

1 **Dear Editor,**

2 Herewith, we resubmit our manuscript (bg-2015-372) for publication in *Biogeosciences* after
3 finishing the required minor revisions.

4 We appreciate the valuable comments from Dr. Alexandra Weigelt. Below, we explain,
5 point-by-point, how we incorporate the suggestions in our revision and give our replies to the
6 reviewer's comments.

7 Besides our responses to the reviewer's comments, we have made some additional
8 improvements to the manuscript. (1) We follow the editor's suggestion to change 'for' to 'of'
9 in the title of the manuscript. (2) As suggested by the editor, we have added a short section on
10 the implication of our findings for soil processes (Line 361-368). (3) We have added some
11 details to the corresponding author's address (Key Laboratory of Tropical Forest Ecology in
12 Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences). This study has
13 been sponsored by an open fund from the laboratory, and we feel this laboratory should be
14 mentioned on the title page.

15 Further, we apologize for any grammatical missteps. We have carefully revised the
16 manuscript (see the version with marked-up change), and believe it now meets the
17 international standards.

18 We look forward to hearing from you in due course.

19

20 Yours sincerely,

21 Deliang Kong

22

23 **Reviewer comments:**

24 In the revised version of their manuscript the authors present trait data on absorptive roots
25 from seven mostly woody dicots to show that fine and thick absorptive roots differ in their
26 root economic strategies. For five root orders of each species a limited amount of
27 morphological traits was assessed together with total C and N content as well as their labile
28 and recalcitrant fractions. One important morphological trait was root cortex diameter (EC).
29 The data supports the conclusion that thin and thick absorptive roots differ in content of
30 almost all C and N fractions and thus might also be differentiated along the
31 acquisition-conservation trait-off from the root economics spectrum.

32 The paper presents valuable data on an important topic in trait ecology. Root traits and their
33 differentiation and importance are currently very much debated and there is a strong need for
34 data as presented in the current manuscript. Even though seven species is on the low side and
35 the selection of species is from my point of view rather non-ideal (for such a low number I
36 would have voted for either a more general spread e.g. including more conifers and other
37 mycorrhiza types or for more specific thus excluding the fern and the one conifer). However,
38 the morphological results are backed up by a much larger data base, which is convincing. The
39 manuscript is well written and argues soundly. I think the concerns of previous reviewers (of
40 which I am not one) are well met. I have only minor remarks on the manuscript which are
41 listed below.

42

43 **Minor remarks:**

44 *Check throughout for double and missing spaces e.g. L72 or L59 before as.*

45 **Response:** We have carefully checked the manuscript for mistakes such as double and
46 missing spaces.

47

48 *L31: 'fractions' 'At first I was not sure what to expect from this without reading the rest of the*
49 *text. I would expect e.g. different C fractions such as sugar, other carbohydrates etc. from this*
50 *description. This obviously is the case as these differentiations are the central point of the*
51 *paper. I would make sure this is understood right away and denote the measured fractions in*
52 *brackets already in the abstract.*

53 **Response:** We have added the three fractions (see Line 31).

54

55 *L34: 'more' species. I would state 94 species here.*

56 **Response:** We have replaced 'more species' with '96 species' (see Line 35). In Fig S3 of the
57 supporting information, we have excluded two outlier species for the 96 species study and the
58 species number, as the reviewer suggests, should be 94. However, we feel that it is proper to
59 refer to the total number of species (96 species) of that study.

60

61 *L42: 'represents' should be 'represent' as it relates to plant traits which is more than one*
62 *either*

63 **Response:** We have changed ‘represents’ to ‘represent’ (Line 43).

64

65 *L76: effects of*

66 **Response:** We have added ‘of’ after the ‘effects’ (Line 76).

67

68 *L79: in relation to*

69 **Response:** We have added ‘to’ after the ‘relation’ (Line 78).

70

71 *L 86ff: you say roots with less labile C and more labile N indicate acquisitive strategy and*

72 *(89) roots with less labile C and N are conservative. Is this true like this, than only the CN*

73 *ratio would be important or only N as C obviously would than not be decisive for a change in*

74 *root mode.*

75 **Response:** We acknowledge that ‘CN ratio, or N as C’, as pointed out by the reviewer, could

76 also be indicative for acquisitive or conservative strategies of plant roots. However,

77 determination of C and N fractions may be more useful for predicting changes of root

78 strategies. For example, given a certain content of total C, it can appear in at least two cases: 1)

79 higher labile C and lower recalcitrant C fractions; 2) lower labile C and higher recalcitrant C

80 fractions. Although the two cases both can lead to a similar content of total C, they may

81 represent different strategies. In the revised version, we have revised this sentence to show

82 that our argument is based on the perspective of root C and N fractions (Line 84-85).

83

84 *L112: Is there any other justification as to why you chose exactly these species? They are a*
85 *subset of the 96 you published on earlier, I presume, but to me it is a rather strange*
86 *sub-selection with one fern and one conifer. I would recommend another sentence to justify*
87 *this.*

88 **Response:** As stressed by the reviewer, we have included two species (a fern and a conifer
89 species) in addition to five angiosperm species. These two species are selected for two
90 reasons: (I) plant economic strategies have been explored and proved in many different plant
91 species, i.e., conifers and angiosperms (Espeleta et al. 2009), ferns (Dong et al. 2015), cycads
92 (Zhang et al. 2015), different kind of species (Wright et al. 2004; Freschet et al. 2010).
93 Therefore, including the fern and conifer species increases the species pool, and more
94 importantly, extrapolates to some extent our idea of root economic strategies across groups of
95 plant species. However, for logistic constraints, we could only include one fern species and a
96 conifer. As such, we advocate in the concluding paragraph that more species should be
97 included in future studies. (II) The anatomical structures have been explored in one of our
98 previous studies (see Long et al. 2013) and their results may be instructive for our current
99 study. See Line 121-125 for the added information.

100 The papers referred to here are listed below and can also be found in the references section
101 of this manuscript.

102 Dong et al. 2015. Root morphology, histology and chemistry of nine fern species
103 (pteridophyta) in a temperate forest. *Plant and soil*.

104 Espeleta et al. 2009. Tree species fine-root demography parallels habitat specialization across
105 a sandhill soil resource gradient. *Ecology*.

106 Freschet et al. 2010. Evidence of the ‘plant economics spectrum’ in a subarctic flora. *Journal*
107 *of Ecology*.

108 Long et al. 2013. Variation of the linkage of root function with root branch order. *Plos One*.

109 Wright et al. 2004. The worldwide leaf economic spectrum. *Nature*.

110 Zhang et al. 2015. Extending the generality of leaf economic design principles in the cycads,
111 an ancient lineage. *New Phytologist*.

112

113 *L122: ‘are mycorrhizas’ is not correct grammar. Either refer to are colonized with*
114 *mycorrhiza or are mycorrhized.*

115 **Response:** We have changed ‘mycorrhizas’ to ‘mycorrhized’ (Line 121).

116

117 *L204: Why would you use thickness of 247 μm as a cut of? Just because it is the mean and*
118 *thus you would split the data set in half? I have my problems with this rather arbitrary split as*
119 *there is not clear ecological or physiological reasoning behind this size. I think this*
120 *separation earns some justification as well.*

121 **Response:** We acknowledge that there is no commonly accepted cutoff point for separating
122 the thin and thick absorptive roots. In this study, we used mean thickness of root EC as a

123 cutoff point. Such a cutoff point seems effective as it is based on the frequency distribution of
124 root EC thickness. On the other hand, some older and more recent studies have provided a
125 range of evidence including root morphology, physiology and demography to show the
126 different entities of the thin and thick absorptive roots. Therefore, it is likely that the thin and
127 thick absorptive roots may have different economic strategies and that our idea of different
128 economic strategies for the two root groups may not be greatly influenced by the selection of
129 cutoff point. Finally, we hope that the physiologically and ecologically based cutoff point
130 could be developed in future studies.

131

132 *L286-294: There should be no need to justify your study in the discussion. Shorten this part to*
133 *one intro sentence without refs. Those have all been cited in the intro.*

134 **Response:** We have shortened this part to one sentence (Line 289-294).

