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Interactive comment on "The root economics spectrum: divergence of absorptive root strategies with root diameter" *by* D. Kong et al.

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General comments The aims of the paper were to evaluate (1) the influence of root diameter on the root economics spectrum (RES) and (2) that the root chemical traits (C, N) vary across branch orders. Recently it has been argued that roots should be categorized based on their function or order with the architecture more than that based on a diameter cutoff, typically 2 mm (see McCormack et al 2015). The distal roots, called absorptive, could be considered as a main group because of their position in the root system. The authors would like to demonstrate this is not the case and that absorptive roots could follow different patterns. The authors consider that a RES exists in plants in general, but it has not been yet demonstrated at large scales (see debates given by Mommer & Weenstra 2012, Reich 2014 or Bardgett et al 2015). Defining

a RES needs to observe similar traits syndromes related to resource acquisition and conservation in a large number of species. In the present study only a limited number of traits (mainly chemical and anatomy) for 7 species were measured. For these reasons the title gives a false message of the paper and RES should be removed from the title.

Response: We appreciate the comments from the reviewer on the issues of our manuscript. In this study, we aimed to give a new view on the topic of root economics spectrum (RES). The results may also have important implication for the emerging controversial views on the existence of root economics spectrum. In order to validate the main idea of this study, divergence of root strategies with root diameter, we used three suits of trait relationships, including root N-root tissue density, root tissue density-root C fractions, root EC-root C and N fractions. Results of these relationships supported our new idea on RES (see the text of this study). As also concerned by the reviewer, the root traits included in this study were relative few. However, the root traits indeed represented key aspects of root morphology (i.e., diameter), chemicals (i.e., C and N fractions) and anatomy (i.e., EC) that are closely related to resource acquisition in absorptive roots. Seven species were included in this study. We admit that seven species are indeed too few to test the big topic of RES. In order to overcome this weakness, we resorted to our recent study of 96 species and reanalyzed the root traits (see Fig. S2,S4 in the supporting information). Interestingly, results of the reanalysis also supported the claim of divergence of absorptive root strategies with root diameter. The analyses added further evidence for the main idea of this study. Nevertheless, we acknowledge that testing whether the RES existed or how the patterns of RES were across species with different root diameter need more work in future studies by selecting more species and more traits related to root resource acquisition and conservation. Therefore, in the conclusion section, we also advocated that these issues should be stressed in future studies.

Additional traits related to resource acquisition (SRL, SRA) in order to confirm the separation between thin and thick roots are expected.

Response: In this study, SRL was not included in our analysis. It has been reported that the diameter-related root traits including SLA and root anatomical structures were strongly inter-correlated and constituted a key ecological dimension for the absorptive roots (see Kong et al. 2014). Here, we presented the relationship between root diameter and SRL (see the Fig. 1a for response, best fitted by an exponential decay regression). It was clear that the root diameter-SRL relationship was strong. The root diameter-SRL was also strong for 96 species of our previous study (see the Fig. 1b for response, data from Kong et al. 2014). Such strong root diameter-SRL relationship could ensure that the divergence of ecological strategies in the thin and thick absorptive roots can also be indicated by SRL. Exactly, in the root diameter-SRL relationship, variation of root diameter can result in change of SRL for fine absorptive roots whereas SRL remained constantly small even with a great change of diameter for the coarse absorptive roots. The SRL, as also stressed by the reviewer, was a key trait related to resource absorption in roots. The much smaller change of SRL in coarse relative fine absorptive suggested a different strategy for the former (greater dependence on mycorrhizal fungi for nutrient acquisition, Baylis 1975) from the latter. Therefore, the root diameter-SRL relationship may also suggest divergence of root strategies with root diameter.

In addition the size of cortex (root EC) seems to be a promising trait more than diameter itself, as it drives values of root tissue density (RTD), C and N. But this trait has not been enough underlined in the hypotheses.

Response: Root EC may be more important than root diameter in relation to root functions. However, as the reviewer noted, root EC has not well been referred to in the hypothesis. Actually, we gave explanations for the usage of root EC instead of root diameter to indict thin and thick roots. On the other hand, we understand that the concern by the reviewer may arise from the special pattern of cortex size in thick roots of monocots where the stele rather than cortex dominates root cross area. As for this issue, we have responded in the specific comments section.

