that of labile C fractions. As such, the patterns of labile and recalcitrant C fractions in thin absorptive roots are in support of RES theory. On the other hand, for thick absorptive roots, their lower tissue density was accompanied with higher extractive and lower acid-insoluble C fraction, possibly because of storage of labile C in their thick cortex (Long et al., 2013; Lux et al., 2004). These patterns of root C fractions for thick absorptive roots run against expectations from the RES. Therefore, our study shows that thick absorptive roots may follow a strategy different from that for thin absorptive roots.

Furthermore, observed relationships between thickness of root EC and root C and N fractions provided indirect evidence for our contention of divergence of ecological strategy with root diameter. Across total absorptive roots, thickness of root EC was positively correlated with root N concentration and the extractive C fraction while being negatively correlated with the acid-soluble C fraction and N in the acid-soluble C fraction. This suggest that compared with thin absorptive roots, thick absorptive roots acquire resources at higher rates as indicated by their higher N concentration and lower C and N in recalcitrant fractions. Meanwhile, thick absorptive roots may also have longer lifespan because of their larger root diameter (Adams et al., 2013; Anderson et al., 2003; McCormack et al., 2012; Wells and Eissenstat, 2001). These findings seem to contrast with an acquisition-conservation tradeoff. Further, we showed that relationships between thickness of root EC and root chemical fractions only hold across the full spectrum from thin to thick absorptive roots. Nevertheless, it was also noted that root tissue density showed a greater range of variation for thin than for thick absorptive roots. For thin absorptive roots, variation in root tissue density might arise from secondary thickening of root EC cell walls (Eissenstat and Achor, 1999; Long et al., 2013; Ryser, 2006; Wahl and Ryser, 2000). This could be associated with lower root activity and hence lower root N concentration (Figs. 1 and S1), which is consistent with the RES theory. However, for thick absorptive roots, the cell size as well as the cortical cell file number (Chimungu et al., 2014a, b) may be more important than cell wall thicken-

ing in determining root activity. If so, root activity may be less affected by thickening of root EC cell walls than by changing the size or number of these cells, and hence no acquisition-conservation trade-off as predicted by the RES for thick absorptive roots. Therefore, relationships between thickness of root EC and root chemical fractions provide further evidence for the idea of divergence of root strategies between the thin and thick absorptive roots which may be underpinned by different mechanisms.

Our finding of different ecological strategies in thin and thick absorptive roots has important implications for the emerging debate on the plant economics spectrum. Although the existence of an economics spectrum for roots (RES) has been recognized (Craine et al., 2005; Espeleta et al., 2009; Freschet et al., 2010; Reich, 2014), some recent studies have shown contrasting findings, suggesting no RES (Chen et al., 2013) or positive relationships between root diameter and root N concentration (Kong et al., 2014). Although there may be other mechanisms, one possible explanation for a lack of trade-offs between acquisitive and conservative root traits in these studies is the inclusion of thick absorptive roots which could have altered root trait relationships.

Besides the prominent role in influencing root strategy, root thickness may also affect patterns of root chemical traits among root branch orders. The extractive C fraction increased with increasing root order for species with thin absorptive roots, whereas it declined for species with thick absorptive roots. Although both the acid-soluble and acid-insoluble fractions showed no consistent trends across root orders, the total recalcitrant fraction (sum of acid-soluble and acid-insoluble fractions) showed a pattern opposite to that of the extractive fraction. On the other hand, root N concentration and N in recalcitrant C fractions showed relative consistent patterns across root orders. Thus, we only found partial support of our second hypothesis. These patterns of root chemical fractions are important in understanding soil ecosystem processes. For example, it is increasingly recognized that lower-order roots, compared with higher-order woody roots, are faster in root turnover but slower in root decomposition which makes the former a disproportionately greater source for soil organic matter (Clemmensen et al., 2013; Fan and Guo, 2010; Goebel et al., 2011; Xiong et al., 2013). This has been ascribed to

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



higher recalcitrant C fractions in lower-order compared with higher-order woody roots (Goebel et al., 2011). However, our results may challenge the generality of slower decomposition of lower-order relative to higher-order roots as some lower-order roots had less recalcitrant C fractions and hence faster decomposition than higher-order roots.

