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1 **Synchronous and asynchronous root and shoot phenology in temperate woody**
2 **seedlings**

3

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24 **Abstract**

25 Understanding variation in root and shoot growth phenology among species is crucial to
26 understanding underlying mechanisms of temporal niche differentiation. However, little
27 is known about the relationship between root and shoot phenology, or how this
28 relationship varies among functional traits. We examined fine root and shoot phenology
29 of 42 seedlings representing a variety of woody species that inhabit the cool temperate
30 forests of northern Japan. Some aspects of phenology were common to the pool of
31 species examined: we found positive relationships between root and shoot phenology
32 for the end of growth, and for the duration of growth, but not for the start of growth.
33 Further, seedlings that started root growth relatively early also ended root growth
34 relatively late. Other aspects of phenology varied predictably with functional traits, i.e.
35 leaf habit and successional status: first, root growth in evergreen species started
36 significantly earlier and ended later than in deciduous species; second, early
37 successional species had the longest duration of shoot growth among all successional
38 types. Our results suggest that niche differentiation may be promoted by differences in
39 phenology between root and shoots, likely contributing to the co-existence of woody
40 seedlings in temperate forests.

41

42 **Keywords:** aboveground-belowground linkage, functional traits, leaf habit, species

43 coexistence, succession, temporal niche differentiation

44

45 **Introduction**

46 Growth phenology is closely linked to temporal variation in resource exploitation
47 because the timing and duration of growth directly links to the quantity of a resource
48 that plants can acquire (Pearman et al. 2008, Huang et al. 2019). Clarifying differences
49 in growth phenology among species, growth forms and functional traits may contribute
50 to understanding mechanisms of temporal niche differentiation (Fargione and Tilman
51 2005, Gonzalez and Loreau 2009).

52 Niche differentiation is known to be important in the early life stages of the trees
53 (e.g. Peet 1985). At the same time, above-ground phenology has been well-documented
54 in the early life stages of trees, and different phenological parameters are linked. For
55 example, woody plants which start their shoot growth earlier often also end their growth
56 earlier (Fu et al. 2014, Keenan and Richardson 2015, but see Panchen et al. 2014). This
57 is thought to be because early bud burst and an early start of shoot growth results in a
58 more rapid accumulation of the degree-days required for inducing dormancy, causing
59 individuals to end their growth earlier (Fu et al. 2014, Keenan and Richardson 2015).
60 Further, differences in growth phenology among individuals are related to functional
61 traits (Lechowicz 2002, Panchen et al. 2014) and successional status. Leaf habit (e.g.
62 evergreen versus deciduous leaves), height-related growth-form (tree or shrub), wood

63 anatomy (ring, diffuse or semi-ring porous) and species-specific successional status
64 (pioneer or late successional) are useful for categorizing differences in aboveground
65 phenology, such as the timing of shoot growth and leaf-out among woody individuals
66 (Marks 1975, Maruyama 1979, Bicknell 1982, Boojh and Ramakrishnan 1982, Panchen
67 et al. 2014).

68 In contrast, root phenology and its relation to shoot phenology have received less
69 attention (Radville et al. 2016). Fine roots in seasonal climates often start to grow later
70 than shoots (Hendrick and Pregitzer 1996, Joslin and Wolfe 1998, Steinaker and Wilson
71 2008, Iivonen et al. 2011, Abramoff and Finzi 2015), although there are notable
72 exceptions to this pattern (Steinaker et al. 2010). Further, fine roots can continue to
73 grow longer than shoots (Steinaker and Wilson 2008, Steinaker et al. 2010, Blume-
74 Werry et al. 2016). Overall, the largest time-lags between the peaks of early shoot
75 growth and later root growth appear to be between evergreen and deciduous trees
76 (Abramoff and Finzi 2015). However the timing and number of pulses of root growth
77 also shows a wide variation among species, as shown by the twelve temperate woody
78 species (10 deciduous and 2 evergreen) studied by McCormack et al. (2014).

79 There are two main pathways linking root and shoot phenology. First, in seasonal
80 ecosystems, similar temporal patterns of temperature and resource availability above-

81 and below ground (i.e., lower resource availability in winter and greater resource
82 availability in summer) should drive convergence in root and shoot phenology. Second,
83 root production is dependent on photosynthates assimilated above ground (Abramoff
84 and Finzi 2015), which should also drive phenological convergence. Based on these
85 facts, we expect shoot and root growth phenology to follow similar seasonal patterns.
86 Specifically, we hypothesize that: 1) root and shoot phenology are correlated among
87 woody plants within a temperate forest; and 2) leaf habit (deciduous vs. evergreen) is a
88 strong predictor of variation in both shoot and root phenology, relative to other traits
89 and successional status.

90 To test these hypotheses, we examined root and shoot phenology in 42 seedlings
91 representing a phylogenetically wide range of species inhabiting the cool temperate
92 forests of northern Japan. These species include both common and rare native species,
93 as well as introduced species, representing a wide range of functional traits and
94 successional status (Table 1). A key feature of our study is that we adopted a common
95 garden approach in order to directly compare growth phenology across species.

