

Fertile forests produce biomass more efficiently

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1 Fertile forests produce biomass more efficiently

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50 Abstract

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

63

65 Introduction

66 Plant physiologists often argue that, across species and biomes, plants respire a nearly constant fraction – approximately 50% – of the carbon taken up during photosynthesis (GPP) (Gifford 67 1994, 1995; Dewar et al. 1998; Waring et al. 1998; Enquist et al. 2007; Van Oijen et al. 2010). 68 69 The remaining carbon – termed net primary production (NPP) – is converted into plant biomass and other complex molecules used for multiple purposes (e.g., root exudation, production of 70 71 volatile organic compounds). The relative constancy of the partitioning of GPP into autotrophic respiration (Ra) and NPP would reflect the interdependence of respiration and photosynthesis. 72 Respiration depends on the substrate provided by photosynthesis, which in turn relies on 73 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 within the ecosystem, NPP includes numerous carbon-consuming processes (plant growth, root 78 exudation, carbon allocation to symbionts and production of volatile organic compounds). The 79 paucity of accurate data on forest ecosystem Ra and NPP globally explains why the partitioning 80 of GPP at the ecosystem scale remains poorly understood. 81

82

Because biomass production constitutes the largest fraction of NPP, biomass production is commonly used as a proxy for NPP (Waring *et al.* 1998; DeLucia *et al.* 2007; Drake *et al.* 2011; Goulden *et al.* 2011). In contrast to theoretical argumentations for a constrained NPP-to-GPP ratio (Dewar *et al.* 1998; Van Oijen *et al.* 2010), field measurements in forests revealed substantial variation in the biomass production-to-GPP ratio (DeLucia *et al.* 2007). The biomass production-to-GPP ratio was reported to be higher in forests of the temperate zone, in particular in broadleaved temperate forests (DeLucia *et al.* 2007), and to decrease with increasing stand age
(DeLucia *et al.* 2007; Goulden *et al.* 2011). These results are, however, tentative because the
effect of stand age is confounded with forest type and climate zone; the majority of the young
forests is located in the temperate zone (DeLucia *et al.* 2007; Drake *et al.* 2011).

93

Because biomass production and GPP data have become increasingly available in recent years, 94 95 we revisited the global variation in ecosystem-scale carbon partitioning patterns using a global forest database (Luyssaert et al. 2007). For the current study, we selected only those forests that 96 provided estimates of above- and belowground biomass production and GPP that were 97 98 independent from each other (i.e., biomass production estimates via biometry and GPP via eddy covariance or in a few cases using a model). Whenever necessary, biomass production estimates 99 100 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 regarding the dataset is provided in Appendix S1. 102

103

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

109

110 Variables explaining variation in biomass production efficiency

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

et al. 2011). Nutrient availability and forest management (unmanaged versus management 113 114 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 relatively less carbon in roots, while plants growing under low nutrient availability use relatively 116 117 more carbon for root growth at the expense of aboveground growth (Chapin 1980). Forest management also has been found to decrease root-to-shoot ratios (Shan et al. 2001) and both 118 119 nutrient availability and forest management are thus potentially important factors influencing BPE. So far, however, they have not been assessed. 120

121

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

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

146

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

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

162

In order to test whether nutrient availability was indeed the key factor explaining variation in 163 164 BPE, we performed a stepwise regression analysis including climate zone (boreal, temperate and tropical), forest type (coniferous, broadleaved and mixed), stand age, nutrient availability and 165 166 forest management (i.e., unmanaged or managed). For more information regarding stepwise regression analysis, see Cohen (1991), Derr & Everitt (2002) and Appendix S4. In contrast to 167 results reported in other analyses (DeLucia et al. 2007; Goulden et al. 2011), analysis of our data 168 set indicated that neither climate zone, nor forest type or stand age significantly affected BPE, 169 170 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 $58\pm3\%$ 172 (mean±SE of 17 forests) of their photosynthates to biomass production, whereas forests with low nutrient availability used on average only 42±2% (mean±SE of 19 forests) of their photosynthates 173 for biomass production (i.e., slopes of lines in Fig. 1; p<0.01 for low versus high nutrient 174 175 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

Figure 2A further suggests that previously reported differences in BPE among boreal, temperate and tropical forests (DeLucia *et al.* 2007) were introduced by the uneven distribution of forests with high nutrient availability (with higher BPE) across the globe, being heavily biased towards the temperate zone. Likewise, the previously reported difference between coniferous and 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 by185 coniferous forests (Fig. 2C).

