

1 **Trees increase their P:N ratio with size.**

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9 41 51

10 Running title: Phosphorus; the treasure nutrient

11 Number of words of abstract: 296

12 Number of words of main body text: 3956

13 Number of references: 73

14

15 Keywords

16 Early-succesional species, forest, late-succesional species, leaf:wood ratio, N:P,
17 nitrogen, phosphorus, soil, stoichiometry.

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29 **ABSTRACT**

30 **Aim** Phosphorus (P) tends to become limiting in aging terrestrial ecosystems, and its
31 resorption efficiency is higher than for other elements such as nitrogen (N). We thus
32 hypothesized that trees should store more P than those other elements such as N
33 when tree size increases and that this process should be enhanced in slow-growing
34 late successional trees.

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36 **Location** Catalan forests.

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38 **Methods** We have used data from the Catalan Forest Inventory that contains field data
39 of the P and N contents of total aboveground, foliar and woody biomasses of the
40 diverse Mediterranean, temperate and alpine forests of Catalonia (1018 sites). We
41 used correlation and general lineal models (GLM) to analyze the allometric
42 relationships between nutrient contents of different aboveground biomass fractions
43 (foliar, branches and stems) and total aboveground biomass.

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45 **Results** Aboveground forest P content increases proportionally more than
46 aboveground forest N content with increasing aboveground biomass. Two mechanisms
47 underlie this. First, woody biomass increases proportionally more than foliar biomass
48 having woody biomass higher P:N ratio than foliar biomass. Second, wood P:N ratio
49 increases with tree size. These results are consistent with the generally higher foliar
50 resorption of P than of N. Slow-growing species accumulate more P in total
51 aboveground with size than fast-growing species mainly as a result of their large
52 capacity to store P in wood.

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54 **Main conclusions** Trees may have thus developed long-term adaptive mechanisms to
55 store P in biomass, mainly in wood, thereby slowing the loss of P from the ecosystems,
56 reducing its availability for competitors, and implying an increase in the P:N ratio in
57 forest biomass with aging. This trend to accumulate more P than N with size is more
58 accentuated in slow-growing, large, long-living species of late successional stages.
59 This way they partly counterbalance the gradual decrease of P in the soil.

60

61 **INTRODUCTION**

62 An increasing number of studies in recent decades have shown that P is a key nutrient
63 in determining the structure and function of both aquatic and terrestrial ecosystems
64 (Walker & Syers, 1976; Margaleff, 1998; Aerts & Chapin, 2000; Richardson *et al.*, 2005;
65 Sardans *et al.*, 2005; Gradowsky & Thomas, 2006; Turner *et al.*, 2012; Peñuelas *et al.*,
66 2013). The limiting role of P has been observed in all types of terrestrial ecosystems
67 (Vitousek *et al.*, 2010), from cold-temperate regions (Richardson *et al.*, 2005; Sardans
68 *et al.*, 2005; Gradowsky & Thomas, 2006; Turner *et al.*, 2012) to tropical areas, where
69 P is most frequently the limiting nutrient (Walker & Syers, 1976; Quesada *et al.*, 2010;
70 Nottingham *et al.*, 2012).

71 Phosphorus is progressively transferred from rock parental material to living and
72 dead biomass and/or becomes occluded in secondary minerals such as organo-clay
73 aggregates and Al, Ca and Fe phosphates, depending on soil traits such as pH,
74 bedrock type, and other general ecosystem characteristics such as climatic conditions
75 or vegetation type (Walker & Syers, 1976). A wide variety of conditions influence P
76 and/or N limitation in both temperate (Finzi, 2009; Sackett *et al.*, 2013) and tropical
77 forests (Tanner *et al.*, 1998; Wright *et al.*, 2011), but despite this soils generally evolve
78 toward increasing P limitation over time after their formation (Walker & Syers, 1976;
79 Vitousek *et al.*, 2010), and several studies have observed a P-limiting role for tree
80 growth in all types of forests and world areas (Sardans *et al.*, 2004; Boyce *et al.*, 2006;
81 Gradowski & Thomas, 2006; Ehlers *et al.*, 2010; Alvarez-Clare *et al.*, 2013; Huang *et al.*
82 *et al.*, 2013; Zhou *et al.*, 2013). Moreover, the P-limitation of N₂-fixation (Binkley *et al.*,
83 2003; Augusto *et al.*, 2013) and of C and N cycling and N availability (Cleveland *et al.*,
84 2002; Kranabetter *et al.*, 2005) in forests can control the ecosystem level mass balance
85 of N. Phosphorus is thus often the ultimate limiting nutrient in forests (Vitousek *et al.*,
86 2010). Related to this limiting role of P in many soils, trees could have developed an
87 efficient resorption of P from leaves. Several studies have observed that more P and N
88 are resorbed in nutrient-poor soil-plant systems (Richardson *et al.*, 2004; Lü *et al.*,

89 2012). Moreover, P:N resorption ratios generally decrease when the soil is N limited
90 and generally increase when the soil is P limited (van Heerwaarden *et al.*, 2003; Zotz,
91 2004). The available information indicates broader ranges for P than for N resorption
92 efficiencies (Hättenschwiler *et al.*, 2008; Vergutz *et al.*, 2012), despite the large
93 variabilities (Vergutz *et al.*, 2012). Third, the proportional concentrations of C and N
94 relative to P are higher in litter than in leaves, 3007:45:1 and 1212:28:1, respectively
95 (Vergutz *et al.*, 2012), indicating a generally higher resorption efficiency of P than of N,
96 especially under nutrient poor conditions (Mulder *et al.*, 2013). It is logical to
97 hypothesize that if the trees reabsorb P more efficiently than N from leaves, P should
98 accumulate more than N in other plant organs.

99 Natural selection should favor the capacity to retain P, more than other
100 elements such as N. Species of advanced successional stages that are adapted to
101 remain long periods should be particularly benefited from storing P in biomass. In fact,
102 the trend to make more internal the control of nutrient cycles has been associated to
103 more advanced successional stages (McDonald & Healey, 2000; Parsons & Congdon
104 2008; Celi *et al.*, 2013). In this way, the old tropical forests growing on old nutrient-poor
105 soils store a large amount of nutrients in wood biomass (Tanner *et al.*, 1998; Wright *et al.*
106 *et al.*, 2011). In tropical forest, total soil P was a better predictor of wood production rates
107 than any of the fractionated organic- or inorganic-P pools (Quesada *et al.*, 2012). This
108 suggests that it is not only the immediately available P forms, but probably the entire
109 soil phosphorus pool that is interacting with forest growth on longer timescales.
110 Because late successional species tend to occupy the soil for long periods of time, it
111 may be adaptive to internalize nutrient cycles, making the P supply more dependent on
112 the relatively fast organic matter cycle than from soil minerals leaching (Vinegla *et al.*,
113 2006).