Similarly for mycorrhiza colonization as it seems to contrast thin and thick absorptive roots.

Response: As referred to by the reviewer, we have not included mycorrhizal colonization in this study. This is because mycorrhizal colonization, despite it can be quantified to some extent (i.e. the percentage of root length or total number of roots infected with mycorrhizal fungi), it is still difficult to accurately determine resource acquisition (rate and quantity) through mycorrhizal fungi. Additionally, there are usually many different mycorrhizal fungi species even in a single absorptive root. Therefore, mycorrhizal colonization may not be a good trait to accurately indicate difference of resource acquisition across species. However, nutrient foraging through mycorrhizal fungi is important for thick absorptive roots (Baylis 1975; St John 1980; Eissenstat et al. 2015). We speculate that future work on mycorrhizal fungi may be important for revealing the nature of economic strategy in thick absorptive roots. We have added this information in the conclusion section.

I consider this paper addresses relevant scientific questions within the scope of BG and presents novel data on absorptive roots by considering separation of thin and thick based on diameter. However the attractive title does not reflect the data shown. The conclusions should take into account this point of view.

Response: We appreciate these valuable comments from the reviewer and respond to the above general comments and below specific comments. To be honestly, we agree with the review that to consolidate the argument of our view of RES, more traits and trait relationships as well as more species should be considered in future studies.

Specific comments Choice of the measured root traits. It is surprising that for absorptive roots (distal part of root system including apices) the authors did not measure specific root length or root surface area, nor mycorrhiza colonization, traits considered to be linked with resource acquisition whereas the chosen traits (anatomy, chemical) are more related to transport or construction cost. How can you estimate acquisition strategy with such traits? Root tissue density is more related to construction cost of tissue (mainly stele, see Wahl & Ryser 2000) and not to resource acquisition. Root diameter in driving root trait spectra.

Response: The anatomy and chemical traits apart from SRL and mycorrhizal colonization are also the key traits influencing resource absorption in plant roots. Furthermore, these traits have been shown to form a trait syndrome, the diameter-related trait dimension or ecological axis (Kong et al. 2014). The relationship between SRL and root diameter (the above figure) can also suggest the divergence of different strategies in thin and thick absorptive. However, the SRL-root diameter relationship was strong, and thus we have not included SRL in our study. As for the mycorrhizal colonization, we also give the reasons for their not inclusion (see the responses for general comments). On the other hand, despite the traits examined in this study are not too many, they (the diameter, chemicals and anatomy) do represent key aspects of resource absorption as well as preservation in roots. We agree with the review that root tissue density is a trait directly reflecting construction cost of root tissues. Theoretically, the construction cost can be related to root lifespan. For example, higher construction cost could be associated with longer lifespan while tissues with lower construction cost could have short lifespan (see Eissenstat et al. 2000. Building roots in a changing environment: implications for root longevity). The longer lifespan may indicate longer preservation of resource acquired. Therefore, root tissue density can be associated with resource preservation. On the other hand, root tissue density can also indirectly affect root activity (i.e., Picon-Cochard et al 2012. Plant and Soil, 353:47-57). For example, higher root tissue density could result from thickened cell walls or more secondary tissues. This can eventually lead to reduced root activity. Therefore, root tissue density might indirectly impact resource acquisition and preservation in roots which is the kernel of the RES.

Comments on two sentences given page 13044, line 21-22: “Traits syndrome for thicker absorptive roots would differ from the predictions of faster acquisition and shorter lifes-

pan”; and page 13044, line 23-24: “This highlights the importance of discriminating the thicker for the thinner absorptive roots when exploring root strategies”. I agree but this is because in case of your species thick roots have higher proportion of cortex than thin roots while for other species including monocots this is the opposite. What is then important is the proportion of cortex in the surface area, more than the diameter per se. Thus the link between diameter and lifespan is not applicable.