96

97

98 **Materials and Methods**

99 *Phenology*

100 Phenology was measured in seedlings at the Forest Research Institute, Forest Research
101 Department, Hokkaido Research Organization, Japan (43°17'N, 141°51'E). The mean
102 annual temperature was 7.2 °C (January: -6.6 °C; August: 21.1 °C), and annual
103 precipitation was 1170 mm between 1981 – 2018 (Japan Meteorological Agency 2019).
104 The climate of the research site is Dfa (humid continental climate) in the Köppen
105 climate classification system.

106 One individual was measured for each of 42 species (Table S1, Supplementary
107 material). The rationale for this is that our focus was not on the growth phenology of
108 individual species, but rather on the relation of growth phenology to functional traits
109 across an evolutionarily large variety of trees. Most of the species are native to the
110 region, while a few (e.g. *Larix kaempferi*) were introduced for forestry and horticulture.
111 Seedlings (four to five years old) were planted in transparent pots (33 x 33 cm x 180 cm
112 deep) which were buried in soil in the nursery (Fig. 1). Pot depth was chosen to avoid
113 the suppression of root growth by shallow soil depth. One side of each pot was covered
114 with wooden blocks to allow periodic root measurements while otherwise eliminating
115 light and temperature fluctuations. Pots were filled with a mixture of brown upland
116 forest soil and volcanic sand.

117 Plants were measured every 1 – 2 weeks one year after planting. Measurements
118 were conducted in 1981 (six species), 1983 (12 species), 1984 (12 species), and 1985
119 (12 species) (Table S1, Supplementary material), due to the time-consuming nature of
120 the measurements. Differences in the year of measurement were taken into account in
121 the statistical analysis (see below), and species of contrasting functional groups were
122 planted in different years. For shoot growth, the length of the current-year’s main shoot
123 was measured. For root growth, the length of all roots that appeared on the transparent
124 wall were measured. The start of growth was identified as the date (DOY) when the first
125 root or shoot growth was detected. The end of growth was identified as the date when
126 the final root or shoot growth was detected. These data were previously reported in the
127 Ph.D thesis of Takao Sato (1994). We extracted data published as figures in the thesis
128 using Web Plot Digitizer (Rohatgi 2012). The duration of growth was calculated as:

129

$$130 \quad \textit{Duration (days)} = \textit{End of growth (DOY)} - \textit{Start of growth (DOY)}$$

131

132 *Functional traits*

133 For each seedling, we determined the following functional traits: leaf habit (evergreen
134 or deciduous, following Sato 2017); growth-form (tree or shrub); wood anatomy (ring-

135 porous, diffuse porous, or semi-ring porous wood, following Carlquist (2001) and using
136 the Database of Wood Specimens run by the Forestry and Forest Product Research
137 Institute in Japan <http://db.ffpri.affrc.go.jp/WoodDB/index-E.html>); successional status
138 (early successional, early to middle successional, middle successional, middle to late
139 successional and late successional, using Maruyama (1979), Koike (1988), and Bazzaz
140 (2003)); and mycorrhizal type (ectomycorrhiza, arbuscular mycorrhiza, and
141 ectomycorrhiza-arbuscular mycorrhiza). Wood anatomy is related to water uptake
142 strategy (Lechowicz 2002, Takahashi et al. 2013). Height-related growth form (tree
143 versus shrub) is related to rooting depth (Schenk and Jackson 2002). Successional status
144 may influence root phenology because both light and soil resource availability vary
145 across among successional stages (Marks 1975, Bicknell 1982, Vitousek et al. 1993).
146 Mycorrhizal type influences the ability of plants to exploit belowground resources
147 (Chen et al. 2016). Because we studied only one species that forms ericoid mycorrhiza,
148 this species was excluded from the analysis of mycorrhizal type.

149

150 *Analysis*

151 We analyzed the relationship between shoot and root phenology with generalized linear
152 mixed model (GLMM). The link function was set as log and the data set followed a

153 Gaussian distribution. The response variables were root phenological parameters and
154 the explanatory variables were shoot phenological parameters. Furthermore, the
155 relationships between the start and end of root growth, and between the start and end of
156 shoot growth, were also analyzed.

157 We analyzed the relationship between phenology and functional traits with
158 GLMM. Response variables were both shoot and root phenological parameters and the
159 explanatory variable was set as each functional trait (see the tested traits, above). The
160 data distribution of the response variables was assumed to follow a Gaussian
161 distribution by setting the link function as log. The random factor was set as the year of
162 the investigation to avoid the over-dispersion of the data across the years of
163 investigation. The statistical significance was evaluated at $p < 0.05$. For the correlation
164 between the two parameters in GLMM, conditional R^2 value (hereafter R^2C) was also
165 calculated to show the variance explained (Nakagawa and Schielzeth 2013). We used
166 the function “lme” in nlme package for GLMM analysis and in R. version 3.5.1. (R
167 Core Team 2018).

168

169 **Results**

170 *Relationships between root and shoot phenology*

171 There was no significant relationship between the start of root and shoot growth (Fig.
172 2A). In contrast, there were significant positive relationships between the end of root
173 and shoot growth (Fig 2B, $p=0.010$ and $R^2C=0.15$) and between the duration of root and
174 shoot growth (Fig 2C, $p=0.018$ and $R^2C=0.15$). Seedlings with later end dates for root
175 growth also had later end dates for shoot growth, resulting in a positive correlation
176 between the duration of root and shoot growth.