114 Moreover, in certain situations the time-scale of the ecosystem P-cycle and of
115 the successional process can be similar. An increase of nutrient cycling rates and
116 losses occurs after disturbance and secondary succession with early successional

117 species substituting late-successional species (Valdespino *et al.*, 2009). Forest
118 disturbances such as fires frequently imply increases in P availability that are
119 accompanied by the recruitment of early successional species as observed in
120 Mediterranean (Escudey *et al.*, 2010; Yildiz *et al.*, 2010; Lane *et al.*, 2011; Turkmean &
121 Duzenli, 2011) tropical (Hughes *et al.*, 2000; Kennard & Gholz, 2001; Ilstedt *et al.*,
122 2003; Blair, 2005) wet temperate (Saa *et al.*, 1993; 1998; Michalzik & Martin, 2013)
123 and cold forests (Lagenstrom *et al.*, 2009; Mitchell & Ruess, 2009). During post-fire
124 events, soil P-availability tends to decrease returning to the values before fire with
125 aging at the time scale of successional processes, because soil-P immobilization
126 increases (Mitchell & Ruess, 2009; Turkmean & Duzenli, 2011; Celi *et al.*, 2013) and
127 soil-P availability decreases (Turkmean & Duzenli, 2011; Huang *et al.*, 2013; Zhou *et al.*
128 *et al.*, 2013) during plant community succession (decades). Consequently, are logical
129 hypotheses that species tend to retain the nutrient most likely to decrease in soil with
130 time, and that this retention should be greater in species of more advanced
131 successional stages because the evolution pressure at this regard should be greater.

132 Very few studies have provided field data for the changes that occur in the
133 contents of P and N in the different ecosystem compartments as forests age and grow,
134 even though P and N play key roles in the function and structure of organisms and
135 ecosystems. In a study of 10 Amazonian tropical forests ranging in age from 0 to 14
136 years since agricultural abandonment, Feldpausch *et al.* (2004) observed that the total
137 stocks of P in soil decreased, with asymmetric behaviors in different compartments: the
138 accumulation of P in stand biomass increased whereas the Olsen P (the P available for
139 plants) of the soil decreased. Similar studies in other forests, however, particularly in
140 temperate regions, have not been conducted. Moreover, regional data sets are lacking
141 that would allow an extensive study of the trends in P and N accumulation in forests
142 over time in the different components of tree biomass, including wood.

143 Given the frequently limiting role of P, the impoverishment of soil P with
144 succession, and the higher resorption efficiency of P than of N, we hypothesized that

145 the evolutionary processes under increasing P-limitation should have selected a
146 greater capacity of retaining and storing P in biomass and do it even more than for
147 other nutrients such as N. We also hypothesized that this storage of P is larger in
148 species of advanced successional stages adapted to remain for longer periods than
149 early-successional fast-growing species. Here, we tested these hypotheses, which
150 have some experimental support in tropical forests (Tanner *et al.*, 1998; Wright *et al.*,
151 2011), using a large data set from the Catalan Forest Inventory.

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175 **MATERIALS AND METHODS**

176 **Study area and climatic data**

177 The study was based on data in the Catalan Forest Inventory (Gracia *et al.*, 2004a).
178 These databases contain information on the concentrations of C, N and P in branches,
179 stems and leaves in 1018 plots, and the corresponding biomasses. The plots were
180 uniformly distributed throughout 19 568 Km² of the forested areas of Catalonia.
181 Catalonia, which has an area of 32 114 Km², is located on the shores of the
182 Mediterranean Sea, and the presence of the Pyrenees and continental gradients
183 generate contrasting climatic regions, including semiarid-Mediterranean, wet-
184 Mediterranean, Atlantic wet temperate and alpine. Coastal areas have Mediterranean
185 climates, and inland areas have mostly continental Mediterranean climates. To the
186 north, the Pyrenees have montane or, at the highest elevations, alpine climates. Data
187 for mean annual precipitation and temperature were obtained from the “Atlas climàtic
188 digital de Catalunya” (Ninyerola *et al.*, 2000).

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190 **Estimation of biomass and growth**

191 In each plot (minimum 28.3 m²), all living trees with a diameter at breast height (DBH)
192 of at least 5 cm were identified to species, and their height and DBH were measured.
193 Bark was measured at a 1.3 m height with a bark calibrator (with an accuracy of 1 mm)
194 in two orientations (north and south) in three trees of each plot. We used the scaling
195 relationships between the DBH without bark and bark thickness to calculate the bark
196 thickness for all the other trees of the same species of this plot. To calculate wood
197 biomass we used the DBH without bark. To calculate the biomass of the different
198 aboveground organs and also total aboveground biomass we used the allometric
199 equations shown in Tables S1-S4 (Appendices 1-4). In these equations we take into
200 account wood density (g cm⁻³) determined in each plot by weighting wood samples
201 dried in a dry-oven at 75 °C during 48 hours. The volume was obtained by wood cores

202 obtained from a stem extraction with a Pressler drill and measured with a Vernier
203 caliper.

204 Then current biomass (t ha^{-1}) per plot of the other aboveground organs of the
205 different species was estimated using allometric equations (See Tables S1-S4 in the
206 Appendices 1-4) obtained for each species and region (Vilà *et al.*, 2003). Briefly, each
207 plot had a minimum diameter of 6 m. This plot area was function of tree density in the
208 plot and was variable to include a minimum of 15-25 trees with a DBH higher than 5 cm.
209 Within the plot all trees were measured. The biomass of the plot was the sum of the
210 biomasses of all the trees of each species within. The 1018 plots used to conduct the
211 chemical analyses plus the biomass estimation were mostly monospecific forest (with
212 more than 90% of trees belong to the same target species). Total wood per tree was
213 the sum of branch and stem wood.

