

BELOWGROUND RESPONSES TO CLIMATE CHANGE

Below-ground carbon flux and partitioning: global patterns and response to temperatureC. M. Litton^{*1} and C. P. Giardina²

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Summary

1. The fraction of gross primary production (GPP) that is total below-ground carbon flux (TBCF) and the fraction of TBCF that is below-ground net primary production (BNPP) represent globally significant C fluxes that are fundamental in regulating ecosystem C balance. However, global estimates of the partitioning of GPP to TBCF and of TBCF to BNPP, as well as the absolute size of these fluxes, remain highly uncertain.

2. Efforts to model below-ground processes are hindered by methodological difficulties for estimating below-ground C cycling, the complexity of below-ground interactions, and an incomplete understanding of the response of GPP, TBCF and BNPP to climate change. Due to a paucity of available data, many terrestrial ecosystem models and ecosystem-level studies of whole stand C use efficiency rely on assumptions that: (i) C allocation patterns across large geographic, climatic and taxonomic scales are fixed; and (ii) *c.* 50% of TBCF is BNPP.

3. Here, we examine available information on GPP, TBCF, BNPP, TBCF : GPP and BNPP : TBCF from a diverse global data base of forest ecosystems to understand patterns in below-ground C flux and partitioning, and their response to mean annual temperature (MAT).

4. MAT and mean annual precipitation (MAP) covaried strongly across the global forest data base (37 mm increase in MAP for every 1 °C increase in MAT). In all analyses, however, MAT was the most important variable explaining observed patterns in below-ground C processes.

5. GPP, TBCF and BNPP all increased linearly across the global scale range of MAT. TBCF : GPP increased significantly with MAT for temperate and tropical ecosystems (> 5 °C), but variability was high across the data set. BNPP : TBCF varied from 0.26 to 0.53 across the entire MAT gradient (–5 to 30 °C), with a much narrower range of 0.42 to 0.53 for temperate and tropical ecosystems (5 to 30 °C).

6. Variability in the data sets was moderate and clear exceptions to the general patterns exist that likely relate to other factors important for determining below-ground C flux and partitioning, in particular water availability and nutrient supply. Still, our results highlight global patterns in below-ground C flux and partitioning in forests in response to MAT that in part confirm previously held assumptions.

Key-words: below-ground carbon cycling, below-ground net primary production (BNPP), carbon allocation, gross primary production (GPP), mean annual temperature (MAT), total below-ground carbon flux (TBCF)

Introduction

BELOW-GROUND CARBON CYCLING

Globally, the flux of carbon (C) to below-ground in terrestrial ecosystems exceeds C emitted to the atmosphere through

combustion of fossil fuels by an order of magnitude (*c.* 60 vs. 6 Gt C year⁻¹; Giardina *et al.* 2005), and exerts a large influence on soils and ecosystems by regulating soil organic C formation and decomposition, and associated soil physical, chemical and biological properties. Despite the magnitude of below-ground C flux, it remains the least understood C flux in terrestrial ecosystems (Clark *et al.* 2001; Gower *et al.* 2001; Giardina *et al.* 2005; Litton, Raich & Ryan 2007). This

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uncertainty is particularly problematic when modelling the role of forests in global C cycling, as forests account for the majority of terrestrial primary productivity and C storage (Jobbágy & Jackson 2000; Geider *et al.* 2001).

In forest ecosystems, the annual total of canopy photosynthesis (gross primary production; GPP) is partitioned between component fluxes to above- and below-ground production and respiration. Importantly, the balance between net primary productivity (NPP) and heterotrophic respiration regulates C storage in terrestrial vegetation and soils (Pendall *et al.* 2004), and this balance may be sensitive to changes in climate (Cox *et al.* 2000). The sensitivity of C allocation (GPP and component fluxes; the partitioning of GPP to above- or below-ground, to plant respiration or biomass production, and to short-lived or long-lived tissues) to climate change will in part determine whether the sink strength of forests changes in response to a warming climate, because any trade-offs in C allocation will impact detrital C availability and C storage in both short- and long-lived pools. In particular, climate-driven changes in below-ground C flux and partitioning have the potential to feedback positively or negatively on climate by slowing or accelerating the accumulation of greenhouse gases in the atmosphere.

