

LETTER

Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale

Allison L. Gill and Adrien C. Finzi*

Department of Biology, Boston University, Boston, MA 02215, USA

*Correspondence: E-mail: afinzi@bu.edu

Abstract

Nutrient limitation is pervasive in the terrestrial biosphere, although the relationship between global carbon (C) nitrogen (N) and phosphorus (P) cycles remains uncertain. Using meta-analysis we show that gross primary production (GPP) partitioning belowground is inversely related to soil-available N : P, increasing with latitude from tropical to boreal forests. N-use efficiency is highest in boreal forests, and P-use efficiency in tropical forests. High C partitioning belowground in boreal forests reflects a 13-fold greater C cost of N acquisition compared to the tropics. By contrast, the C cost of P acquisition varies only 2-fold among biomes. This analysis suggests a new hypothesis that the primary limitation on productivity in forested ecosystems transitions from belowground resources at high latitudes to aboveground resources at low latitudes as C-intensive root- and mycorrhizal-mediated nutrient capture is progressively replaced by rapidly cycling, enzyme-derived nutrient fluxes when temperatures approach the thermal optimum for biogeochemical transformations.

Keywords

Belowground carbon allocation, global biogeochemical cycle, nitrogen limitation, resource use efficiency.

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INTRODUCTION

Terrestrial productivity is limited by light and soil resource availability and plants preferentially allocate fixed carbon (C) to access the most strongly limiting resources (Valentine & Mäkelä 2012; McMurtrie & Dewar 2013). While C allocation aboveground promotes competition for light, plants simultaneously allocate C belowground to produce roots and root exudates, support mycorrhizal associations, and compete for soil nitrogen (N) and phosphorus (P) (Litton *et al.* 2007). Plants grown in nutrient-limited environments or exposed to elevated atmospheric CO₂ may allocate a larger fraction of fixed carbon to roots at the expense of aboveground growth (Jackson *et al.* 2009), whereas N fertilisation decreases the proportion of fixed carbon allocated belowground (Axelsson & Axelsson 1986; Jones *et al.* 2012).

Belowground carbon allocation necessarily trades-off with aboveground growth and it is useful to define a metric to assess the magnitude of this trade-off (Chen *et al.* 2013). The C partitioning coefficient, defined here as the ratio of total belowground C flux (g C m⁻² year⁻¹) to gross primary production (GPP, g C m⁻² year⁻¹), is one such metric and provides an incisive view into the magnitude of above vs. belowground resource limitation (McMurtrie & Dewar 2013). C partitioning coefficients < 0.5 indicate that plants allocate the majority of GPP aboveground to stem and foliage production and suggest a preponderance of light limitation to primary production (Valentine & Mäkelä 2012). In contrast, C partitioning coefficients > 0.5 indicate a preponderance of soil resource limitation to primary production because a majority of GPP is allocated belowground. As residence times of plant C pools vary widely (Bird & Torn 2006) and

root input is a major source of mineral-soil C (Schmidt *et al.* 2011), plant C allocation schemes strongly affect the terrestrial C cycle. The relationship between soil N and P availability and C allocation patterns, however, remains poorly defined.

Belowground resource limitation varies among biomes and across large-scale environmental gradients. As ecosystems age, N accumulates in soil through biological fixation, whereas available P is depleted through mineral weathering and occlusion in iron and aluminium oxides and calcium phosphates (Walker & Syers 1976; Vitousek & Farrington 1997). These processes are observable at the global scale as, for example N often limits primary productivity in geologically young arctic and boreal ecosystems (Nohrstedt 2001; Jones *et al.* 2012) whereas P limits productivity in ancient lowland tropical forests (Chadwick *et al.* 1999). Given that plant uptake and use of N and P differ, as do the biogeochemical factors regulating their availability, the effect of soil nutrient limitation on plant growth and C allocation is likely to differ between N and P limited ecosystems (Harrington *et al.* 2001).

At present, we lack an empirically rooted, global-scale understanding of the linkages between terrestrial productivity, plant C allocation and the cycles of N and P. Such an understanding would be an important step in describing the coupling of three important biogeochemical cycles. Here, we ask and answer three questions that contribute to this understanding: (1) are there predictable relationships between terrestrial productivity and C partitioning belowground; (2) how does C allocation vary as a function of N and P availability and how does this in turn influence N- and P-use efficiency and (3) are the C costs of N and P acquisition the same or different

among biomes and how do these costs relate to the biogeochemical controls over their supply rates? To answer these questions, we synthesise information on GPP from the FLUXNET database, and belowground carbon allocation, and annual rates of net N and P mineralisation from the published literature. We find that belowground C partitioning is inversely related to the ratio of available N-to-P and increases with latitude from tropical to boreal forests. Along this same gradient, we find that N-use efficiency is highest in the high-latitude boreal forest biome where the N : P is lowest and conversely that P-use efficiency is highest in the low-latitude tropical forest biome where N : P is highest. The large partitioning of C belowground in the boreal forest reflects a 13-fold greater C cost of N acquisition compared to that of tropical forests, which we hypothesise reflects the high C cost of ectomycorrhizal symbiosis (Smith & Read 2008). In comparison to N, the C cost of P acquisition is less variable among biomes and despite high P-use efficiency and soil N : P in the tropics, GPP is preferentially allocated aboveground. The results suggest that the primary limitation on productivity transitions from nutrients at high latitudes to light at low latitudes as C-intensive root- and mycorrhizal-mediated nutrient capture is progressively replaced by rapidly cycling, enzyme-derived nutrient fluxes when mean annual temperatures approach the thermal optimum for biogeochemical transformations.

