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4 "Low-cost" initial burst of root development in whole *Fagus crenata* seedlings: The key to survival?

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Abstract

Terrestrial plants are rooted in one place, and therefore their metabolism must be flexible to adapt to continuously changing environments. This flexibility is probably influenced by the divergent metabolic traits of plant organs. However, direct measurements on organ-specific metabolic rates are particularly scarce and little is known about their roles in determining whole-individual meatabolism. To reveal this on seedlings of *Fagus crenata*, which is one of the most widespread dominant genus in temperate deciduous broad leaf forests in the circum-polar Northern Hemisphere, we measured respiration, fresh mass and surface area for total leaves, stems and roots of 55 individuals in two years from germination and analyzed their relationships with individual metabolism. Proportion of roots to whole plant in mass increased from approximately 17% to 74%, and that in surface area increased from about 11% to 82% in the two years. Nonetheless, the increment of the proportion of root respiration to whole-plant respiration was from 9.2% to only 40%, revealing that the increment in mass and surface area of roots was much larger than the increment in energetic cost. As a result, only the roots showed a substantial decline in both respiration/surface area and respiration/mass among the three organs; roots had about 90% decline in their respiration/surface area, and 84% decline in their respiration/mass, while those in leaves and stems were relatively constant. The low-cost and rapid root development is specific to the two years after germination and would be effective for avoiding water and nutrient deficit, and possibly helps seedling survival. This drastic shift in structure and function with efficient energy use in developmental change from seeds to seedlings may underpin the establishment of *F. crenata* forests. We discuss significance of lowering energetic cost for various individual organisms to effectively acquire resources from a wide perspective of view.

Introduction

Individual metabolism is a fundamental process that transforms energy and materials to

50 support various biological processes as a base for adaptation to changing environments [1,2].

51 Therefore, the metabolic rate has profound physiological, ecological and evolutionary implications

52 [3,4], which would be a key to understand and predict the effects of climate change on organisms

53 and ecosystems [1,2].

54   In general, the metabolic rate (i.e. respiration rate, R) of individual organisms scales with body

55 size (X), and is usually described as the simple power function of body mass:

56 $$R \ = \ aX^b \#(\mathbf{1})$$

57 where a is a normalization constant, and b is the scaling exponent (slope on the log-log coordinates)

58 [5–7]. The equation (1) represents the emergent outcomes of the metabolism of individuals under

59 various constraints [2,8,9]. Therefore, to obtain a mechanistic insight into the regulation of scaling of

60 metabolic rate, we need empirical evidence of whole-organism measurements. However, little is

61 known about the relationships between metabolic rate and body size with the reliable data from small

62 to giant individuals [10]. This is because most of the studies on metabolic scaling have been based on

63 indirect evidence and aimed to construct theoretical models to explain the exponent b, which has

64 widely been assumed to be 3/4 as suggested by the WBE model [5–9]. The size scaling of individual

65 organisms results from the sum of differentiated organs with distinctive functions and structure, each

66 one showing contrasting responses under changing environments [11–13]. Therefore, evaluating

67 metabolic rate of each organ is crucial to understand the scaling of metabolism associating with body

68 size, namely mass or surface area.

69   Terrestrial plants are supposed to adapt to various environments by adjusting the biomass

70 partitioning among organs, as typically shown in the root/shoot ratio [11–17]. To date, the optimal

71 partitioning theory has mainly evaluated allocation between shoot and roots in mass. It suggests that

72 plants should allocate more biomass to the shoot when limiting resource is carbon and to the roots

73 when limiting resource is water or nutrient [11,17]. However, in spite of the significant implication

74 of metabolic rate, few studies have compared metabolic rate of shoot (leaves + stems) and roots at

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75 the whole-plant level [18]. The comparison of respiration rate between shoot and roots, with

76 measurement of organ-specific respiration at the individual level, would provide a new insight into

77 the energy partitioning and would progress our understanding about whole-plant adaptation for

78 resource acquisition.

79   The purpose of this study is to understand the processes of establishment of individual

80 seedlings of *Fagus crenata* under varying environments on the basis of the partitioning theory

81 [11,17], considering the allocation of individual mass, surface area, and energy to the different

82 organs. *Fagus* is one of the most widespread dominant genus in temperate deciduous broad leaf

83 forests in the circum-polar Northern Hemisphere [19–21]. Under low light conditions, *Fagus*

84 seedlings are characterized by high mortality in current year of germination, which is called as

85 bottleneck phase [22–26]. We hypothesize that the effective adaptation of seedlings for survival

86 beyond the bottleneck phase is largely dependent on the partitioning of energy within each

87 individual. To test this assumption, we need size-scaling of respiration that cover seedlings in

88 current-year of germination and 1-year old.

89   Here, we show the respiration rates of total leaves, stems, and roots of various sized seedlings

90 and size-scaling of organ-specific respiration to discuss the shift of the partitioning of energy within

91 individuals during the two years after germination. To date, little is known about the whole-plant

92 physiology of *Fagus* seedlings in the bottleneck phase. Our empirical study on the partitioning of

93 energy would clarify how seedlings survive over the bottleneck phase, which would greatly affect

94 the population dynamics of forest in the circum-polar Northern Hemisphere under changing

95 environment [14,26,27]. Finally, we discuss efficient energy use in divergent individual organisms to

96 effectively acquire resources.