While terrestrial ecosystems exert a large influence on the global C cycle (Cox *et al.* 2000), fundamental aspects of C allocation remain poorly quantified (Giardina *et al.* 2005; Litton *et al.* 2007). Critical questions remaining in terrestrial C cycle science include: (i) how much of GPP do forests partition below-ground and what is the ultimate fate of this C; and (ii) how will climate change impact both the overall partitioning of GPP to below-ground C flux, and the partitioning of below-ground C flux to production vs. respiration?

Prior syntheses have identified positive relationships across diverse forests between mean annual temperature (MAT) and above-ground net primary production (ANPP), and between MAT and total below-ground carbon flux (TBCF) (Giardina *et al.* 2005; Raich *et al.* 2006). These findings suggest that total C inputs to soils will increase with warming but TBCF includes C used for both autotrophic respiration and below-ground net primary production (BNPP), and only the latter contributes directly to soil organic C formation. Raich *et al.* (2006) identified an increase in TBCF with increasing MAT in moist tropical forests. However, soil organic C storage decreased across a similar MAT gradient, suggesting that an increase in the total flux of C to below-ground with climate change may not lead to increased soil C storage.

How the partitioning of TBCF to production vs. respiration varies with temperature is unknown and unlikely to be straightforward. For example, autotrophic respiration may show a strong, short-term response to experimentally manipulated temperature. However, this appears to be a transient response where plant respiration rapidly acclimates to warmer temperatures (see King *et al.* 2006), including below-ground (Bryla, Bouma & Eissenstat 1997; Dewar, Medlyn & McMurtrie 1999). Further, the fraction of GPP used for plant respiration appears to show little or no response to experimentally manipulated temperatures (Gifford 1994; Tjoelker,

Oleksyn & Reich 1999; Atkin, Scheurwater & Pons 2007). Moreover, where seasonal changes in temperature have been used to quantify the relationship between respiration and temperature, phenological changes in GPP may confound patterns (Fitter *et al.* 1999; Höglberg *et al.* 2001).

Increasingly sophisticated approaches have been employed to examine how the distribution of plant and animal species, the timing of life-history events, and the structure of ecosystems may change in response to modern climate change (Root *et al.* 2003; Walther *et al.* 2005). However, enormous logistical hurdles and a lack of adequate methodologies, particularly for quantifying below-ground processes, have constrained efforts to predict the impact of climate change on the physiological and biogeochemical process rates that control terrestrial C storage (Pendall *et al.* 2004; Giardina *et al.* 2005; Litton *et al.* 2007). Multiple studies have demonstrated that below-ground processes are tightly coupled to forest canopy physiology (Ekblad & Höglberg 2001; Höglberg *et al.* 2001; Giardina *et al.* 2004; Höglberg & Read 2006), and across large scales to above-ground C fluxes (Litton *et al.* 2007). However, the fate of C allocated below-ground, especially C that ultimately resides in longer lived pools, has rarely been quantified in response to environmental change (Giardina *et al.* 2005).

Efforts to quantify the role that forest ecosystems play in global C cycling under a changing climate are largely accomplished with the use of terrestrial ecosystem models (e.g. Cox *et al.* 2000; Schimel *et al.* 2000; Thornton *et al.* 2002; Ise & Moorcroft 2006). Yet confidence in resulting scenarios is constrained by the high uncertainty of underlying climate-process relationships (Giardina & Ryan 2000; Grace & Rayment 2000; Holland *et al.* 2000) and an incomplete understanding of C allocation in forests (Friedlingstein *et al.* 1999; Landsberg 2003; Litton *et al.* 2007). While MAT is predicted to rise by 1.8–4.0 °C over the next 100 years (IPCC 2007), the effects of this rise in temperature on below-ground C flux and partitioning are largely unknown (Giardina *et al.* 2005).

