IDEA AND PERSPECTIVE

Fertile forests produce biomass more efficiently

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Abstract

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 response to nutrient availability: forests with high-nutrient availability use $58 \pm 3\%$ (mean $\pm$ SE; 17 forests) of their photosynthates for plant biomass production (BP), while forests with low-nutrient availability only convert $42 \pm 2\%$ (mean $\pm$ SE; 19 forests) of annual photosynthates to biomass. This nutrient effect largely overshadows previously observed differences in carbon allocation patterns among climate zones, forest types and age classes. If forests with low-nutrient availability use $16 \pm 4\%$ less of their photosynthates for plant growth, what are these used for? Current knowledge suggests that lower BP per unit photosynthesis in forests with low- versus forests with high-nutrient availability reflects not merely an increase in plant respiration, but likely results from reduced carbon allocation to unaccounted components of net primary production, particularly root symbionts.

Keywords

biomass production, biomass production efficiency, carbon allocation, global forest database, nutrients, photosynthesis, root symbionts.

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INTRODUCTION

Plant physiologists often argue that, across species and biomes, plants respire a nearly constant fraction – approximately 50% – of the carbon taken up during photosynthesis (gross primary production, GPP) (Gifford 1994, 1995; Dewar *et al.* 1998; Waring *et al.* 1998; Enquist *et al.* 2007; Van Oijen *et al.* 2010). 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 volatile organic compounds, VOC). The relative constancy of the partitioning of GPP into autotrophic respiration (Ra) and NPP would reflect the interdependence of respiration and photosynthesis. Respiration depends on the substrate provided by photosynthesis, which in turn relies on respiration to provide the energy required for construction of complex compounds such as carbon skeletons for protein synthesis (Krömer 1995; Hoefnagel *et al.* 1998). Unfortunately, the verification of this theory at the ecosystem scale is severely hampered by the fact that NPP and 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 exudation, carbon allocation to symbionts and production of VOC). The paucity of accurate data on forest ecosystem Ra and NPP globally explains why the partitioning of GPP at the ecosystem scale remains poorly understood.

Because biomass production (BP) constitutes the largest fraction of NPP, BP 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 BP-to-GPP ratio (DeLucia *et al.* 2007). The BP-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).

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Because BP and GPP data have become increasingly available in recent years, 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 provided estimates of above- and belowground BP and GPP that were independent from each other (i.e. BP estimates via biometry and GPP via eddy covariance or in a few cases using a model). Whenever necessary, BP estimates of the resulting 49 forests were complemented with estimates of missing biomass components. This procedure did not affect our conclusions (see Appendix S1). Further detailed information regarding the dataset is provided in Appendix S1.

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

VARIABLES EXPLAINING VARIATION IN BPE

Previous studies focussed on climate, forest type and stand age to explain the observed differences in the BP-to-GPP ratio among forests (DeLucia *et al.* 2007; Goulden *et al.* 2011). Nutrient availability and forest management (unmanaged versus management involving harvesting, thinning, etc.) significantly affect allocation patterns in forests (Shan *et al.* 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 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 nutrient availability and forest management are thus potentially important factors influencing BPE. So far, however, they have not been assessed.

While information on climate, forest type, stand age and management practices is easily available, measured nutrient availability is not. Estimation of comparable nutrient availability is not a simple task and requires standardised measurements. Effective plant nutrient availability 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 soil nitrogen contents but different soil texture. Furthermore, comparison of nutrient availability among ecosystems requires consideration of all plant nutrients, and not only nitrogen, as was demonstrated for a range of hardwood forests in northern US and Canada (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 nutrient availability, we therefore assigned each of the 49 forests in our dataset to one of three categories: low-, medium-, or high-nutrient availability following the information available in literature (see Table S3 in Appedix S2).