METHODS

Database compilation

We compiled a global database of annual gross primary productivity (GPP, $\text{g C m}^{-2} \text{ year}^{-1}$), total belowground carbon flux (TBCF, $\text{g C m}^{-2} \text{ year}^{-1}$), and annual net N and P mineralisation rates (g N or $\text{g P m}^{-2} \text{ year}^{-1}$) (Fig. 1; Table 1). We obtained annual GPP estimates from eddy covariance measurements of net ecosystem exchange (NEE) found in the LaThuile FLUXNET database. NEE measurements were standardised, gap-filled and separated into flux components using standard methodology (Reichstein *et al.* 2005). The LaThuile database contains daily GPP estimates collected between 1991 and 2006 for 256 FLUXNET sites (data availability varies by site, Table S1). We considered site years with a minimum of 80% data coverage (< 65 missing days) and a minimum mean annual quality control (QC) value of 0.75. We accounted for missing data by fitting polynomial functions to the daily GPP estimates for each site year and used individual functions to interpolate missing estimates where necessary (R Package 'zoo'; Zeileis & Grothendieck 2005). We calculated the mean annual GPP across all useable measurement years for each site. The final data set comprised 90 FLUXNET sites and 298 site years. Because only six tropical observations in the LaThuile database met QC requirements, we supplemented the tropical forest data set with nine additional GPP estimates derived from biometric measurements (Fig. 1a,b; Table S1).

Total belowground carbon flux ($\text{g C m}^{-2} \text{ year}^{-1}$) is the amount of fixed C allocated belowground in support of the maintenance and production of roots, mycorrhizal

associations and the release of C via exudation (Raich & Nadelhoffer 1989). TBCF is estimated via mass-balance under the assumption that C inputs (litterfall) must equal outputs (soil respiration), minus any change in belowground carbon stocks (Raich & Nadelhoffer 1989). In practice most studies do not account for changes in root biomass or soil C pools because they are difficult to measure and changes are small relative to respiration and litterfall C fluxes at the annual time scale (Davidson *et al.* 2004). Most TBCF calculations also do not account for dissolved organic carbon (DOC) losses, which may lead to underestimation of TBCF particularly in high-latitude ecosystems where DOC is a significant component of the annual carbon budget (Oquist *et al.* 2014). We performed a literature search to collect published total belowground carbon flux estimates (*Web of Science* search engine, search strings 'total belowground carbon flux' and 'total belowground carbon allocation', 543 search returns, 1 April 2014). After accessing and reading all papers, we compiled TBCF estimates from 50 publications incorporating 120 independent observations (Fig. 1c,d; Table S2). We extracted data from text and tables when available and used DataThief (Version 1.6 2010; Tummers 2005) to extract data presented in figures. See Supporting Information for further discussion of TBCF calculations.

Annual N and P uptake are often estimated as net primary productivity multiplied by tissue-specific N and P concentrations. Given that most estimates of NPP are for aboveground biomass and not independent of GPP and TBCF, we used the annual rate of N mineralisation as an independent proxy for plant N uptake. Annual rates of net N mineralisation and N uptake are highly correlated and widely measured (Nadelhoffer *et al.* 1984; Reich *et al.* 1997; Finzi *et al.* 2002). The one exception to correlation with annual mineralisation is boreal forests where annual N uptake can exceed mineralisation rates owing to the uptake of organic N species (Näsholm *et al.* 1998). Annual mineralisation rates nevertheless remain useful for comparative purposes because the difference between N uptake and N mineralisation in the boreal forest biome is at least an order of magnitude smaller than annual N mineralisation in other biomes (Cleveland *et al.* 2013).

We performed a Web of Science search (search string, 'annual net nitrogen mineralisation', 1321 search returns, 1 April 2014) and compiled a database of 81 publications incorporating 290 independent observations (Fig. 1e,f; Table S3). We limited the nitrogen mineralisation dataset to those studies reporting annually realised mineralisation rates derived from sequential monthly-to-seasonal *in situ* field incubations and excluded studies that calculated annual flux rates based on growing season mineralisation measurements alone.

There are few estimates of annual P mineralisation rates outside of wetland ecosystems. We therefore developed a three step process to estimate P mineralisation: (1) collect published data on soil P pools based on the Hedley fractionation procedure; (2) estimate the turnover time of the labile P pool based on MAT and (3) estimate the P mineralisation rate as the product of (1) and (2).

Soil P pool estimates were taken from a published synthesis of studies that report Hedley Fractionation measurements (Yang & Post 2011) (22 studies and 127 observations met our