214 **Sampling and chemical analyses**

215 In each plot, samples of leaves, stems and branches were collected and analyzed.
216 These samples were pools of the leaves, stems and branches, respectively, of at least
217 three different trees collected and sampled in all directions of the canopy. The leaves
218 were sampled from the upper central part of the crown by using extensible loppers.
219 The final foliar sample included all foliar cohorts present in the different branches
220 sampled from the selected trees. For more information on the method of sampling, see
221 Vilà *et al.* (2003).

222 Samples were ground with a Braun Mikrodismembrator-U (B. *Braun* Biotech
223 International, Melsungen, Germany). Concentrations of N were determined by
224 combustion coupled to gas chromatography using a Thermo Electron Gas
225 Chromatograph (model NA 2100, CE instruments-Thermo Electron, Milan, Italy). To
226 determine the concentrations of P, samples were solubilized in 50 mL Teflon centrifuge
227 tubes (Nalge Nunc International, Rochester, NY, USA) containing a 2:1 acidic mixture

228 of HNO₃ (60%) (143255, purissimum, PANREAC, Barcelona) and HClO₄ (60%)
229 (141054, purissimum, PANREAC, Barcelona) in a microwave oven (SAMSUNG, TDS,
230 Seoul, South Korea). A standard certified biomass (DC73351, poplar leaf, China
231 National Analysis Centre for Iron & Steel) assessed the accuracy of the digestions and
232 analytical procedures. After digestion, the concentrations of P were determined using
233 ICP-OES (Optic Emission Spectroscopy with Inductively Coupled Plasma) (JOBIN
234 YBON JI 38 Jobin, France).

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236 **Statistical analyses**

237 We analyzed all allometric relationships among log-transformed biomasses and P and
238 N concentrations (in mass basis), contents and ratios and conducted a GLM to test for
239 differences between fast-growing species (*Pinus halepensis*, *Pinus sylvestris*, *Pinus*
240 *nigra*, *Pinus pinaster*, *Castanea sativa*, *Pseudotsuga menziesii*, *Pinus radiata*, *Populus*
241 *tremula*, *Populus hybridus*, *Populus nigra*, *Fraxinus angustifolia*, *Fraxinus excelsior*,
242 *Prunus avium*, *Cedrus deodara*) versus slow-growing species (*Pinus uncinata*,
243 *Quercus ilex*, *Quercus suber*, *Abies alba*, *Quercus cerrifolia*, *Quercus humilis*,
244 *Quercus petraea*, *Fagus sylvatica*). We used major axis regression (MA) and
245 standardized major axis (SMA) using SMATR package
246 (<http://www.bio.mq.edu.au/ecology/SMATR>) (Warton & Weber, 2002; Warton *et al.*,
247 2006) to compare differences in regression slopes between allometric relationships
248 (Figures 1a, 2a, 4, 5a, 5b, Supplementary Figures S1 and S3). We conducted general
249 linear models using successional status, mean annual temperature (MAT) and mean
250 annual precipitation (MAP) as independent factors and P:N ratios in tree organs as
251 dependent variables. We used with Statistica 6.0 (StatSoft, Inc. Tule, Oklahoma,
252 USA). The simple allometric relationships (Figures S2a, S2b in Appendix 6, Figure S4
253 in Appendix 8 and Figures 2b, 3a, 3b) were analyzed by using the unbiased Theil-
254 Sen's slope estimator (Sen, 1968; Theil, 1950) from the R (Core Team, 2013) package

255 "mblm" (median-based linear models) to avoid outlier influence in scaling relationships
256 (Komsta, 2012).

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281 RESULTS

282 P and N accumulation patterns

283 Woody biomass, especially stem biomass, increases proportionally more than foliar
284 biomass as total aboveground biomass increases (Fig. 1A). This difference implies that
285 the ratio of woody (branches + stem) to foliar biomass increases with increasing total
286 aboveground biomass in all forest types (See Fig. S1 in Appendix 5). This increase is
287 higher in wet temperate deciduous forests than in the other forest types (coniferous
288 and Mediterranean evergreen) (See Fig. S1 in Appendix 5). On the other hand, P:N
289 ratio is higher in branches and stems than in foliar biomass (Fig 1B). The large
290 increase in the wood/leaf ratio with increasing forest aboveground biomass, however,
291 indicates that the ratio of P stocks in wood over foliage also increases when total
292 aboveground biomass increases, thus functional P (leaf) ratio versus non-functional P
293 (wood) decreases (See Fig. S2 in Appendix 6). In contrast, the increase of functional N
294 (leaf) versus non functional decreases less ($P < 0.001$, SMA test of common slopes)
295 when total aboveground biomass increases (See Fig. S2 in Appendix 6). As a result,
296 the total P content of the aboveground biomass increases more than the total N
297 content ($P < 0.001$, SMA test of common slopes) (Fig. 2A), so the P:N ratio in the
298 aboveground biomass consequently increases as the aboveground biomass rises (Fig.
299 2B). This higher proportional increase of the total P content than N content with
300 increasing aboveground biomass is observed both in angiosperms ($P < 0.001$ SMA test
301 of common slopes) (See Fig. S3A in Appendix 7) and in gymnosperms ($P < 0.001$, test
302 of common slopes) (See Fig. S3B in Appendix 7).

303 The P:N ratios of the foliar biomass only increase slightly in forests, but the P:N
304 ratios of the woody biomass increase strongly when the total aboveground biomass
305 also increases ($P < 0.001$ SMA test of common slopes) (Fig. 3), and similar results are
306 observed with the total P content of aboveground biomass also increases ($P < 0.001$
307 SMA test of common slopes) (See Fig. S4 in Appendix S8).

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309 **Differences in P accumulation intensity depending on forest species**

310 The slow-growing tree species have higher aboveground P contents than fast-growing
311 species and even increase their total P contents with biomass more than do the fast-
312 growing species (See Fig. S5 in Appendix 9) ($P < 0.001$, SMA test of common slopes).
313 Slow growing species had higher P:N ratios wood and total aboveground biomass and
314 lower leaf P:N ratios than fast-growing species (Figure 4). Within angiosperms and
315 within gymnosperms by separate this general tendencies were also observed (see
316 Table S5 in Appendix 10) and also when comparing slow- and fast-growing species
317 within species growing under Mediterranean climate and also within the species
318 growing under wet-temperate climatic conditions (see Table S6 in Appendix 11).
319 Moreover, the increases of P:N ratio with total aboveground biomass also increase
320 more in slow-growing than in fast-growing species, mainly in wood (Figure 5).