FLUX AND PARTITIONING OF GPP TO TBCF AND BNPP

Raich & Nadelhoffer (1989) proposed a mass balance approach that relies on conservation of mass to estimate TBCF (originally termed 'TRCA' and/or 'TBCA'), which includes coarse and fine root production, coarse and fine root respiration, root exudates and plant C used by mycorrhizae (Raich & Nadelhoffer 1989; Giardina & Ryan 2002; Litton *et al.* 2007). Based on conservation of mass, the total flux of C below-ground (i.e. TBCF) will either alter below-ground C storage (e.g. a net change in the storage of soil C or root C), or will be lost from the system (e.g. autotrophic or heterotrophic respiration). This approach to quantifying TBCF has been examined across a wide diversity of ecosystem types, and the required assumptions tested under diverse conditions. See Giardina & Ryan (2002) for a more complete discussion of terminology and methods for quantifying TBCF in forest ecosystems.

The fraction of TBCF that is not used for autotrophic respiration is often termed BNPP, which includes coarse and fine root production, root mortality and losses to herbivory,

root exudation, and mycorrhizal growth and turnover. Root exudates and mycorrhizae are likely to be a large portion of BNPP in most ecosystems (Fogel & Hunt 1979; Sylvia 1998; Hobbie 2006). However, most studies of BNPP do not account for these components (Giardina *et al.* 2005; Litton *et al.* 2007), and their contribution to BNPP remains poorly quantified (Eissenstat *et al.* 2000; Stevens, Jones & Mitchell 2002; Wells, Glenn & Eissenstat 2002). In general, BNPP estimates include sequential coring, sequential coring coupled with analysis of root production, and loss and survivorship from mini-rhizotron imagery. For a more complete discussion of terminology and methods pertaining to BNPP see Giardina *et al.* (2005) and Litton *et al.* (2007).

Litton *et al.* (2007) presented a global data set of annual forest C budgets that documents a decrease in partitioning to TBCF (TBCF : GPP) as GPP increases – presumably as below-ground resource supply also increases. While GPP and its components increase globally with increasing MAT (Giardina *et al.* 2005; Raich *et al.* 2006; Luyssaert *et al.* 2007), we are not aware of any study that has examined how the partitioning of GPP (e.g. TBCF : GPP) varies across a broad range of MATs. The fraction of TBCF that is BNPP is also poorly quantified, yet both of these ratios are critical to efforts seeking to correctly model ecosystem C cycling. In the past, efforts to estimate stand level carbon use efficiency (CUE) and BNPP have often assumed that *c.* 50% of TBCF is BNPP (e.g. Law, Ryan & Anthoni 1999; Giardina *et al.* 2003; Vitousek 2004; Newman, Arthur & Muller 2006). Moreover, while some terrestrial ecosystem models have dynamic, albeit simplified, C allocation schemes that vary partitioning to below-ground based on water and/or nutrient availability (e.g. 3-PG; Landsberg & Waring 1997), many models assume a constant CUE of *c.* 50% (Delucia *et al.* 2007; Litton *et al.* 2007).

Available data to justify these assumptions are conspicuously lacking (Clark *et al.* 2001; Giardina *et al.* 2005). Nadelhoffer & Raich (1992) looked at a variety of ecosystems where fine root production had been estimated using the N budget technique, and estimated that *c.* 33% of TBCF goes to fine root production. McDowell *et al.* (2001) estimated that BNPP accounted for 53–63% of TBCF in *Pseudotsuga menziesii* forests but fine root and mycorrhizal production, which accounted for most of BNPP, were not directly quantified. Based on central tendency of relationships between TBCF and ANPP, and between BNPP and ANPP, Giardina *et al.* (2005) identified that BNPP was *c.* 50% of TBCF. Because TBCF can account for 21–75% of GPP (Litton *et al.* 2007), uncertainty surrounding the fraction of TBCF that is BNPP severely constrains efforts to accurately model terrestrial C cycling and ecosystem C balance.