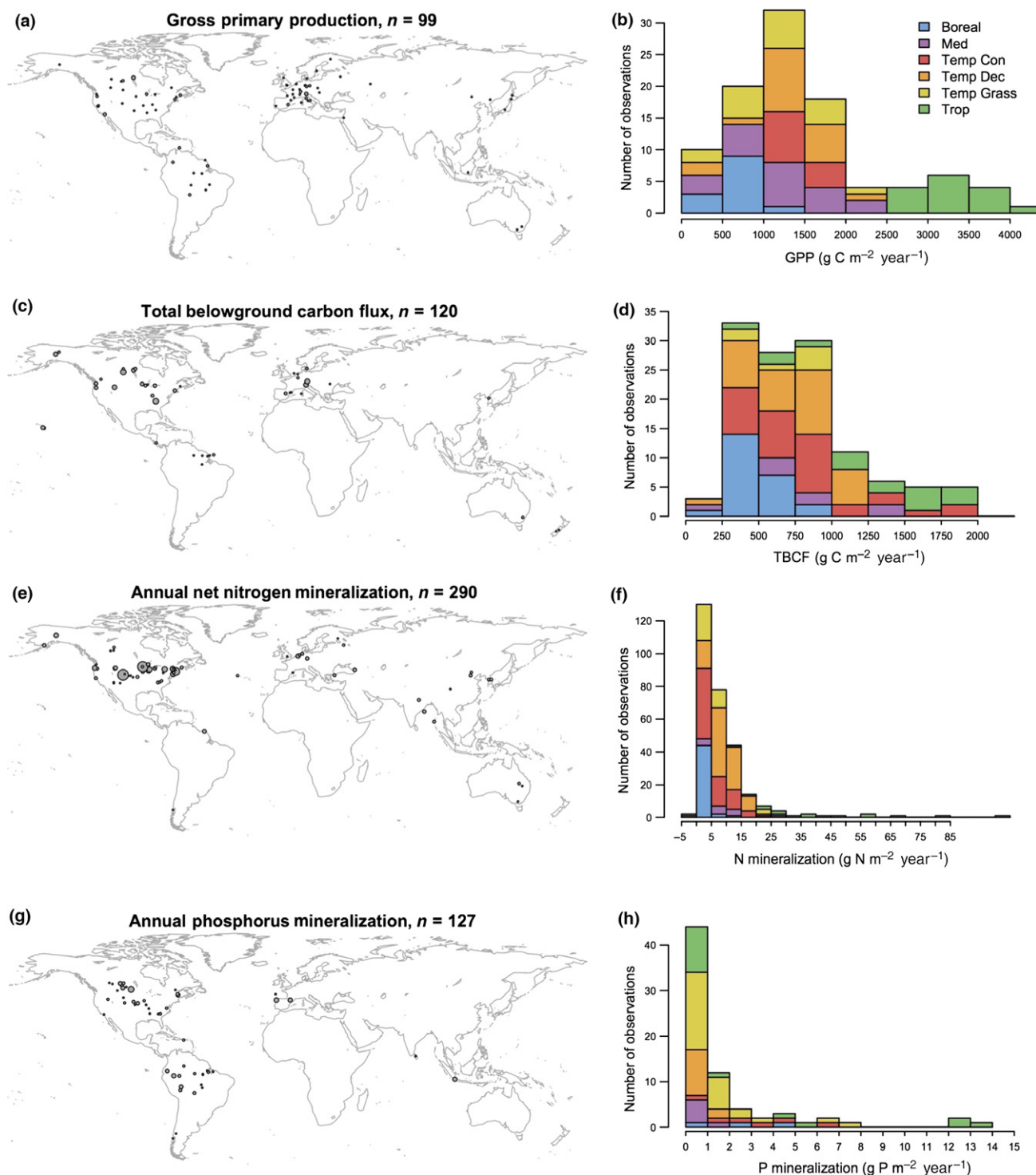


Figure 1 Resource flux distributions. Maps show site locations for each resource flux considered in the analysis. Point size indicates the relative number of observations at each location. Histograms show distribution of resource fluxes compiled from the literature and the FLUXNET database. Data are colour-coded by biome.

biome criteria; Fig. 1g,h; Table S4). The Hedley fractionation applies increasingly strong chemical and physical processes to extract P from soil (water to sonication to sulphuric acid). The water ('resin-extractable' pool) and bicarbonate-extracted P_i and P_o pools are frequently cited as the plant-available

pool of P and assumed to represent the annual rate of P mineralisation (Cross & Schlesinger 1995; Yang & Post 2011). We note, however, even the most weakly bound, water-extractable P pool exceeded modelled estimates of P mineralisation by > 2-fold in most biomes (Wang *et al.* 2007; Cleveland *et al.*

Table 1 Biome-level fluxes of C, N, P and moisture

Biome	GPP (g C m ⁻² year ⁻¹)	TBCF (g C m ⁻² year ⁻¹)	P Min. (g P m ⁻² year ⁻¹)	N Min. (g N m ⁻² year ⁻¹)	MAT (°C)	MAP (mm)
Boreal forest	613 ^c (511–728) <i>n</i> = 13	397 ^c (343–451) <i>n</i> = 19	0.42 ^{abc} (0.08–0.76) <i>n</i> = 6	1.57 ^c (1.10–2.05) <i>n</i> = 47	−0.4	590
Temperate coniferous	1416 ^b (1281–1546) <i>n</i> = 12	638 ^b (542–733) <i>n</i> = 38	0.93 ^{ab} (0.43–1.43) <i>n</i> = 9	4.69 ^b (3.80–5.59) <i>n</i> = 78	7.6	990
Temperate deciduous	1266 ^b (1071–1472) <i>n</i> = 20	597 ^b (516–678) <i>n</i> = 33	0.40 ^b (0.30–0.49) <i>n</i> = 19	7.24 ^b (6.47–8.01) <i>n</i> = 97	7.2	1070
Temperate grassland	1152 ^b (939–1377) <i>n</i> = 18	560 ^{bc} (430–689) <i>n</i> = 7	0.40 ^b (0.26–0.54) <i>n</i> = 40	5.00 ^b (3.42–6.59) <i>n</i> = 40	8.0	970
Mediterranean	1181 ^b (971–1406) <i>n</i> = 21	639 ^{abc} (429–850) <i>n</i> = 8	0.28 ^c (0.20–0.36) <i>n</i> = 8	5.68 ^b (3.69–7.67) <i>n</i> = 13	12.3	660
Tropical forest	3329 ^a (3094–3570) <i>n</i> = 15	998 ^a (815–1180) <i>n</i> = 17	0.77 ^a (0.58–1.06) <i>n</i> = 45	36.10 ^a (26.67–45.54) <i>n</i> = 15	26.4	2540

Notes. Mean, 95% confidence interval (in parentheses), and sample size, *n*, of data derived from the published literature and FLUXNET Database. Abbreviations as follows: GPP, gross primary production; N Min., N mineralisation; P Min., P mineralisation; TBCF, total belowground carbon flux; MAT, mean annual temperature. Superscript letters above the mean value indicate significant differences among biomes at *P* < 0.05.