Response: We admit that we have neglected the studies in monocots. It is indeed that the root diameter is contributed mainly by the cortex rather than the stele in many species (i.e., Gu et al. 2014 in Tree Physiology, Kong et al. 2014 in New Phytologist, and the current study). However, in monocots or some other species, the stele rather than the cortex may dominate the size of root diameter or root cross section area. Despite no much data of root lifespan in monocots, we speculate that the thick roots in monocots may also have longer lifespan than thin roots because construction cost for thick roots is usually higher than that for thin roots. However, it is possible, as the reviewer referred to, that roots in monocots may follow the positive root diameter-lifespan relationship but with the slope or R square different from other species. Different from the prediction of the reviewer, we speculate that in thick roots of monocots the size of stele instead of cortex may be more important in influencing trait relationships as the stele dominates the root size. For the thick monocot roots, the majority of stele may be accounted by the parenchyma cells that can serve the storage function. This may be similar to our study where the cortex, we argue, may serve storage of resources. However, we can’t make further prediction as no such data available. Anyways, the authors appreciate much for these valuable comments pointing out an important group of species that should be taken into account. As such, in the revised version we have added some information in this regards.

Furthermore, the presence of mycorrhiza in thick roots also changes the capacity of the roots to uptake nutrients, independently of their morphology. Thus defining a RES with/without mycorrhiza should be explored. Response: It has been acknowledged that the thick absorptive roots depend mainly on mycorrhizal fungi for resource acquisition (see Baylis 1975, Kong et al. 2014, Eissenstat et al. 2015 in New Phytologist). The great dependence on mycorrhizal fungi may be the reason of no acquisition-conservation tradeoff in thick absorptive roots. However, we know little about how mycorrhizal fungi alter the trait relationships in these thick roots. In the revised version, as put in the conclusion, we advocate further studies to reveal the nature of economic strategy in thick roots by emphasizing on the mycorrhizal fungi.

Page 13044, line 24-25: Contrary to the sentence, the effect of root diameter in driving root traits spectra has been tested in monocots (see Drouet et al 2005. European Journal of Agronomy, 22:185–193 ; Picon-Cochard et al 2012. Plant and Soil, 353:47–57; and see Zobel. 2003. New Phytologist, 160:276–279).

Response: The authors thank the review for providing the important information. We have examined the literatures suggested by the review. Despite they have explored effects of root diameter on root trait spectra, the roots used in these studies may not belong to absorptive roots. For example, the coarse roots in Picon-Cochard et al. (2012) refer to the shoot-born roots. The shoot-born roots are similar to the higher-order roots in our studies and Guo et al. (2008 in New Phytologist). In a previous study of grasses, we have revealed significant heterogeneity between shoot-born roots and root-derived roots (roots produced from shoot-born roots, similar to the fine roots in Picon-Cochard's study) with less active for the former than the latter (see Kong et al. 2010 in Plant Soil). We speculate that the shoot-born roots in Picon-Cochard's study may not be the dominant parts of the absorptive roots or even non-absorptive relative to the abundant and active root-derived roots. Therefore, despite previous studies have considered the role of root diameter (i.e., the studies in monocots, and Prieto et al., 2015), the absorptive roots have not been clearly separated, and roots used in these studies may be a mixture of absorptive roots with non- or weakly absorptive roots. Anyway, we appreciate the reminding by the reviewer of studies in monocots.

Methods. Page 13046, line 6-12: precise if all species hold mycorrhiza

Response: The species examined in this study hold mycorrhiza which can refer to Long et al. 2013 and Kong et al. 2014.

Page 13047, line 1-2: Precise if the roots collected in plastic bags were washed or not before or after freezing. This is important for chemical analyses.

Response: Root samples collected in plastic bags and transported in coolers were not washed. Before the chemical measurements, root samples were washed in deionized water. The procedure of root sampling and collection followed previous studies, i.e., Pregitzer et al. (2002) in Ecological Monographs and Guo et al. (2008) in New Phytologist. In the revised version, we have added the information in the corresponding parts of the manuscript.

Page 13047, line 7: The type and company of the stereomicroscope should be given Response: we have added this information in the revised manuscript.

Page 13048, line 1-2: determination of absorptive roots should be developed a bit even always described earlier. Response: we have added some detailed information for determination of the absorptive roots.

