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1 Fertile forests produce biomass more efficiently

2
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40
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49

50 **Abstract**

51 Trees with sufficient nutrition are known to allocate carbon preferentially to aboveground plant
52 parts. Our global study of 49 forests revealed an even more fundamental carbon allocation
53 response to nutrient availability: forests with high nutrient availability use $58\pm 3\%$ (mean \pm SE; 17
54 forests) of their photosynthates for plant biomass production, while forests with low nutrient
55 availability only convert $42\pm 2\%$ (mean \pm SE; 19 forests) of annual photosynthates to biomass.
56 This nutrient effect largely overshadows previously observed differences in carbon allocation
57 patterns among climate zones, forest types and age classes. If forests with low nutrient
58 availability use $16\pm 4\%$ less of their photosynthates for plant growth, what are these used for?
59 Current knowledge suggests that lower biomass production per unit photosynthesis in forests
60 with low- versus forests with high nutrient availability reflects not merely an increase in plant
61 respiration, but likely results from reduced carbon allocation to unaccounted components of net
62 primary production, particularly root symbionts.

63

64

65 **Introduction**

66 Plant physiologists often argue that, across species and biomes, plants respire a nearly constant
67 fraction – approximately 50% – of the carbon taken up during photosynthesis (GPP) (Gifford
68 1994, 1995; Dewar *et al.* 1998; Waring *et al.* 1998; Enquist *et al.* 2007; Van Oijen *et al.* 2010).
69 The remaining carbon – termed net primary production (NPP) – is converted into plant biomass
70 and other complex molecules used for multiple purposes (e.g., root exudation, production of
71 volatile organic compounds). The relative constancy of the partitioning of GPP into autotrophic
72 respiration (Ra) and NPP would reflect the interdependence of respiration and photosynthesis.
73 Respiration depends on the substrate provided by photosynthesis, which in turn relies on
74 respiration to provide the energy required for construction of complex compounds such as carbon
75 skeletons for protein synthesis (Krömer 1995; Hoefnagel *et al.* 1998). Unfortunately, the
76 verification of this theory at the ecosystem scale is severely hampered by the fact that NPP and
77 Ra are difficult to quantify for the entire ecosystem. While Ra occurs in every living plant cell
78 within the ecosystem, NPP includes numerous carbon-consuming processes (plant growth, root
79 exudation, carbon allocation to symbionts and production of volatile organic compounds). The
80 paucity of accurate data on forest ecosystem Ra and NPP globally explains why the partitioning
81 of GPP at the ecosystem scale remains poorly understood.

82
83 Because biomass production constitutes the largest fraction of NPP, biomass production is
84 commonly used as a proxy for NPP (Waring *et al.* 1998; DeLucia *et al.* 2007; Drake *et al.* 2011;
85 Goulden *et al.* 2011). In contrast to theoretical argumentations for a constrained NPP-to-GPP
86 ratio (Dewar *et al.* 1998; Van Oijen *et al.* 2010), field measurements in forests revealed
87 substantial variation in the biomass production-to-GPP ratio (DeLucia *et al.* 2007). The biomass
88 production-to-GPP ratio was reported to be higher in forests of the temperate zone, in particular

89 in broadleaved temperate forests (DeLucia *et al.* 2007), and to decrease with increasing stand age
90 (DeLucia *et al.* 2007; Goulden *et al.* 2011). These results are, however, tentative because the
91 effect of stand age is confounded with forest type and climate zone; the majority of the young
92 forests is located in the temperate zone (DeLucia *et al.* 2007; Drake *et al.* 2011).

93
94 Because biomass production and GPP data have become increasingly available in recent years,
95 we revisited the global variation in ecosystem-scale carbon partitioning patterns using a global
96 forest database (Luyssaert *et al.* 2007). For the current study, we selected only those forests that
97 provided estimates of above- and belowground biomass production and GPP that were
98 independent from each other (i.e., biomass production estimates via biometry and GPP via eddy
99 covariance or in a few cases using a model). Whenever necessary, biomass production estimates
100 of the resulting 49 forests were complemented with estimates of missing biomass components.
101 This procedure did not affect our conclusions (see Appendix S1). Further detailed information
102 regarding the dataset is provided in Appendix S1.

103
104 Last, to make a clear distinction with the NPP-to-GPP ratio (which comprises not only plant
105 biomass production, but also production of volatile organic compounds, root exudates and root
106 symbionts), we here introduce the term Biomass Production Efficiency (BPE) when referring to
107 the biomass production-to-GPP ratio. Biomass production contains all the biomass produced
108 within a year irrespective of whether this biomass dies within the same or subsequent years.