2013), suggesting that this pool alone is too large to represent the annual flux.

The P turnover time (years) was first estimated for boreal and tropical growth forms as the water-extracted P pool (g P m⁻²) from our database divided by the average rate of P mineralisation (g P m⁻² year⁻¹) presented in models of Cleveland *et al.* (2013) and Wang *et al.* (2007). We use these values to generate coefficients for the exponential function relating P turnover time to MAT (P turnover time [years] = 8.41e^{-0.082MAT}, see Supporting Information). We then calculated the P turnover time for each site in the database using the reported MAT. Finally, we calculated the annual P mineralisation rate as the size of the P pool (g P m⁻²) divided by the P turnover time (years). The advantage of this approach is its generality and ability to characterise large spatial scale variations in P mineralisation. The disadvantage to this approach is that it is not a direct measurement of P mineralisation in the soil and does not account for factors other than temperature that may affect P mineralisation. See Supporting Information for further discussion of the P mineralisation calculation.

Data analysis

We collected site-level information on mean annual temperature (MAT), precipitation (MAP) and latitude as recorded in individual publications and divided studies into biome categories using site descriptions and the Whittaker biome diagram (Whittaker 1962). Due to limitations in data availability, we did not acquire sufficient sample sizes across all variables to consider wetland (high-latitude forested wetlands were included in boreal forest biome), tundra, desert, subtropical forest or tropical grassland sites in our analysis. This analysis did not include studies performed in agricultural systems,

plantation forests, recently burned sites or clear cuts. We included lightly managed temperate grasslands (mowed sites), but excluded sites amended with fertiliser. In cases of experimental manipulations (e.g. nitrogen fertilisation experiments), we used measurements obtained in the reference plots only. We assessed the relationship between individual resource fluxes and site temperature, precipitation, and latitude and computed mean annual rates of net nitrogen mineralisation (g N m⁻² year⁻¹), P mineralisation (g P m⁻² year⁻¹), total belowground carbon flux (g C m⁻² year⁻¹) and GPP (g C m⁻² year⁻¹) for each biome. We used 95% confidence intervals to compare differences across biomes.

The information in this database is from studies that measured one or at most two of the fluxes of interest (Fig. 1). The variables were not paired at the time of collection, and are not evenly distributed among biomes or across the globe (Fig. 1). Therefore, we used a parametric bootstrapping approach (Good 2005) to assess among-biome variation in nutrient use-efficiency, C partitioning and the quantity of C allocated belowground relative to nutrient availability. In parametric bootstrapping, the original data are fit to probability density distributions (PDD) using the method of maximum likelihood (Table S6). To prevent random draws of negative fluxes, we truncated each PDD at 0 and rescaled so that its integral equalled unity. We computed the mean of *n* random draws from each PDD where *n* equalled the number of observations used to generate each distribution. We resampled each distribution 1000 times and estimated the variability using 95% confidence bands (0.025 and 0.975 quantiles of the resampled data).

The bootstrapping approach creates randomly paired observations from which we calculated biome-scale estimates of N- and P-use efficiency viz:

$$\text{NUE (g C g}^{-1} \text{ N)} = \text{GPP (g C m}^{-2} \text{ year}^{-1}) \div \text{Net N Mineralisation (g N m}^{-2} \text{ year}^{-1}) \quad (1)$$

$$\text{PUE (g C g}^{-1} \text{ P)} = \text{GPP (g C m}^{-2} \text{ year}^{-1}) \div \text{Net P Mineralisation (g P m}^{-2} \text{ year}^{-1}) \quad (2)$$

The belowground C partitioning coefficient was estimated viz:

$$\text{C partitioning [dimensionless]} = \text{TBCF (g C m}^{-2} \text{ year}^{-2}) \div \text{GPP (g C m}^{-2} \text{ year}^{-2}) \quad (3)$$

We used the C partitioning estimate to evaluate the magnitude of below- vs. aboveground resource limitation across biomes. The coefficient is based on two gross fluxes, GPP and TBCF, which represent the total amount of C fixed through photosynthesis and the total amount of fixed C allocated belowground respectively. The logic for the use of gross rather than net fluxes rests on the fundamental requirement for autotrophic respiration in resource acquisition; leaves, stems and roots are the means by which resources are acquired and the cost of their maintenance is an integral part of C allocation, resource-use efficiency and assessments of above- vs. belowground resource limitation. For the partitioning of C belowground we applied the logic that a value not significantly different than 0.5 indicates co-limitation by above and belowground resources. C partitioning values significantly > 0.5 indicate a preponderance of belowground resource limitation, whereas those significantly < 0.5 indicate a preponderance of aboveground limitation.

The C cost of N and P acquisition represents the amount of carbon allocated belowground to either N or P uptake, assuming a simplified two-resource pool and that TBCF is not allocated to other soil resources (e.g. water, base cations, etc.). This approach is an obvious oversimplification but the purpose of this calculation is to compare among-biome variations in the C costs of N and P acquisition rather than the 'actual' C cost of N or P acquisition, which would be very difficult under even the most controlled conditions, in addition to their relationship with biome-level variations in NUE and PUE. We also note that for purposes of benchmarking, simulation models could export variables like GPP, TBCF, Nmin and Pmin and directly calculate the ratios (TBCF : GPP, TBCF : Nmin, etc.) to compare model output to the empirical data presented here.