135

136 *L 296: relatively*

137 **Response:** We have changed 'relative' to 'relatively' (Line 296).

138

139 *L352 strategy*

140 **Response:** We have changed 'strategies' to 'strategy' (Line 349).

141

142 *L361 Notably*

143 **Response:** We have changed ‘Notable’ to ‘Notably’ (Line 358).

144

145 *L391: including*

146 **Response:** We have changed ‘include’ to ‘including’ (Line 395).

147 |

148 | Economic strategies ~~for~~of plant absorptive roots vary with root diameter

149 | Deliang Kong^{1,2*}, Junjian Wang³, Paul Kardol⁴, Huifang Wu⁵, Hui Zeng⁶, Xiaobao Deng¹,

150 | Yun Deng¹

151

152 | ¹ Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden,

带格式的: 字体: (默认) Times
New Roman, (中文) 宋体, 小四

153 | Chinese Academy of Sciences, Mengla, Yunnan, China

154 | ² College of Biosciences and Biotechnology, Shenyang Agricultural University, Shenyang,

155 | China

156 | ³ Belle W. Baruch Institute of Coastal Ecology & Forest Science, Clemson University,

157 | Georgetown, South Carolina, USA

158 | ⁴ Department of Forest Ecology and Management, Swedish University of Agricultural

159 | Sciences, Umeå Sweden

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

161 | ⁶ Key Laboratory for Urban Habitat Environmental Science and Technology, Peking

162 | University Shenzhen Graduate School, Shenzhen, China

163

164 | Author for correspondence:

165 | Tel: +86-024-88487163, Fax: +86-024-88492799

166 | E-mail: deliangkong1999@126.com

167

168

169 **Abstract**

170 Plant roots typically vary along a dominant ecological axis, the root economics spectrum,
171 depicting a tradeoff between resource acquisition and conservation. For absorptive roots,
172 which are mainly responsible for resource acquisition, we hypothesized that root economic
173 strategies differ with increasing root diameter. To test this hypothesis, we used seven plant
174 species (a fern, a conifer, and five angiosperms from south China) for which we separated
175 absorptive roots into two categories: thin roots (thickness of root cortex plus epidermis < 247
176 μm) and thick roots. For each category, we analyzed a range of root traits related to resource
177 acquisition and conservation, including root tissue density, different carbon (C) and nitrogen
178 (N) fractions (i.e., extractive, acid-soluble and acid-insoluble fractions) as well as root
179 anatomical traits. The results showed significant relationships among root traits indicating an
180 acquisition-conservation tradeoff for thin absorptive roots while no such trait relationships
181 were found for thick absorptive roots. Similar results were found when reanalyzing data of a
182 previous study including more96 plant species. The contrasting economic strategies between
183 thin and thick absorptive roots, as revealed here, may provide a new perspective on our
184 understanding of the root economics spectrum.–

185

186 **Key-words:** chemical fractions, plant functional traits, root diameter, root economics
187 spectrum, root tissue density

188

189 **1 Introduction**

190 | Plant traits reflecting a tradeoff between resource acquisition and conservation represents an
191 | essential ecological axis for plant strategies that is important for our understanding of how
192 | plants drive ecosystem processes and ~~ecosystem~~ responses to environmental change
193 | (Cornwell et al., 2008; Freschet et al., 2010; Reich, 2014; Westoby et al., 2002). On the one
194 | end of this ~~ecological~~ axis, there are species with acquisitive strategies, i.e., fast acquisition of
195 | resources (e.g., CO₂ for leaves and nutrients for roots) accompanied with a short lifespan. On
196 | the other end of the axis, there are species with conservative strategies, i.e., slow resource
197 | acquisition accompanied with a long lifespan. Originally, such an ecological axis has been
198 | demonstrated for leaves, which is widely known as the leaf economics spectrum (Diaz et al.,
199 | 2004; Osnas et al., 2013; Wright et al., 2004). More recently, similar trait spectra have been
200 | demonstrated across plant organs from leaves to stems and roots, thus forming a whole ‘plant
201 | economics spectrum’ (Freschet et al., 2010; Laughlin et al., 2010; Prieto et al., 2015; Reich,
202 | 2014).

203 | Resource acquisition in plant roots is performed by absorptive roots, i.e., the first two or
204 | three orders of a root branch with primarily-developed tissues which are part of the commonly
205 | used category of ‘fine roots’ (< 2mm in diameter) (Guo et al., 2008; Long et al., 2013;
206 | Pregitzer et al., 2002). For absorptive roots, ~~the~~ tissue density, i.e., root dry mass per unit root
207 | volume, is a key trait of the root economics spectrum –as tissue density is closely linked to
208 | the acquisition-conservation tradeoff (Bardgett et al., 2014; Birouste et al., 2014; Craine et al.,
209 | 2005; Espeleta et al., 2009; Mommer and Weemstra, 2012; Roumet et al., 2006). In general,
210 | absorptive roots with higher tissue density are slower in nutrient acquisition and longer in
211 | lifespan whereas absorptive roots with lower tissue density may enable faster acquisition but

212 maintain a shorter lifespan (Ryser, 1996; Wahl and Ryser, 2000; Withington et al., 2006).
213 Recently, tissue density for absorptive roots was found to negatively correlate with root
214 diameter. This could be because root cortex is less dense than root stele and because in thicker
215 roots a larger proportion of the root cross-sectional area is accounted for by the cortex (Chen
216 et al., 2013; Kong et al., 2014; Kong and Ma, 2014). On the other hand, compared with
217 thinner absorptive roots, thicker absorptive roots may acquire resources faster because of their
218 greater dependence on mycorrhizal fungi (Eissenstat et al., 2015; Kong et al., 2014; Kong and
219 Ma, 2014; St John, 1980), and may also have a longer lifespan due to the larger diameter.
220 (Adams et al., 2013; Eissenstat and Yanai, 1997; Wells and Eissenstat, 2001). As such, the
221 trait syndrome for thicker absorptive roots would differ from the predictions of faster
222 acquisition and shorter lifespan. This highlights the importance of discriminating thicker and
223 thinner absorptive roots when exploring root strategies. However, ~~we are aware of~~ few studies
224 ~~that~~ have tested for effects of root diameter in driving trait economics spectra in absorptive
225 roots.

226 In addition to structural traits such as density, the chemical composition of absorptive roots
227 may constitute another important aspect of testing root strategies in relation to root diameter
228 (Hidaka and Kitayama, 2011; Meier and Bowman, 2008; Poorter and Bergkotte, 1992;
229 Poorter et al., 2009). For example, carbon (C) and nitrogen (N), the two most abundant
230 elements in plant tissues, are usually bound to organic compounds which may contain labile
231 fractions (e.g., soluble sugars and proteins in living cells) and recalcitrant fractions (e.g.,
232 cellulose and lignin in structural tissues) (Atkinson et al., 2012; Berg and McClaugherty, 2008;
233 Feng et al., 2009; Poorter et al., 2009; Shipley et al., 2006). From the perspective of C and N

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

247 | Here, we selected a variety of plant species common to tropical and subtropical forests in
248 | south China with contrasting phylogeny and root structure. The aim of our study was two-fold.
249 | First, we examined the influence of root diameter on the root economic strategies in
250 | absorptive roots. We hypothesized that the root economic strategies differ between thinner
251 | and thicker absorptive roots, with trait relationships indicating acquisitive-conservative
252 | trade-off for thinner roots but not for thicker roots. The hypothesis was tested using a series of
253 | trait relationships involving both structural and chemical traits. Second, root C and N
254 | fractions have been suggested to vary in predictive ways across branch orders (Fan and Guo,

255 2010; Goebel et al., 2011). However, we hypothesized that patterns of root C and N fractions
256 across branch orders differ in species varying in absorptive root diameter.

257

258 **2 Materials and methods**

259 **2.1 Plant species and sampling sites**

260 We selected seven plant species with contrasting phylogeny and root structure (Table S1) in
261 tropical and subtropical forests in south China. Three species were sampled at the Heshan
262 Hilly Land Interdisciplinary Experimental Station (22°41'N, 112°54'E), Guangdong province.