109
110 **Variables explaining variation in biomass production efficiency**

111 Previous studies focussed on climate, forest type and stand age to explain the observed
112 differences in the biomass production-to GPP ratio among forests (DeLucia *et al.* 2007; Goulden

113 *et al.* 2011). Nutrient availability and forest management (unmanaged versus management
114 involving harvesting, thinning, etc.) significantly affect allocation patterns in forests (Shan *et al.*
115 2001; Litton *et al.* 2007; LeBauer & Treseder 2008). Plants exposed to ample nutrients invest
116 relatively less carbon in roots, while plants growing under low nutrient availability use relatively
117 more carbon for root growth at the expense of aboveground growth (Chapin 1980). Forest
118 management also has been found to decrease root-to-shoot ratios (Shan *et al.* 2001) and both
119 nutrient availability and forest management are thus potentially important factors influencing
120 BPE. So far, however, they have not been assessed.

121
122 While information on climate, forest type, stand age and management practices is easily
123 available, measured nutrient availability is not. Estimation of comparable nutrient availability is
124 not a simple task and requires standardized measurements. Effective plant nutrient availability
125 depends on multiple factors besides soil nutrient content (soil texture, pH, cation exchange
126 capacity, moisture), such that it can differ substantially among sites with, for example, similar
127 soil nitrogen contents but different soil texture. Furthermore, comparison of nutrient availability
128 among ecosystems requires consideration of all plant nutrients, and not only nitrogen, as was
129 demonstrated for a range of hardwood forests in northern United States and Canada
130 (Vadeboncoeur 2010). Unfortunately, such a uniform estimation of nutrient availability in forests
131 across the globe does not currently exist. In order to test whether BPE increased with increasing
132 nutrient availability, we therefore assigned each of the 49 forests in our dataset to one of three
133 categories: low-, medium-, or high-nutrient availability following the information available in
134 literature (see Table S3 in Appedix S2).

135

136 Although this classification is not a simple task, information for forests of the low and high
137 nutrient availability class was generally very clear. Forests of the low nutrient availability class
138 were typically located on soils with extremely low nutrient content due to weathering, leaching,
139 or low mineralization rates. In contrast, some of the forests assigned to the high nutrient
140 availability class grew on former (fertilized) agricultural land, while others were located on soil
141 types that are renowned as very fertile (see Appendix S2). Moreover, for 14 of the 17 forests of
142 the high nutrient availability class, an explicit statement of the nutrient status was provided in
143 publications (see Appendix S2). Last, a sensitivity analysis revealed that potential
144 misclassification of sites with relatively little information would not influence our conclusions
145 (Table S4).

146
147 As expected, differences in absolute biomass production between forests of similar nutrient status
148 growing in different climate zones were large (Tables 1 and 3), but these differences were
149 entirely attributable to differences in GPP, with BPE changing little within nutrient classes (Table
150 1). In contrast, the large differences in biomass production among temperate-zone forests of
151 different nutrient availability were not solely due to variation in GPP. Whereas GPP did not
152 significantly differ between temperate forests of the low and high nutrient availability class
153 (+31%, $p=0.19$; Table 1), biomass production was 78% higher in temperate forests of the high
154 nutrient availability class than in temperate forests with low nutrient availability ($p=0.01$; Table
155 1). This disproportionate increase in biomass production relative to GPP was most pronounced in
156 woody biomass, with three-fold higher aboveground wood production at high compared to low
157 nutrient availability ($p=0.02$; Table 2), while foliage and root biomass production remained
158 largely unchanged (Table 2; $p=0.49$ and $p=0.83$, respectively). As a consequence of the much
159 larger nutrient effect on biomass production compared to GPP, BPE was $35\pm 9\%$ (mean \pm SE)

160 higher for temperate forests of high nutrient availability than in temperate forests of low nutrient
161 availability ($p=0.03$; Table 1).

162
163 In order to test whether nutrient availability was indeed the key factor explaining variation in
164 BPE, we performed a stepwise regression analysis including climate zone (boreal, temperate and
165 tropical), forest type (coniferous, broadleaved and mixed), stand age, nutrient availability and
166 forest management (i.e., unmanaged or managed). For more information regarding stepwise
167 regression analysis, see Cohen (1991), Derr & Everitt (2002) and Appendix S4. In contrast to
168 results reported in other analyses (DeLucia et al. 2007; Goulden et al. 2011), analysis of our data
169 set indicated that neither climate zone, nor forest type or stand age significantly affected BPE,
170 whereas nutrient availability affected BPE highly significantly ($p<0.01$). Independently of
171 climate or forest type, forests with high nutrient availability allocated on average $58\pm 3\%$
172 (mean \pm SE of 17 forests) of their photosynthates to biomass production, whereas forests with low
173 nutrient availability used on average only $42\pm 2\%$ (mean \pm SE of 19 forests) of their photosynthates
174 for biomass production (i.e., slopes of lines in Fig. 1; $p<0.01$ for low versus high nutrient
175 availability). This result of nutrient availability being the primary determinant of BPE was
176 confirmed also by other statistical tests (see Appendix S4), irrespective of whether or not we
177 accounted for measurement uncertainties.