177

178 *Relationships between the start and end of growth*

179 For roots, there was a negative correlation between the start and end of growth (Fig. 3A,
180 $p<0.01$, $R^2C=0.31$). Seedlings with an early start of root growth tended to end root
181 growth later than seedlings with a late start (Fig. 3A), suggesting that both an early start
182 and late end of root growth contributed to a greater duration of root growth (note the
183 distribution of circle sizes in Fig. 3A).

184 For shoots, there was no significant relationship between the start and end of growth
185 (Fig.3B). Only the later end of shoot growth contributed to an increase of the duration
186 of shoot growth (note circle size in Fig. 3B).

187

188 *Phenology, functional traits and successional status*

189 Evergreen seedlings started root growth significantly earlier and ended root growth
190 significantly later than deciduous seedlings (Fig. 4A, B, Table 1, $p < 0.05$). Consequently,
191 the duration of root growth of evergreen seedlings was about 30% longer than that of
192 deciduous seedlings (Fig. 4C). Root phenology did not vary significantly with any other
193 functional trait (Table 1).

194 For shoots, deciduous species started growth roughly 15 days earlier than evergreen
195 species (Fig. 5A, Table 1, $p < 0.05$). The end and duration of shoot growth did not vary
196 significantly between deciduous and evergreen species (Fig. 5B and C).

197 The end and the duration of shoot growth varied significantly with successional
198 status (Table 1, $p < 0.05$). Early successional species had a significantly earlier start of
199 shoot growth than late successional species (Fig. 6A). Further, seedlings of early
200 successional species showed a later end of shoot growth as compared to mid and mid-
201 late successional species (Fig. 6B). Overall, the seedlings of early successional species
202 had the longest duration of shoot growth among all successional types (Fig. 6C). Life-
203 form, mycorrhizal type and wood structure did not influence any aspect of the shoot
204 growth variables (Table 1).

205

206 **Discussion**

207 Our examination of 42 woody species showed relationships between shoot and root
208 phenology for the end and duration of growth. Further, we found that different
209 functional traits predicted some aspects of root and shoot phenology. Together these
210 findings imply that belowground phenological differentiation may contribute to co-
211 existence in guilds of woody species with a given aboveground phenology.

212

213 *Relationships between root and shoot phenology*

214 There were significant positive correlations between roots and shoots for the duration
215 and the end of growth, but not for the start of growth (Fig. 2). To our knowledge, this is
216 the first study which demonstrates the presence and absence of correlations of growth
217 phenology between shoot and fine root among woody seedlings within a forest type.
218 The significant positive correlations might be due to the fact that fine root growth
219 depends on the production and translocation of photosynthates (Abramoff and Finzi
220 2015, Radville et al. 2016). The later end of shoot growth might result in the later end of
221 photosynthesis, resulting in later end dates for root growth. Another possibility is that
222 similar seasonal patterns of resource availability above and below ground could
223 contribute to the positive correlations, because both root and shoot phenology are
224 influenced by environmental factors such as temperature and moisture (Pregitzer et al.

225 2000).

226 We note that, while significantly correlated, the proportion of variation in root
227 phenology explained by shoot phenology was small both for the end and the duration of
228 root growth (Fig. 2), which implies that factors beyond aboveground phenology (i.e.,
229 soil temperature and moisture) influence the growth phenology of fine roots. For
230 example soil temperature and carbon allocation are both important regulators of root
231 growth phenology in grapes (Comas et al. 2005).

232 Surprisingly, the start of shoot and root growth were not related (Fig. 2A). A reason
233 for this could be that root growth may be fueled by the previous-year's carbon storage,
234 thus translocation of non-structural carbohydrate from stems or coarse roots to fine root
235 growth before the start of the shoot growth could make fine roots independent of the
236 need to await the translocation of recently assimilated photosynthates. In fact, non-
237 structural carbohydrates are known to influence the rate of root growth in spring
238 (Nguyen et al. 1990, Eissenstat and Duncan 2012), although their importance for the
239 timing of growth initiation is unclear. Our results provide further evidence that not only
240 the duration of growth, but also the initiation of growth, may be influenced by
241 photosynthate translocation (Abramoff and Finzi 2015).

242 In our study, root growth ended later than shoot growth, and the duration of root

243 growth was longer than shoot growth (Fig. 2B, C), which is consistent with previous
244 studies of temperate trees and grasses, as well as arctic trees and shrubs (Steinaker and
245 Wilson 2008, Steinaker et al. 2010, Blume-Werry et al. 2016). Underlying causes may
246 include photosynthate translocation and high nutrient availability in autumn (Yokobe et
247 al. 2018). Furthermore, the soil in our region does not freeze throughout the year owing
248 to the thick snowpack in spite of air temperatures as low as -20 °C (Takagi et al. 2005),
249 which may allow root growth in early winter, after shoots have stopped growing.