To estimate the C cost of N (i.e. g C g N⁻¹) and P (i.e. g C g P⁻¹) acquisition for each biome, we partitioned TBCF in two parts: the amount of C allocated toward N acquisition (g C g⁻¹ N) and that allocated to P acquisition (g C g⁻¹ P). To partition TBCF, we first calculated the proportion of annual net N mineralisation in each biome (N_i) as the ratio of net N mineralisation in that biome (Nmin_i) relative to the sum of annual net N mineralisation across all biomes (Nmin_{sum}). We similarly calculated the proportion of annual net P mineralisation in each biome (P_i) as the ratio of annual net P mineralisation in that biome (Pmin_i) relative to the sum of annual net P mineralisation across biomes (Pmin_{sum}). Under the model that C is preferentially allocated

belowground to the more limiting resource (i.e. 1 - N_i or 1 - P_i), we estimate the C cost of N and P acquisition as:

$$\text{C cost of N (g C g}^{-1} \text{ N)} = \frac{\left[\frac{1-N_i}{(1-N_i)+(1-P_i)} \right] \text{TBCF}_i}{\text{Nmin}_i} \quad (4)$$

$$\text{C cost of P (g C g}^{-1} \text{ P)} = \frac{\left[\frac{1-P_i}{(1-N_i)+(1-P_i)} \right] \text{TBCF}_i}{\text{Pmin}_i} \quad (5)$$

From here one can see that the parenthetical term in the numerator represents the proportion of TBCF allocated to each resource relative to the total supply of both resources. This prevents any double counting of TBCF and ensures that the sum of TBCF_i used in eqns 4 and 5 is equal to the original estimate for each biome. All statistical analyses were conducted in R (R Core Team 2015).

RESULTS

Site-specific estimates of GPP and TBCF increased linearly with temperature (GPP: $R^2 = 0.60$, $P < 0.001$; TBCF: $R^2 = 0.27$, $P < 0.001$; Fig. 2a) and precipitation (GPP: $R^2 = 0.63$, $P < 0.001$; TBCF: $R^2 = 0.15$, $P < 0.001$; Fig. 2b). The annual N mineralisation rate increased exponentially with temperature and precipitation (MAT: $R^2 = 0.56$, $P < 0.001$, Fig. 2c; MAP: $R^2 = 0.16$, $P < 0.001$, Fig. 2d). Annual P mineralisation rate was exponentially albeit weakly related to temperature ($R^2 = 0.06$, $P < 0.01$, Fig. 2e) and precipitation ($R^2 = 0.08$, $P < 0.01$, Fig. 2f).

Annual GPP, TBCF, N mineralisation and P mineralisation differed significantly across biomes (Table 1). The ratio of annual N mineralisation to P mineralisation increased significantly from boreal to tropical forests (Fig. 3a). NUE was 4-fold higher in the boreal forest than the tropics, whereas PUE was only 2-fold greater in the tropics than the boreal forest (Fig. 3b).

The partitioning of GPP belowground (TBCF to GPP ratio) varied > 2-fold among biomes (Fig. 3a). In the tropical forest biome, the fraction of GPP allocated belowground (0.30) was significantly lower than temperate forest and grassland (~0.5), boreal (0.65) and Mediterranean (0.55) biomes. Accordingly, boreal forests allocated 2-fold more carbon belowground per unit available N than the temperate biome, and 13 times more than the tropical forest biome (Fig. 3c). In contrast, the quantity of C allocated belowground per unit P mineralised was only two times higher in the tropical forest and Mediterranean biomes than the boreal forest and less variable among biomes (Fig. 3b,c).

DISCUSSION

We used a data synthesis activity to understand the linkages among GPP, plant C partitioning and the cycling of N and P. The results reported here suggest coherence between soil N and P availability and patterns in C partitioning, as among-biome variation in the partitioning of GPP belowground is positively correlated with latitude and increases from