In conclusion, our study revealed for the first time divergence of absorptive root strategies and patterns of root chemical fractions with root diameter and root order. Specifically, the axis of the RES dominated in thin absorptive roots, while thick absorptive roots did not seem to be constrained by an acquisition-conservation tradeoff. The different strategies for the two groups of roots are important in advancing our understanding of root ecology and the links with aboveground plant counterparts. Yet, our knowledge on the functioning of plant roots and their roles in driving soil ecosystem processes is still limited. Future studies should test to what extent our results hold for other (groups of) plant species, include more functional traits (including those associated with interactions with rhizosphere biota), and unravel the mechanisms underlying the economic strategy for thick absorptive roots.

The Supplement related to this article is available online at doi:10.5194/bgd-12-13041-2015-supplement.

Acknowledgements. We thank Zhengxia Chen and Yingqian Long for their assistance in measuring root chemicals and anatomical structures, and Chengen Ma and Xin Jing in Peking University for their valuable contribution to this work. This study was sponsored by the open fund of Key Laboratory of Tropical Forest Ecology in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences and Natural Science Foundation of China (No. 31200344).

References

Adams, T. S., McCormack, M. L., and Eissenstat, D. M.: Foraging strategies in trees of different root morphology: the role of root lifespan, *Tree Physiol.*, 33, 940–948, 2013.

13055

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Anderson, L. J., Comas, L. H., Lakso, A. N., and Eissenstat, D. M.: Multiple risk factors in root survivorship: a four-year study in Concord grape, *New Phytol.*, 158, 489–501, 2003.
- Atkinson, R. R. L., Burrell, M. M., Osborne, C. P., Rose, K. E., and Rees, M.: A non-targeted metabolomics approach to quantifying differences in root storage between fast- and slow-growing plants, *New Phytol.*, 196, 200–211, 2012.
- Baylis, G.: Magnolioid mycorrhiza and mycotrophy in root systems derived from it, in: *Endomycorrhizas*, edited by: Sanders, F. E., Mosse, B., and Tinker, P. B., Academic Press, 1975.
- Berg, B. and McClaugherty, C.: *Plant litter: decomposition, humus formation, carbon sequestration*, Springer, 2008.
- Birouste, M., Zamora-Ledezma, E., Bossard, C., Pérez-Ramos, I., and Roumet, C.: Measurement of fine root tissue density: a comparison of three methods reveals the potential of root dry matter content, *Plant Soil*, 374, 299–313, 2014.
- Chapin III, F. S.: The mineral nutrition of wild plants, *Annu. Rev. Ecol. Evol. S.*, 11, 233–260, 1980.
- Chen, W., Zeng, H., Eissenstat, D. M., and Guo, D.: Variation of first-order root traits across climatic gradients and evolutionary trends in geological time, *Global Ecol. Biogeogr.*, 22, 846–856, 2013.
- Chimungu, J. G., Brown, K. M., and Lynch, J. P.: Large root cortical cell size improves drought tolerance in maize, *Plant Physiol.*, 166, 2166–2178, 2014a.
- Chimungu, J. G., Brown, K. M., and Lynch, J. P.: Reduced root cortical cell file number improves drought tolerance in maize, *Plant Physiol.*, 166, 1943–1955, 2014b.
- Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A., and Lindahl, B. D.: Roots and associated fungi drive long-term carbon sequestration in boreal forest, *Science*, 339, 1615–1618, 2013.
- Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V., and Westoby, M.: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide, *Ecol. Lett.*, 11, 1065–1071, 2008.