Although this classification is not a simple task, information for forests of the low- and high-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, or low mineralisation rates. In contrast, some of the forests assigned to the high-nutrient availability class grew on former (fertilised) 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 the high-nutrient availability class, an explicit statement of the nutrient status was provided in publications (see Appendix S2). Last, a sensitivity analysis revealed that potential misclassification of sites with relatively little information would not influence our conclusions (Table S4).

As expected, differences in absolute BP between forests of similar nutrient status 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 1). In contrast, the large differences in BP among temperate-zone forests of different nutrient availability were not solely due to variation in GPP. Whereas GPP did not significantly differ between temperate forests of the low- and high-nutrient availability class (+31%, $P = 0.19$; Table 1), BP was 78% higher in temperate forests of the high-nutrient availability class than in temperate forests with low-nutrient availability ($P = 0.01$; Table 1). This disproportionate increase in BP relative to GPP was most pronounced in woody biomass, with three-fold higher aboveground wood production (AWP) at high compared to low-nutrient availability ($P = 0.02$; Table 2), while foliage and root BP remained largely unchanged (Table 2; $P = 0.49, 0.83$, respectively).

Table 1 Mean and standard deviation (in brackets) for GPP, total BP and the BP-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 Fig. 2a

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

Table 2 Mean and standard deviation (in brackets) for the ratio of belowground to aboveground BP (BBP:ABP), AWP, FP, root production (RP) and the ratio of AWP to GPP (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

Climate zone, nutrient availability	BBP:ABP	AWP (g C m^{-2} y^{-1})	FP (g C m^{-2} y^{-1})	RP (g C m^{-2} y^{-1})	AWP:GPP
Boreal, low	0.65 (0.29)[5]	100 (46)[5]	61 (24)[5]	125 (65)[5]	0.11 (0.02)[5]
Temperate, low	0.66 (0.31)[6]	166 (80)[6]	153 (98)[6]	205 (97)[6]	0.13 (0.03)[6]
Tropical, low	0.28 (0.09)[5]	348 (85)[5]	404 (151)[5]	282 (47)[5]	0.11 (0.03)[5]
Boreal, medium	0.45 (0.27)[5]	116 (32)[5]	72 (36)[5]	117 (68)[5]	0.15 (0.03)[5]
Temperate, medium	0.88 (0.90)[7]	212 (129)[6]	149 (97)[7]	238 (122)[7]	0.14 (0.07)[6]
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 GPP, BP, the BP-to-GPP ratio (BPE), the ratio of belowground to aboveground BP (BBP:ABP), AWP, FP, RP, and the AWP-to-GPP ratio (AWP:GPP). The column 'stepwise fit' 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 results of ANOVA with the variables selected by the stepwise regression as fixed factors (or as covariable in case of stand age). ANOVA (2) gives results of a two-way ANOVA with climate zone and nutrient availability as fixed variables and thus corresponds to data shown in Tables 1 and 2

Variable	Stepwise fit	ANOVA(1)	ANOVA(2)
GPP	C, N	Boreal < Temperate < Tropical ($P < 0.01$) Nutrients: low = medium < high ($P = 0.05$)	C: $P < 0.01$; N: $P = 0.05$
BP	A, C, N	Boreal < Temperate < Tropical ($P < 0.01$) Nutrients: low = medium < high ($P < 0.01$) negative age effect ($P = 0.01$)	C: $P < 0.01$; N: $P < 0.01$
BPE	N, M	low = medium < high ($P < 0.01$) Unmanaged < Managed ($P = 0.07$)	C: $P = 0.69$; N: $P < 0.01$
BBP:ABP	N	Nutrients: low = medium > high ($P = 0.07$)	C: $P = 0.69$; N: $P < 0.01$
AWP	C, N	Boreal = Temperate < Tropical ($P < 0.01$) Nutrients: low = medium < high ($P < 0.01$)	C: $P < 0.01$; N: $P < 0.01$
FP	C, F	Boreal < Temperate < Tropical ($P < 0.01$) Needle-leaved < broadleaved ($P < 0.01$)	C: $P < 0.01$; N: $P = 0.13$
RP	C	Boreal < Temperate = Tropical ($P < 0.01$)	C: $P < 0.01$; N: $P = 0.92$
AWP:GPP	N	Nutrients: low = medium < high ($P < 0.01$)	C: $P = 0.94$; N: $P = 0.01$

As a consequence of the much larger nutrient effect on BP compared to GPP, BPE was 35 ± 9% (mean ± SE) higher for temperate forests of high-nutrient availability than in temperate forests of low-nutrient availability ($P = 0.03$; Table 1).