263 The species were: *Dicranopteris dichotoma* (Gleicheniaceae) (a fern), *Cunninghamia*
264 *lanceolata* (Taxodiaceae) (a conifer) and *Acacia auriculiformis* (Leguminosae) (a tree).

265 Another tree species, *Paramichelia baillonii* (Magnoliaceae), was sampled in Wutongshan
266 National Forest Park (22°27'-22°52'N, 113°37'-114°37'E) in Shenzhen, Guangdong province.

267 Three other tree species, *Gordonia axillaris* (Theaceae), *Endospermum chinense*

268 (Euphorbiaceae) and *Cryptocarya chinensis* (Lauraceae), were sampled in Jianfengling

269 Nature Reserve (18°23'-18°50'N, 108°36'-109°05'E), Hainan province. Roots of these species

270 are mycorrhizal. Including plant species from the fern, conifer to angiosperms could
271 extrapolate to some extent our idea of root economic strategies across different groups of
272 plant species. In addition, anatomical structures of some species have been explored in one of
273 our previous studies (see Long et al., 2013) and their results may be instructive for our current
274 study. More information on sites and species can be found in Table S1 and [in](#) Long et al.

275 (2013).

276

277 **2.2 Root sampling**

278 Roots were collected at a soil depth of 0-10 cm in June and July 2011. For each species, at
279 least three mature trees were selected. We first tracked the main lateral roots by carefully
280 removing surface soil at the base of each plant with a specially manufactured fork. Root
281 branch order was defined according to Pregitzer's study with the most terminal branch as the
282 first-order (Pregitzer et al., 2002). The intact roots were collected and soil adhering to the
283 roots was carefully removed. We distinguished all four root orders for *D. dichotoma* and the
284 first five orders for the other species. A portion of each root sample was immediately put into
285 Formalin-Aceto-Alcohol (FAA) solution (90 ml 100% ethanol, 10 ml 100% glacial acetic
286 acid) for later anatomical assessments. The remaining unwashed part of each root sample was
287 placed in plastic bags and transported in a cooler to the laboratory. These root samples were
288 then frozen until measurements of root morphology and chemistry (Pregitzer et al., 2002).

289

290 **2.3 Root tissue density**

291 For each species, 50 root segments for the first order, 30 segments for the second order, and
292 20 segments for the third to the fifth order were randomly picked for measuring root diameter
293 and length. Depending on root size, the root diameter was measured under a 40× or 20×
294 stereomicroscope (MZ41-2B, MshOt, Guangzhou, China). The length of comparatively short
295 roots was assessed using a stereomicroscope with an ocular micrometer (± 0.025 mm) while a
296 measuring tape with the minimum scale of 0.5 mm was used for relatively long roots (Guo et
297 al., 2008). After root diameter and length were recorded, roots were oven-dried at 65 °C for
298 48 h and weighed. Root tissue density was calculated by dividing root dry mass by root

299 volume assuming roots are cylindrically shaped (Kong et al., 2014). In addition, specific root
300 length (SRL) was calculated as the root length divided by its dry mass.

301

302 **2.4 Root anatomy**

303 Root segments from the FAA solution were cleaned with deionized water (4 °C) and then
304 transferred to glass Petri dishes for dissection into different branch orders. Root anatomy was
305 determined according to Long et al. (2013). Briefly, a minimum of 10 root segments were
306 randomly chosen for each root order. All root segments were dehydrated in an ethanol
307 solution series to absolute ethanol, purified in 100% xylene and embedded in paraffin. Root
308 cross-sections were then cut into slices of 8 μm thick using a microtome (Rotary Microtome
309 KD-2258, Zhejiang, China). After deparaffinage, the root slices were stained first by safranin
310 and then by fast green. Following this staining procedure, the cortex and epidermis was in
311 blue and the stele was in red. The root slices were then photographed by a light microscope
312 (Carl Zeiss Axioscop 20, Jena, Germany). The size of anatomical structures including
313 epidermis, cortex and stele was measured using Image J software (NIH Image, Bethesda, MD,
314 USA). Absorptive roots in a root branch were defined based on root anatomy (Guo et al.,
315 2008). Here, root orders were classified as absorptive roots when they had no or little
316 secondary xylem (Long et al., 2013). Specifically, absorptive roots referred to the first two
317 orders for *D. dichotoma*, the first three orders for *A. auriculiformis*, *G. axillaris*, *C. lanceolata*,
318 *E. chinense* and *C. chinensis*, and the first four orders for *P. baillonii*, respectively (Fig. S1).

319

320 **2.5 Chemical analyses**

带格式的：字体：非倾斜

带格式的：字体：非倾斜

带格式的：字体：非倾斜

321 The frozen root samples were put into deionized water to carefully remove any soil particles
322 or dead organic matter that adhered to but was not a-part of the root (Pregitzer et al., 2002).
323 The samples of each root branch order were then oven-dried (65 °C for 24 h), milled (ZM200,
324 Retsch, Germany), and mixed homogeneously for chemical analyses. Root C and N
325 concentrations were determined using an element analyzer (VarioEl, Elementar
326 Analysen-systeme GmbH, Germany). Root C fractions (extractive, acid-soluble fraction,
327 acid-insoluble fraction) were determined by a sulfuric acid digestion method. First, we
328 separated the extractive and labile C fraction from other C fractions. A subsample of c. 100
329 mg (m_0) was extracted with 15 ml of cetyl trimethylammonium bromide (CTAB) solution for
330 3 h, filtered, repeatedly washed with de-ionized water until pH was 7.0, and then oven-dried
331 at 60 °C to a constant weight (m_1). Second, the filtered residue was digested with 30 ml
332 sulfuric acid (72 %) at 22 °C for 3 h, filtered, repeatedly washed (until pH was 7.0), dried and
333 weighed (m_2). After the acid-digestion step, the ash content (m_3), was determined by
334 combusting 15-30 mg of sample at 550 °C for 4 h. Finally, the extractive ~~fraction~~, acid-soluble-
335 ~~fraction~~, and acid-insoluble fractions were calculated as $100\% \times (m_0 - m_1) / (m_0 - m_3)$, $100\% \times$
336 $(m_1 - m_2) / (m_0 - m_3)$, and $100\% \times (m_2 - m_3) / (m_0 - m_3)$, respectively. Here, the extractive fraction
337 was considered as the labile C fraction while acid-soluble and acid-insoluble fractions were
338 considered as the recalcitrant C fraction.

339 An about 5mg subsample of residue left after the above acid-digestion procedure was used
340 to measure N concentration and N allocation in the acid-insoluble C fraction. The N in the
341 extractive fraction was too low to measure. Thus, estimates of N in the acid-soluble fraction
342 were calculated as the difference between total N and N in the acid-insoluble fraction.

343

344 | 2.6 Statistical Data analyses

345 Relationships between root tissue density and root N concentration and each of the three C
346 fractions were assessed by linear regressions. Here, we introduced a new term, 'root EC'
347 | referring to tissues outside the stele including the epidermis ~~plus and~~ cortex. Root EC was
348 used for two reasons. First, the thickness of root EC can be a proxy of the size of root
349 diameter ($R^2=0.91$ and $R^2=0.99$ for linear regressions in this study and in Kong et al. (2014),
350 respectively). Second, root EC can be used as an indicator of root chemical composition as
351 the storage of root labile C and most of root N is found in root EC (Chen et al., 2013). The
352 relationships between the thickness of root EC and root tissue density and root chemical
353 fractions were also investigated with linear regressions. In addition, the relationship between
354 SRL and thickness of root EC was fitted by exponential regression.

355 To explore the effect of root diameter on root ecological strategies, the above analyses were
356 repeated for thin and thick absorptive roots, respectively. A mean thickness of 247 μm was
357 used for root EC as the cut-off point between thin and thick absorptive roots. The mean
358 thickness of root EC was used because the thickness of root EC for absorptive roots followed
359 a normal distribution ($p>0.05$, indicating that thickness was statistically no different from a
360 normal distribution; Fig. S2a). To avoid the influence of biological N fixation on relationships
361 between root N and root tissue density and root EC, a legume species, *A. auriculiformis*, was
362 excluded in these analyses. In addition, the relationship between the extractive C fraction and
363 root tissue density was further explored by a quadratic polynomial regression using moving
364 average data (Fig. S4). Polynomial regressions were run both for the thin and thick absorptive

365 roots. The moving average data were obtained as follows. First, the extractive C fraction was
366 sorted along with the ascending order of root tissue density. Then, the extractive C fraction
367 and root tissue density were averaged by bins (Reich and Oleksyn, 2004), with bins referring
368 to each of the two neighboring data of extractive C fraction or root tissue density, respectively.
369 Moving average analyses were used as it improved the goodness of fit. No polynomial
370 regression relationships were found for the other two C fractions.