97

Materials and methods

Ethics statement

Our study included fieldwork activities for collecting *F. crenata* seeds and seedlings, and were conducted in Japanese National Forest. The field work was permitted by the Shonai District Forest Office and did not involve any endangered or protected species.

Seed collection and plant materials

The measurements were performed on current-year (n = 46) and 1-year-old (n = 9) seedlings of *F. crenata*, raised from seeds in pots outside the Yamagata University Tsuruoka Campus (38°73′N, 139°82′E). The seeds were collected from a mature forest of *F. crenata* in Tsuruoka (38°30′N, 139°57′E), Yamagata prefecture in 2015 and 2016 to prepare 1-year-old and current-year seedlings, respectively.

The pots were filled with commercially available Kanuma pumice mixed with leaf mold, and kept in a place with sufficient natural light and well-watered. We conducted every measurement at the whole-plant level, using total leaves (including cotyledon), stems, and roots. The whole-plant fresh mass ranged between 41.2×10^{-5} and 23.5×10^{-3} (kg) from the smallest current-year seedling to the largest 1-year-old individual, as compiled in Table 1.

Table 1. Compilation of the minimum and maximum values of fresh mass, surface area, and respiration of whole plant, roots, leaves, and stems at the individual level among all seedlings (n = 55).

	Fresh mass $(\times 10^{-5}\,\mathrm{kg})$			Surface area $(\times 10^{-4}\,\mathrm{m}^2)$			Respiration rate $(\times 10^{-4}\,\mathrm{\mu mol\ sec}^{-1})$		
	min.	max.	max./min.	min.	max.	max./min.	min.	max.	max./min.
Whole plant	41.2	2350	57.0	23.6	1210	51.3	8.70	131	15.1
Roots	7.04	1730	246	2.54	998	393	0.800	52.6	65.8
Leaves	19.3	172	8.91	19.2	185	9.64	4.60	53.3	11.6
Stems	8.52	480	56.3	1.43	31.8	22.2	1.10	42.3	38.5

119 Every measurement is including both current-year and 1-year-old seedlings.

120

Measurement of respiration rates and surface area

122 We separated the seedlings into leaves, stems, and roots, and enclosed them separately in

123 custom-made chambers (80 or 160 cm³), promoting air circulation within the chamber using a DC

124 fan. We confirmed that the separation did not have an effect on the measured values of whole-plant

125 respiration, as reported by Mori et al. [10]. Increment rates of CO_2 concentrations within the closed

126 air-circulation system were measured every 5 seconds using an infrared CO_2 analyzer (GMP343,

127 Vaisala, Helsinki, Finland), and normalized to 20℃ assuming a standard $Q_{10} = 2$. During the

128 measurements, we kept the plant materials wrapped in wet paper to prevent transpiration, and the

129 measurements were taken within 20 minutes of the excavation for each seedling.

130 Leaf surface area was measured with an area meter (LI-3100C, LICOR, Lincoln, NE, USA),

131 and stem surface area was determined as sum of the surface area of stem sections, following a

132 cylindrical approximation from their diameter and length. Roots were scanned at 800 dpi resolution

133 with a flatbed scanner (Epson Perfection V800, Seiko Epson, Japan), followed by the measurements

134 of root surface area with image analytical software (WinRhizo, Regent Instruments, Quebec,

135 Canada).

136

Data analysis

137

138   We fitted the respiration–fresh mass and respiration–area scaling relationships using a

139   simple-power function on log-log coordinates, based on reduced major axis regression (RMA) [28]

140   of the log transformed version of equation (1), using all the measurement data of the 55 seedlings

141   from current-year to 1-year-old. We also analyzed the size-scaling values for surface area in relation

142   to fresh mass (based on RMA) for organs, and their respiration per unit mass and surface area in

143   relation to whole-plant mass (based on ordinary least squares regression, OLS) on the log-log

144   coordinates. In the analysis for the size-scaling of respiration per unit mass and surface area, OLS

145   analysis performed adequately rather than RMA. All of the data used for the regression analysis

146   were compiled in S1 File.

147

Results

Whole-plant respiration

150   Whole-plant respiration reflects individual adaptation as an integrated use of energy

151   partitioned to leaves, stems, and roots. To consider the total energy use of individuals, we showed

152   relationships of whole-plant respiration (R; μmol s^{-1}) to fresh mass (M; kg) and surface area (S; m^2)

153   of the seedlings from current-year to 1-year old on log-log coordinates. We fitted them with a simple

154   power function (1) (Fig. 1, Table 2). Astonishingly, there was no significant difference between the

155   exponents for the scaling of R to M ($b = 0.647$, 95% CI of b: 0.584 to 0.702, $r^2 = 0.898$; Fig.1a) and

156   that of R to S ($b = 0.685$, 95% CI of b: 0.625 to 0.738, $r^2 = 0.892$; Fig. 1b). The $b = 0.647$ for R to M

157   was closer to $2/3 \approx 0.667$, being significantly different from the $b = 3/4 = 0.75$ that was predicted by

158   the WBE model.