186

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

196

197 Underlying mechanisms

The significantly higher BPE in forests with high nutrient availability as compared to forests of 198 the medium or low nutrient availability class implies that either a smaller fraction of GPP is being 199 respired in the forests with high nutrient availability, or a smaller fraction of GPP is partitioned to 200 201 unaccounted NPP components (VOC emissions, root symbionts, root exudation), or a combination of both. Because estimates of carbon transfers to volatile organic compounds 202 (VOC), and to root exudates and symbionts are not available for any of the forests in our 203 204 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 often estimated as the residual of GPP minus biomass production, rendering these Ra estimatesuseless to test whether or not variation in the ratio of Ra to GPP could explain variation in BPE.

209

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

222

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

231

232 Our analysis of 49 forest sites where biomass production and GPP were independently measured revealed that nutrient availability may be the unifying mechanism controlling the ratio of biomass 233 production-to-GPP that encompasses climate, forest type, and stand age as influencing factors. 234 235 The carbon sink potential of forests largely depends on how carbon taken up during 236 photosynthesis is partitioned. Photosynthates partitioned to Ra do not contribute to carbon sequestration but those converted into long-lived biomass do contribute. The observed pattern of 237 higher carbon partitioning to plant biomass with increasing nutrient availability thus adds to our 238 understanding of the processes governing long-term carbon sequestration in forests and may have 239 far-reaching consequences for carbon cycle management. Further research is needed to verify 240 241 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

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

253

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266

267 SUPPORTING INFORMATION

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

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280

281 **References**

- Amthor, J.S. (2000). The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30
- 283 years later. Ann. Bot., 86, 1-20.
- Amthor, J.S. & Baldocchi, D.D. (2001). Terrestrial higher plant respiration and net primary
 production. In: *Terrestrial Global Productivity* (eds. Roy J, Saugier B & Mooney HA). Academic
- 286 Press San Diego, pp. 33-59.
- Atkin, O.K., Scheurwater, I. & Pons, T.L. (2007). Respiration as a percentage of daily
 photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. *New Phytol.*, 174, 367-380.
- Burton, A.J., Pregitzer, K.S., Ruess, R.W., Hendrik, R.L. & Allen, M.F. (2002). Root respiration
- in North American forests: effects of nitrogen concentration and temperature across biomes. *Oecologia*, 131, 559-568.
- Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O. & Hurry, V. (2007).
 Acclimation of photosynthesis and respiration is asynchronous in response to changes in
 temperature regardless of plant functional group. *New Phytol.*, 176, 375-389.
- 296 Chapin, F.S. (1980). The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst., 11, 233-260.
- 297 Courty, P.E., Buée, M., Diedhiou, A.G., Frey-Klett, P., Le Tacon, F., Rineau, F., et al. (2010).
- 298 The role of ectomycorrhizal communities in forest ecosystem processes: New perspectives and 299 emerging concepts. *Soil Biol. Biochem.*, 42, 679-698.
- 300 DeLucia, E.H., Drake, J.E., Thomas, R.B. & Gonzalez-Meler, M. (2007). Forest carbon use
- 301 efficiency: is respiration a constant fraction of gross primary production? *Global Change Biol.*,
- 302 13, 1157-1167.

- 303 Dewar, R.C., Medlyn, B.E. & McMurtrie, R.E. (1998). A mechanistic analysis of light and
 304 carbon use efficiencies. *Plant Cell Environ.*, 21, 573-588.
- Drake, J.E., Davis, S.C., Raetz, L.M. & DeLucia, E.H. (2011). Mechanisms of age-related
 changes in forest production: the influence of physiological and successional changes. *Global Change Biol.*, 17, 1522-1535.
- Enquist, B.J., Kerkhoff, A.J., Huxman, T.E. & Economo, E.P. (2007). Adaptive differences in
 plant physiology and ecosystem paradoxes: insights from metabolic scaling theory. *Global Change Biol.*, 13, 591-609.
- Gifford, R.M. (1994). The global carbon cycle: a viewpoint on the missing sink. *Austr. J. Plant Physiol.*, 21, 1-15.
- Gifford, R.M. (1995). Whole plant respiration and photosynthesis of wheat under increased CO₂
 concentration and temperature: long-term vs. short-term distinctions for modelling. *Global Change Biol.*, 1, 385-396.
- Goulden, M.L., McMillan, A.M.S., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W., *et al.* (2011). Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biol.*, 17, 855-871.
- Heinemeyer, A., Wilkinson, M., Vargas, R., Subke, J.A., Casella, E., Morison, J.I.L., *et al.*(2012). Exploring the "overflow tap" theory: linking forest soil CO₂ fluxes and individual
 mycorrhizosphere components to photosynthesis. *Biogeosci.*, 9, 79-95.
- Hobbie, E.A. (2006). Carbon allocation to ectomycorrhizal fungi correlates with belowground
 allocation in culture studies. *Ecology*, 87, 563-569.
- 324 Hoefnagel, M.H.N., Atkin, O.K. & Wiskich, J.T. (1998). Interdependence between chloroplasts
- and mitochondria in the light and the dark. *Biochim. Biophys. Acta*, 1366, 235-255.