GLOBAL SYNTHESIS

Ecosystems are dynamic, with C allocation patterns and below-ground process rates dependent upon a multitude of factors such as species composition, stand age, climate and nutrient supply (Pendall *et al.* 2004; Giardina *et al.* 2005; Litton *et al.* 2007). To date, a paucity of available data has

prevented detailed analyses of how climate change will impact stand level C budgets. Here, we examine global-scale patterns of GPP, TBCF, BNPP, partitioning of GPP to TBCF (TBCF : GPP) and partitioning of TBCF to BNPP (BNPP : TBCF) across a global MAT gradient to examine how they vary with temperature.

We hypothesized that partitioning of GPP to below-ground (TBCF : GPP) will increase with increasing MAT because both TBCF and ANPP have been shown to increase with temperature but the slope is steeper for TBCF (Giardina *et al.* 2005; Raich *et al.* 2006). Based on C allocation theory and a recent global analysis (see Litton *et al.* 2007), the most likely mechanism explaining an increase in partitioning to TBCF with increasing MAT is that as MAT increases, below-ground limitations to GPP (e.g. nutrients, water) become more important than above-ground limitations (e.g. light, temperature) (Fig. 1). This proposed mechanism is compatible with MAT driven increases in both above- and below-ground resource supply. How increasing MAT affects the balance between above- and below-ground resource limitations to GPP has not been examined in forest ecosystems, and is outside the scope of this analysis. Nonetheless, a better understanding of how climate variables impact C allocation patterns in forests is clearly warranted. We also hypothesized that partitioning

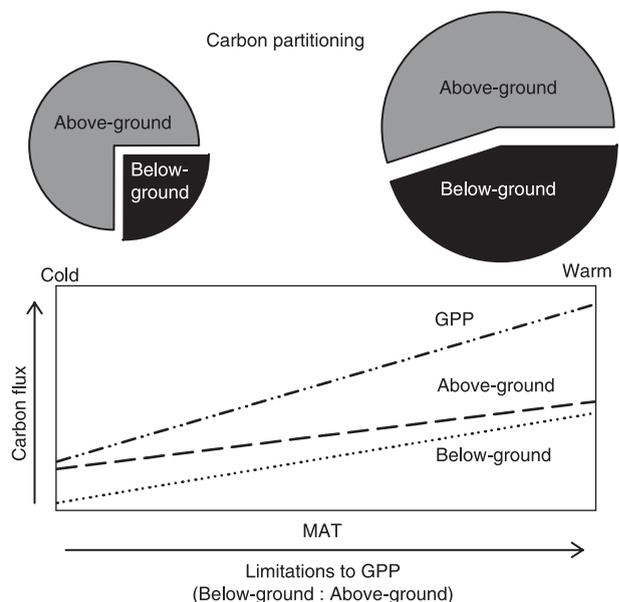


Fig. 1. Hypothesized relationship between mean annual temperature and the partitioning of GPP (carbon flux as a fraction of GPP) to aboveground vs. belowground (top panel). While GPP, aboveground C flux, and belowground C flux all increase with MAT (Giardina *et al.* 2005; Raich *et al.* 2006; Luyssaert *et al.* 2007), the slopes of the aboveground and belowground relationships differ because the factors constraining GPP change as MAT increases (bottom panel). At colder sites, air temperature presents the strongest limitation to GPP, and belowground resource supply (e.g., nutrients and water) is high by comparison. Conversely, at warmer sites, air temperature constraints are alleviated and belowground resource supply exerts a stronger limitation to GPP. As a result, partitioning of GPP to belowground increases with MAT.

of TBCF to production (BNPP : TBCF) will approximate 0.50 across a wide range of MAT, as originally proposed by Giardina *et al.* (2005).

Because below-ground processes are likely to respond simultaneously to a suite of factors, including MAT and water availability, we also explored how below-ground C flux and partitioning respond to mean annual precipitation (MAP), and whether MAT, MAP or their interaction is the most important variable for explaining observed global patterns. Changes in temperature and/or precipitation, in turn, are likely to have both direct and indirect impacts on nutrient supply, an important determinant of GPP and its partitioning (Litton *et al.* 2007). However, the impact of nutrient supply on below-ground C processes was outside of the scope of this analysis. Global observational analyses like that used here are unable to control for all factors that influence the variable of interest – in this case the effect of MAT on below-ground C processes. However, we contend that these analyses provide compelling insights into global-scale processes and their drivers and, as such, help to identify important areas of future research.