159

160   **Fig. 1 Relationship between whole-plant respiration and (a) whole-plant fresh mass and (b)**

161   **whole-plant surface area.** Each point is an individual seedling of current-year (filled, n = 46) and

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162   1-year-old (open, n = 9). An exponent b (with 95% confidence interval) is the RMA slope fit to all

163   points in each relationship.

164

165   **Table 2. Scaling of respiration rate (μmol sec^{-1}) of whole plant, roots, leaves, and stems with**

166   **their fresh mass (kg) and surface area (m^2) fitted by equation (1).**

Independent variable		Exponent (b)	95% CI of b	Normalization constant (a)	95% CI of a	r^2
Whole plant	Mass	0.647	0.584, 0.702	0.185	0.122, 0.258	0.898
	Surface area	0.685	0.625, 0.738	0.0637	0.0487, 0.0807	0.892
Roots	Mass	0.712	0.641, 0.774	0.158	0.0913, 0.247	0.917
	Surface area	0.631	0.588, 0.675	0.0288	0.0228, 0.0359	0.944
Leaves	Mass	1.09	0.977, 1.20	6.37	2.69, 13.9	0.792
	Surface area	1.12	0.921, 1.27	0.598	0.203, 1.27	0.739
Stems	Mass	0.811	0.756, 0.875	0.292	0.187, 0.490	0.883
	Surface area	0.972	0.896, 1.06	0.791	0.464, 1.54	0.879

167   In all regression, number of observation = 55, using RMA on log-log coordinates (for all cases, P <

168   0.001).

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170   # **Respiration of organs**

171   To see how organ-specific respiration contribute to the size-scaling of R shown in Fig. 1, we

172   analyzed the size-scaling values for area in relation to mass (Fig. 2), and evaluated the relationships

173   between respiration of roots, leaves, and stems (R_R, R_L, R_S; μmol s^{-1}) and their fresh mass (M_R, M_L,

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174   M_S; kg) and surface area (S_R, S_L, S_S; m²) separately, at the whole-organ level (Fig. 3, Table 2).

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176   **Fig. 2 Relationships between surface area and fresh mass in plant organs at the whole-organ**

177   **level.** Each point is total leaves (diamonds, n = 55), stems (triangles, n = 55), and roots (circles and

178   squares, n = 97) of current-year (filled) and 1-year-old seedlings (open). Roots depicted by squares

179   (n = 42) were obtained from current-year seedlings (n = 16) and 1-year-old seedlings (n = 26) that

180   were not used for respiration measurement. An exponent b (with 95% confidence interval) is the

181   RMA slope of equation (1) fit to all points in each organ-specific relationship on log-log coordinates.

182

183   **Fig. 3 Relationships between respiration and (a) fresh mass and (b) surface area in plant**

184   **organs.** Each point is total leaves (diamonds), stems (triangles), and roots (circles) of the individual

185   seedling in Fig. 1 of current-year (filled, n = 46) and 1-year-old (open, n = 9). An exponent b (with

186   95% confidence interval) is the RMA slope fit of equation (1) to all points (n = 55) in each

187   relationship.

188

189   The roots had a 246-fold range in mass (M_R) and 393-fold range in surface area (S_R), revealing

190   that S_R–M_R relationship showed a significantly positive allometry, as shown in Fig. 2. On the other

191   hand, root respiration (R_R) varied within only 65.8-fold range, providing significantly low b values

192   for the size-scaling of R_R to M_R (b = 0.712, 95% CI of b: 0.641 to 0.774, r² = 0.917; Fig. 3a) and R_R

193   to S_R (b = 0.631, 95% CI of b: 0.588 to 0.675, r² = 0.944; Fig. 3b). Although the difference of b

194   values was not significant, the exponent b of R_R to S_R was relatively lower than that of R_R to M_R,

195   indicating that the increase in S_R was more efficient than that in M_R. This seems to represent an

196   energetically efficient growth to effectively enhance water acquisition by increasing absorptive

197   surface area with minimum carbon cost.

198   The leaves showed an 8.91-fold range of mass (M_L) and 9.64-fold range of surface area (S_L),

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199   providing nearly isometric scaling of S_L–M_L relationship in Fig. 2. Further, the 11.6-fold range of

200   leaf of respiration (R_L) was close to that of M_L and S_L. Consequently, we found that leaves had

201   isometric scaling for both relationships of R_L to M_L ($b = 1.09$, 95% CI of b: 0.977 to 1.20, $r^2 = 0.792$;

202   Fig. 3a) and R_L to S_L ($b = 1.12$, 95% CI of b: 0.921 to 1.27, $r^2 = 0.739$; Fig. 3b).

203   The stems had a 56.3-fold variation in mass (M_S) and 22.2-fold range of surface area (S_S),

204   revealing a negative allometric scaling of the S_S–M_S relationship in Fig. 2. Respiration (R_S) showed a

205   38.5-fold range, which was smaller than the range of M_S, but larger than that of S_S. Consequently, the

206   scaling of R_S to M_S was negatively allometric ($b = 0.811$, 95% CI of b: 0.756 to 0.875, $r^2 = 0.883$;

207   Fig. 3a), whereas the scaling of R_S to S_S was nearly isometric ($b = 0.972$, 95% CI of b: 0.896 to 1.06,

208    $r^2 = 0.879$; Fig. 3b).