178
179 Figure 2A further suggests that previously reported differences in BPE among boreal, temperate
180 and tropical forests (DeLucia *et al.* 2007) were introduced by the uneven distribution of forests
181 with high nutrient availability (with higher BPE) across the globe, being heavily biased towards
182 the temperate zone. Likewise, the previously reported difference between coniferous and
183 broadleaved forests (DeLucia *et al.* 2007) was not apparent when taking nutrient availability into

184 account, probably because nutrient-rich soils were occupied more by broadleaved than by
185 coniferous forests (Fig. 2C).

186
187 In addition to nutrient availability, which was by far the dominant determinant of variation in
188 BPE, management also affected BPE significantly according to the stepwise regression analysis
189 ($p=0.02$). Managed forests exhibited higher BPE than unmanaged forests for both low and high
190 nutrient availability classes (Fig. 2B), but quantification of this effect remains premature because
191 of the uneven distribution of unmanaged and managed forests among nutrient classes (Fig. 2B).
192 Nonetheless, the distinction between unmanaged and managed forests appeared an important
193 factor in the relationship between stand age and BPE, because the tendency for a negative age
194 effect on BPE as observed in Figure 2D only became significant ($p=0.04$) if management regime
195 was not included in the stepwise regression analysis.

196

197 **Underlying mechanisms**

198 The significantly higher BPE in forests with high nutrient availability as compared to forests of
199 the medium or low nutrient availability class implies that either a smaller fraction of GPP is being
200 respired in the forests with high nutrient availability, or a smaller fraction of GPP is partitioned to
201 unaccounted NPP components (VOC emissions, root symbionts, root exudation), or a
202 combination of both. Because estimates of carbon transfers to volatile organic compounds
203 (VOC), and to root exudates and symbionts are not available for any of the forests in our
204 database, the only way to test why BPE differs between forests of different nutrient availability is
205 by comparing estimates of the Ra-to-GPP ratio. Many pitfalls arise when measuring Ra at the
206 ecosystem level (Ryan *et al.* 1997; Amthor & Baldocchi 2001), ecosystem Ra is therefore most

207 often estimated as the residual of GPP minus biomass production, rendering these Ra estimates
208 useless to test whether or not variation in the ratio of Ra to GPP could explain variation in BPE.

209
210 Only 11 of our sites provided ecosystem Ra and GPP estimates that were independent from
211 biomass production. These 11 forests revealed no effect of nutrient availability on the Ra-to-GPP
212 ratio (see Fig. 3 in BOX 1), suggesting that variation in the ratio of Ra to GPP does not explain
213 the higher BPE in nutrient-rich forests. Obviously, the limited data availability constrains the
214 robustness of this analysis. Nonetheless, in addition to this lack of empirical evidence for a
215 difference in the Ra-to-GPP ratio among nutrient availability classes, it appears unlikely that
216 nutrient-rich forests that grow faster (which would lead to more growth respiration) and that
217 likely exhibit higher protein levels (which would lead to higher maintenance respiration would
218 exhibit considerably lower Ra-to-GPP ratios than nutrient-poor forests (see BOX 1 for a more
219 thorough elaboration of the underlying rationale). We therefore hypothesize that the unmeasured
220 NPP components explain the difference in BPE among nutrient availability classes. Particularly
221 root symbionts are a plausible candidate (BOX 2).

222
223 Finally, managed forests exhibited higher BPE than unmanaged forests for both the high and low
224 nutrient availability class. Management via thinning sometimes implies removal of biomass
225 expected to grow sub-optimally, such as suppressed trees with large autotrophic respiration
226 relative to GPP. Such removals may decrease the relative amount of maintenance respiration and
227 consequently also the Ra-to-GPP ratio. The higher BPE in managed than in unmanaged forests
228 may thus reflect this reduced Ra-to-GPP ratio. In addition, managed forests may exhibit higher
229 BPE than unmanaged forests because frequent anthropogenic disturbances tend to (further)
230 increase nutrient availability.

231
232 Our analysis of 49 forest sites where biomass production and GPP were independently measured
233 revealed that nutrient availability may be the unifying mechanism controlling the ratio of biomass
234 production-to-GPP that encompasses climate, forest type, and stand age as influencing factors.
235 The carbon sink potential of forests largely depends on how carbon taken up during
236 photosynthesis is partitioned. Photosynthates partitioned to R_a do not contribute to carbon
237 sequestration but those converted into long-lived biomass do contribute. The observed pattern of
238 higher carbon partitioning to plant biomass with increasing nutrient availability thus adds to our
239 understanding of the processes governing long-term carbon sequestration in forests and may have
240 far-reaching consequences for carbon cycle management. Further research is needed to verify
241 how the higher BPE in forests with high nutrient availability, together with the previously
242 reported decrease of soil organic matter decomposition in response to fertilization (Janssens *et al.*
243 2010) determines ecosystem carbon sequestration.