371 We acknowledge that the seven species we used represent a relative small species pool. To
372 validate the results of our study, another dataset of 96 woody species from one of our
373 previous studies was used where only the first-order roots were ~~included~~ measured (Kong et
374 al., 2014). For these 96 species, we did not use the average root EC thickness as the cut-off
375 between thin and thick absorptive roots. This was because root EC of these species followed a
376 skewed normal distribution with abundant species having thinner root EC ($p < 0.05$, indicating
377 that thickness was statistically different from a normal distribution; Fig. S2b). In the case of a
378 skewed normal distribution, the cut-off point based on mean root EC might cause bias ~~for~~ in
379 separating thin and thick absorptive roots. Here, a thickness of 182.8 μm for root EC was used
380 as a cut-off between thin and thick absorptive roots for these species (Kong et al., 2014). The
381 thickness of 182.8 μm for root EC corresponded to a transition from lower to higher
382 mycorrhizal colonization with increasing root diameter (Kong et al., 2014). This transition
383 may also indicate a divergence of strategy between thin absorptive roots (depending mainly
384 on roots themselves for resource acquisition) and thick absorptive roots (depending mainly on
385 mycorrhizal fungi for resource acquisition, or the mycotrophy) (Baylis, 1975; Eissenstat et al.,
386 2015; Liu et al., 2015; St John, 1980). In this dataset, relationships between root tissue density

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

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

394

395 **3 Results**

396 **3.1 Root trait relationships for thin and thick absorptive roots**

397 Root tissue density was negatively correlated with root N concentration for total and thin but
398 not for thick absorptive roots (Fig. 1). Similarly, using a larger species pool, negative
399 relationships between root tissue density and root N concentration were found for total and
400 thin but not for thick absorptive roots (Fig. S3).

401 For thin absorptive roots, the extractive C fraction peaked at medium root tissue density
402 (Fig. 2a). Moving average analysis revealed a quadratic relationship between the extractive C
403 fraction and root tissue density in thin absorptive roots (Fig. S4a), while no relationships were
404 found between acid-soluble and acid-insoluble fractions and root tissue density. The
405 recalcitrant C fraction (acid-soluble C + acid insoluble C) in thin absorptive roots showed a
406 quadratic relationship with root tissue density (Fig. S4b). It was also noted that in the thin
407 absorptive roots, the acid-soluble and [acid](#)-insoluble fractions were relatively higher in the

408 higher and lower range of root tissue density, respectively (Fig. 2b,c). For thick absorptive
409 roots, none of the three C fractions were correlated with root tissue density (Fig. 2, Fig. S4).

410 Across total absorptive roots, thickness of root EC was positively correlated with total root
411 N concentration (Fig. 3a) and negatively with root N in the acid-insoluble fraction (Fig. 3b).
412 Thickness of root EC was also positively correlated with the extractive C fraction (Fig. 3c)
413 and negatively with the acid-insoluble fraction (Fig. 3e). However, in each of thin and thick
414 absorptive roots, no relationships were found between thickness of root EC and either of these
415 chemical fractions (all p values > 0.05, Fig. 3a-e).

416 Thickness of root EC decreased linearly with root tissue density (Fig. 4), but no
417 relationships were found when separated between thin and thick absorptive roots. Using a
418 large species pool we found a very similar pattern: a significant relationship between
419 thickness of root EC and root tissue density for total absorptive roots, a weaker relationship
420 for thin absorptive roots and no relationship for thick absorptive roots (Fig. S5). In addition,
421 we found exponential relationships between SRL and thickness of root EC for the species in
422 our current study as well as for [the](#) larger species pool from a previous study (Fig. S6).

423

424 **3.2 Effects of plant species and root order on root C and N fractions**

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

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

436

437 4 Discussion

438 ~~The acquisition-conservation tradeoff in plants has been suggested to be consistent across~~
439 ~~plant organs (roots, leaves, and stems), as such constituting a key ecological axis, i.e., the~~
440 ~~‘plant economics spectrum’ (Freschet et al., 2010; Prieto et al., 2015; Reich, 2014). The~~
441 negative relationship between root tissue density and root N concentration ~~across total~~
442 ~~absorptive roots~~ supports the acquisition-conservation tradeoff, and hence, the existence of
443 economic strategies in absorptive roots. ~~This is~~ because absorptive roots with higher tissue
444 density usually have longer lifespan (Eissenstat and Yanai, 1997; Ryser, 1996; Withington et
445 al., 2006); while their lower N concentration ~~would be associated with~~ indicates slow resource
446 acquisition (Kong et al., 2010; Mommer and Weemstra, 2012; Reich et al., 2008). However,
447 our results further showed that the negative relationship between root tissue density and root
448 N concentration held for thin but not for thick absorptive roots (Fig. 1). Although these results
449 were based on a relatively small number of species, reanalysis of data from a previous study
450 including 96 species (Kong et al., 2014) revealed very similar patterns (Fig. S1). As such, trait

451 relationship between root N concentration and root tissue density supports our first hypothesis
452 of different economic strategies for ~~the~~ thin and thick absorptive roots.

453 The trait relationships between root tissue density and root C fractions provide further
454 support for ~~our~~ hypothesis. Theoretically, absorptive roots with lower tissue density would
455 have higher activity, while higher root activity also consumes more labile C thus leaving less
456 labile and more recalcitrant C fractions in these roots. In contrast, in absorptive roots with
457 higher tissue density, more C is used for structural tissues demanding recalcitrant C fractions
458 (Fan and Guo, 2010). Therefore, we would expect an inverted U-shaped relationship for labile
459 C fractions and a U-shaped relationship for recalcitrant C fractions when these C fractions
460 would be correlated with root tissue density. As expected, for thin absorptive roots we found
461 an inverted U-shaped relationship between the labile C fraction and root tissue density (Fig.
462 S4a) and a U-shaped relationship between recalcitrant C fractions (acid-soluble C + acid
463 insoluble C) and root tissue density (Fig. S4b). The higher acid-soluble C fraction with
464 increasing root tissue density (Fig. 2b) suggest that thin absorptive roots with higher tissue
465 density are constructed with more acid-soluble C compounds, such as cellulose, rather than
466 acid-insoluble C compounds, such as lignin, possibly because of higher energy demands for
467 the production of lignin than for the production of cellulose (Novaes et al., 2010).. However,
468 different from thin absorptive roots, there were no relationships between root C fractions and
469 root tissue density for thick absorptive roots (Fig. 2, Fig. S4). Therefore, trait relationships
470 between root C fractions and root tissue density provides further evidence for an
471 acquisition-conservation tradeoff ~~economics strategy infor~~ thin absorptive roots, but not for
472 thick absorptive roots.

473 Furthermore, observed relationships between thickness of root EC and root C and N
474 fractions provides the third piece of support for our hypothesis of ~~different-contrasting~~
475 economic strategies with root diameter. Across total absorptive roots, thickness of root EC
476 was positively correlated with root N concentration and the extractive C fraction while ~~being~~
477 negatively correlated with the acid-soluble C fraction and N in the acid-soluble C fraction.
478 This suggests that compared with thin absorptive roots, thick absorptive roots acquire
479 resources at higher rates as indicated by their higher N concentration and lower C and N in
480 recalcitrant fractions. Meanwhile, thick absorptive roots may also have longer lifespan
481 because of their larger root diameter (Adams et al., 2013; Anderson et al., 2003; McCormack
482 et al., 2012; Wells and Eissenstat, 2001). These findings seem to contrast with an
483 acquisition-conservation tradeoff. Further, we showed that relationships between thickness of
484 root EC and root chemical fractions only held across the full spectrum from thin to thick
485 absorptive roots. Nevertheless, it was also noted that root tissue density showed a greater
486 range of variation for thin than for thick absorptive roots. For thin absorptive roots, variation
487 in root tissue density might arise from secondary thickening of root EC cell walls (Eissenstat
488 and Achor, 1999; Long et al., 2013; Ryser, 2006; Wahl and Ryser, 2000). This could be
489 associated with lower root activity and hence lower root N concentration (Fig. 1, Fig. S3). ~~As~~
490 ~~such, and~~ an acquisition-conservation tradeoff in thin absorptive roots ~~ew~~ould be expected.
491 However, for thick absorptive roots, the cell size, as well as the cortical cell file number
492 (Chimungu et al., 2014a, b), may be more important than cell wall thickening in determining
493 root activity. If so, root activity may be less affected by thickening of root EC cell walls than

494 | by changing the size or number of these cells. As such, ~~and~~ there would ~~thus~~ be no ~~clear~~
495 | obvious economic strategies for thick absorptive roots.