- Högberg, M.N., Baath, E., Nordgren, A., Arnebrant, K. & Högberg, P. (2003). Contrasting
 effects of nitrogen availability on plant carbon supply to mycorrhizal fungi and saprotrophs a
 hypothesis based on field observations in boreal forest. *New Phytol.*, 160, 225-238.
- Högberg, M.N., Briones, M.J.I., Keel, S.G., Metcalfe, D.B., Campbell, C., Midwood, A.J., et al.
- 330 (2010). Quantification of effects of season and nitrogen supply on tree below-ground carbon
- transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytol.*,
 187, 485-493.
- Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., et al.
- (2010). Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geosci.*, 3,
 315-322.
- 336 Krömer, S. (1995). Respiration during photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol.*337 *Biol.*, 46, 45-70.
- LeBauer, D.S. & Treseder, K.K. (2008). Nitrogen limitation of net primary productivity in
 terrestrial ecosystems is globally distributed. *Ecology*, 89, 371-379.
- Lilleskov, E.A., Fahey, T.J., Horton, T.R. & Lovett, G.M. (2002). Belowground ectomycorrhizal
- fungal community change over a nitrogen deposition gradient in Alaska. *Ecology*, 83, 104-115.
- Litton, C.M., Raich, J.W. & Ryan, M.G. (2007). Carbon allocation in forest ecosystems. *Global Change Biol.*, 13, 2089-2109.
- Loveys, B.R., Atkinson, L.J., Sherlock, D.J., Roberts, R.L., Fitter, A.H. & Atkin, O.K. (2003).
- 345 Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and 346 slow-growing plant species. *Global Change Biol.*, 9, 895-910.
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichsteins, M., Papale, D., et al. (2007).
- CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global*
- 349 *Change Biol.*, 13, 2509-2537.

- Piao, S., Luyssaert, S., Ciais, P., Janssens, I.A., Chen, A., Cao, C., et al. (2010). Forest annual
- 351 carbon cost: a global-scale analysis of autotrophic respiration. *Ecology*, 91, 652-661.
- Read, D.J. & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems a journey towards relevance? *New Phytol.*, 157, 475-492.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., Vose, J.M., Volin, J.C., Gresham, C., et al. (1998).
- Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, 114, 471-482.
- 357 Ryan, M.G., Lavigne, M.B. & Gower, S.T. (1997). Annual carbon cost of autotrophic respiration
- in boreal forest ecosystems in relation to species and climate. J. Geophys. Res., 102, 2887128883.
- Schulze, E.D. (2000). The carbon and nitrogen cycle in forest ecosystems. In: *Carbon and Nitrogen Cycling in European Forest Ecosystems* (ed. Schulze ED). Springer, Berlin, p. 500.
- Shan, J.P., Morris, L.A. & Hendrick, R.L. (2001). The effects of management on soil and plant
 carbon sequestration in slash pine plantations. *J. Appl. Ecol.*, 38, 932-941.
- 364 Treseder, K.K. (2004). A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and
 365 atmospheric CO₂ in field studies. *New Phytol.*, 164, 347-355.
- 366 Turnbull, M.H., Tissue, D.T., Griffin, K.L., Richardson, S.J., Peltzer, D.A. & Whitehead, D.
- 367 (2005). Respiration characteristics in temperate rainforest tree species differ along a long-term
 368 soil-development chronosequence. *Oecologia*, 143, 271-279.
- Vadeboncoeur, M.A. (2010). Meta-analysis of fertilization experiments indicates multiple
 limiting nutrients in northeastern deciduous forests. *Can. J. For. Res.*, 40, 1766-1780.
- van der Heijden, M.G.A., Bardgett, R.D. & van Straalen, N.M. (2008). The unseen majority: soil
- microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.*, 11,
- 373 296-310.

| 374 | Van Oijen, M., Schapendonk, A. & Hoglind, M. (2010). On the relative magnitudes of |
|-----|--|
| 375 | photosynthesis, respiration, growth and carbon storage in vegetation. Ann. Bot., 105, 793-797. |
| 376 | Wallenda, T. & Kottke, I. (1998). Nitrogen deposition and ectomycorrhizas. New Phytol., 139, |