244
245 It remains unresolved whether the increased partitioning to biomass production relative to GPP
246 associated with higher nutrient availability is related to a lower R_a -to-GPP ratio or to a small
247 fraction of NPP going to typically unaccounted for components such as VOC production, root
248 symbionts, and root exudates in forests of high versus low nutrient availability. The present study
249 points in the direction of the latter (see also BOX 2). Future (large-scale) experiments in which
250 nutrient availability is manipulated and where all measurements needed to unravel carbon
251 partitioning are made (i.e., independent estimates for all NPP components, GPP and R_a) would
252 help resolve these questions.

253
254

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266

267 **SUPPORTING INFORMATION**

268 Additional Supporting Information may be found in the online version of this article:

269

270 **Appendix S1:** Detailed information about the data used

271 **Appendix S2:** Nutrient classification

272 **Appendix S3:** Additional discussion regarding uncertainties on fine root production estimates

273 **Appendix S4:** Detailed information about statistical analyses

274

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380

381 **BOX 1: Autotrophic respiration-to-GPP ratio**

382

383 The biomass production-to-photosynthesis ratio is typically used as a proxy for the ratio of net
384 primary production (NPP) to photosynthesis (GPP), termed carbon use efficiency (CUE) (e.g.
385 DeLucia *et al.* 2007). Alternatively, CUE can be determined using autotrophic respiration (Ra)
386 instead of biomass production, i.e., $CUE=1-(Ra:GPP)$. Estimates of Ra (not derived from
387 biomass production measurements) are usually obtained by upscaling respiration measured on
388 parts of the vegetation (foliage, stem, branch) or by subtracting heterotrophic respiration from
389 eddy covariance-based estimates of ecosystem respiration (see e.g. Piao *et al.* (2010)). Estimates
390 of Ra (independent of biomass production) are less abundant than biomass production estimates,
391 which is the primary reason why we focus on the biomass production-to-GPP ratio and not on the
392 ratio of Ra to GPP. Nonetheless, we show the results of the 11 forests in our dataset that provided
393 estimates of Ra that were independent of GPP and biomass production (Fig. 3). The Ra-to-GPP
394 ratio did not significantly differ among nutrient availability classes ($p=0.34$ for ANOVA with
395 nutrient availability as fixed factor), but with only two nutrient-rich forests, it is premature to
396 draw meaningful conclusions.

397

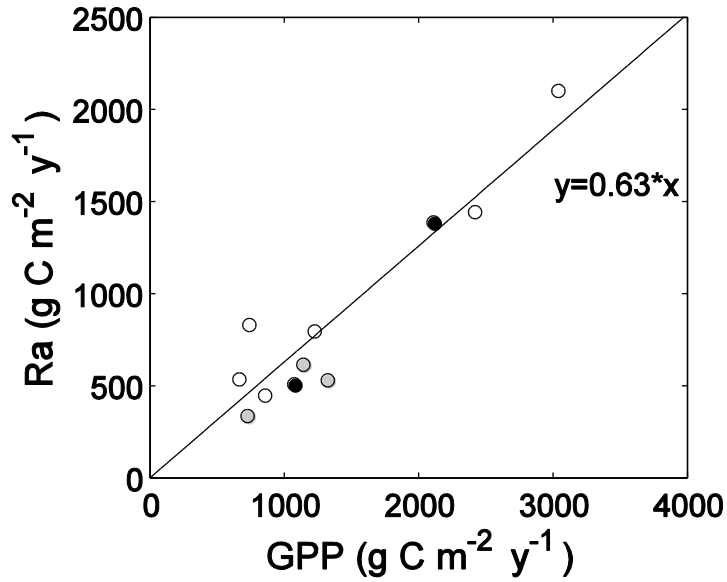
398 Literature on respiration measurements at organ level (root, woody tissue, foliage) also provides
399 no definite answer because both increases and decreases in the Ra-to-GPP ratio with increasing
400 nutrient availability appear possible. Autotrophic respiration (Ra) is typically positively related to
401 tissue nitrogen concentrations (Chapin 1980). Because photosynthesis also increases with
402 increasing nitrogen concentration, the Ra-to-GPP ratio of leaves appears relatively constant
403 across species, climates and ecosystem types (Reich *et al.* 1998; Loveys *et al.* 2003; Turnbull *et*
404 *al.* 2005; Atkin *et al.* 2007; Campbell *et al.* 2007), although under extreme conditions this ratio

405 may increase (Atkin *et al.* 2007; Campbell *et al.* 2007) and potentially indicates an increase of
406 ‘wastage’ respiration needed to discard excess energy and prevent cell damage (Amthor 2000). In
407 one study, the leaf respiration-to-photosynthesis ratio was higher in two forests suffering severe
408 nutrient limitations as compared to neighbouring less nutrient-stressed forests (Turnbull *et al.*
409 2005).