496 | Recent studies have revealed different nutrient foraging strategies for thin and thick
497 | absorptive roots with the former depending on roots themselves and the latter depending more
498 | on mycorrhizal fungi (Baylis, 1975; Eissenstat et al., 2015; Liu et al., 2015). These
499 | observations are supported by the SRL-thickness relationship we found in our study where
500 | thin roots had larger SRL ~~and SRL of than~~ thick roots ~~was constantly smaller~~ (Fig. S6). Here,
501 | our results further indicate that thin and thick absorptive roots may follow different economic
502 | strategies when foraging for nutrients. These findings may have important implications for the
503 | emerging debate on the root economics spectrum. For example, the existence of an economic
504 | ~~strategies~~ for plant roots has been commonly accepted (Craine et al., 2005; Espeleta et al.,
505 | 2009; Freschet et al., 2010; Reich, 2014). However, some recent studies have challenged the
506 | ubiquity of root economics spectra by showing no (Chen et al., 2013) or positive (Kong et al.,
507 | 2014) relationships between root diameter and root N concentration. One possible explanation
508 | for ~~these contrasting conflicting~~ findings ~~of these studies~~ is the inclusion of many species with
509 | thick absorptive roots. Including these species may potentially obscure trait relationships
510 | indicating acquisition-conservation tradeoffs. On the other hand, the lack of evidence of an
511 | acquisition-conservation tradeoff may have resulted from the larger proportion of root
512 | cross-section area accounted for by root EC compared to the stele (Table S2; Kong et al.,
513 | 2014). ~~Notably~~, for species like monocots, the area of root stele is much larger than the area
514 | of root EC. We did not ~~include~~ monocots in our study, but it would be interesting to test
515 | whether the contrasting economic strategies for thin and thick absorptive roots, as presented

516 here, can be applied across mono-dicots. Furthermore, our findings of different economic
517 strategies for thin and thick absorptive roots are important for understanding plant impacts on
518 soil processes. Acquisitive species are usually associated with bacterial-dominated soil
519 microbial communities, faster carbon and nutrient cycling, and stronger plant-soil feedbacks,
520 while conservative species are usually associated with fungal-dominated soil microbial
521 communities, slower carbon and nutrient cycling, and weaker plant-soil feedbacks (Bardgett
522 et al., 2014; Kardol et al., 2015; Wardle et al., 2004). This suggests that the impacts of
523 absorptive roots on soil processes would depend on root diameter.

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

538 recalcitrant C fractions in lower-order compared with higher-order woody roots (Goebel et al.,
539 2011). However, our results may challenge the generality of slower decomposition of
540 lower-order relative to higher-order roots as some lower-order roots had less recalcitrant C
541 fractions and hence faster decomposition than higher-order roots.

542 In conclusion, the results of our study suggest an acquisition-conservation tradeoff for thin
543 absorptive roots but not for thick absorptive roots. In addition, we found different patterns of
544 root chemical fractions with root diameter and root order. The contrasting economic strategies
545 between thin and thick absorptive roots are important in advancing our understanding of root
546 ecology and the links with aboveground plant counterparts. Yet, our knowledge on the
547 functioning of plant roots and their roles in driving soil ecosystem processes is still limited.

548 We hope that our study presents an instructive perspective on the root economics spectrum
549 that will stimulate further research in this field. Future studies may test to what extent our
550 results hold for other (groups of) plant species (e.g., monocots, ferns, or conifers), including
551 a larger spectrum of functional traits (including those associated with interactions with
552 rhizosphere biota), and unravel the mechanisms underlying the ‘non-economics strategy’ for
553 thick absorptive roots. Further, we anticipate that the mycotrophy (i.e., plant species
554 association with mycorrhizal fungi for resource acquisition) may underlie economics
555 strategies in thick absorptive roots; however, empirical studies are needed to confirm this.

556

557 **References**

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

带格式的: 行距: 2 倍行距

域代码已更改

带格式的: 字体: (默认) Times
New Roman, 小四

560 Anderson, L. J., Comas, L. H., Lakso, A. N., and Eissenstat, D. M.: Multiple risk factors in
561 root survivorship: a four-year study in Concord grape, *New Phytologist*, 158, 489-501, 2003.

562 Atkinson, R. R. L., Burrell, M. M., Osborne, C. P., Rose, K. E., and Rees, M.: A non-targeted
563 metabolomics approach to quantifying differences in root storage between fast- and
564 slow-growing plants, *New Phytologist*, 196, 200-211, 2012.

565 Bardgett, R., D., , Mommer, L., and De Vries, F., T.: Going underground: root traits as drivers
566 of ecosystem processes, *Trends in Ecology and Evolution*, 29, 692-699, 2014.

567 Baylis, G.: Magnolioid mycorrhiza and mycotrophy in root systems derived from it. In:
568 *Endomycorrhizas*, Sanders, F. E., Mosse, B., and Tinker, P. B. (Eds.), Academic Press, 1975.

569 Berg, B. and McClaugherty, C.: *Plant litter: decomposition, humus formation, carbon*
570 *sequestration*, Springer, 2008.

571 Birouste, M., Zamora-Ledezma, E., Bossard, C., Pérez-Ramos, I., and Roumet, C.:
572 Measurement of fine root tissue density: a comparison of three methods reveals the potential
573 of root dry matter content, *Plant and Soil*, 374, 299-313, 2014.

574 Chapin III, F. S.: The mineral nutrition of wild plants, *Annual Review of Ecology, Evolution*
575 *and Systematics*, 11, 233-260, 1980.

576 Chen, W., Zeng, H., Eissenstat, D. M., and Guo, D.: Variation of first-order root traits across
577 climatic gradients and evolutionary trends in geological time, *Global Ecology and*
578 *Biogeography*, 22, 846-856, 2013.

579 Chimungu, J. G., Brown, K. M., and Lynch, J. P.: Large root cortical cell size improves
580 drought tolerance in maize, *Plant Physiology*, 166, 2166-2178, 2014a.

581 Chimungu, J. G., Brown, K. M., and Lynch, J. P.: Reduced root cortical cell file number

582 improves drought tolerance in maize, *Plant Physiology*, 166, 1943-1955, 2014b.

583 Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H.,

584 Stenlid, J., Finlay, R. D., Wardle, D. A., and Lindahl, B. D.: Roots and associated fungi drive

585 long-term carbon sequestration in boreal forest, *Science*, 339, 1615-1618, 2013.

586 Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy,

587 O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Queded, H. M.,

588 Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P.,

589 Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E.,

590 Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V., and Westoby, M.:

591 Plant species traits are the predominant control on litter decomposition rates within biomes

592 worldwide, *Ecology Letters*, 11, 1065-1071, 2008.

593 Craine, J. M., Lee, W. G., Bond, W. J., Williams, R. J., and Johnson, L. C.: Environmental

594 constraints on a global relationship among leaf and root traits of grasses, *Ecology*, 86, 12-19,

595 2005.

596 Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A.,

597 Montserrat-Martí G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S.,

598 Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N.,

599 Pérez-Rontomé M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R.,

600 Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V.,

601 Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez,

602 M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M. R.: The plant traits

603 that drive ecosystems: Evidence from three continents, *Journal of Vegetation Science*, 15,

604 295-304, 2004.