321 Different increases in total P contents with biomass were also observed in
322 comparing the angiosperms with the gymnosperms of those Catalan forests ($P < 0.001$,
323 SMA test of common slopes) and also between evergreen angiosperms and deciduous
324 angiosperms ($P < 0.001$, SMA test of common slopes) (see Fig. S6 in Appendix 12).

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337 **DISCUSSION**

338 Trees respond to the frequent P limitation by the P losses during soil aging and
339 ecological succession by increasingly accumulating P (Walker & Syers, 1976;
340 Izquierdo *et al.*, 2013; Celi *et al.*, 2013; Huang *et al.*, 2013; Zhou *et al.*, 2013). This
341 allows slowing down the plant-soil-plant P-cycle for longer time and avoiding P losses
342 by soil leaching. Two mechanisms appear to underlie the increasing capacity to store P
343 and the increasing P:N ratio as aboveground biomass increases. First, woody biomass
344 increases proportionally more than foliar biomass. Second, wood has higher P:N ratio
345 than foliar biomass and moreover wood P:N ratio increases when plants increase in
346 size. Increasing size thus not only increases the proportion of wood but also the P:N
347 ratio in the wood. This trend is observed both in angiosperm and in gymnosperm
348 forests.

349 Some previous studies have focused on the scaling relationships among total
350 plant biomass and nutrient content and stoichiometric relationships (Kerkhoff *et al.*,
351 2005; Kerkhoff & Enquist, 2006). These studies focused on all types of plants and
352 considered that the total plant nutrient content reflects the metabolically active fraction
353 of plant mass, which in turn should scale isometrically in direct proportion with total leaf
354 mass, and that whole plant P:N ratio should be independent of plant biomass and
355 equivalent to leaf P:N ratio. This can be adequate in herbs, but our results demonstrate
356 that in morphologically more complex plants such as trees, we cannot expect that foliar
357 nutrient content and stoichiometric relationships reflect directly all tree nutrient content
358 and stoichiometric relationships. Several studies have observed that the scaling
359 relationships between N and P observed in leaves are also confirmed in other major
360 plant organs (Kerkhoff *et al.*, 2006; Elser *et al.*, 2010). Although these relationships can
361 differ between woody and herbaceous species and among different tissues of the
362 same species, P increases disproportionately with N in all them (Niklas *et al.*, 2005;
363 Reich *et al.*, 2010).

364 Despite some studies and models observed and projected decreases of P:N
365 with plant size, this relationship can be very complex, among several reasons, because
366 it can vary in function of how the stoichiometry of plant organs affect growth and
367 production and how allocation to different organs vary with plant size (Niklas *et al.*,
368 2005; Elser *et al.*, 2010). Moreover, Elser *et al.* (2010) i observed that “functional” and
369 “non functional” pools of nutrients can change with plant size which has not been
370 adequately assessed in most current models. Our data also shows that the proportion
371 of functional (in leaves) versus non functional (in wood) P tends to decrease with size
372 in higher proportion than for N, because P accumulates proportionally more than N in
373 wood and less in leaves. This suggests that in the stoichiometrical allometrical
374 relationships apart from plant production considerations other factors such as storing
375 capacity can strongly determine the N and P scaling relationships, especially in species
376 with most biomass (wood) not directly linked to production. Our study also agrees with
377 the previous studies reporting that leaf $P_{(F/noF)}:N_{(F/noF)}$ ratio tends to decrease with
378 increasing size of plants (Elser *et al.*, 2010). Our study showed that large size and long
379 life trees are related with their great capacity to continuously accumulate wood tissues
380 not directly related with active mechanisms underlying production capacity. This wood
381 can thus become an effective reservoir of sources. The slopes of the relationships of P
382 content and N content with total aboveground biomass were 1.1 and 0.88 respectively,
383 showing that the overall aboveground P concentration increases whereas N
384 aboveground concentration decreases. This phenomenon occurs as a result of the
385 increase in wood/leaf ratio (with wood with higher P:N ratio) and also as direct result of
386 the higher P:N ratio in leaves and mainly in wood when aboveground biomass
387 increases. In other words, P concentration in aboveground biomass increases because
388 P has a higher proportional content enhancement in leaves and mainly in wood than N
389 when aboveground biomass increases and also by the increasingly wood/leaf ratio with
390 size. This higher retention of P in wood resulting from internal mobility differences
391 between N and P could be interpreted as an evolutionarily acquired mechanism

392 resulting from the selective pressure to retain as much P as possible to counteract the
393 natural trend of soils to lose P thus also taking profit of the wood accumulation with age.
394 The higher resorption efficiency of P than of N at global scale (Mulder *et al.*, 2013) is a
395 key process that can generate these differences between foliar P and N concentrations
396 and P:N ratios in leaves and wood. The trend to accumulate P is even more
397 accentuated and important in species of advanced successional stages. In this case,
398 the slow-growing species (see Figure 4) such as *Q. ilex*, *Q. suber*, *A. alba*, *Q. petraea*,
399 *F. sylvatica*, *Q. humilis*, *Q. cerrroides* or *Pinus uncinata*) are species of advanced forest
400 succesional stages (Gracia *et al.*, 2004b). The slow-growing plant species have been
401 associated with low foliar P:N ratio (Elser *et al.*, 2010; Reich *et al.*, 2010), large growth
402 and long life, coupled to a large capacity to store P in wood (Reich *et al.*, 2010;
403 Sardans & Peñuelas, 2013). In contrast, the capacity to store P in wood is less
404 important in species of early successional stages with higher foliar P:N ratios, that are
405 usually fast-growing species in this study (Gracia *et al.*, 2004b). In fact, fast-growing
406 plants have normally higher P:N ratios in photosynthetic tissues (Yu *et al.*, 2010; 2011).
407 The fact that most early successional species in Catalan forests are gymnosperms that
408 present low wood/foliar ratio can influence the previous results. This is translated into
409 lower allometrical slopes in the increase of P accumulation with biomass in
410 gymnosperms than in angiosperms. In any case, gymnosperms, as angiosperms, also
411 increase the accumulation of P proportionally more than the accumulation of N with
412 biomass increase. Thus, the results show that all types of forests accumulate more P
413 than N with increasing biomass, and suggest that early-successional fast-growing tree
414 species allocate proportionally more P to leaves than to wood with respect to N,
415 favoring higher foliar P:N ratios and lower wood P:N ratios than late-successional slow-
416 growing species. However, they have lower global capacity of storing P than slow-
417 growing long-living late-successional species since wood/leaf ratio increases with tree
418 aging. Slow-growing species make a conservative use of limiting resources such as P
419 because wood/leaf ratios increase with age and their higher allocation of P to wood