Materials and methods

Analyses of how GPP and TBCF : GPP vary with MAT (Fig. 3) were based on a global data set of forest C budgets (Litton *et al.* 2007). Sites from this data set span a wide gradient of species (evergreen needleleaf, deciduous and evergreen broadleaf), stand ages (young regenerating forests to mature old-growth forests), forest types (natural and plantation forests), resource availability (with and without nutrient and water amendments) and climate (−5 to 27 °C) (Table 1). For this analysis we utilized all reviewed studies ($n = 34$), including both natural forests and plantations, that quantified all components of GPP (ANPP in foliage and wood, above-ground autotrophic respiration in foliage and wood, and TBCF). GPP was determined as the sum of these components and the fraction of GPP to below-ground as TBCF : GPP.

Analyses of how BNPP, TBCF and BNPP : TBCF varied with MAT (Fig. 4) were based on two global data sets from Giardina *et al.* (2005) and Litton *et al.* (2007), and published data from additional forested sites that did not appear in these earlier syntheses (Table 1). Where necessary, biomass values were converted to C assuming a C content of 48%. We excluded all forests that received supplemental resources (fertilization, irrigation, etc.) and exotic plantations from the BNPP, TBCF and BNPP : TBCF analyses because enhanced resource supply and improved genetics can result in productivity rates and allocation patterns that are substantially different than for native forests at similar MATs (Litton *et al.* 2007). While partitioning of TBCF to BNPP may not vary with stand productivity, inclusion of intensively managed plantation data would have increased variation in the MAT relationships. For BNPP, data are from studies that used either sequential coring or a paired sequential coring/minirhizotron approach (Giardina *et al.* 2005). Few studies included estimates of mycorrhizal production or exudation, yet these components can amount to a significant fraction of BNPP (Vogt *et al.* 1983; Giardina *et al.* 2004; Hobbie 2006). As a result, these missing components will lead to underestimates of BNPP and BNPP : TBCF. Overall, the results we report for BNPP are better described as fine + coarse root production (Giardina *et al.* 2005). For individual studies in all data sets that did not report MAT or

MAP for their study site, they were determined from site locations and a readily available on-line data set <www.worldclimate.com>.

We estimated TBCF as soil-surface CO₂ efflux minus litterfall (Raich & Nadelhoffer, 1989) such that all estimates of TBCF would be directly comparable across the MAT gradient. This approach assumes that below-ground C pools in soil organic matter, litter and roots are at steady state, an assumption that is not always valid. Excluding coarse roots from estimates of TBCF may underestimate TBCF by ≥ 10% in some cases, while excluding the other fluxes contributing to TBCF would alter final estimates by < 5% (Giardina *et al.* 2003; Litton, Ryan & Knight 2004). Seldom, however, are these variables estimated in the TBCF literature. In this analysis, for studies that included estimates of change in coarse roots or other soil C pools in the mass balance equation for TBCF (see Litton *et al.* 2007), we recalculated TBCF as above to be consistent across studies.

Because BNPP and TBCF were seldom quantified for the same study, we analyzed the fraction of TBCF partitioned to BNPP by: (i) establishing the independent MAT responses of TBCF and BNPP; (ii) using these relationships to predict the effects of MAT on TBCF and BNPP at 1 °C increments; and (iii) calculating BNPP : TBCF across the entire MAT range from the predicted values of TBCF and BNPP. To account for the variance associated with estimates of TBCF and BNPP for any given temperature, we also modelled the 95% confidence intervals (CIs) for the BNPP : TBCF relationship with MAT by: (i) fitting a quadratic polynomial equation to the 95% CI data points for each observation in the BNPP or TBCF vs. MAT relationships ($R^2 > 0.99$ in all cases); (ii) using the resulting quadratic equations to predict upper and lower CIs for both BNPP and TBCF across a standard set of temperatures spanning our data set (−5 to 30 °C with 1 °C increments); and (iii) calculating the ratio of the modelled upper or lower CI fits for the BNPP vs. MAT relationship against the TBCF vs. MAT relationship.