250

251 *Relationships between the start and end of shoot and fine root growth*

252 Previous studies have shown that species with an earlier start of shoot growth also end
253 their growth earlier (Fu et al. 2014, Keenan and Richardson 2015), or that the start and
254 end of aboveground growth were unrelated (Panchen et al. 2015). Surprisingly, when
255 we tested these relationships for roots, we found that individuals with an early start of
256 root growth ended their root growth later (Fig. 3). Data from McCormack et al. (2014)
257 also suggest this pattern, but our study expands this finding to a larger array of species
258 and functional traits. It is possible that an earlier start of root growth results in increased
259 uptake of soil nutrients and water, which might stimulate shoot growth. This, in turn,
260 may result in a positive feedback involving a longer period of shoot growth and

261 photosynthesis, allowing roots to grow for a longer period. Alternatively, species with
262 short growth duration might have a more concentrated pattern of growth with a
263 relatively high production of new tissue within a short period, which might be beneficial
264 if resources are also temporally heterogeneous (McCormack et al. 2014).

265 For roots, both an earlier start and later end of growth contributed to longer growth
266 duration, but for shoots, only growth at the end of the growing season contributed to a
267 longer duration (Fig. 3). The reason that shoot duration was not influenced by the start
268 of growth may be the well-known environmental constraints that exist early in the
269 growing season in cool temperate forests. An earlier start of shoot growth is limited by
270 the increasing risk of frost damage, while a later start is limited by seasonal light
271 attenuation in temperate forests (Marks 1975, Bicknell 1982, Boojh and Ramakrishnan
272 1982). In cool temperate forests, suitable conditions for starting shoot growth (between
273 spring frost and light attenuation) might last only briefly, which results in the
274 simultaneous start of shoot growth (Lenz et al. 2016). As a result, the early start of shoot
275 growth did not contribute to a longer duration of growth. In the case of roots,
276 temperature generally fluctuates less in soil than in air, especially so in northern Japan
277 where a thick snow cover prevents soil frost even at air temperature as low as -20 °C
278 (Shibata et al. 2013). Therefore, fine roots are less threatened by frost than shoots,

279 which may result in divergence in the timing of root growth start between roots and
280 shoots.

281

282 *Phenology, functional traits and successional status*

283 Among functional traits, only the evergreen-deciduous dichotomy contributed to
284 differences in growth phenology of fine roots, probably because of the importance of
285 the seasonality of carbon fixation and its allocation to root growth. Temperate evergreen
286 species start photosynthesis earlier and end it later than deciduous species (Warren et al.
287 2011), and may start allocation to root growth earlier and end it later than do deciduous
288 plants. Steinaker et al. (2010) reported the growth phenology of roots of four deciduous
289 woody species and one evergreen woody species (*Picea*) from temperate forests. In
290 their study, no clear difference between evergreen and deciduous plants was observed,
291 which highlights the usefulness of including many species to categorize differences in
292 root phenology among woody seedlings.

293 Our study found no evidence that differences in fine root growth phenology were
294 related to wood anatomy, which relates to water uptake (Lechowicz 2002, Takahashi et
295 al. 2013). Further, our results suggest that neither mycorrhizal type, which relates to the
296 importance of fine root for its nutrient uptake (Chen et al. 2016), height-related growth-

297 form, which relates to rooting depth (Schenk and Jackson 2002), nor successional status
298 were related to the difference in fine root phenology among woody species. These
299 results suggest that the drivers of variation in root phenology may be less related to
300 belowground resource availability than the activity of photosynthesizing apparatus.

301 Successional status explained variation in shoot phenology (Fig. 6) but not root
302 phenology (Table 1), suggesting that different factors drive the evolution of growth
303 phenology in fine roots and shoots. Successional status has been reported to be useful
304 for categorizing interspecific differences in shoot phenology because light availability
305 determines survival and growth (Marks 1975, Bicknell 1982, Boojh and Ramakrishnan
306 1982), which is consistent with our study. Here, seedlings of late successional species
307 started shoot growth later than early successional species, possibly because they are
308 typically shade-tolerant and can photosynthesize under the closed canopies that occur
309 after leaf-out (Koike 1988). On the other hand, middle and middle-late successional
310 species, which are sometimes categorized as gap species, have less shade tolerance than
311 late successional species, which may be related to relatively greater carbon loss due to
312 the higher rates of respiration (Loach 1967). Consequently, middle and middle-late
313 successional species grew for a shorter period than did seedlings of early successional
314 species (Fig. 6C).

315 Although soil resource availability, which varies across the successional stages
316 (Walker and del Moral 2003), was expected to be related to root phenology, this
317 relationship was not detected in our study. The lack of root phenological differences
318 associated with successional status does not support a link between successional-
319 determined nutrient availability and root phenology. Other aspects of root function may
320 be important, e.g. early successional species have deeper roots than late successional
321 species (Gale and Grigal 2008). However, our results indicate that co-existence of
322 several species of the same successional status might be attributed partly to differences
323 in belowground resource use between evergreen and deciduous species, which could
324 promote forest diversity. However, we included too few early and middle successional
325 evergreen species to explicitly examine variation in traits within a successional stage.

326 Our study examined only one seedling per species, and within-species differences
327 could be quite large. One such source of intraspecific variation is the tremendous
328 difference in size between seedlings and older trees. Seedlings and mature individuals
329 of *Acer mono* differed greatly in shoot phenology (Seiwa 1999). Future studies could
330 overcome this with replicates of each species, and including individual age or size as a
331 factor. Further, the rooting volume in the pots used in our study differed from the
332 rooting volume under the natural conditions experienced by seedlings in the field, but

333 we expect the range of responses revealed in the study to be representative of the range
334 that would appear in the field.