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Craine, J. M., Lee, W. G., Bond, W. J., Williams, R. J., and Johnson, L. C.: Environmental constraints on a global relationship among leaf and root traits of grasses, *Ecology*, 86, 12–19, 2005.
- Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M. R.: The plant traits that drive ecosystems: evidence from three continents, *J. Veg. Sci.*, 15, 295–304, 2004.
- Eissenstat, D. M. and Achor, D. S.: Anatomical characteristics of roots of citrus rootstocks that vary in specific root length, *New Phytol.*, 141, 309–321, 1999.
- Eissenstat, D. M. and Yanai, R. D.: The ecology of root lifespan, *Adv. Ecol. Res.*, 27, 1–60, 1997.
- Espeleta, J. F., West, J. B., and Donovan, L. A.: Tree species fine-root demography parallels habitat specialization across a sandhill soil resource gradient, *Ecology*, 90, 1773–1787, 2009.
- Fan, P. and Guo, D.: Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil, *Oecologia*, 163, 509–515, 2010.
- Feng, Y. L., Lei, Y. B., Wan, R. F., Callaway, R. M., Valiente-Banuet, I., Li, Y. P., and Zheng, Y. L.: Evolutionary tradeoffs for nitrogen allocation to photosynthesis vs. cell walls in an invasive plant, *P. Natl. Acad. Sci. USA*, 106, 1853–1856, 2009.
- Freschet, G. T., Cornelissen, J. H., Van Logtestijn, R. S., and Aerts, R.: Evidence of the “plant economics spectrum” in a subarctic flora, *J. Ecol.*, 98, 275–301, 2010.
- Goebel, M., Hobbie, S. E., Bulaj, B., Zadworny, M., Archibald, D. D., Oleksyn, J., Reich, P. B., and Eissenstat, D. M.: Decomposition of the finest root branching orders: linking belowground dynamics to fine-root function and structure, *Ecol. Monogr.*, 81, 89–102, 2011.
- Guo, D., Xia, M., Wei, X., Chang, W., Liu, Y., and Wang, Z.: Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species, *New Phytol.*, 180, 673–683, 2008.

The root economics spectrum

D. Kong et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[I◀](#)

[▶I](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Hidaka, A. and Kitayama, K.: Allocation of foliar phosphorus fractions and leaf traits of tropical tree species in response to decreased soil phosphorus availability on Mount Kinabalu, Borneo, *J. Ecol.*, 99, 849–857, 2011.

Kong, D. L. and Ma, C. E.: Acquisition of ephemeral module in roots: a new view and test, *Sci. Rep.*, 4, 5078, doi:10.1038/srep05078, 2014.

Kong, D., Wu, H., Wang, M., Simmons, M., Lü, X., Yu, Q., and Han, X.: Structural and chemical differences between shoot- and root-derived roots of three perennial grasses in a typical steppe in Inner Mongolia China, *Plant Soil*, 336, 209–217, 2010.

Kong, D., Ma, C., Zhang, Q., Li, L., Chen, X., Zeng, H., and Guo, D.: Leading dimensions in absorptive root trait variation across 96 subtropical forest species, *New Phytol.*, 203, 863–872, 2014.

Laughlin, D. C., Leppert, J. J., Moore, M. M., and Sieg, C. H.: A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora, *Funct. Ecol.*, 24, 493–501, 2010.

Long, Y., Kong, D., Chen, Z., and Zeng, H.: Variation of the linkage of root function with root branch order, *PLoS ONE*, 8, e57153, doi:10.1371/journal.pone.0057153, 2013.

Lux, A., Luxova, M., Abe, J., and Morita, S.: Root cortex: structural and functional variability and responses to environmental stress, *Root Res.*, 13, 117–131, 2004.

McCormack, M. L., Adams, T. S., Smithwick, E. A., and Eissenstat, D. M.: Predicting fine root lifespan from plant functional traits in temperate trees, *New Phytol.*, 195, 823–831, 2012.

Meier, C. L. and Bowman, W. D.: Links between plant litter chemistry, species diversity, and below-ground ecosystem function, *P. Natl. Acad. Sci. USA*, 105, 19780–19785, 2008.

Mommer, L. and Weemstra, M.: The role of roots in the resource economics spectrum, *New Phytol.*, 195, 725–727, 2012.