420 favors P storing in stand biomass. Thus, the natural successional process seems to
421 favor the ecosystem capacity to retain P (mainly in wood), more than N. This
422 differential retention is of particular importance in preventing ecosystem P losses with
423 soil aging. In addition, this different capacity of tree species to accumulate more or less P,
424 may have significant consequences in many forest ecosystem due to the outstanding role
425 of P:N at the community level including in soil trophic webs (Sterner & Elser, 2002; Sardans
426 *et al.*, 2012).

427 Summarizing, in Catalan forests, P accumulates in forest aboveground biomass
428 more than N; the P concentration of aboveground biomass increases whereas the N
429 concentration decreases with increasing aboveground biomass. This is mainly due to
430 the higher capacity of wood to store P than N, a difference that it is enhanced with
431 increasing aboveground biomass. These data coincided with previous observations in
432 tropical forest and could be a general trend to compensate the long-term soil-P
433 depletion with time. In this way this storage of P in wood would be a strategy to remove
434 P from the soil to avoid soil immobilization and losses and also could be and strategy
435 to reduce its availability to competitors. Whether or not this P accumulated in wood is
436 used as an active reservoir for the growing trees remains to be investigated. However
437 this trend could not exist in forests evolved on soils with specific N-limitation and/or
438 especially rich in P. Moreover, late-successional slow-growing long-living species have
439 higher capacity to store more P in aboveground biomass than early-successional fast-
440 growing species. In any case, this increasing storage of P and the consequent shift in
441 P:N ratios, which are very important in physiological and ecological processes, are
442 likely to have large implications for ecosystem functioning and services.

443

444 **ACKNOWLEDGEMENTS**

445 This research was supported by the Spanish Government grants CGL2013-48074-P
446 and Consolider-Ingenio Montes CSD2008-00040, the Catalan Government project

447 SGR 2014-274 and the European Research Council Synergy grant ERC-SyG-610028

448 IMBALANCE-P.

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SUPPORTING INFORMATION

675 Additional supporting information may be found in the online version of this article at
676 the publisher's web-site.

677

678 Appendix 1. Table S1. Allometries to the calculation of leaf biomass per tree.

679

680 Appendix 2. Table S2. Allometries to the calculation of leaf biomass + branch biomass
681 per tree.

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683 Appendix 3. Table S3. Allometries to the calculation of stem biomass per tree.

684

685 Appendix 4. Table S4. Allometries to the calculation of total aboveground biomass per
686 tree.

687

688 Appendix 5. Supplementary Figure S1. Relationships of wood/leaf ratios with total
689 aboveground biomass in different forest types

690

691 Appendix 6. Supplementary Figure S2. Allometric relationships of log-transformed
692 ratios of leaf P content/total wood P content and of leaf N content/total wood N
693 content with log-transformed total aboveground biomass.

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695 Appendix 7. Supplementary Figure S3. Allometric relationships of log-transformed total
696 aboveground N and P contents with total aboveground biomass in angiosperms
697 and in gymnosperms forest.

698

699 Appendix 8. Supplementary Figure S4. Allometric relationships of log-transformed
700 woody and foliar P:N ratios with log-transformed total P in aboveground biomass

701

702 Appendix 9. Supplementary Figure S5. Allometric relationships of log-transformed total
703 aboveground P contents with log-transformed aboveground biomass in slow- and
704 fast-growing species.

705

706 Appendix 10. Table S5. Allometric relationships of total aboveground P contents and
707 total aboveground biomass in fast-growing species and slow-growing species.

708

709 Appendix 11. Table S6. Leaf, wood and total aboveground biomass in slow- and fast-
710 growing species.

711

712 Appendix 12. Supplementary Figure S6. Allometric relationships of total aboveground
713 P contents with total aboveground biomass in angiosperms and gymnosperms,
714 and in evergreens and deciduous angiosperms.

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718 BIOSKETCH

719 Dr. Jordi Sardans and Prof Josep Peñuelas research is focused on the field of plant
720 ecophysiology, biogeochemical cycles and atmosphere-biosphere interactions. JS
721 mainly focuses his research on the elemental stoichiometry relationships with terrestrial
722 ecosystems structure and function and in the metabolomic plant responses to abiotic
723 and biotic changes. JP research covers a wide range of ecological disciplines:
724 chemical ecology, biogeochemistry, global change, climate change, atmospheric
725 pollution, biogenic VOCs emissions, remote sensing, and functioning and structure of
726 terrestrial plants and ecosystems.

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761 **Figure legends**

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764 Figure 1. Allometric relationships of foliar, branch and stem biomasses with total
765 aboveground biomass (A). Boxplots of the P:N ratios of leaves, branches and
766 stems median (the continuous line into the boxes) with the corresponding
767 quartiles. The dashed lines into the boxes represent the mean values \pm (S.E.).
768 Different letters indicate statistically significant differences ($P < 0.05$) (B). (SMA =
769 Slope Major Axis).