335 In summary, our survey of 42 species found (1) positive relationships between shoot
336 and root phenology for the end and the duration of growth but not for its initiation, (2)
337 seedlings that started fine root growth relatively early ended their fine root growth
338 relatively late, (3) root growth in evergreen species started significantly earlier and
339 ended later than that in deciduous species and (4) early successional species had the
340 longest duration of shoot growth among all successional types. Together, our results
341 suggest that niche differentiation may be promoted by differences among species in the
342 phenology of both above- and belowground tissues.

343

344

345 **Contributions**

346 MK designed the study, ST conducted the experiment, GBW, SDW and JHCC
347 consulted on the analysis, and MK wrote the manuscript with help from SDW, GBW
348 and JHCC.

349

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354

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452

453 **Table**

454 **Table 1:** The statistical significance of the influence of functional traits and
455 successional status on interspecific differences of fine root and shoot growth phenology
456 of seedlings tested by GLMM, “*” indicates statistical significance at $p < 0.05$, “n.s.”
457 indicates no significant effect.

Parameter	Leaf habit	Growth form	Mycorrhizal type	Wood structure	Successional status
Start of shoot growth	*	n.s.	n.s.	n.s.	*
End of shoot growth	n.s.	n.s.	n.s.	n.s.	*
Duration of shoot growth	n.s.	n.s.	n.s.	n.s.	*
Start of root growth	*	n.s.	n.s.	n.s.	n.s.
End of root growth	*	n.s.	n.s.	n.s.	n.s.
Duration of root growth	*	n.s.	n.s.	n.s.	n.s.

458

459

460 **Figure Captions**

461 **Figure 1:** The rhizo-box used for root growth observations. The glass panel was
462 covered with wooden blocks to avoid temperature fluctuation and light penetration into
463 the soil profile.

464

465 **Figure 2:** Relationship of the A) start, B) end, and C) duration of growth between roots
466 and shoots. The statistical significance for the relationship between the two parameters
467 is shown as p value and the variation explained is shown as conditional R^2 value (R^2C).
468 The solid line is the estimated relationship based on the GLMM analysis and the dashed
469 line is the 1:1 line between the two parameters.

470

471 **Figure 3:** Relationship between the start and end of growth in fine roots (A) and shoots
472 (B). Each circle shows the data of each individual. The size of each point shows the
473 duration of growth. The statistical significance for the relationship between the two
474 parameters is shown as p value and the variation explained is shown as conditional R^2
475 value (R^2C) respectively in each figure. The solid line is the estimated relationship
476 based on the GLMM analysis.

477

478 **Figure 4:** The start (A), end (B) and duration (C) of fine root growth in deciduous and
479 evergreen woody species. Different lower-case letters indicate significant differences
480 between the groups ($p < 0.05$) analyzed with GLMM.

481

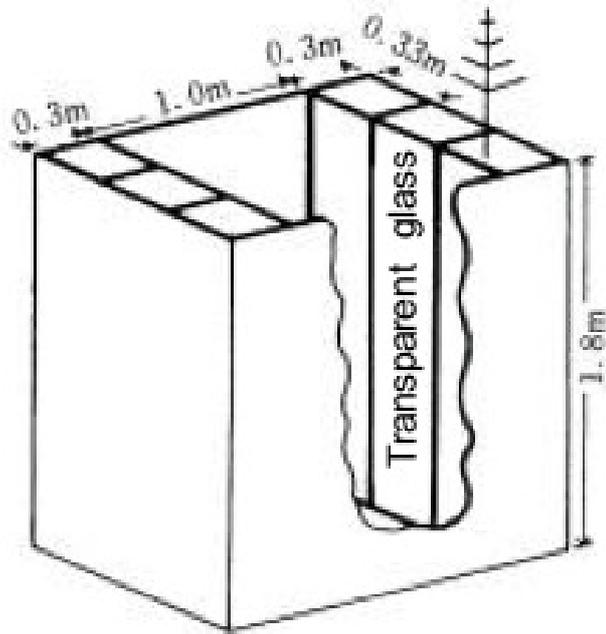
482 **Figure 5:** The start (A), end (B) and duration (C) of shoot growth in deciduous and
483 evergreen woody species. Different lower-case letters indicate the statistically
484 significant difference between the groups ($p < 0.05$) analyzed with GLMM.

485

486 **Figure 6:** The start (A), end (B) and duration (C) of shoot growth in woody species of
487 contrasting successional stages. Early: early successional species; Early-Mid: species
488 between early successional and middle successional species; Mid: middle successional
489 species; Mid-Lat: species between middle successional and late successional species;
490 and Late: late successional species. Different lower-case letters indicate statistically
491 significant differences among the successional stages ($p < 0.05$, Tukey HSD).