Novaes, E., Kirst, M., Chiang, V., Winter-Sederoff, H., and Sederoff, R.: Lignin and biomass: a negative correlation for wood formation and lignin content in trees, *Plant Physiol.*, 154, 555–561, 2010.

Osnas, J. L., Lichstein, J. W., Reich, P. B., and Pacala, S. W.: Global leaf trait relationships-mass, area, and the leaf economics spectrum, *Science*, 340, 741–744, 2013.

Poorter, H. and Bergkotte, M.: Chemical composition of 24 wild species differing in relative growth rate, *Plant Cell Environ.*, 15, 221–229, 1992.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., and Villar, R.: Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis, *New Phytol.*, 182, 565–588, 2009.

The root economics spectrum

D. Kong et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Pregitzer, K. S., DeForest, J. L., Burton, A. J., Allen, M. F., Ruess, R. W., and Hendrick, R. L.: Fine root architecture of nine North American trees, *Ecol. Monogr.*, 72, 293–309, 2002.
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao, Z., Pierret, A., Portillo, N., Rouspard, O., Thammahacksa, C., and Stokes, A.: Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum, *J. Ecol.*, 103, 361–373, 2015.
- Reich, P. B.: The world-wide “fast–slow” plant economics spectrum: a traits manifesto, *J. Ecol.*, 102, 275–301, 2014.
- Reich, P. B., Tjoelker, M. G., Pregitzer, K. S., Wright, I. J., Oleksyn, J., and Machado, J. L.: Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants, *Ecol. Lett.*, 11, 793–801, 2008.
- Ryser, P.: The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses, *Funct. Ecol.*, 10, 717–723, 1996.
- Ryser, P.: The mysterious root length, *Plant Soil*, 286, 1–6, 2006.
- Shiple, B., Lechowicz, M. J., Wright, I., and Reich, P. B.: Fundamental trade-offs generating the worldwide leaf economics spectrum, *Ecology*, 87, 535–541, 2006.
- St John, T. V.: Root size, root hairs and mycorrhizal infection: a re-examination of Baylis’s hypothesis with tropical trees, *New Phytol.*, 84, 483–487, 1980.
- Wahl, S. and Ryser, P.: Root tissue structure is linked to ecological strategies of grasses, *New Phytol.*, 148, 459–471, 2000.
- Wells, C. E. and Eissenstat, D. M.: Marked differences in survivorship among apple roots of different diameters, *Ecology*, 82, 882–892, 2001.
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., and Wright, I. J.: Plant ecological strategies—some leading dimensions of variation among species, *Annu. Rev. Ecol. Evol. S.*, 33, 125–159, 2002.
- Withington, J. M., Reich, P. B., Oleksyn, J., and Eissenstat, D. M.: Comparisons of structure and life span in roots and leaves among temperate trees, *Ecol. Monogr.*, 76, 381–397, 2006.
- 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., Midgley, J. J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.: The worldwide leaf economics spectrum, *Nature*, 428, 821–827, 2004.

Xiong, Y. M., Fan, P. P., Fu, S. L., Zeng, H., and Guo, D. L.: Slow decomposition and limited nitrogen release by lower order roots in eight Chinese temperate and subtropical trees, *Plant Soil*, 363, 19–31, 2013.

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



The root economics spectrum

D. Kong et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**Table 1.** *F* values of two-way ANOVAs testing effects of plants species and root branch order on the extractive C fraction, acid-soluble C fraction, acid-insoluble C fraction, N concentration, and N in acid-insoluble C fraction. *, **, *** were significant level at 0.05, 0.01, 0.001, respectively.