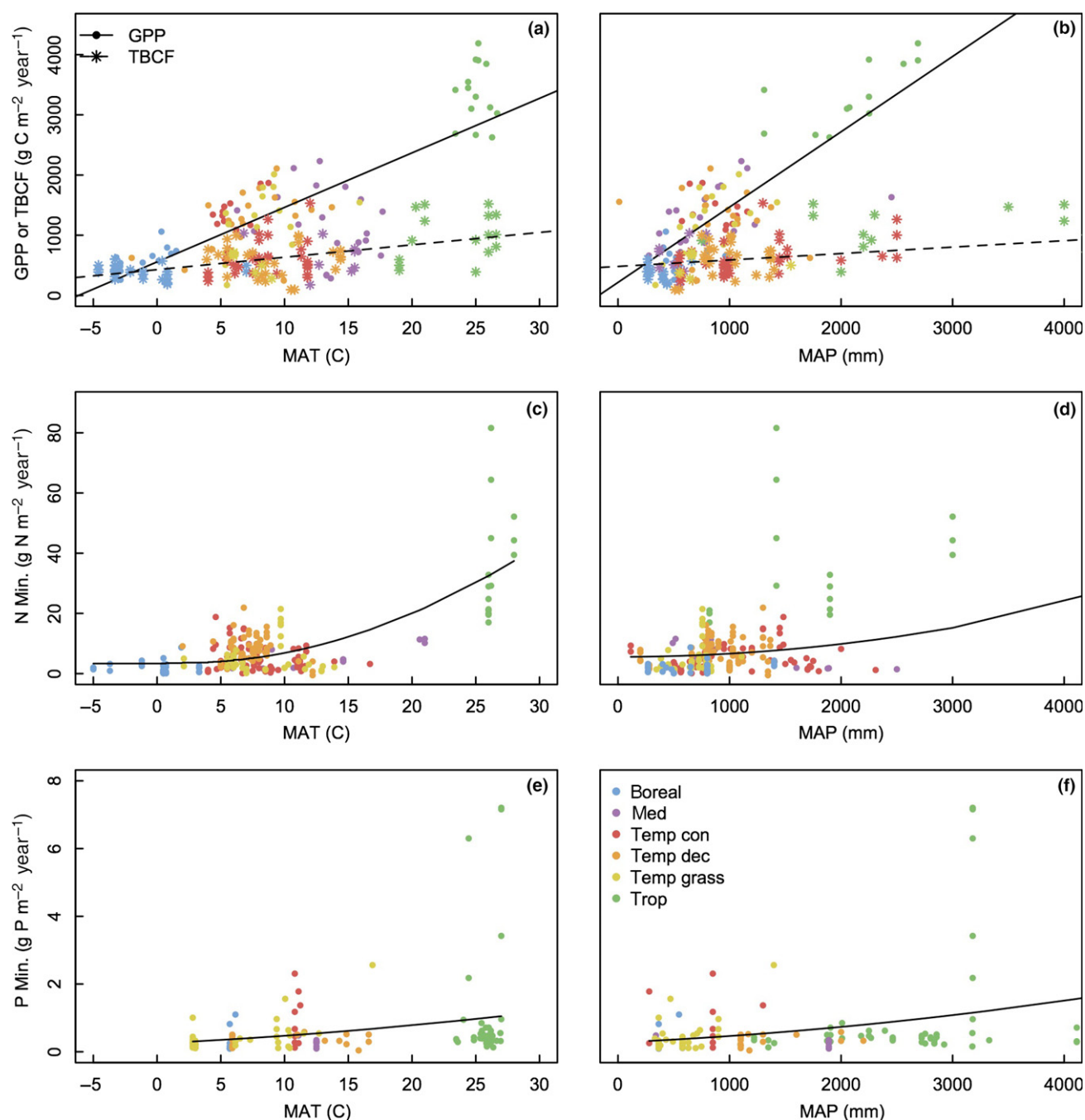


Figure 2 Relationship with site meteorological characteristics. Relationship between site MAT and MAP with GPP, TBCF, N mineralisation and P mineralisation. Colours indicate biome distribution; lines represent significant linear (a,b) or quadratic (c,d,e,f) relationships. GPP increased more rapidly than TBCF across gradients of both temperature (GPP: $m = 89.4 \text{ g C m}^{-2} \text{ year}^{-1} \text{ }^{\circ}\text{C}^{-1}$; TBCF: $m = 20.6 \text{ g C m}^{-2} \text{ year}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Fig. 2a) and precipitation (GPP: $m = 1.24 \text{ g C m}^{-2} \text{ year}^{-1} \text{ mm}^{-1}$; TBCF: $m = 0.10 \text{ g C m}^{-2} \text{ year}^{-1} \text{ mm}^{-1}$; Fig. 2b).

potentially P-limited tropical forests to N-limited boreal forests. The coherence between belowground C partitioning and nutrient availability implies that biogeophysical controls over nutrient cycling have a major influence on C allocation among several of the Earth's major biomes.

Among-biome variation in the N-to-P ratio of annual mineralisation rates support putative patterns of resource limitation described by biogeochemical theory in that NUE and PUE peak in the biome in which the resource is presumed to

be most limiting (Walker & Syers 1976; Chadwick *et al.* 1999). In general, resource use efficiency increases as resource supply becomes more limiting (Harrington *et al.* 2001) and high PUE in the putatively P-limited tropical forest biome suggests that tropical plants adopt growth strategies to maximise production under low-P conditions. High NUE in the boreal forest biome corroborates N limitation identified by boreal forest fertilisation experiments (Axelsson & Axelsson 1986; Jones *et al.* 2012).