Page 13048, line 25: "root EC": why there is no link with hypotheses? Response: In the first hypothesis, we tested divergence of root strategies with root diameter. Here, we used root EC to indicate the size of root diameter. We then separated the fine and coarse absorptive roots according to the thickness of root EC. In the sentences following line 25, we gave detailed explanations for the using of root EC in this study. Therefore, the "root EC" is in fact related to the hypothesis in this study.

Page 13049, line 9: 247_m for root EC: have you tested the normal distribution of fig S1a, because it seems there are 2 groups, 250-300_m being in the middle.

Response: We did test the normal distribution of the data in Fig. S1a. The statistical test showed that the frequency distribution in Fig. S1a had no difference from normal distribution (P=0.995). In other words, they exactly followed the normal distribution.

Page 13049, line 16: Moving average analyses should be more described as there are different methods

Response: We have added some more information about procedures by which we conducted the moving average analyses.

Page 13049, line 17: a point is missing between fit and No.

Response: The authors appreciate the careful comment on this error. We have added a point between fit and No.

Results. thin vs thick absorptive roots: thick roots do not follow the same pattern as thin one: in conclusion can you consider that thick roots are still absorptive roots? The use of RES is not correct in your work (see comments above).

Response: Our results showed that the thick absorptive roots did not follow the same pattern as the thin ones. Nevertheless, these thick roots were still thick absorptive roots. As for these thick roots, they may follow a different strategy, i.e., depending mainly on mycorrhizal fungi for nutrient foraging.

Fig S3: different symbols between thin and thick should be shown

Response: In Fig. S3, we showed the relationship for the thin absorptive roots. There was no significant relationship for the thick roots (see Fig. 2a), and then we had not conducted this analysis here.

Discussion. Page 13052, line 8-10: fig S1 shows distribution of root EC thickness for your species and previous work, but the two distributions seem to be different not similar. The comparison of your dataset with previous studies (supplementary material) raises more questions than answers. For example, fig S1: the two distributions seem different.

Response: Yes, as the reviewer stressed, distributions of the current study and previous study were different. Here, the presentation of the two different distributions was

used to explain the different cutoff points between the thin and thick absorptive roots for the two studies. As data of the current study followed a normal distribution, we used the average of absorptive root diameter (root EC=247 μm) as the cutoff point. While in previous study dominated by thin roots, a smaller root diameter (root EC=182.8 μm) corresponding to the transition of mycorrhizal colonization was used as a cutoff point. Therefore, we give the two different distribution patterns just aiming to justify the selection of cutoff points in the two studies. We also acknowledge that there is no commonly accepted cutoff point to separate the thin from the thick absorptive roots. The method used here represents only one way to discriminate the two root groups. Alternative ways in this regards may be proposed in future studies.

The revised version can refer to the supplement file.

Please also note the supplement to this comment:
http://www.biogeosciences-discuss.net/12/C6371/2015/bgd-12-C6371-2015-supplement.pdf

Interactive comment on Biogeosciences Discuss., 12, 13041, 2015.

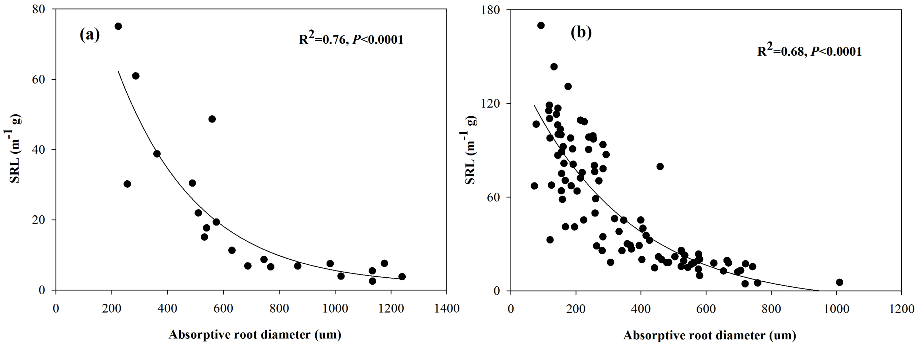

Fig. 1. The relationship between specific root length (SRL) and absorptive root diameter using the current data (a) and a previous study (b). The figure is used in our responses to reviewer 1.