410
411 On the other hand, in forests with high nutrient availability, a larger fraction of photosynthates
412 typically is invested in wood compared to the fraction invested in wood in forests with low
413 nutrient availability (Litton *et al.* 2007). This was also the case for the forests in our dataset
414 (Table 1 and 2). Higher wood relative to foliage production may thus increase the Ra-to-GPP
415 ratio in forests of high nutrient availability compared to forests of low nutrient availability.
416 Further, several studies show a positive relation between root respiration per unit mass and root
417 nutrient concentrations (Chapin 1980; Burton *et al.* 2002), but this may be counterbalanced by a
418 decrease in standing root biomass as indicated by the negative fertilization effect on root
419 respiration found in a recent meta-analytical study (Janssens *et al.* 2010).

420
421 While the effects of nutrient availability on the ratio of Ra to GPP remain unclear, a decrease in
422 the Ra-to-GPP ratio for forests with high nutrient availability relative to forests of low nutrient
423 availability seems unlikely according to the theory that plants respire a relatively constant
424 fraction of GPP (Dewar *et al.* 1998; Van Oijen *et al.* 2010) due to interdependencies of
425 respiration and photosynthesis (Hoefnagel *et al.* 1998).

426 .



427
 428 **Figure 3:** Field estimates of autotrophic respiration (Ra) versus gross primary production (GPP).
 429 Each single data point represents one forest site and is the average value over all years for which
 430 data were available in the database. White, gray and black circles indicate sites of low-, medium-
 431 and high-nutrient availability, respectively. The equation refers to the linear fit through the data.
 432 One nutrient-poor site with Ra:GPP>1 was removed. We found no statistically significant
 433 nutrient-availability effect on Ra:GPP (p=0.34), but these results remain tentative due to the
 434 small number of data points

435 **BOX 2: Testing where the missing carbon is going**

436

437 In this study, we identified a gap in the current knowledge of forest carbon allocation: forests
438 with high nutrient availability use $16\pm 4\%$ more of their photosynthates for biomass production
439 than forests with low nutrient availability ($16\pm 4\%$ represents the difference between mean of 17
440 forests of high nutrient availability and mean of 19 forests of low nutrient availability; SE
441 calculated as $SE_{\text{difference}} = \sqrt{SE_1^2 + SE_2^2}$, with SE_1 and SE_2 the SE for low- and high nutrient
442 availability, respectively). This difference is, however, unlikely attributable to a difference in
443 carbon partitioning to autotrophic respiration. It therefore appears likely that forests of low
444 nutrient availability invest more photosynthates in non-biomass components of net primary
445 production (NPP), which usually are not quantified in experiments or reported in the literature
446 and therefore could not be taken into account in our analysis. These unaccounted for NPP
447 components include volatile organic compounds, root exudates, and root symbionts. We
448 hypothesize that carbon allocation to root symbionts in particular is a key factor explaining the
449 higher biomass production efficiency in nutrient-rich relative to nutrient-poor forests. First
450 support for this hypothesis is given in literature:

451

452 Symbiotic fungi are essential for the growth and health of forest trees (Courty *et al.* 2010), as
453 they transport nutrients from soil to tree (van der Heijden *et al.* 2008; Courty *et al.* 2010). Up to
454 80% of plant nitrogen and 75% of plant phosphorus can be fungal-derived in forests (van der
455 Heijden *et al.* 2008). In return for these nutrients, considerable amounts of carbon are transferred
456 from tree to fungus (van der Heijden *et al.* 2008; Courty *et al.* 2010). Recent reviews (Hobbie
457 2006; Courty *et al.* 2010), mostly based on controlled short-term studies, state that the overall
458 carbon flux to mycorrhizal fungi can constitute up to 30% of NPP (but observational estimates

459 remain scarce and highly variable; see Hobbie 2006 and Courty *et al.* 2010). Nonetheless, one
460 long-term field study in a nutrient-rich, temperate oak forest (Heinemeyer *et al.* 2012) where the
461 mycorrhizal soil carbon flux contribution was estimated at about 20% of NPP, confirms this
462 order of magnitude.