209

Respiration per unit mass and surface area of organs

211   We evaluated the respiration rate (energetic cost) per unit mass and surface area of organs, as

212   related to total individual mass (M) on the log-log coordinates, fitting the relationships with a simple

213   power function (1) (Fig. 4 and Table 3). For the roots, both R_R/M_R ($b = -0.456$, 95% CI of b: -0.541

214   to -0.381, $r^2 = 0.751$; Fig. 4a) and R_R/S_R ($b = -0.575$, 95% CI of b: -0.642 to -0.497, $r^2 = 0.781$; Fig.

215   4b) decreased with increasing M, resulting in the steepest change among the three organs.

216   Conversely, for the leaves both R_L/M_L ($b = 0.00415$, 95% CI of b: -0.0470 to 0.0516, $r^2 = 0.\,000379$;

217   Fig. 4a) and R_L/S_L ($b = -0.00695$, 95% CI of b: -0.0720 to 0.0511, $r^2 = 0.000846$; Fig. 4b) were

218   almost constant, regardless of M. Finally, for the stems R_S/M_S declined with increasing M ($b =$

219   -0.242, 95% CI of b: -0.309 to -0.167, $r^2 = 0.460$; Fig. 4a), but R_S/S_S was independent of M ($b =$

220   -0.0644, 95% CI of b: -0.135 to 0.0216, $r^2 = 0.0511$; Fig. 4b).

221

222   **Fig. 4 (a) Respiration/fresh mass and (b) respiration/surface area of plant organs in relation to**

223   **whole-plant fresh mass.** Each point is total leaves (diamonds), stems (triangles), and roots (circles)

224 of the individual seedling in Fig. 1 of current-year (filled, n = 46) and 1-year-old (open, n = 9). Lines

225 are OLS regression line of equation (1) fit to all points in each relationship, and details of the

226 regression analysis are compiled in Table 3.

227

228 **Table 3. Scaling of respiration per unit mass (µmol sec^{-1} kg $^{-1}$) and per unit surface area (µmol**

229 **sec^{-1} m^{-2}) of roots, leaves, and stems (n = 55) with whole-plant mass fitted by equation (1).**

Dependent variable	Exponent (b)	95% CI of b	Normalization constant (a)	95% CI of a	r^2
R_R/M_R	−0.456	−0.541, −0.381	0.0708	0.0389, 0.109	0.751
R_R/S_R	−0.575	−0.642, −0.497	0.00565	0.00380, 0.00930	0.781
R_L/M_L	0.00415	−0.0470, 0.0516	3.25	2.35, 4.24	0.000379
R_L/S_L	−0.00695	−0.0720, 0.0511	0.300	0.200, 0.425	0.000846
R_S/M_S	−0.242	−0.309, −0.167	0.285	0.189, 0.458	0.460
R_S/S_S	−0.0644	−0.135, 0.0216	0.652	0.405, 1.12	0.0511

230 In all regression, number of observation = 55, using OLS on log-log coordinates.

231

232 These results indicate that only roots show a significant decline in the energetic cost per unit

233 surface area as well as per unit mass with increasing whole-plant mass. On the regression line, the

234 R_R/S_R declined about 90% and the R_R/M_R declined about 84%, indicating that energetic cost per unit

235 surface area declined more rapidly than that per unit mass.

236

237 # Partitioning of individual mass, surface area, and respiration to organs

238 The scaling of whole-plant respiration is determined by 1) the relative contribution of each

239 organ to total mass and surface area, and 2) the organ-specific respiration per unit mass and surface

240 area. Table 1 shows the maximum and minimum values of respiration, mass, and surface area of

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241 organs in the seedlings from current-year to 1-year old. It indicates that the proportion of roots to

242 whole plant increased greatly both in mass and surface area with increasing M; the proportion of

243 roots to whole plant in mass increased from approximately 17% (7.04/41.2) to 74% (1730/2350) and

244 that in surface area increased from about 11% (2.54/23.6) to 82% (998/1210). Nonetheless, the

245 increment of the proportion of root respiration was from 9.2% (0.800/8.70) to only 40% (52.6/131),

246 revealing that the increment in the proportion of roots to whole plant is much more larger in mass

247 and surface area than in energetic cost.

248   These results revealed that the similarity between the R–M (Fig. 1a) and R–S (Fig. 1b)

249 relationships in their scaling exponents (Table 2) was largely due to the equally significant increase

250 in the proportion of root mass and area. Hence, the combined effect of increasing root proportion and

251 the decreasing mass- and area-specific respiration in the roots induced the negative allometry in the

252 scaling of whole-plant respiration.

253

Discussion

Role of low-cost initial burst of root development

256   The significantly negative allometry of R_R to S_R (Fig. 3b) that provided the drastic decrease in

257 R_R/S_R (Fig. 4b) indicate that the root development in two years after germination is energetically

258 efficient and effective for enhancing water and nutrient acquisition with minimum energy cost. The

259 decrese in the energetic cost at root surface area (R_R/S_R) is probably mainly due to consumption of

260 energy reserves in seeds. During the initial growth stage after the exhaustion of energy reserves, the

261 photosynthetic performance remains lowest among whole life stages [29–31], and gradually

262 increases accompanied by accumulation of nutrient with leaves thickening [29]. Therefore, the

263 low-cost burst in root development seems to be reasonable and indispensable process for seedlings to

264 induce the increase in photosynthesis. At the same time, this process would help to avoid water and

265 nutrient deficit of tiny seedlings.