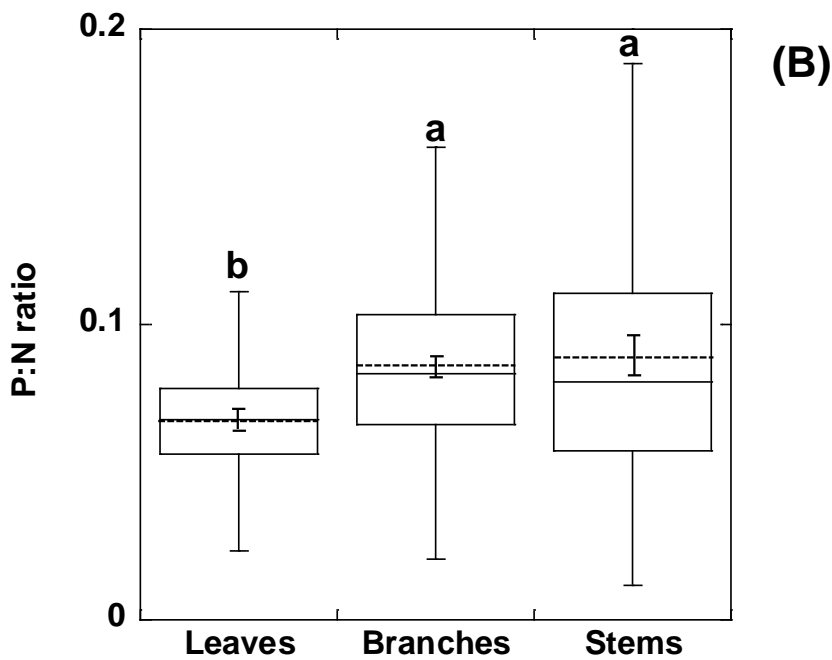
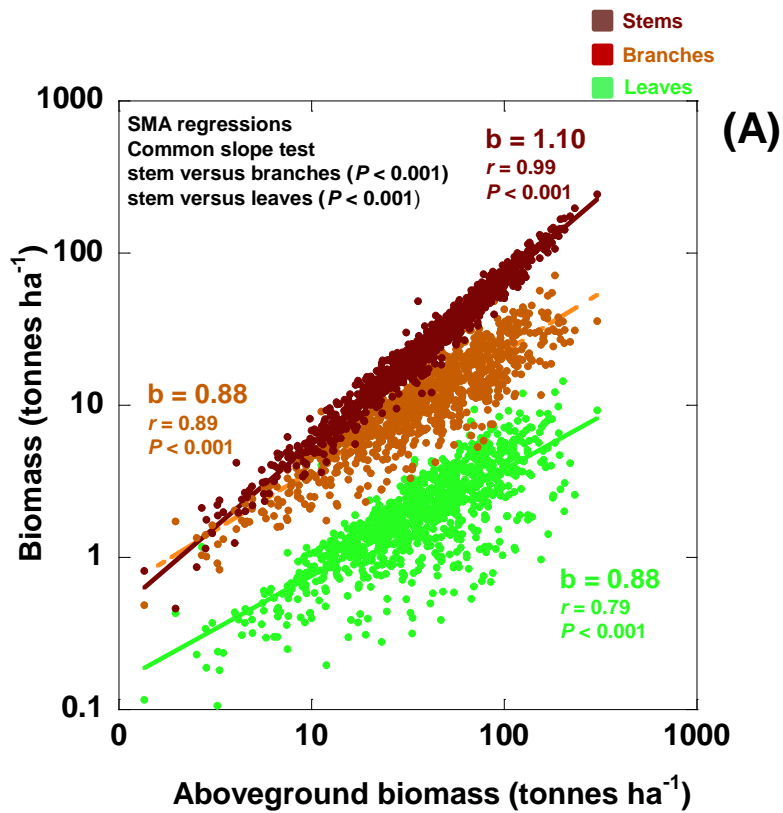
770 Figure 2. Allometric relationships of P and N contents in total aboveground biomass
771 with total aboveground biomass (A). Allometric relationships of P:N ratios in
772 total aboveground biomass with total aboveground biomass (B). (SMA = Slope
773 Major Axis).

774 Figure 3. Allometric relationships of (A) woody P:N ratios and (B) foliar P:N ratios with
775 log-transformed total aboveground biomass. (SMA = Slope Major Axis).

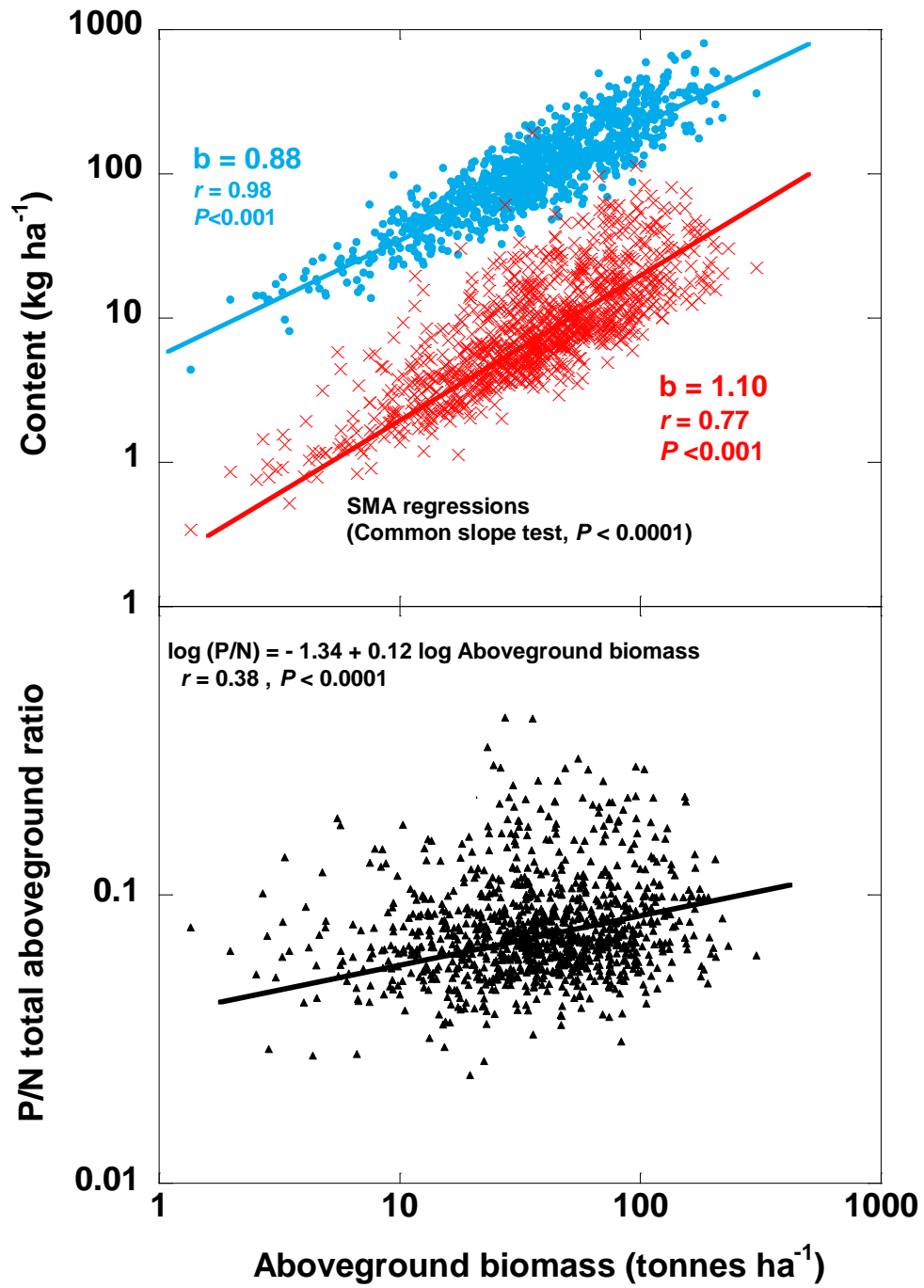
776 Figure 4. Figure 4. Boxplot of P:N ratios of wood, leaves and total aboveground
777 biomass median (the continuous line into the boxes) with the corresponding
778 quartiles in slow- and fast-growing tree species. The dashed lines into the
779 boxes represent the mean values \pm (S.E.). Different letters indicate statistically
780 significant differences ($P < 0.05$) between slow- and fast-growing species. Slow-
781 growing (*Pinus uncinata*, *Quercus ilex*, *Quercus suber*, *Abies alba*, *Quercus*
782 *cerrioides*, *Quercus humilis*, *Quercus petraea*, *Fagus sylvatica*) and fast-
783 growing tree species (*Pinus halepensis*, *Pinus sylvestris*, *Pinus nigra*, *Pinus*
784 *pinaster*, *Castanea sativa*, *Pseudotsuga menziesii*, *Pinus radiata*, *Populus*
785 *tremula*, *Populus hybrides*, *Populus nigra*, *Fraxinus angustifolia*, *Fraxinus*
786 *excelsior*, *Prunus avium*, *Cedrus deodara*).