463
464 It has been shown repeatedly that carbon transfer to fungal symbionts are strongly inversely
465 related to nutrient availability (Wallenda & Kottke 1998; Lilleskov *et al.* 2002; Högberg *et al.*
466 2003; Read & Perez-Moreno 2003; Treseder 2004; Högberg *et al.* 2010), opening the door for a
467 substantial effect on the biomass production efficiency (BPE). According to a meta-analytical
468 review, mycorrhizal abundance declines substantially in response to nitrogen and phosphorus
469 fertilization (15% and 32%, respectively) (Treseder 2004). Similar responses were observed
470 along natural gradients in nutrient availability. Both biodiversity and proteolytic capabilities of
471 ectomycorrhizal fungi declined along a gradient of increasing mineral nitrogen availability
472 through Europe (Schulze 2000), phospholipid fatty acid attributed to mycorrhizal fungi
473 dramatically decreased along a natural soil nitrogen gradient in a boreal forest (Högberg *et al.*
474 2003), and both taxonomic richness and sporocarp abundance decreased over an anthropogenic
475 nitrogen deposition gradient in Alaska (Lilleskov *et al.* 2002).

476
477 Following this well-reported and strong relation between root symbionts and nutrient availability,
478 we hypothesize that forests with high nutrient availability produce more biomass per unit
479 photosynthesis than forests with low nutrient availability because the latter need to invest
480 relatively more photosynthates in root symbionts.

481

482 **Tables**

483 **Table 1:** Mean and standard deviation (in brackets) for gross primary production (GPP), total
484 biomass production (BP) and the biomass production-to-GPP ratio (BPE) in boreal, temperate
485 and tropical forests of different nutrient availability (low, medium and high). For statistics, see
486 Table 3. The number of forests per group is indicated in Figure 2A.

487

| 488 Climate zone, | GPP | BP | BPE |
|----------------------------------|--|--|-------------|
| 489 nutrient availability | (g C m⁻² y⁻¹) | (g C m⁻² y⁻¹) | |
| 490 Boreal, low | 911 (184) | 355 (124) | 0.39 (0.10) |
| 491 Temperate, low | 1320 (718) | 565 (264) | 0.43 (0.05) |
| 492 Tropical, low | 2985 (591) | 1233 (315) | 0.41 (0.11) |
| 493 Boreal, medium | 803 (204) | 390 (112) | 0.49 (0.10) |
| 494 Temperate, medium | 1328 (372) | 659 (208) | 0.50 (0.11) |
| 495 Temperate, high | 1724 (408) | 1008 (354) | 0.58 (0.13) |

496

497

498 **Table 2:** Mean and standard deviation (in brackets) for the ratio of belowground to aboveground
 499 biomass production (BBP:ABP), aboveground wood production (AWP), foliage production (FP),
 500 root production (RP) and the ratio of aboveground wood production to gross primary production
 501 (AWP:GPP) in boreal, temperate and tropical forests of different nutrient availability (low,
 502 medium and high). For statistics, see Table 3. The number of forests per group are indicated in
 503 superscript.

504

| 505 Climate zone, | BBP:ABP | AWP | FP | RP | AWP:GPP |
|----------------------------------|---------------------------|--|--|--|---------------------------|
| 506 nutrient availability | | (g C m⁻² y⁻¹) | (g C m⁻² y⁻¹) | (g C m⁻² y⁻¹) | |
| 507 Boreal, low | 0.65 (0.29) ⁵ | 100 (46) ⁵ | 61 (24) ⁵ | 125 (65) ⁵ | 0.11 (0.02) ⁵ |
| 508 Temperate, low | 0.66 (0.31) ⁶ | 166 (80) ⁶ | 153 (98) ⁶ | 205 (97) ⁶ | 0.13 (0.03) ⁶ |
| 509 Tropical, low | 0.28 (0.09) ⁵ | 348 (85) ⁵ | 404 (151) ⁵ | 282 (47) ⁵ | 0.11 (0.03) ⁵ |
| 510 Boreal, medium | 0.45 (0.27) ⁵ | 116 (32) ⁵ | 72 (36) ⁵ | 117 (68) ⁵ | 0.15 (0.03) ⁵ |
| 511 Temperate, medium | 0.88 (0.90) ⁷ | 212 (129) ⁶ | 149 (97) ⁷ | 238 (122) ⁷ | 0.14 (0.07) ⁶ |
| 512 Temperate, high | 0.33 (0.17) ¹⁷ | 493 (335) ¹⁶ | 184 (50) ¹⁶ | 218 (88) ¹⁷ | 0.27 (0.14) ¹⁶ |