In order to test whether nutrient availability was indeed the key factor explaining variation in 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 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 results reported in other analyses (DeLucia *et al.* 2007; Goulden *et al.* 2011), analysis of our data set indicated that neither climate zone, nor forest type or stand age significantly affected BPE, whereas nutrient availability affected BPE highly significantly ($P < 0.01$). Independently of climate or forest type, forests with high-nutrient availability allocated on average 58 ± 3% (mean ± SE of 17 forests) of their photosynthates to BP, whereas forests with low-nutrient availability used on average only 42 ± 2% (mean ± SE of 19 forests) of their photosynthates for BP (i.e. slopes of lines in Fig. 1; $P < 0.01$ for low- versus high-nutrient availability). This result of nutrient availability being the primary determinant of BPE was
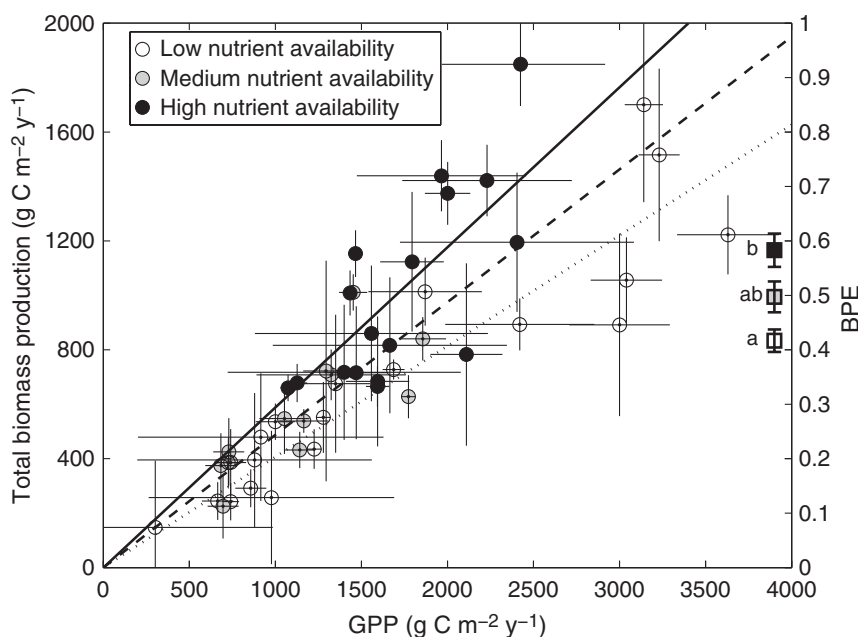