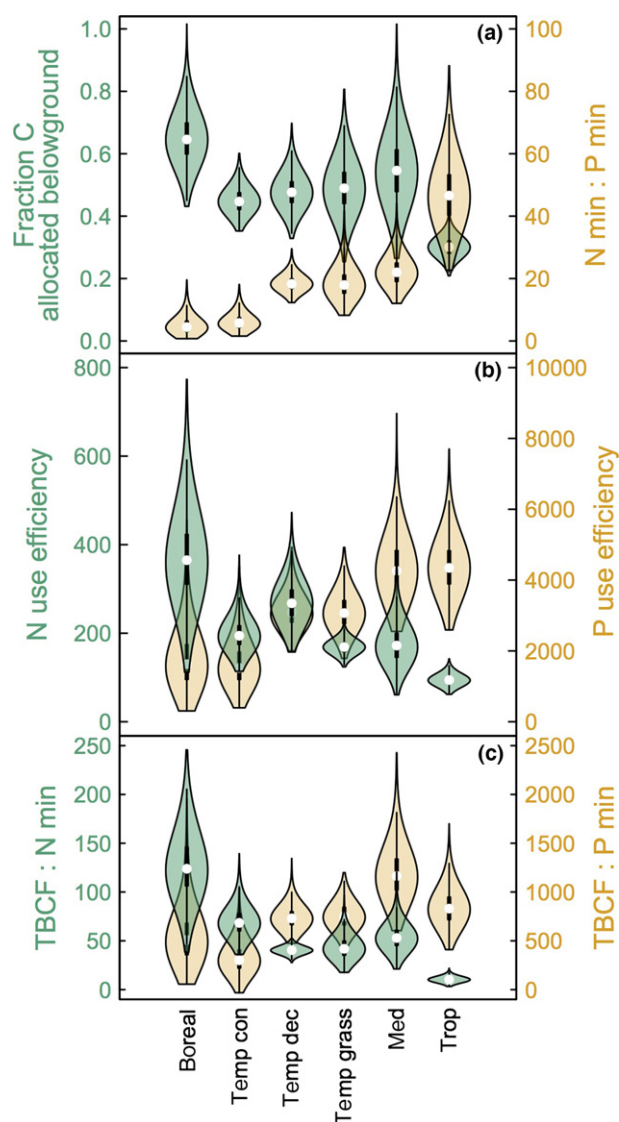


Figure 3 Violin plots of the C partitioning coefficients, ratio of N to P mineralisation, resource use efficiencies and the C cost of N and P acquisition by biome. Plots show the median value of bootstrapped ratios (open circles) with balloons representing the probability density distribution of each ratio (1000 bootstrapped values). Letters indicate non-overlapping 95% confidence intervals. (a) Significant declines in C partitioning belowground are inversely related to the N : P mineralisation ratio. (b) NUE declines from high to low latitude, whereas the opposite holds true for PUE. (c) The C cost of N (TBCF : N mineralisation) varies 13-fold among biomes and declines with latitude, whereas the amount of C allocated belowground relative to available P is less variable among biomes. Abbreviations as follows: boreal, boreal forest; temp con, temperate coniferous forest; temp dec, temperate deciduous forest; temp grass, temperate grassland; med, Mediterranean shrubland; trop, tropical forest.

While nutrient use efficiency calculations support putative patterns of N and P limitation to primary production, the C partitioning coefficients identify the relative strength of belowground vs. aboveground resource limitation. In the boreal forest biome, *c.* 65% of GPP is allocated belowground suggesting substantial belowground resource limitation (*c.f.*, Nohrstedt 2001). This analysis expands on the idea of

traditional N limitation by showing that there is a high C-cost of N acquisition. The quantity of C allocated belowground per unit available N is two times higher than the temperate biomes and fully 13 times higher than the tropical forest biome (Fig. 3c).

Why is the C cost of N so high in boreal forests? Much of the N pool in boreal forests is bound to organic material and must be depolymerised by microbially produced oxidative and hydrolytic enzymes whose overall activity is limited by low temperature. To overcome these constraints, boreal plants are heavily dependent on symbiotic ericoid and ectomycorrhizal fungal communities for N acquisition (Näsholm *et al.* 1998; Höglberg *et al.* 2010). The importance of this dependency and the role of belowground C allocation in N acquisition are highlighted by the response of the boreal forest to N fertilisation. Fertilisation decreases the fraction of C allocated belowground (Axelsson & Axelsson 1986) and the colonisation of roots by ectomycorrhizal fungi (Jones *et al.* 2012). Given the strong relationship between photosynthesis and foliar N (Reich *et al.* 1997) and the environmental constraints on N supply (Averill *et al.* 2014), the results suggest that boreal forests may maximise productivity through a large proportional C allocation to roots and mycorrhizal fungi.

In contrast to the boreal forest, high PUE in the tropical forest biome suggests that P is the more strongly limiting soil resource. Despite the high PUE, the proportion of fixed C partitioned belowground in tropical forests (*c.* 30%) is significantly lower than mid- and high-latitude ecosystems (Fig. 3a). It therefore appears that while P may be the most strongly limiting soil resource, the availability of aboveground resources such as light may more strongly influence plant growth strategies in the tropical forest biome where intense vertical competition drives a substantial partitioning of GPP aboveground (Dybziński *et al.* 2011).

High tropical PUE despite low C partitioning coefficients raises two questions regarding the role of P in regulating tropical productivity and C allocation. First, what evidence is there for P limitation of tropical forest productivity? High PUE indicates that tropical forests experience greater P limitation than other forested biomes (Fig. 3b). Cleveland *et al.* (2011) identified a similar but noisy pattern in a pan-tropical analysis showing that aboveground net primary production (NPP) per unit soil P was higher in low-P sites than high-P sites. Tropical forest responses to P fertilisation, however, remain less clear (Alvarez-Clare *et al.* 2013). Phosphorus fertilisation significantly increased diameter growth of *Metrosideros polymorpha* on millions-of-years old substrate in Hawai'i (Vitousek & Farrington 1997) and in a secondary growth forest in the Yucatán Peninsula, Mexico (Campo & Vázquez-Yanes 2004). In a Venezuelan montane forest both N and P addition were required to stimulate stem growth and litterfall (Tanner *et al.* 1992) and in a young secondary tropical forest regrowing from pastureland in Brazil, P addition had no significant effect on tree growth (Davidson *et al.* 2004). Similarly, in primary-growth lowland tropical forests, primary production has not responded significantly to P fertilisation (Mirmanto *et al.* 1999; Newbery *et al.* 2002; Wright *et al.* 2011). Evidence of P limitation from fertilisation experiments is mixed. Thus identifying the spatial and temporal

scales over which P alone or in combination with N may limit tropical forest productivity should remain a high priority for research as should measurements of plant-available P across a wide range of tropical ecosystems.