787 Figure 5. Allometric relationships of (A) woody P:N ratios and (B) foliar P:N ratios with
788 log-transformed total aboveground biomass in slow- and fast-growing. (SMA =
789 Slope Major Axis).

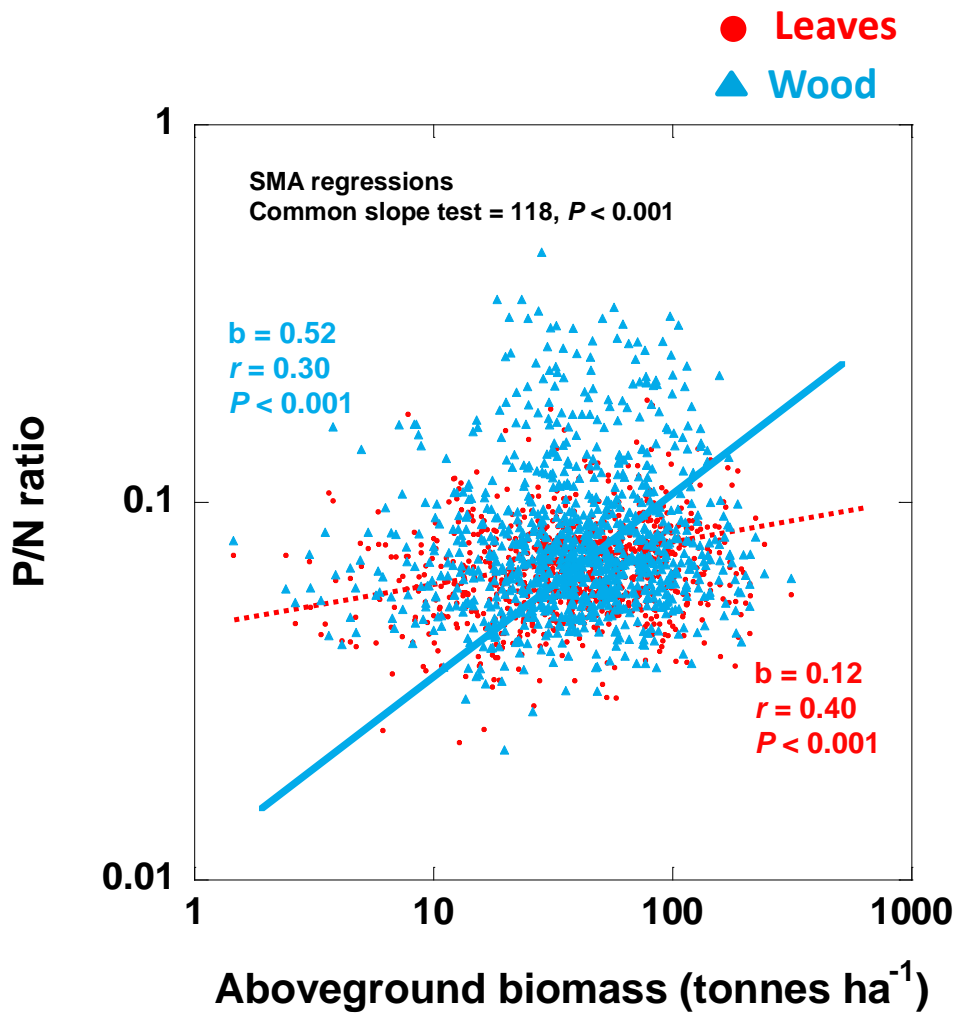
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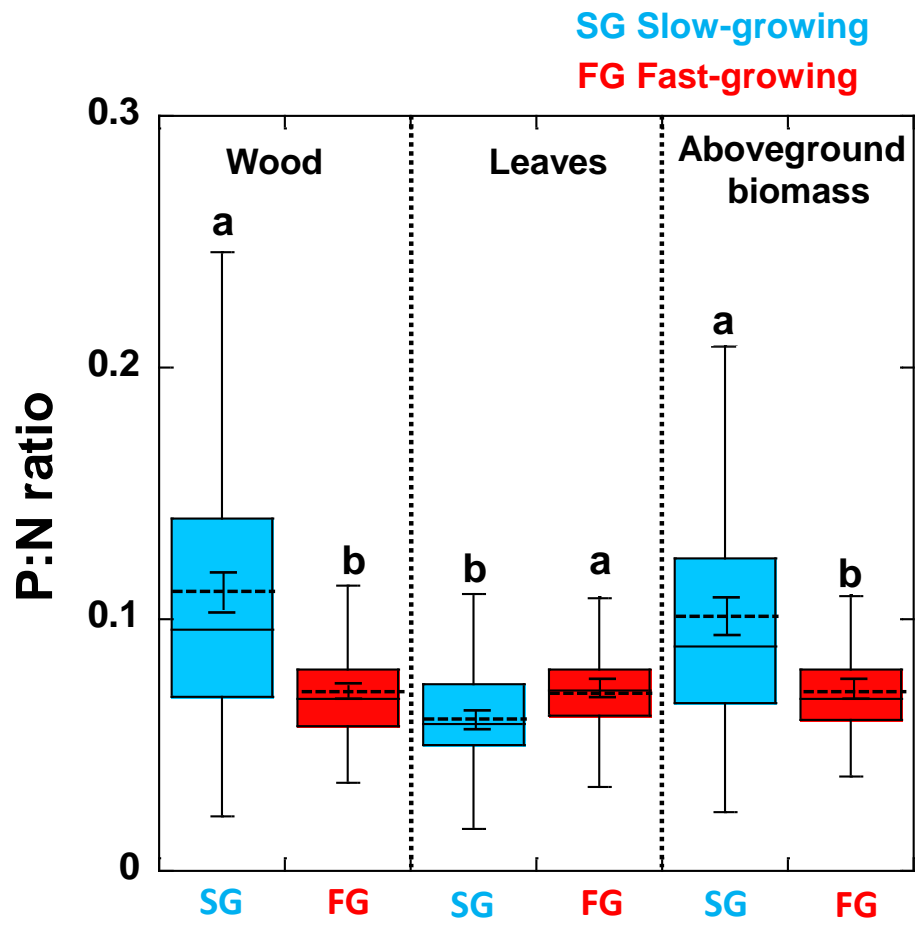