492

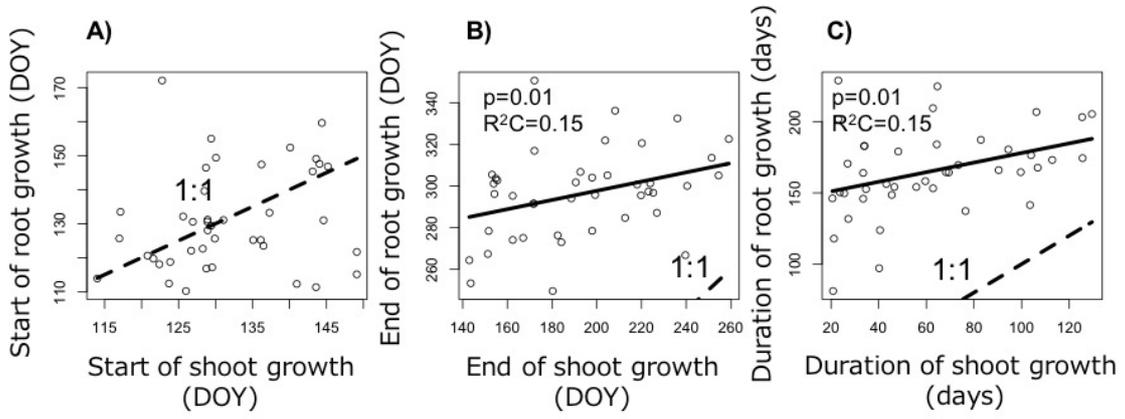
493 **Figure 1**



494

495

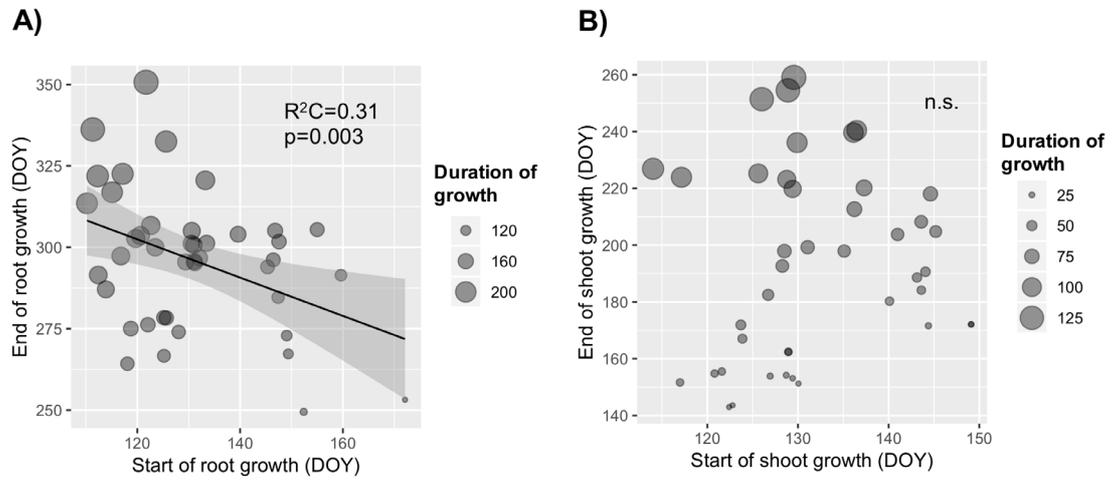
496 **Figure 2**



497

498

499 **Figure 3**

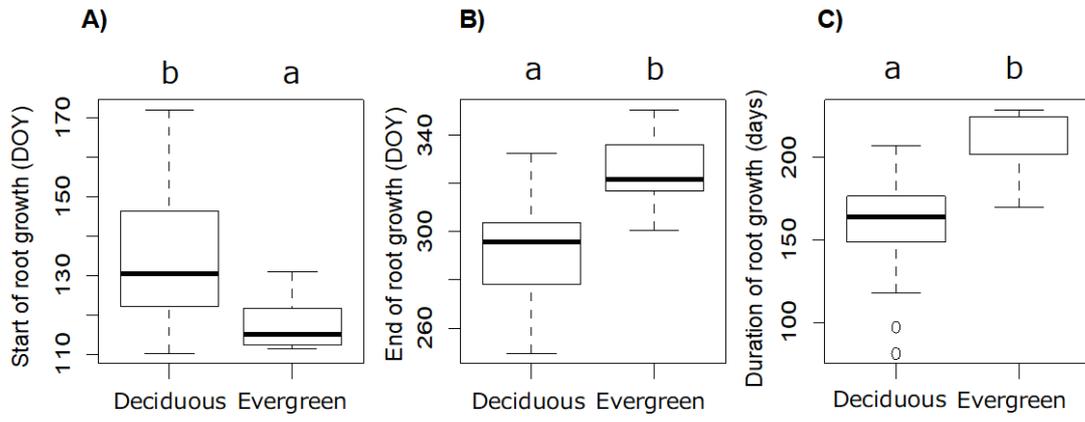


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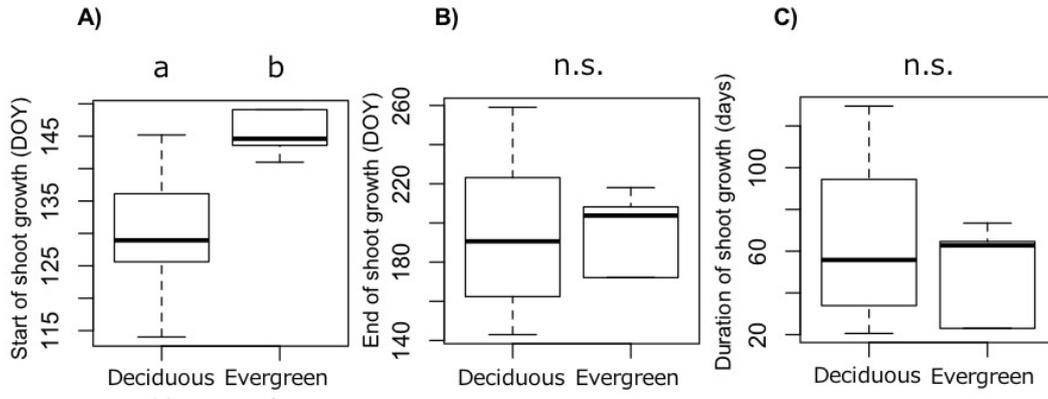
503 **Figure 4**



504

505

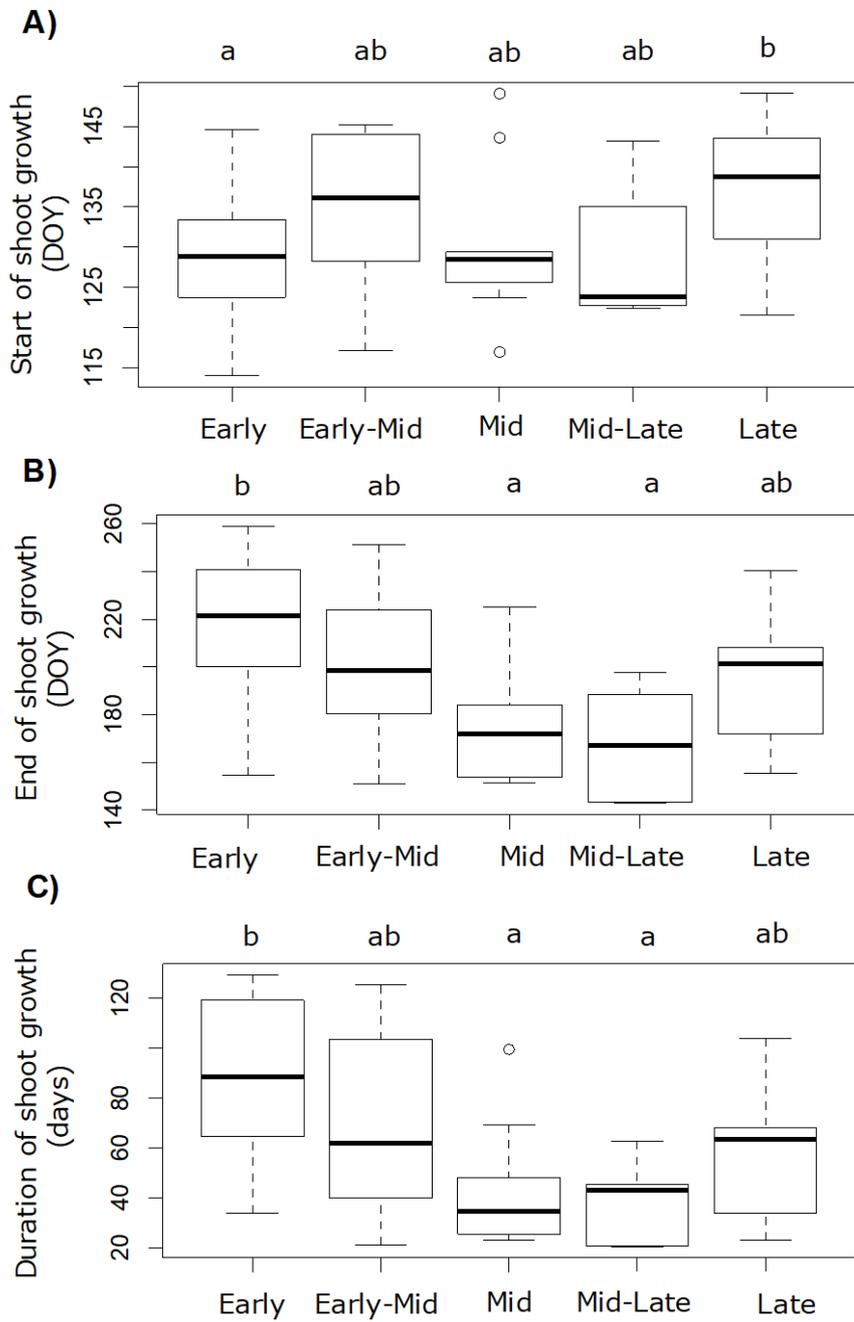
506 **Figure 5**



507

508

509 **Figure 6**



510

511

512 **Supplementary material:**

513 **Table S1:**

514 The list of the 42 woody species and their functional traits used in this study (derived
 515 from Carlquist (2001), Database of Wood Specimens of the Forestry and Forest Product
 516 Research Institute in Japan Maruyama (1979), Koike (1988), Bazzaz (2003), Lechowicz
 517 (2002), Takahashi et al. (2013)).