Second, why is the quantity of C allocated belowground relative to available P less variable among biomes than that allocated relative to available N? Despite the potential for P limitation, the small tropical C partitioning coefficient (Fig. 3a) in combination with low among-biome variation in the quantity of C allocated belowground per unit P (Fig. 3c) suggest that the C cost of P acquisition is no greater in the tropics than other biomes, despite the presence of old soils potentially depleted of P resources. In general, rates of foliar P translocation prior to leaf senescence vary more with soil P availability than rates of foliar N translocation (McGroddy *et al.* 2004), which may be one mechanism by which plants reduce soil P demand and moderate the apparent C cost of P acquisition in P-limited or tropical ecosystems. In the case of low-latitude tropical forests, we also propose that warm temperatures and high N availability minimise the quantity of C required for P acquisition despite high P demand (Cleveland *et al.* 2013). Tropical forests are N rich as a result of symbiotic-N₂ fixation and the accrual of N via atmospheric deposition for hundreds of thousands of years (Chadwick *et al.* 1999; Houlton *et al.* 2008). In these ecosystems, N is readily available (Table 1) and allocated to the synthesis of extracellular phosphatase enzymes that release phosphate (PO₄³⁻) from ester-bound organic molecules (Treseder & Vitousek 2001). While there is a modest C cost of N₂ fixation (~ 7.4 g C g N⁻¹ or 16.2 g C m⁻² year⁻¹; Cleveland *et al.* 1999) and N cost of phosphatase enzyme synthesis (15 g N g P⁻¹ cleaved; Wang *et al.* 2007), enzyme activity reaches its peak at 25–30 °C (Houlton *et al.* 2008). Mean annual temperature in the tropics is near the thermal optimum for enzyme activity (Table 1). Therefore, fewer moles of enzyme are needed to cleave a given amount of P from organic matter in warm tropical soils compared to temperate and boreal forests. This argument is analogous to that proposed for high rates of symbiotic biological N fixation in neotropical forests (Houlton *et al.* 2008). This suggests that while P may be the most limiting soil resource, light availability and perhaps atmospheric CO₂ place larger constraints on tropical forest productivity (Nemani *et al.* 2003).

While this analysis focused on patterns in soil N and P availability, many other soil-derived resources may simultaneously impact plant growth and C-partitioning. There are strong gradients in water availability across the biomes considered in this analysis (Fig. 2), which may also influence the patterns described here. In particular, while the ratio of TBCF to N mineralisation decreases linearly between the boreal and tropical forests, TBCF : P mineralisation peaks in the Mediterranean ecosystem (Fig. 3c). The Mediterranean biome is characterised by an intermediate N-to-P mineralisation ratio (Fig. 3a), high PUE (Fig. 3b) and the greatest C cost of P acquisition (Fig. 3c). We posit that the high C cost of P reflects some combination of water limitation driving root production and the need for chelator- or organic-acid containing root exudates to mobilise P bound to carbonates in Mediterranean regions underlain by calcareous substrates where soil pH can

be in excess of 7 (Lindsey & Vlek 1977). Water limitation could also contribute to the large proportional allocation of C belowground in boreal forests, which may experience increased drought frequency as climate warms (Wu *et al.* 2012). Other important soil nutrients such as potassium (K) and calcium (Ca) may place additional constraints on plant growth (Likens & Bormann 1995), but were not considered here.

The data synthesised in this analysis are derived from hundreds of individual studies and come together to describe large-scale patterns in soil resource availability and plant C partitioning across the globe. While we can draw many important inferences from such large and diverse empirical datasets, they also have their limitations. For example site-level observations of C and nutrient fluxes are biased toward the northern hemisphere and the Brazilian Amazon, which may influence the patterns described here. Similarly, the individual flux measurements (e.g. GPP, TBCF, N mineralisation, etc.) were not measured simultaneously at the site level and are not equally distributed across biomes or regions (Fig. 1). Although TBCF : GPP ratios derived from the bootstrapping approach match closely with those calculated from the few site-matched TBCF and GPP estimates (see Supporting Information), the small number of site-matched estimates limit our ability to draw robust conclusions. This is especially true for the nutrient fluxes relative to C fluxes. Thus we cannot be certain that the coherence among the literature-aggregated data reflects what one might observe at the site-level across gradients in nutrient supply, temperature or soil moisture. Efforts to collect co-located measurements of plant productivity, C allocation, and nutrient availability, particularly in underrepresented regions, are critical to our understanding of coupled global biogeochemical cycles.

This analysis provides applied and fundamental insights into the coupled biogeochemical cycles of C, N, P and water in terrestrial ecosystems. The coupling of eddy-covariance data with published estimates of TBCF and N and P mineralisation rates enable biome-scale estimates of resource-use efficiency, carbon allocation patterns, and the role of element interactions in determining the strength of above vs. belowground resource limitation. We find that the proportion of GPP allocated belowground is highly sensitive to soil development history, biophysical controls over soil resource supply, and nutrient use and acquisition strategies, which results in > 2-fold variation in C partitioning schemes among biomes. Together the data and analysis presented here suggest a new hypothesis that the primary limitation to plant productivity in forested ecosystems transitions from belowground soil resources at high latitudes to aboveground resources at low latitudes because C-intensive root- and mycorrhizal-mediated nutrient capture is progressively replaced by rapidly cycling, enzyme-derived nutrient fluxes as MAT approaches the thermal optimum for biogeochemical transformations.

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AUTHOR CONTRIBUTIONS

ALG collected data from the literature, processed FLUXNET data, conducted data analysis, wrote and edited the manuscript; ACF conceived the idea and data approach, wrote and edited the manuscript.

DATA ACCESSIBILITY STATEMENT

All data used in this analysis are tabulated in the Supporting Information. Data will also be permanently archived with the Carbon Dioxide Information Analysis Center at Oak Ridge National Lab.

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