513

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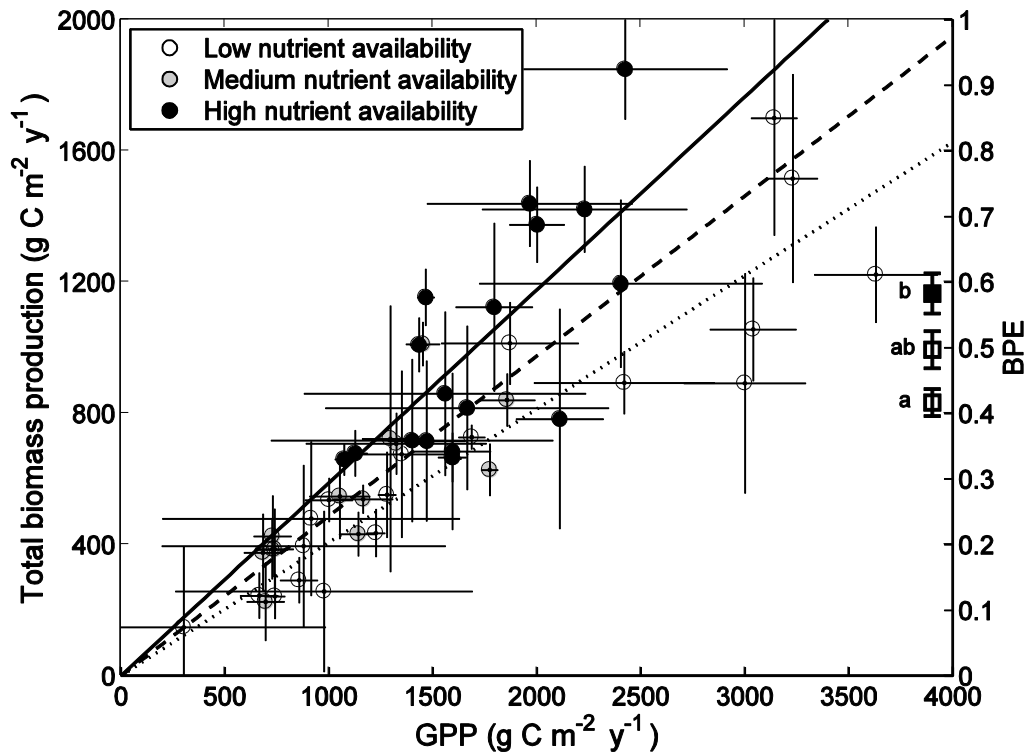
515 **Table 3:** Statistical analysis for gross primary production (GPP), biomass production (BP), the
516 biomass production-to-GPP ratio (BPE), the ratio of belowground to aboveground biomass
517 production (BBP:ABP), aboveground wood production (AWP), foliage production (FP), root
518 production (RP), and the wood production-to-GPP ratio (AWP:GPP). The column ‘stepwise fit’
519 indicates the predictor variable(s) (climate zone (C), forest type (F), management (M), stand age
520 (A), nutrient availability (N)) selected by the stepwise regression at $p < 0.05$. ANOVA(1) shows
521 results of ANOVA with the variables selected by the stepwise regression as fixed factors (or as
522 covariable in case of stand age). ANOVA(2) gives results of a two-way ANOVA with climate
523 zone and nutrient availability as fixed variables and thus corresponds to data shown in Tables 1
524 and 2.

525

| 526 | Variable | Stepwise fit | ANOVA(1) | ANOVA(2) |
|-----|-----------------|---------------------|---|-------------------------------|
| 527 | GPP | C, N | Boreal<Temperate<Tropical ($p < 0.01$) | C: $p < 0.01$; N: $p = 0.05$ |
| 528 | | | Nutrients: low=medium<high ($p = 0.05$) | |
| 529 | BP | A, C, N | Boreal<Temperate<Tropical ($p < 0.01$) | C: $p < 0.01$; N: $p < 0.01$ |
| 530 | | | Nutrients: low=medium<high ($p < 0.01$) | |
| 531 | | | negative age effect ($p = 0.01$) | |
| 532 | BPE | N, M | low=medium<high ($p < 0.01$) | C: $p = 0.69$; N: $p < 0.01$ |
| 533 | | | Unmanaged<Managed ($p = 0.07$) | |
| 534 | BBP:ABP | N | Nutrients: low=medium>high ($p = 0.07$) | C: $p = 0.69$; N: $p < 0.01$ |
| 535 | AWP | C, N | Boreal=Temperate<Tropical ($p < 0.01$) | C: $p < 0.01$; N: $p < 0.01$ |
| 536 | | | Nutrients: low=medium<high ($p < 0.01$) | |
| 537 | FP | C, F | Boreal<Temperate<Tropical ($p < 0.01$) | C: $p < 0.01$; N: $p = 0.13$ |
| 538 | | | Needle-leaved<broadleaved ($p < 0.01$) | |
| 539 | RP | C | Boreal<Temperate=Tropical ($p < 0.01$) | C: $p < 0.01$; N: $p = 0.92$ |
| 540 | AWP:GPP | N | Nutrients: low=medium<high ($p < 0.01$) | C: $p = 0.94$; N: $p = 0.01$ |