605 Eissenstat, D. M. and Achor, D. S.: Anatomical characteristics of roots of citrus rootstocks
606 that vary in specific root length, *New Phytologist*, 141, 309-321, 1999.

607 Eissenstat, D. M., Kucharski, J. M., Zadworny, M., Adams, T. S., and Koide, R. T.: Linking
608 root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest, *New
609 Phytologist*, 208, 114-124, 2015.

610 Eissenstat, D. M. and Yanai, R. D.: The ecology of root lifespan, *Advances in Ecological
611 Research* 27, 1-60, 1997.

612 Espeleta, J. F., West, J. B., and Donovan, L. A.: Tree species fine-root demography parallels
613 habitat specialization across a sandhill soil resource gradient, *Ecology*, 90, 1773-1787, 2009.

614 Fan, P. and Guo, D.: Slow decomposition of lower order roots: a key mechanism of root
615 carbon and nutrient retention in the soil. , *Oecologia*, 163, 509-515, 2010.

616 Feng, Y. L., Lei, Y. B., Wan, R. F., Callaway, R. M., Valiente-Banuet, I., Li, Y. P., and Zheng,
617 Y. L.: Evolutionary tradeoffs for nitrogen allocation to photosynthesis versus cell walls in an
618 invasive plant, *Proceedings of the National Academy of Sciences USA*, 106, 1853-1856,
619 2009.

620 Freschet, G. T., Cornelissen, J. H., Van Logtestijn, R. S., and Aerts, R.: Evidence of the 'plant
621 economics spectrum' in a subarctic flora, *Journal of Ecology*, 98, 275-301, 2010.

622 Goebel, M., Hobbie, S. E., Bulaj, B., Zadworny, M., Archibald, D. D., Oleksyn, J., Reich, P.
623 B., and Eissenstat, D. M.: Decomposition of the finest root branching orders: linking
624 belowground dynamics to fine-root function and structure, *Ecological Monographs*, 81,
625 89-102, 2011.

626 Guo, D., Xia, M., Wei, X., Chang, W., Liu, Y., and Wang, Z.: Anatomical traits associated
627 with absorption and mycorrhizal colonization are linked to root branch order in twenty-three
628 Chinese temperate tree species, *New Phytologist*, 180, 673-683, 2008.

629 Hidaka, A. and Kitayama, K.: Allocation of foliar phosphorus fractions and leaf traits of
630 tropical tree species in response to decreased soil phosphorus availability on Mount Kinabalu,
631 Borneo, *Journal of Ecology*, 99, 849-857, 2011.

632 Kardol, P., Veen, G. F., Teste, F. P., and Perring, M. P.: Peeking into the black box: a
633 trait-based approach to predicting plant–soil feedback, *New Phytologist*, 206, 1-4, 2015.

634 Kong, D., Ma, C., Zhang, Q., Li, L., Chen, X., Zeng, H., and Guo, D.: Leading dimensions in
635 absorptive root trait variation across 96 subtropical forest species, *New Phytologist*, 203,
636 863-872, 2014.

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

640 Kong, D. L. and Ma, C. E.: Acquisition of ephemeral module in roots: a new view and test,
641 *Scientific Reports*, 4, 5078, 2014.

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

645 Liu, B., Li, H., Zhu, B., Koide, R. T., Eissenstat, D. M., and Guo, D.: Complementarity in
646 nutrient foraging strategies of absorptive fine roots and arbuscular mycorrhizal fungi across
647 14 coexisting subtropical tree species, *New Phytologist*, 208, 125-136, 2015.

648 Long, Y., Kong, D., Chen, Z., and Zeng, H.: Variation of the linkage of root function with root
649 branch order, PLoS ONE, 8, e57153, 2013.

650 Lux, A., Luxova, M., Abe, J., and Morita, S.: Root cortex: structural and functional variability
651 and responses to environmental stress, Root Research, 13, 117-131, 2004.

652 McCormack, M. L., Adams, T. S., Smithwick, E. A., and Eissenstat, D. M.: Predicting fine
653 root lifespan from plant functional traits in temperate trees, New Phytologist, 195, 823-831,
654 2012.

655 Meier, C. L. and Bowman, W. D.: Links between plant litter chemistry, species diversity, and
656 below-ground ecosystem function, Proceedings of the National Academy of Sciences USA,
657 105, 19780-19785 2008.

658 Mommer, L. and Weemstra, M.: The role of roots in the resource economics spectrum, New
659 Phytologist, 195, 725-727, 2012.

660 Novaes, E., Kirst, M., Chiang, V., Winter-Sederoff, H., and Sederoff, R.: Lignin and biomass:
661 a negative correlation for wood formation and lignin content in trees., Plant Physiology, 154,
662 555-561, 2010.

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

665 Poorter, H. and Bergkotte, M.: Chemical composition of 24 wild species differing in relative
666 growth rate, Plant Cell and Environment, 15, 221-229, 1992.

667 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., and Villar, R.: Causes and consequences
668 of variation in leaf mass per area (LMA): a meta-analysis, New Phytologist, 182, 565-588,
669 2009.

670 Pregitzer, K. S., DeForest, J. L., Burton, A. J., Allen, M. F., Ruess, R. W., and Hendrick, R. L.:
671 Fine root architecture of nine North American trees, *Ecological Monographs*, 72, 293-309,
672 2002.

673 Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao,
674 Z., Pierret, A., Portillo, N., Rouspard, O., Thammahacksa, C., and Stokes, A.: Root functional
675 parameters along a land-use gradient: evidence of a community-level economics spectrum,
676 *Journal of Ecology*, 103, 361-373, 2015.

677 Reich, P. B.: The world-wide 'fast-slow' plant economics spectrum: a traits manifesto,
678 *Journal of Ecology*, 102, 275-301, 2014.

679 Reich, P. B. and Oleksyn, J.: Global patterns of plant leaf N and P in relation to temperature
680 and latitude, *Proceedings of the National Academy of Sciences USA*, 101, 11001-11006, 2004.

681 Reich, P. B., Tjoelker, M. G., Pregitzer, K. S., Wright, I. J., Oleksyn, J., and Machado, J. L.:
682 Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants, *Ecology*
683 *Letters*, 11, 793-801 2008.

684 Roumet, C., Urcelay, C., and Díaz, S.: Suites of root traits differ between annual and perennial
685 species growing in the field, *New Phytologist*, 170, 357-368, 2006.

686 Ryser, P.: The Importance of Tissue Density for Growth and Life Span of Leaves and Roots: A
687 Comparison of Five Ecologically Contrasting Grasses, *Functional Ecology*, 10, 717-723,
688 1996.

689 Ryser, P.: The mysterious root length, *Plant and Soil*, 286, 1-6, 2006.

690 Shipley, B., Lechowicz, M. J., Wright, I. J., and Reich, P. B.: Fundamental trade-offs
691 generating the worldwide leaf economics spectrum, *Ecology*, 87, 535-541, 2006.

692 St John, T. V.: Root size, root hairs and mycorrhizal infection: a re- examination of Baylis's
693 hypothesis with tropical trees, *New Phytologist*, 84, 483-487, 1980.

694 Wahl, S. and Ryser, P.: Root tissue structure is linked to ecological strategies of grasses, *New*
695 *Phytologist*, 148, 459-471, 2000.

696 Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä H., van der Putten, W. H., and Wall,
697 D. H.: Ecological Linkages Between Aboveground and Belowground Biota, *Science*, 304,
698 1629-1633, 2004.

699 Wells, C. E. and Eissenstat, D. M.: Marked Differences in Survivorship among Apple Roots
700 of Different Diameters, *Ecology*, 82, 882-892, 2001.

701 Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., and Wright, I. J.: Plant ecological
702 strategies- some leading dimensions of variation among species, *Annual Review of Ecology,*
703 *Evolution and Systematics*, 33, 125-159, 2002.

704 Withington, J. M., Reich, P. B., Oleksyn, J., and Eissenstat, D. M.: Comparisons of structure
705 and life span in roots and leaves among temperate trees, *Ecological Monographs*, 76, 381-397,
706 2006.

707 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F.,
708 Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E.,
709 Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J.
710 J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L.,
711 Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.:
712 The worldwide leaf economics spectrum, *Nature*, 428, 821-827, 2004.