266

Ontogenetic shift in root/shoot ratio from seedlings to mature trees

268   Our study suggests the need for further work at the whole-plant level up to mature trees, to

269   clarify the role of low-cost rapid root development, beyond the initial seedling stage. Figure 5 depicts

270   the relationship between root/shoot ratio in mass ($M_R/M_{Shoot} = M_R/(M_L + M_S)$) and whole-plant mass

271   (M) of *F. crenata* from seedlings to mature trees (n = 346, compiled in S1 File), including the

272   materials in this study (n = 55) and pot- (n = 178) and field-grown (n = 113) individuals from our

273   prior work [10,32]. This figure also shows root/shoot ratio in respiration ($R_R/R_{Shoot} = R_R/(R_L + R_S)$)

274   for the 55 current-year and 1-year-old seedlings, and indicates that their M_R/M_{Shoot} increases much

275   greater than R_R/R_{Shoot} with increasing M.

276

277   **Fig. 5 Plot of root/shoot ratios against whole-plant mass of *Fagus crenata* from germination to**

278   **mature trees.** The total plot number of the root/shoot ratio in mass is 346 (compiled in S1 File). Red

279   and blue symbols represent the root/shoot ratio of the 55 seedlings in mass and respiration,

280   respectively (circles; current-year seedlings; n = 46, triangles; 1-year-old seedlings; n = 9). Filled and

281   open diamonds represent root/shoot ratio in mass of pot-grown (n = 178) and field-grown (n = 113)

282   individuals, respectively that were obtained from our prior work.

283

284   As to M_R/M_{Shoot}, the rapid increment is specific of the seedling stage, but after that, it gradually

285   declines with size (and presumably age) in both pot- and field-grown individuals. The decrease in

286   M_R/M_{Shoot} after the seedling stage should coincide with the gradual increase in photosynthetic

287   performance during ontogenetic transition [29–31], entailing a decrease in R_R/R_{Shoot}. Since

288   measurements were performed in healthy individuals, it is probable that the individuals that did not

289   reach high M_R/M_{Shoot} during the first year after germination had already died. Therefore, keeping low

290   M_R/M_{Shoot} during the initial growth stage may be one of the physiological reasons for death of

291 seedlings in the bottleneck phase [22–25], and seedling survival under natural conditions is likely to

292 depend on the rapid and low-cost development of roots at the individual level.

293   During the development from seeds to seedlings, the source that activates individual

294 metabolism shift from chemical energy in seeds to current assimilation after initiation of

295 photosynthesis [1,2,33]. This shift in the energy source may successively generate the low-cost burst

296 in root development with shifting individual structure and function that would help to avoid water

297 and nutrient deficit [11,17], and reduce mortality of seedlings.

298

Importamce of lowering energetic cost for various individual organisms

301   Banavar et al. [34] suggested that plants and animals have reached equivalent energetic

302 efficiencies through their independent evolution, using our prior data on whole-plant respiration from

303 seedlings to giant trees [10]. Fundamentally, the studies on improvement of energetic efficiency have

304 focused on animal locomotion and often suggested energy-saving mechanism as a strategy for

305 effective resource acquisition [35–38]. On the other hand, although the resource acquisition is

306 essential for all individual organisms including both plants and animals, very few studies have

307 focused on energetic efficiency of terrestrial plants. Hence, whole-plant level empirical data on

308 energetic cost in shoot and root would be important for us to obtain the understanding of physical

309 and physiological constraints on metabolic scaling of terrestrial plants [10,39].

310   Plants are rooted in one place and they must acquire resources under continuously changing

311 environment. Therefore, it is expected that plant metabolism must be flexible, relying on rapid

312 adjustments in energetic efficiency. In this respect, the negative allometry of whole-plant respiration

313 shown in Fig. 1 seems to indicate an improvement in flexibility for resource acquisition with body

314 size, involving changes in the energy partitioning among organs. Therefore, the initial spurt and

315 reduction in energetic cost in root development (shown in Figs. 2–4) could be considered as one of

14

316　the underlying processes to effectively improve whole-plant energetic efficiency. In that case, it may

317　be an energy-saving process of seedlings that is comparable to that in animal locomotion for resource

318　acquisition [35–38]. In the present study, the measurement at the whole-plant level revealed the

319　drastic reduction in energetic cost for rapid root development that would underpin the population

320　dynamics and sustainability of the Northern Hemisphere forests that are dominated by *Fagus* trees

321　[19–21]. The understanding of metabolic scaling of individual organisms would help to scale up the

322　structure and function from organ level to ecosystem level [40–42].