C fraction	Extractive C fraction	Acid-soluble C fraction	Acid-insoluble C fraction	N concentration C fraction	N in acid-insoluble C fraction
Species	132.97***	51.57***	188.51***	1578.85***	142.40***
Root order	1.63	11.76***	17.78***	521.22***	19.61***
Species × Root order	4.46***	2.59**	3.53***	29.33***	3.83***

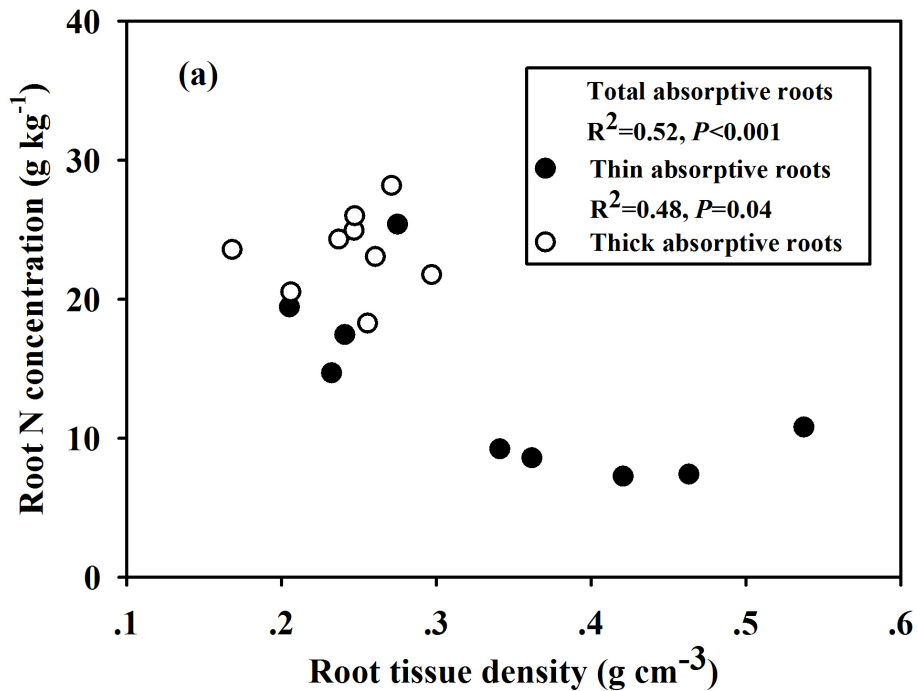


Figure 1. Relationships between root tissue density and root N concentration over the total, thin (solid circles) and thick (open circles) absorptive roots.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The root economics spectrum

D. Kong et al.

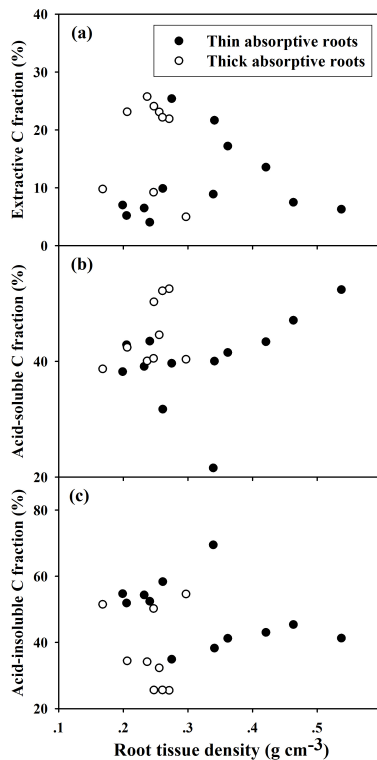


Figure 2. Relationships between root tissue density and three C fractions, extractive C fraction (a), acid-soluble C fraction (b) and acid-insoluble C fraction (c), for the thin (solid circles) and thick (open circles) absorptive roots.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