713 Xiong, Y. M., Fan, P. P., Fu, S. L., Zeng, H., and Guo, D. L.: Slow decomposition and limited

714 | nitrogen release by lower order roots in eight Chinese temperate and subtropical trees., Plant
715 | and Soil, 363, 19-31, 2013.

716

717 **Acknowledgements**

718 | We thank Dr. Zhengxia Chen and Ms Yingqian Long for their assistance in measuring root
719 | chemicals and anatomical structures, and Dr. Chengen Ma and Dr. Xin Jing (Peking
720 | University) for their valuable contribution to this work. We also appreciate two anonymous
721 | reviewers, [Dr. Alexandra Weigelt](#) and the editor Michael Bahn for their valuable comments
722 | on [discussion-earlier](#) versions of this manuscript. This study was sponsored by the open fund
723 | of Key Laboratory of Tropical Forest Ecology in Xishuangbanna Tropical Botanical Garden,
724 | Chinese Academy of Sciences and Natural Science Foundation of China (No. 31200344).

带格式的: 字体: (默认) Times
New Roman, 小四, 字体颜色: 自
动设置, 检查拼写和语法, 图案:
清除

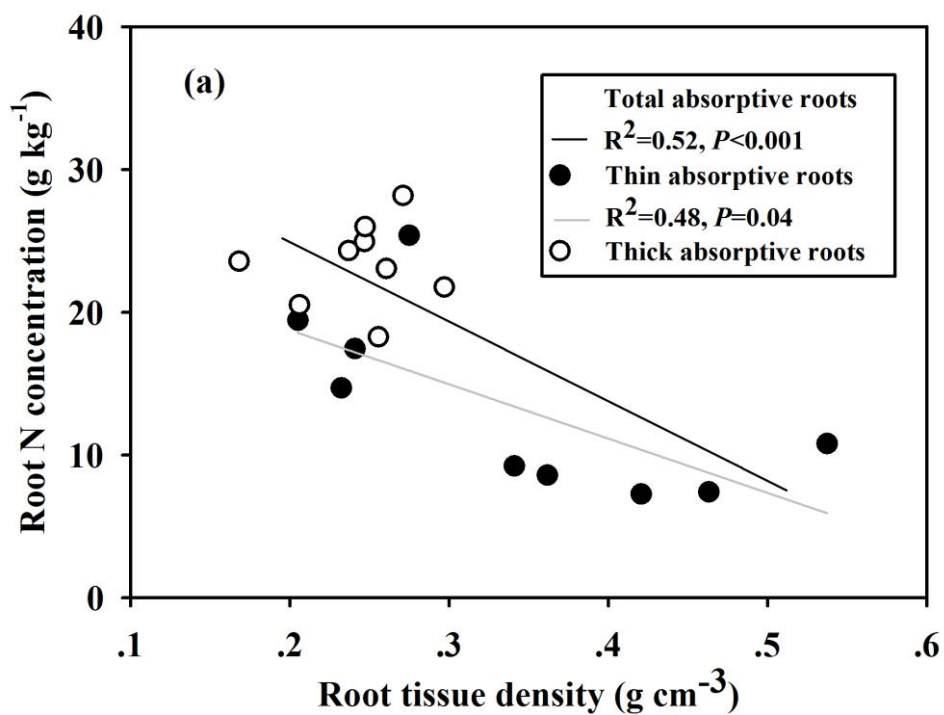
725 **Table 1.** *F* values of two-way ANOVAs testing effects of plants species and root branch
 726 order on the extractive C fraction, acid-soluble C fraction, acid-insoluble C fraction, N
 727 concentration, and N in acid-insoluble C fraction. *, **, *** arewere significant level at 0.05,
 728 0.01, 0.001, respectively.

	Extractive C fraction	Acid-soluble C fraction	Acid-insoluble C fraction	N concentration	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***

729 **Figures**

730 Fig. 1 Relationships between root tissue density and root N concentration for total (black line),

731 thin (solid circles, grey line) and thick (open circles) absorptive roots.

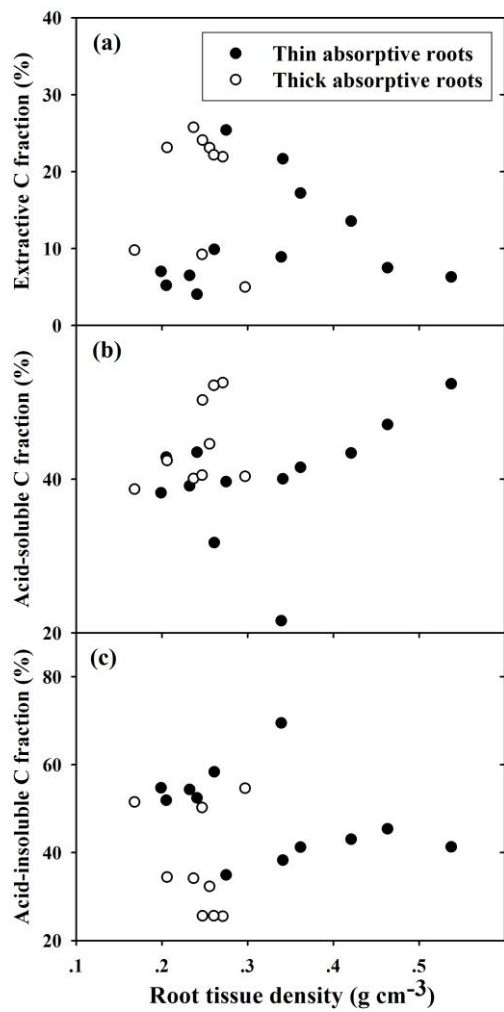


732

733

734

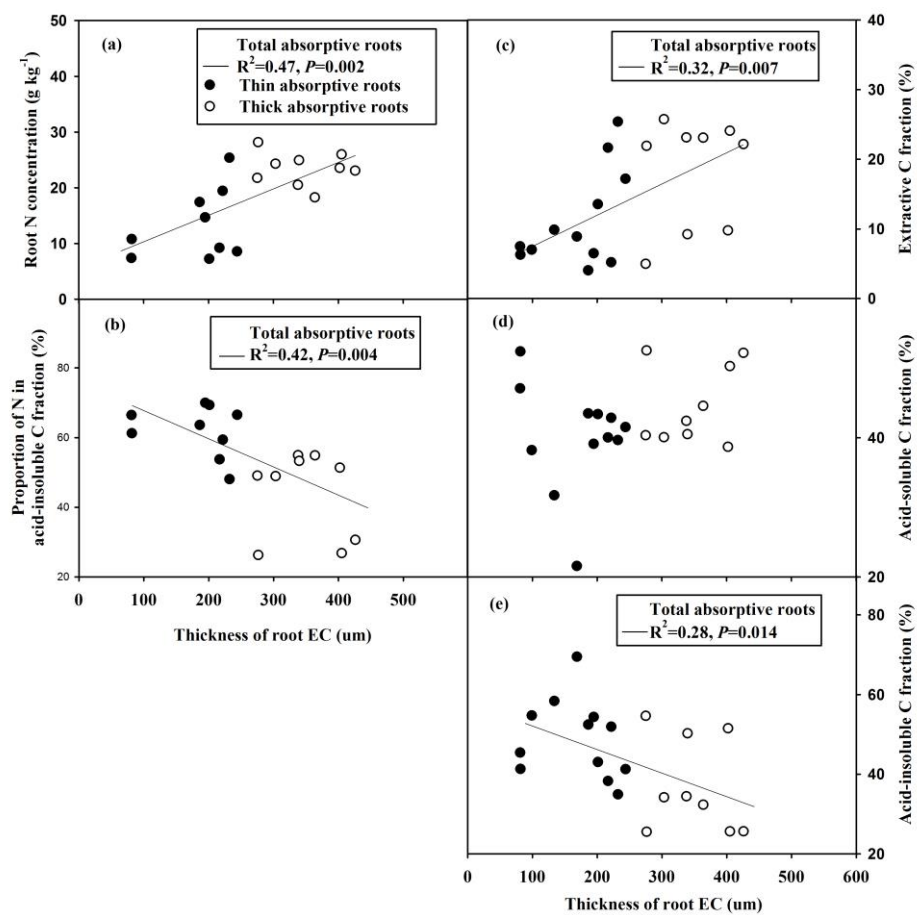
735 Fig. 2 Relationships between root tissue density and extractive C fraction (a), acid-soluble C
736 fraction (b) and acid-insoluble C fraction (c), for thin (solid circles) and thick (open circles)
737 absorptive roots.