Figure 1 Each circle represents the mean annual total BP ± SE versus mean annual gross primary production (GPP ± SE) for one forest. Colours indicate nutrient availability classes, error bars reflect uncertainties (see Appendix S1). Dotted, dashed and solid lines are linear fits ($y = ax$) for the low-, medium- and high-nutrient availability class, respectively ($R^2 = 0.84, 0.66, 0.56$, respectively; $P < 0.01$ for low- versus high-nutrient availability (GLM analysis)). The squares on the right represent the mean BPE (BP-to-GPP ratio). Error bars on these squares are standard errors on the means, 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; ANOVA with nutrient availability as fixed factor).
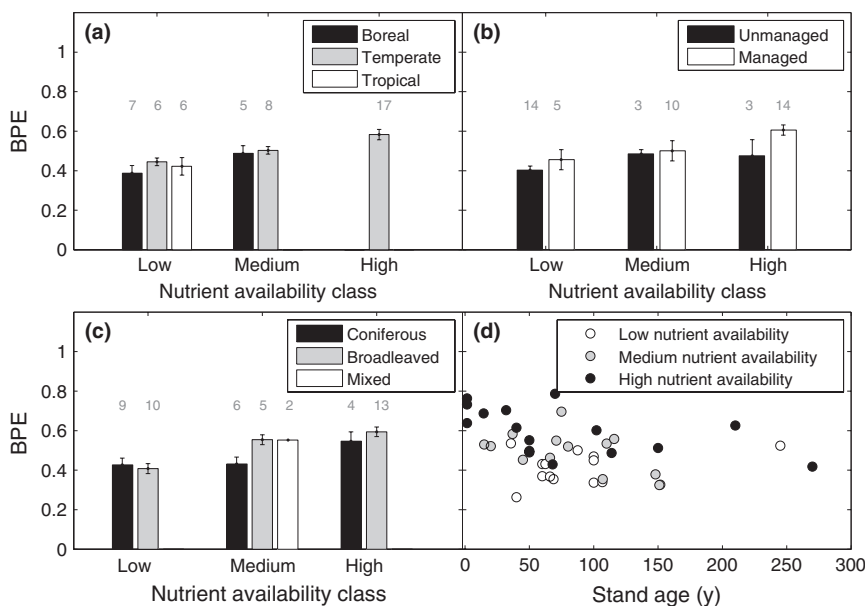
Figure 2 Mean BPE versus nutrient availability class for (a) different climate zones, (b) management practices, (c) forest types and (d) BPE versus stand age for the three nutrient availability classes. Error bars represent the standard error on the mean and numbers indicate the number of forests per 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).

confirmed also by other statistical tests (see Appendix S4), irrespective of whether or not we accounted for measurement uncertainties.

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 account, probably because nutrient-rich soils were occupied more by broad-leaved than by coniferous forests (Fig. 2c).

In addition to nutrient availability, which was by far the dominant determinant of variation in 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-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). Nonetheless, the distinction between unmanaged and managed forests appeared an important factor in the relationship between stand age and BPE, because the tendency for a negative age effect on BPE as observed in Fig. 2d only became significant ($P = 0.04$) if management regime was not included in the stepwise regression analysis.

UNDERLYING MECHANISMS

The significantly higher BPE in forests with high-nutrient availability as compared to forests of the medium- or low-nutrient availability class implies that either a smaller fraction of GPP is being respired in the forests with high-nutrient availability, or a smaller fraction of GPP is partitioned to unaccounted NPP components (VOC emissions, root symbionts, root exudation), or a combination of both. Because estimates of carbon transfers to VOC, and to root exudates and symbionts are not available for any of the forests in our database, the only way to test why BPE differs between forests of different nutrient availability is by comparing estimates of the Ra-to-GPP ratio. Many pitfalls arise when measuring Ra at the ecosystem level (Ryan *et al.* 1997; Amthor & Baldocchi 2001), ecosystem Ra is therefore most often estimated as the residual of GPP minus BP, rendering these Ra estimates useless to test whether or not variation in the ratio of Ra to GPP could explain variation in BPE.

Only 11 of our sites provided ecosystem Ra and GPP estimates that were independent from BP. 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 the higher BPE in nutrient-rich forests. Obviously, the limited data availability constrains the robustness of this analysis. Nonetheless, in addition to this lack of empirical evidence for a difference in the Ra-to-GPP ratio among nutrient availability classes, it appears unlikely that 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 exhibit considerably lower Ra-to-GPP ratios than nutrient-poor forests (see Box 1 for a more thorough elaboration of the underlying rationale). We therefore hypothesise that the unmeasured NPP components explain the difference in BPE among nutrient availability classes. Particularly root symbionts are a plausible candidate (Box 2).