541 **Figures**

542 **Figure 1:** Each circle represents the mean annual total biomass production \pm SE versus mean
543 annual gross primary production (GPP \pm SE) for one forest. Colours indicate nutrient availability
544 classes, error bars reflect uncertainties (see Appendix S1). Dotted, dashed and solid lines are
545 linear fits ($y=ax$) for the low-, medium- and high nutrient availability class, respectively
546 ($R^2=0.84$, $R^2=0.66$, $R^2=0.56$, respectively; $p<0.01$ for low- versus high nutrient availability (GLM
547 analysis)). The squares on the right represent the mean biomass production efficiency (BPE:
548 biomass production-to-GPP ratio). Error bars on these squares are standard errors on the means,
549 reflecting measurement uncertainties and inter-annual variability in case of multi-year data.
550 Letters next to the squares indicate significant differences at $p<0.05$ (Tukey post-hoc test;
551 ANOVA with nutrient availability as fixed factor).

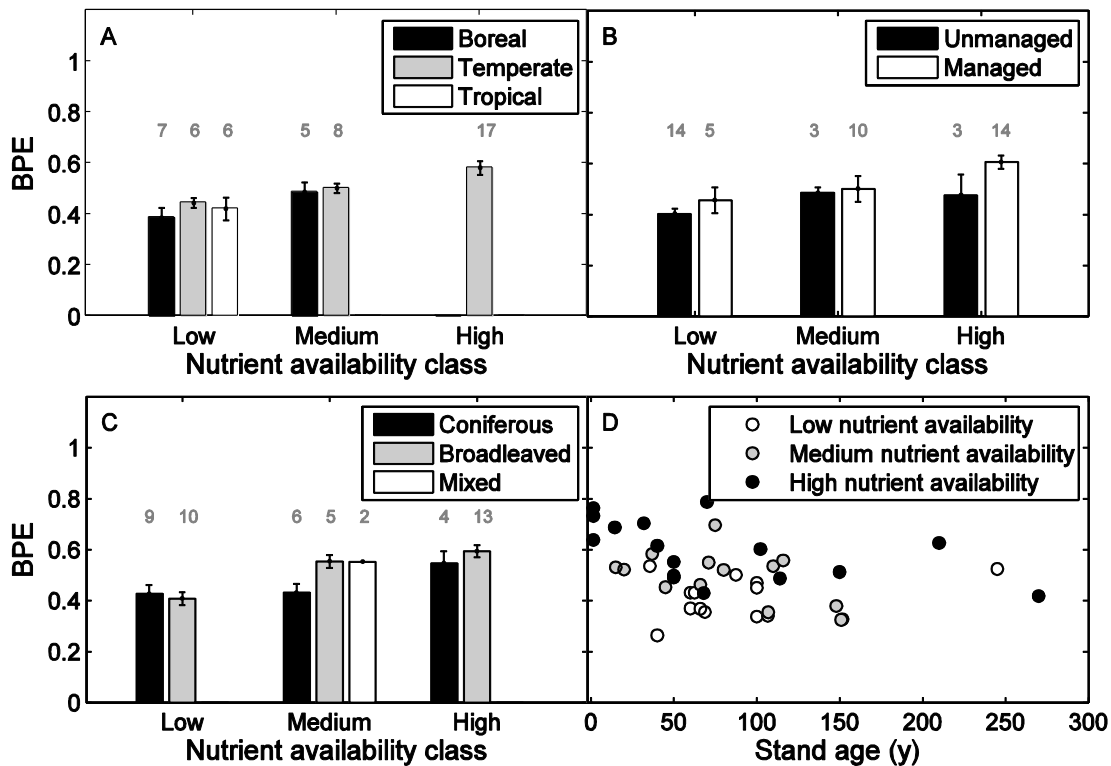


552

553

554 **Figure 2:** Mean biomass production efficiency (BPE) versus nutrient availability class for (A)
 555 different climate zones, (B) management practices, (C) forest types and (D) BPE versus stand age
 556 for the three nutrient availability classes. Error bars represent the standard error on the mean and
 557 numbers indicate the number of forests per group. Stepwise regression analysis revealed a
 558 significant effect of nutrient availability ($p < 0.01$) and forest management ($p = 0.02$). Climate zone,
 559 forest type and stand age were not statistically significant ($p > 0.1$). Note that for six forests no
 560 estimate for stand age was available and these sites were thus omitted from this analysis.
 561 Removing stand age from the regression model, which allows inclusion of these six sites, did not
 562 alter the outcome (data not shown).

563



564

565

566