All statistical analyses were performed in SPSS 15.0 (SPSS Inc., Chicago, IL). Least-squares regression techniques were used to examine how GPP, TBCF, BNPP, TBCF : GPP and BNPP : TBCF vary with MAT. We fit both linear and nonlinear regression models, but ultimately used linear models in all cases. Multiple regressions with a backward elimination variable selection procedure were used to determine significant effects of climate variables (MAT, MAP and their interaction) on global scale patterns for each variable of interest. In all cases, goodness-of-fit and final model selection were determined by examining P values, the sum of squares of the residuals, mean square of error, coefficient of determination (R^2) and by visual inspection of plots of residuals. In all cases, conformance to homogeneity of variance and normality assumptions were examined at $\alpha = 0.05$. Normality assumptions were met for all data sets, but the TBCF and BNPP data sets were mildly heteroscedastic. We examined these relationships with log-transformed data and recalculated linear regression equations, but as we found almost identical regression fits and significance values between untransformed and transformed data we present non-transformed data in all cases.

Results and discussion

RESPONSE OF BELOW-GROUND PROCESSES TO CLIMATE VARIABLES

MAT and MAP covaried across the global forest data base (Fig. 2). For all sites, MAP increased by 80 mm for every 1 °C increase in MAT ($n = 56$; $P < 0.01$; $r^2 = 0.40$; $Y = 473 + 80.2 \times X$). However, a small number of sites that receive > 1500 mm

Table 1. Studies used to examine the response of below-ground C cycling to a global scale range of mean annual temperature (MAT)