- 377 169-187.
- 378 Waring, R.H., Landsberg, J.J. & Williams, M. (1998). Net primary production of forests: a
- constant fraction of gross primary production? *Tree Physiol.*, 18, 129-134.
- 380

381 BOX 1: Autotrophic respiration-to-GPP ratio

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

397

Literature on respiration measurements at organ level (root, woody tissue, foliage) also provides no definite answer because both increases and decreases in the Ra-to-GPP ratio with increasing nutrient availability appear possible. Autotrophic respiration (Ra) is typically positively related to tissue nitrogen concentrations (Chapin 1980). Because photosynthesis also increases with increasing nitrogen concentration, the Ra-to-GPP ratio of leaves appears relatively constant across species, climates and ecosystem types (Reich *et al.* 1998; Loveys *et al.* 2003; Turnbull *et al.* 2005; Atkin *et al.* 2007; Campbell *et al.* 2007), although under extreme conditions this ratio may increase (Atkin *et al.* 2007; Campbell *et al.* 2007) and potentially indicates an increase of
'wastage' respiration needed to discard excess energy and prevent cell damage (Amthor 2000). In
one study, the leaf respiration-to-photosynthesis ratio was higher in two forests suffering severe
nutrient limitations as compared to neighbouring less nutrient-stressed forests (Turnbull *et al.*2005).

410

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

420

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

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

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

436

In this study, we identified a gap in the current knowledge of forest carbon allocation: forests 437 with high nutrient availability use $16\pm4\%$ more of their photosynthates for biomass production 438 439 than forests with low nutrient availability $(16\pm4\%$ represents the difference between mean of 17 forests of high nutrient availability and mean of 19 forests of low nutrient availability; SE 440 calculated as $SE_{difference} = sqrt(SE_1^2 + SE_2^2)$, with SE_1 and SE_2 the SE for low- and high nutrient 441 availability, respectively). This difference is, however, unlikely attributable to a difference in 442 carbon partitioning to autotrophic respiration. It therefore appears likely that forests of low 443 444 nutrient availability invest more photosynthates in non-biomass components of net primary production (NPP), which usually are not quantified in experiments or reported in the literature 445 446 and therefore could not be taken into account in our analysis. These unaccounted for NPP components include volatile organic compounds, root exudates, and root symbionts. We 447 hypothesize that carbon allocation to root symbionts in particular is a key factor explaining the 448 higher biomass production efficiency in nutrient-rich relative to nutrient-poor forests. First 449 450 support for this hypothesis is given in literature:

451

Symbiotic fungi are essential for the growth and health of forest trees (Courty *et al.* 2010), as they transport nutrients from soil to tree (van der Heijden *et al.* 2008; Courty *et al.* 2010). Up to 80% of plant nitrogen and 75% of plant phosphorus can be fungal-derived in forests (van der Heijden *et al.* 2008). In return for these nutrients, considerable amounts of carbon are transferred from tree to fungus (van der Heijden *et al.* 2008; Courty *et al.* 2010). Recent reviews (Hobbie 2006; Courty *et al.* 2010), mostly based on controlled short-term studies, state that the overall carbon flux to mycorrhizal fungi can constitute up to 30% of NPP (but observational estimates remain scarce and highly variable; see Hobbie 2006 and Courty *et al.* 2010). Nonetheless, one long-term field study in a nutrient-rich, temperate oak forest (Heinemeyer *et al.* 2012) where the mycorrhizal soil carbon flux contribution was estimated at about 20% of NPP, confirms this order of magnitude.

463

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

476

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

481

482 Tables

Table 1: Mean and standard deviation (in brackets) for gross primary production (GPP), total biomass production (BP) and the biomass production-to-GPP ratio (BPE) in boreal, temperate and tropical forests of different nutrient availability (low, medium and high). For statistics, see 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 | | | | |

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

| 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 |
| | | | | | | |

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

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

541 Figures

542 Figure 1: Each circle represents the mean annual total biomass production ±SE versus mean 543 annual gross primary production (GPP±SE) for one forest. Colours indicate nutrient availability 544 classes, error bars reflect uncertainties (see Appendix S1). Dotted, dashed and solid lines are linear fits (y=ax) for the low-, medium- and high nutrient availability class, respectively 545 546 (R²=0.84, R²=0.66, R²=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. Letters next to the squares indicate significant differences at p<0.05 (Tukey post-hoc test; 550 551 ANOVA with nutrient availability as fixed factor).



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