I ◀

▶ I

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



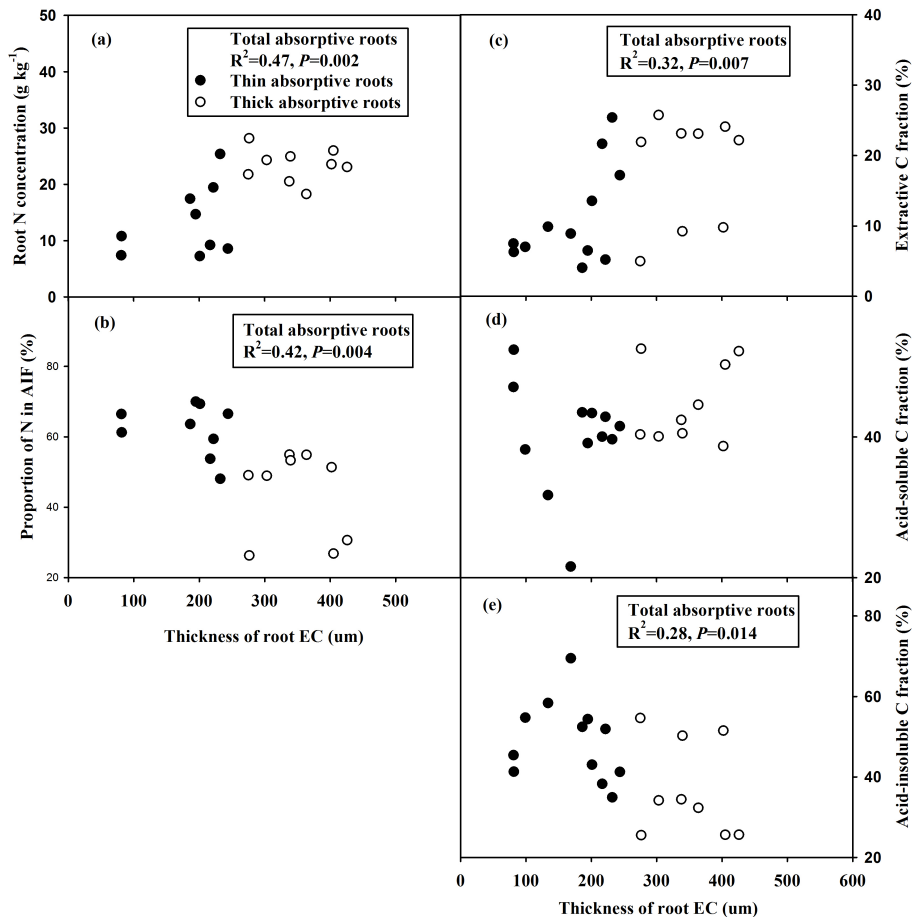


Figure 3. Relationships between thickness of root EC and root N concentration **(a)**, N in acid-insoluble C fraction **(b)**, extractive C fraction **(c)**, acid-soluble C fraction **(d)** and acid-insoluble C fraction **(e)** for the thin (solid circles) and thick (open circles) absorptive roots.

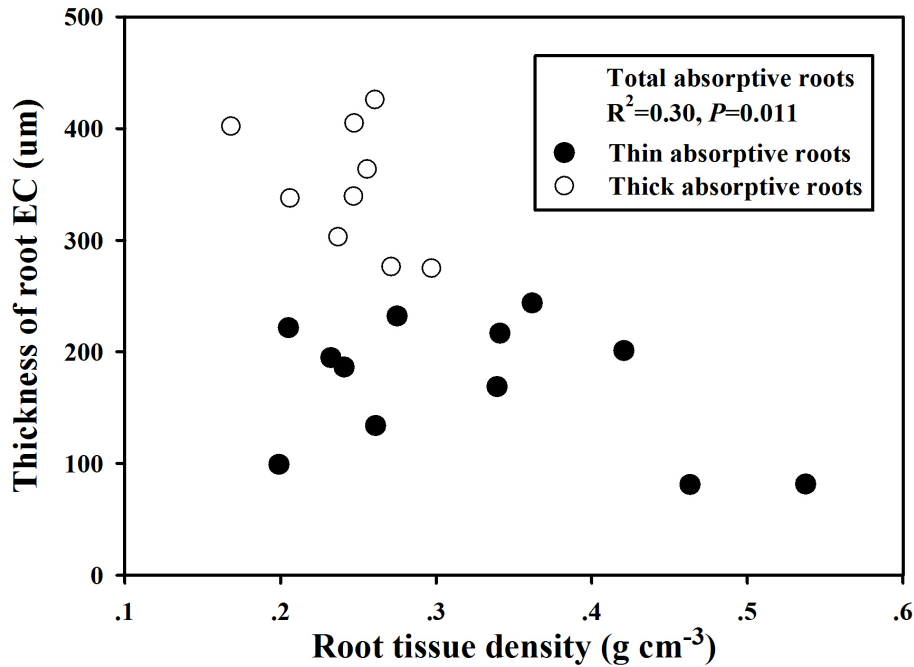


Figure 4. Relationships between root tissue density and thickness of root EC over the total, thin (solid circles) and thick (open circles) absorptive roots.