738

739

740 Fig. 3 Relationships between thickness of root EC and root N concentration (a), N in
 741 acid-insoluble C fraction (b), extractive C fraction (c), acid-soluble C fraction (d) and
 742 acid-insoluble C fraction (e) for total (black line), thin (solid circles) and thick (open circles)
 743 absorptive roots.

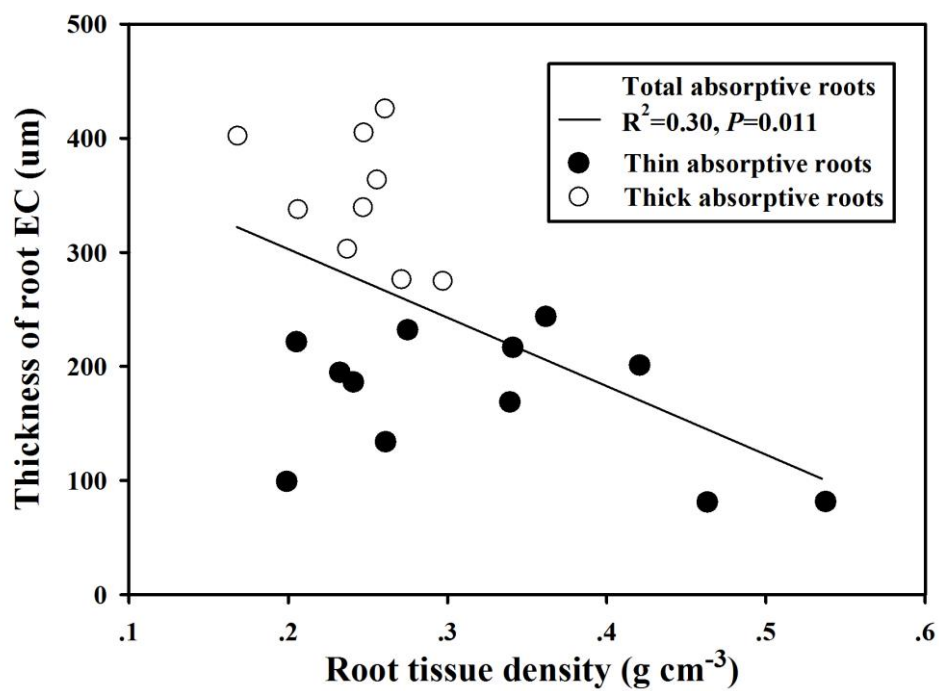


744

745

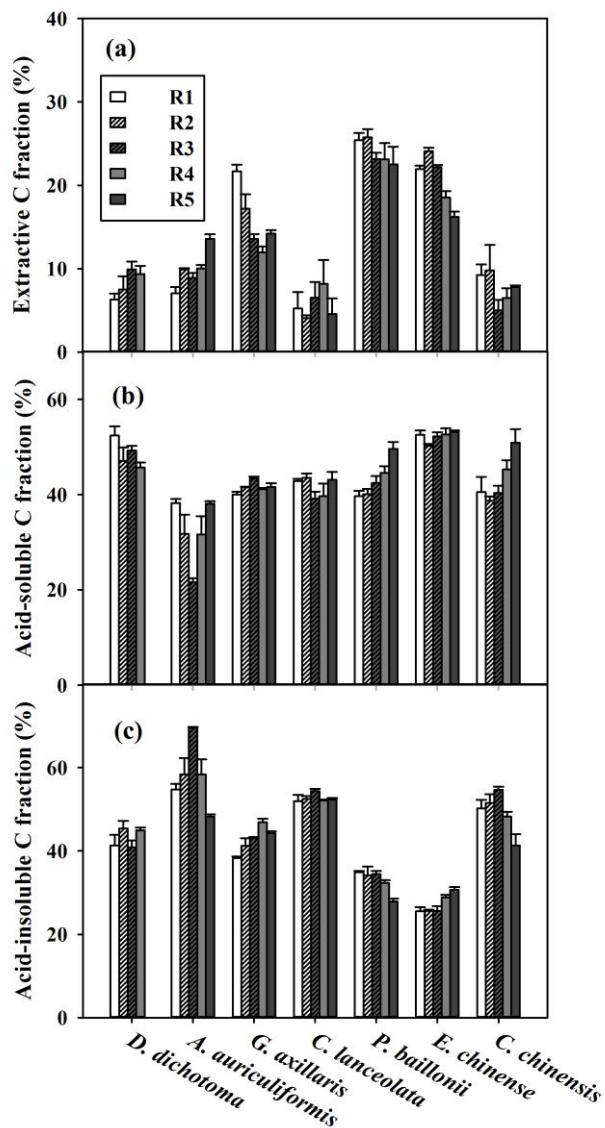
746

747 Fig. 4 Relationships between root tissue density and thickness of root EC for total, thin (solid
748 circles, black line) and thick (open circles) absorptive roots.



749
750
751

752 Fig. 5 The extractive C fraction (a), acid-soluble C fraction (b) and acid-insoluble C fraction
 753 (c) for the first five root orders for each of seven plant species. R1-R5 refer to the first to fifth
 754 order.

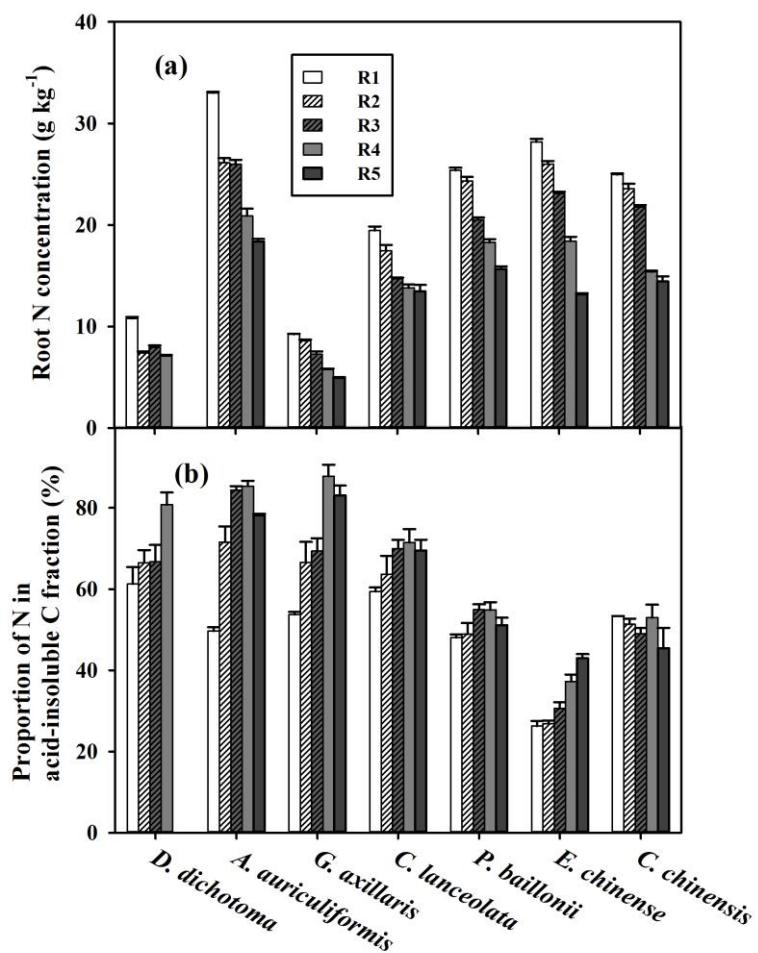


755

756

757 Fig. 6 Root N concentration (a) and N in acid-insoluble C fraction (b) for the first five root

758 branch orders for each of seven plant species. R1-R5 refer to the first to fifth order.



759