Species	Family	Investigation year	Growth form	Leaf habit	Mycorrhizal type	Wood structure	Successional status
<i>Abies sachalinensis</i>	Phaceae	1981	tree	ev	ECM	Tracheids	Late
<i>Acer ginnala</i> Maxim. var. <i>aidzuense</i>	Sapindaceae	1983	trub	dc	AM	Diffuse	Mid-Late
<i>Acer mono</i>	Sapindaceae	1983	tree	dc	AM	Diffuse	Late
<i>Acer palmatum</i> var. <i>matsumurae</i>	Sapindaceae	1983	tree	dc	AM	Diffuse	Late
<i>Acer ukurunduense</i>	Sapindaceae	1983	trub	dc	AM	Diffuse	Early-Mid
<i>Aesculus turbinata</i>	Sapindaceae	1983	tree	dc	AM	Diffuse	Early-Mid
<i>Alnus hirsuta</i>	Betulaceae	1984	tree	dc	AM-ECM	Diffuse	Early
<i>Alnus maximowiczii</i>	Betulaceae	1984	tree	dc	AM-ECM	Diffuse	Early
<i>Betula platyphylla</i>	Betulaceae	1983	tree	dc	ECM	Diffuse	Early
<i>Carpinus cordata</i>	Betulaceae	1984	tree	dc	ECM	Diffuse	Late
<i>Castanea crenata</i>	Fagaceae	1984	tree	dc	ECM	Ring	Early-Mid
<i>Cerasus sargentii</i>	Rosaceae	1983	tree	dc	AM-ECM	Diffuse	Mid-Late
<i>Cercidiphyllum japonicum</i>	Cercidiphyllaceae	1981	tree	dc	AM	Diffuse	Mid
<i>Cornus controversa</i>	Cornaceae	1985	tree	dc	AM	Diffuse	Mid
<i>Corylus sieboldiana</i>	Betulaceae	1984	shrub	dc	ECM	Diffuse	Early-Mid
<i>Elaeagnus umbellata</i>	Elaeagnaceae	1985	shrub	dc	AM	Ring	
<i>Euonymus alatus</i>	Celastraceae	1985	shrub	dc	AM-ECM	Diffuse	Mid
<i>Fraxinus mandshurica</i> var. <i>japonica</i>	Oleaceae	1984	tree	dc	AM	Ring	Early-Mid
<i>Hydrangea paniculata</i>	Hydrangeaceae	1985	shrub	dc	AM	Diffuse	Early
<i>Ilex crenata</i> var. <i>pakidosa</i>	Aquifoliaceae	1984	shrub	ev	ECM	Diffuse	Early
<i>Juglans mandshurica</i> var. <i>sachalinensis</i>	Juglandaceae	1984	tree	dc	AM	Sem i-ring	Mid
<i>Kalopanax septemlobus</i>	Araliaceae	1983	tree	dc	AM	Ring	Mid
<i>Larix kaempferi</i>	Phaceae	1981	tree	dc	ECM	Tracheids	Early
<i>Lonicera caerulea</i> var. <i>emphylocalyx</i>	Caprifoliaceae	1985	shrub	dc	AM	Diffuse	
<i>Maackia amurensis</i> var. <i>buergeri</i>	Fabaceae	1985	tree	dc	AM-ECM	Ring	Mid
<i>Magnolia praecoxissima</i> var. <i>borealis</i>	Magnoliaceae	1981	tree	dc	AM	Diffuse	Early-Mid
<i>Malus toringo</i>	Rosaceae	1985	trub	dc	AM-ECM	Diffuse	Early-Mid
<i>Morus australis</i>	Moraceae	1984	trub	dc	AM-ECM	Ring	Early-Mid
<i>Padus grayana</i>	Rosaceae	1983	tree	dc	AM-ECM	Diffuse	Mid-Late
<i>Phellodendron amurense</i>	Rutaceae	1984	tree	dc	AM	Ring	Early-Mid
<i>Picea glehnii</i>	Phaceae	1981	tree	ev	ECM	Tracheids	Late
<i>Populus suaveolens</i>	Salicaceae	1985	tree	dc	AM-ECM	Diffuse	Early
<i>Quercus crispula</i>	Fagaceae	1983	tree	dc	ECM	Ring	Mid-Late
<i>Rhamnus japonica</i> var. <i>decipiens</i>	Rhamnaceae	1985	shrub	dc	AM	Diffuse	
<i>Rhododendron brachycarpum</i>	Ericaceae	1984	shrub	ev	ERM	Sem i-ring	Mid
<i>Rosa rugosa</i>	Rosaceae	1985	shrub	dc	AM-ECM	Ring	Early
<i>Sorbus commixta</i>	Rosaceae	1983	tree	dc	AM-ECM	Diffuse	Mid
<i>Styrax japonica</i>	Styraceae	1985	trub	dc	AM	Diffuse	
<i>Syringa reticulata</i>	Oleaceae	1985	tree	dc	AM	Diffuse	Mid
<i>Taxus cuspidata</i>	Taxaceae	1981	tree	ev	AM	Tracheids	Late
<i>Tilia japonica</i>	Malvaceae	1984	tree	dc	ECM	Diffuse	Mid-Late
<i>Ulmus davidiana</i> var. <i>japonica</i>	Ulmaceae	1983	tree	dc	AM	Ring	Early-Mid

518