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Acknowledgments

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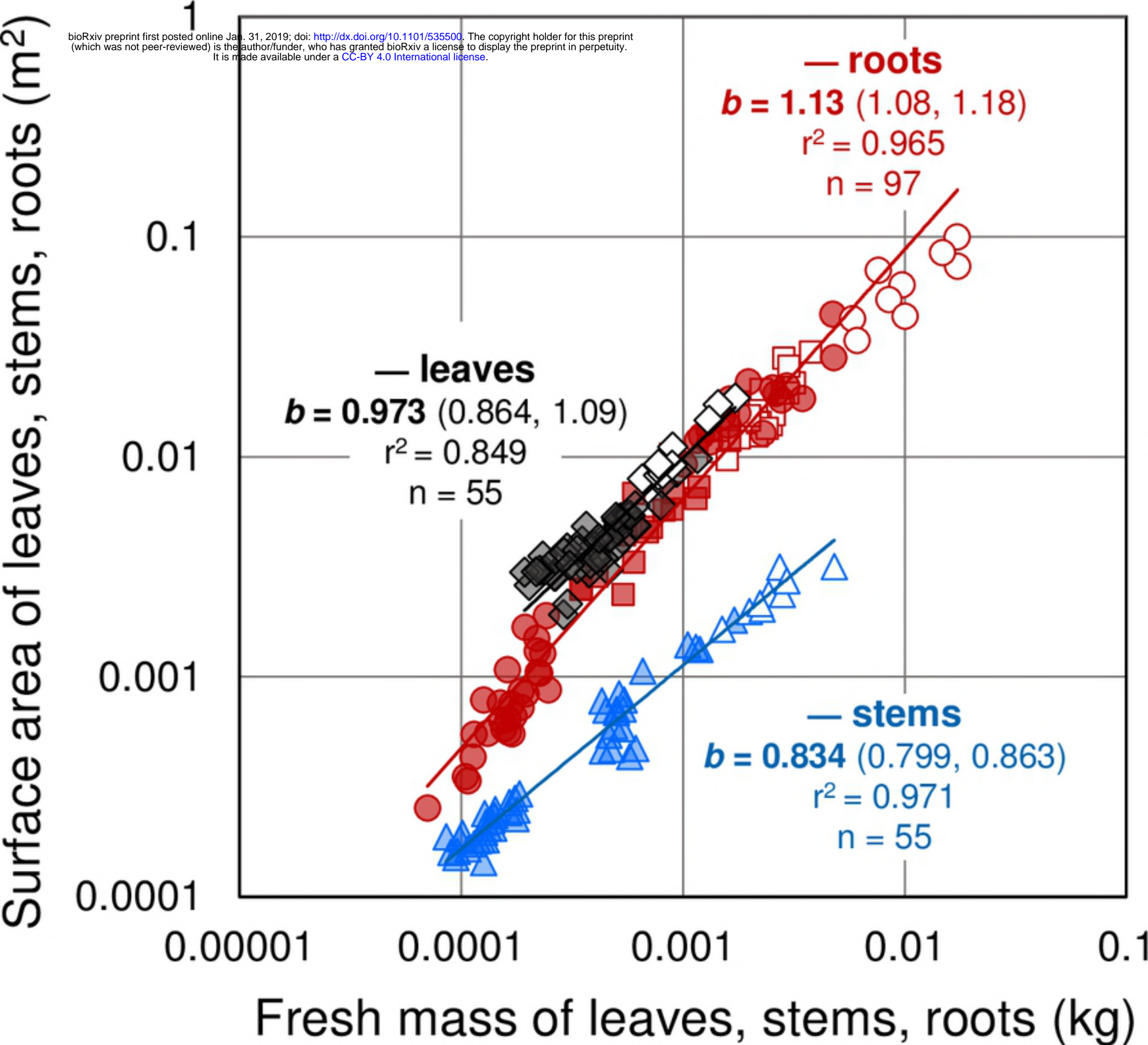
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