BGD

12, 13041–13067, 2015

The root economics spectrum

D. Kong et al.

[Title Page](#)

[Abstract](#) | [Introduction](#)

[Conclusions](#) | [References](#)

[Tables](#) | [Figures](#)

[◀](#) | [▶](#)

[◀](#) | [▶](#)

[Back](#) | [Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



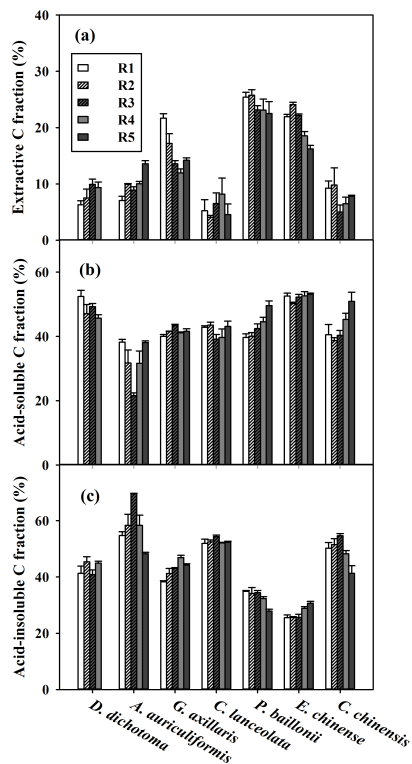


Figure 5. Three C fractions, extractive C fraction (a), acid-soluble C fraction (b) and acid-insoluble C fraction (c), among different root orders in seven species. R1–R5 were the first to the fifth root branch order.

The root economics spectrum

D. Kong et al.

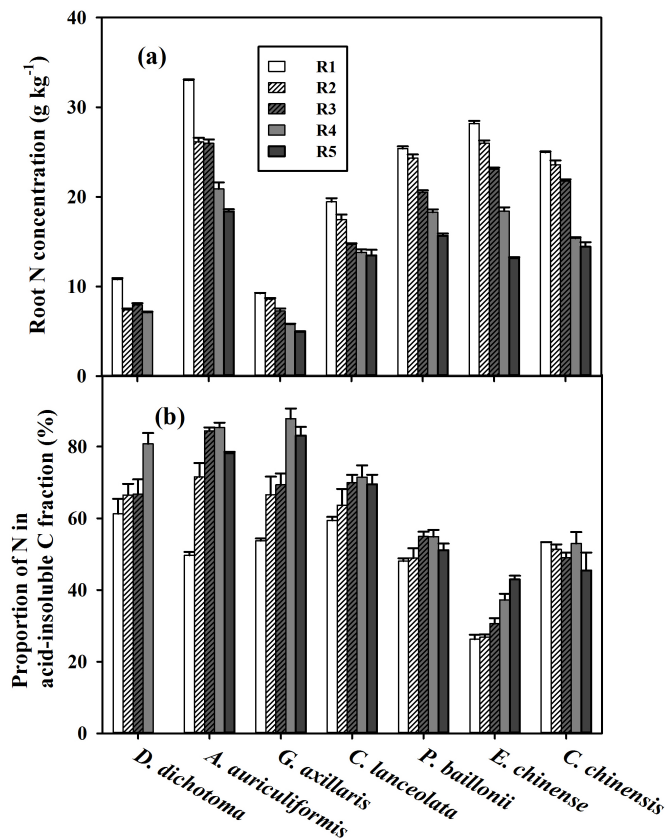


Figure 6. Root N concentration (a) and N in acid-insoluble C fraction (b) among different orders for seven species. R1–R5 were the first to the fifth root branch order.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