Box 1 Autotrophic Respiration-to-Photosynthesis Ratio

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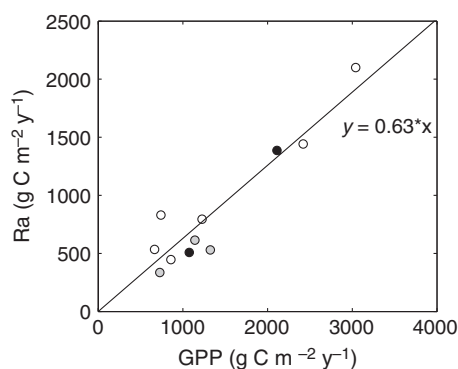

Figure 3 Field estimates of autotrophic respiration (Ra) versus gross primary production (GPP). Each single data point represents one forest site and is the average value over all years for which data were available in the database. White, gray and black circles indicate sites of low-, medium- and high-nutrient 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.

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 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).

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-nutrient availability (Litton *et al.* 2007). This was also the case for the forests in our dataset (Tables 1 and 2). Higher wood relative to foliage production may thus increase the Ra-to-GPP 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 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 fertilisation effect on root respiration found in a recent meta-analytical study (Janssens *et al.* 2010).

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).

Box 2 Testing Where the Missing Carbon is Going

In this study, we identified a gap in the current knowledge of forest carbon allocation: forests with high-nutrient availability use 16 ± 4% more of their photosynthates for BP than forests with low-nutrient availability (16 ± 4% represents the difference between mean of 17 forests of high-nutrient availability and mean of 19 forests of low-nutrient availability; SE calculated as $SE_{difference} = sqrt(SE_1^2 + SE_2^2)$, with SE_1 and SE_2 the SE for low- and high-nutrient availability, respectively). This difference is, however, unlikely attributable to a difference in carbon partitioning to autotrophic respiration. It therefore appears likely that forests of low-nutrient availability invest more photosynthates

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Box 2 (Continued)

in non-biomass components of NPP, which usually are not quantified in experiments or reported in the literature and therefore could not be taken into account in our analysis. These unaccounted for NPP components include VOC, root exudates, and root symbionts. We hypothesise that carbon allocation to root symbionts in particular is a key factor explaining the higher BPE in nutrient-rich relative to nutrient-poor forests. First support for this hypothesis is given in literature.

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; 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.

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

Following this well-reported and strong relation between root symbionts and nutrient availability, we hypothesise 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.

Finally, managed forests exhibited higher BPE than unmanaged forests for both the high and low-nutrient availability class. Management via thinning sometimes implies removal of biomass expected to grow sub-optimally, such as suppressed trees with large autotrophic respiration relative to GPP. Such removals may decrease the relative amount of maintenance respiration and 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 BPE than unmanaged forests because frequent anthropogenic disturbances tend to (further) increase nutrient availability.

Our analysis of 49 forest sites where BP and GPP were independently measured revealed that nutrient availability may be the unifying mechanism controlling the ratio of BP-to-GPP that encompasses climate, forest type, and stand age as influencing factors. The carbon sink potential of forests largely depends on how carbon taken up during 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 higher carbon partitioning to plant biomass with increasing nutrient availability thus adds to our understanding of the processes governing long-term carbon sequestration in forests and may have far-reaching consequences for carbon cycle management. Further research is needed to verify how the higher BPE in forests with high-nutrient availability, together with the previously reported decrease of soil organic matter decomposition in response to fertilisation (Janssens *et al.* 2010) determines ecosystem carbon sequestration.

It remains unresolved whether the increased partitioning to BP relative to GPP 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 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 nutrient availability is manipulated and where all measurements needed to unravel carbon partitioning are made (i.e. independent estimates for all NPP components, GPP and Ra) would help resolve these questions.

AUTHORSHIP

SV, SL, JP and IAJ conceived the paper; SV performed the analyses and wrote the paper; all authors contributed substantially to discussions and revisions.

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