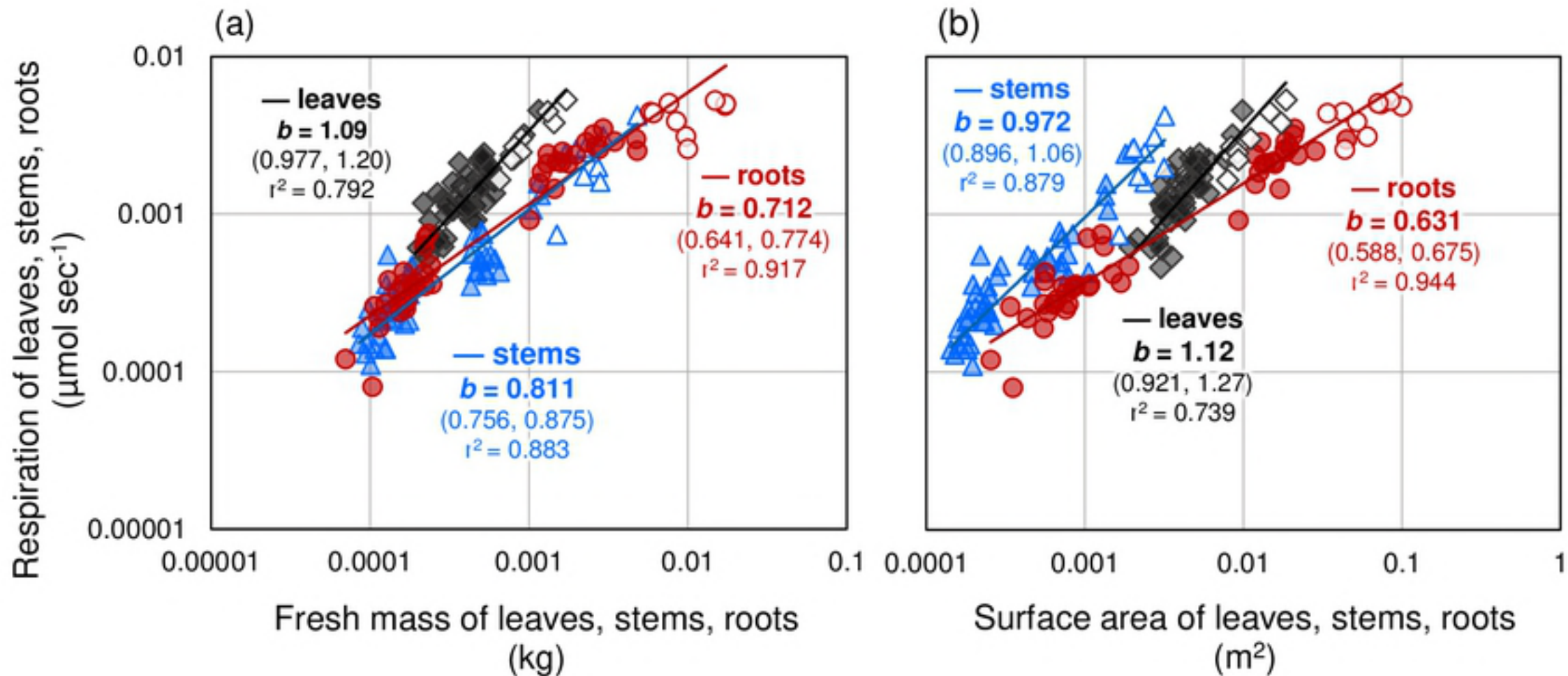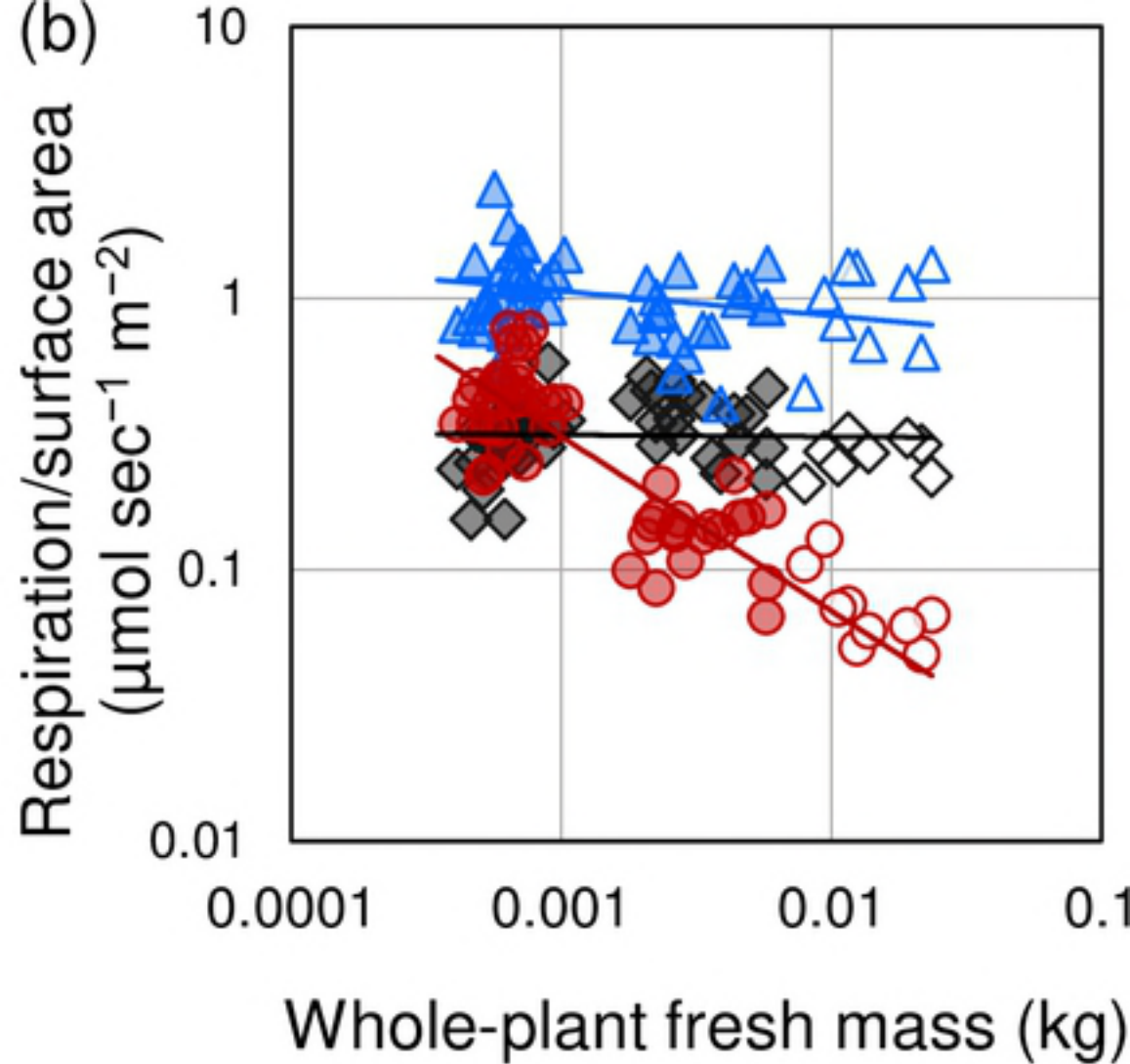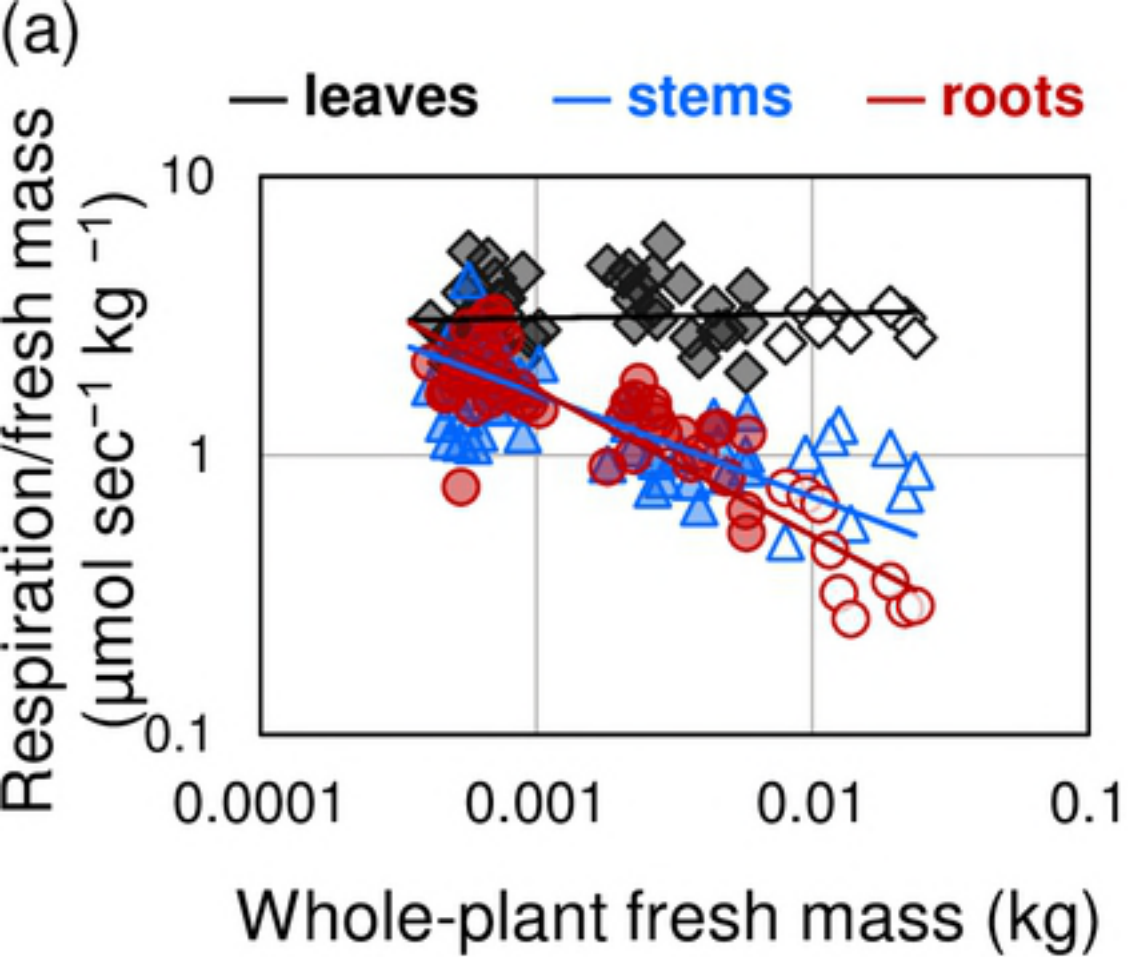
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Supporting information