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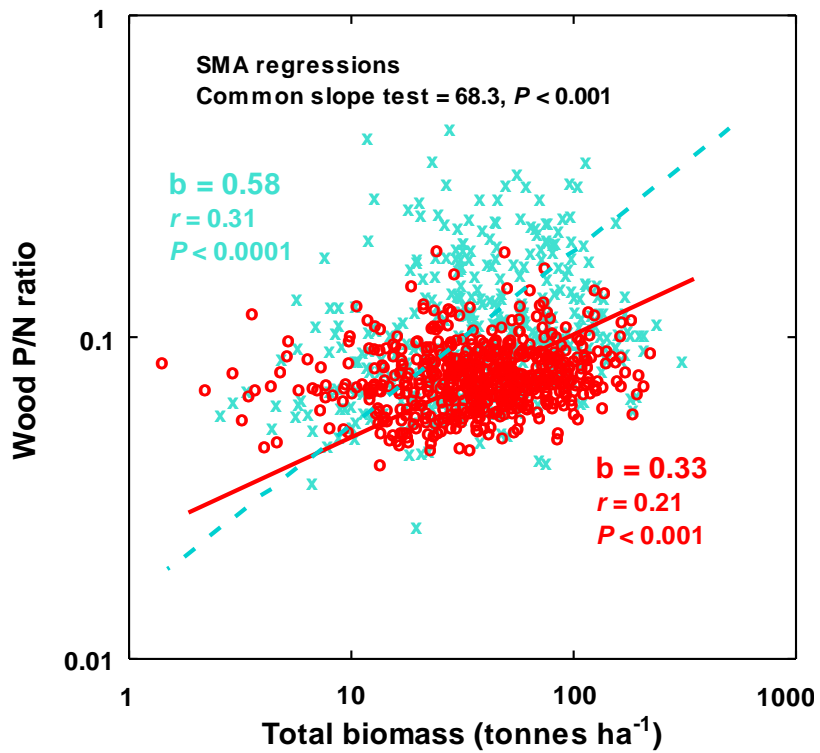
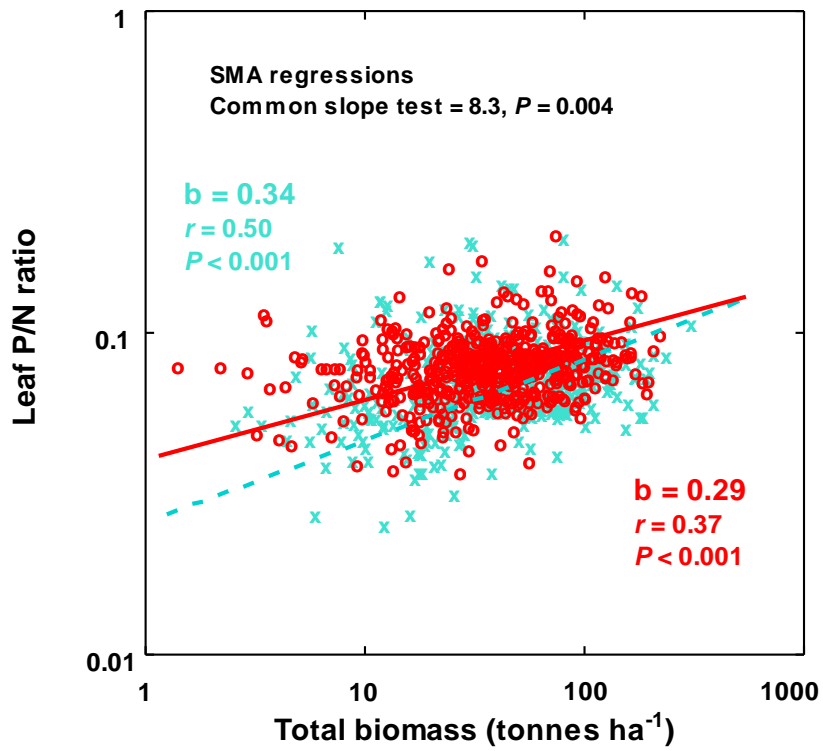
Figure 3



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Figure 4

x Slow-growing
o Fast-growing



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832 Figure 5