442   **S1 File. Primary data.** Fresh mass, surface area, and respiration rate of total leaves, stems, and roots

443   at the individual level.

Figure

(a)

Respiration of leaves, stems, roots (μmol sec^{-1})

leaves
b = 1.09
(0.977, 1.20)
r^2 = 0.792

roots
b = 0.712
(0.641, 0.774)
r^2 = 0.917

stems
b = 0.811
(0.756, 0.875)
r^2 = 0.883

Fresh mass of leaves, stems, roots (kg)

(b)

stems
b = 0.972
(0.896, 1.06)
r^2 = 0.879

roots
b = 0.631
(0.588, 0.675)
r^2 = 0.944

leaves
b = 1.12
(0.921, 1.27)
r^2 = 0.739

Surface area of leaves, stems, roots (m^2)

Figure

(a)

Respiration/fresh mass (μmol sec^{-1} kg^{-1})

— leaves — stems — roots

Whole-plant fresh mass (kg)

(b)

Respiration/surface area (μmol sec^{-1} m^{-2})

Whole-plant fresh mass (kg)

Figure

Figure

(a) — Whole-plant fresh mass (kg)

$b = 0.647$ (0.584, 0.702)
$r^2 = 0.898$

(b) — Whole-plant surface area (m²)

$b = 0.685$ (0.625, 0.738)
$r^2 = 0.892$

y-axis: Whole-plant respiration (μmol sec^{-1})

Figure