| Dominant vegetation | Location | BNPP* | TBCF* | GPP* | MAT (°C) | MAP (mm) | Reference |
|--|---------------------------|-------|------------|------|----------|----------|---|
| <i>Picea mariana</i> ; 150 years‡§ | Manitoba, Canada | 89 | 502 | 863 | −4.6 | 536 | (Ryan <i>et al.</i> 1997; Gower <i>et al.</i> 2001) |
| <i>Pinus banksiana</i> ; 63 years‡§ | " | 100 | 428 | 677 | " | " | " |
| <i>Populus tremuloides</i> ; 53 years‡§ | " | 66 | 390 | 903 | " | " | " |
| <i>Picea mariana</i> ; 115 years‡§ | Saskatch., Canada | 119 | 352 | 785 | −1.1 | 405 | " |
| <i>Pinus banksiana</i> ; 63 years‡§ | " | 105 | 273 | 556 | " | " | " |
| <i>Populus tremuloides</i> ; 68 years‡§ | " | 42 | 393 | 1044 | " | " | " |
| <i>Picea mariana</i> ; 120 years¶ | Fairbanks, AK | | 399 | | −3.3 | 269 | (Vogel <i>et al.</i> 2008) |
| <i>Picea mariana</i> ; 75 years¶ | " | | 314 | | " | " | " |
| <i>Picea mariana</i> ; 110 years¶ | " | | 266 | | " | " | " |
| <i>Picea mariana</i> ; 180 years¶ | Bonanza Creek, AK | | 566 | | " | " | " |
| <i>Picea mariana</i> ; 78 years¶ | Delta Junction, AK | | 386 | | −2.1 | 290 | " |
| <i>Picea mariana</i> ; 75 years¶ | " | | 426 | | " | " | " |
| <i>Picea mariana</i> ; 120 years¶¶ | Saskatch., Canada | 117 | 263 | | −1.1 | 405 | " |
| <i>Picea mariana</i> ; 70 years¶¶ | Manitoba, Canada | 168 | 210 | | 0.8 | 439 | " |
| <i>Picea mariana</i> ; 150 years¶¶ | " | 73 | 186 | | 0.8 | 439 | " |
| <i>Larix gmelinii</i> ; 40 years§ | Daxing'anling, China | 54 | | | −5.4 | 500 | (Gower <i>et al.</i> 2001) |
| <i>Picea glauca</i> ; 250 years§ | Bonanza Creek, AK | 111 | | | −3.5 | 269 | " |
| <i>Picea glauca</i> ; 130 years§ | " | 71 | | | " | " | " |
| <i>Picea mariana</i> ; 200 years§ | " | 105 | | | " | " | " |
| <i>Populus/Alnus</i> ; 30 years§ | " | 160 | | | " | " | " |
| <i>Betula papyrifera</i> ; 77 years§ | " | 124 | | | " | " | " |
| <i>Populus balsamifera</i> ; 90 years§ | " | 197 | | | " | " | " |
| <i>Picea abies</i> ; 100 years§ | Ilomantsi, Finland | 158 | | | 2.2 | 636 | " |
| <i>Pinus sylvestris</i> ; 45 years§ | " | 117 | | | " | " | " |
| <i>Pinus sylvestris</i> ; 50 years§ | " | 55 | | | " | " | " |
| <i>Betula pubescens</i> ; 50 years§ | " | 45 | | | " | " | " |
| <i>Pinus sylvestris</i> ; 20 years§ | Jadraas, Sweden | 285 | | | 3.0 | 731 | " |
| <i>Pinus sylvestris</i> ; 120 years§ | " | 103 | | | " | " | " |
| <i>Pinus contorta</i> ; 110 years¶ | Yellowstone N.P., WY | | 354 | | −0.5 | 484 | (Litton <i>et al.</i> 2004) |
| <i>Populus tremuloides</i> ; 15–25 years¶ | Med. Bow Mtns., WY | | 393 | | 2.5 | 600 | (Fornwalt 1999) |
| <i>Populus tremuloides</i> ; 60–100 years¶ | " | | 500 | | " | " | " |
| <i>Pseudotsuga menziesii</i> ; 98 years§ | Cibola N.F., NM | 391 | | | 4.0 | 773 | (Gower, Vogt & Grier 1992) |
| <i>Picea abies</i> ; 47 years¶ | Bavaria, Germany | | 470 | | 5.6 | 768 | (Buchmann 2000) |
| <i>Pseudotsuga menziesii</i> ; 50 years¶ | Kettle River Range, WA | | 700 | | 5.7 | 660 | (McDowell <i>et al.</i> 2001) |
| <i>Pinus ponderosa</i> ; 15 years‡§¶ | Cascade Mtns., OR | 281 | 614 (602)† | 1043 | 7.5 | 552 | (Law <i>et al.</i> 2001) |
| <i>Pinus ponderosa</i> ; 50/250 years‡§¶ | " | 299 | 671 (648)† | 817 | 8.1 | 524 | " |
| <i>Fagus sylvatica</i> ¶ | Vielsalm, Belgium | | 712 | | 7.9 | 794 | (Longdoz, Yernaux & Aubinet 2000) |
| <i>Pseudotsuga menziesii</i> ¶ | " | | 369 | | " | " | " |
| <i>Pseudotsuga menziesii</i> ; 20 years¶ | Cascade Mtns., WA | | 1263 | | 8.7 | 2500 | (Klopatek 2002) |
| <i>Pseudotsuga menziesii</i> ; 40 years¶ | " | | 628 | | " | " | " |
| <i>Pseudotsuga menziesii</i> ; old growth¶ | " | | 1002 | | " | " | " |
| <i>Picea abies</i> ; 180 years¶ | Province of Trento, Italy | | 900 | | 4.2 | 1008 | (Rodeghiero & Cescatti 2006) |

Table 1 Continued

| Dominant vegetation | Location | BNPP* | TBCF* | GPP* | MAT (°C) | MAP (mm) | Reference |
|---|------------------------|-------|-------------|------|----------|----------|----------------------------------|
| <i>Picea abies</i> ¶ | " | | 497 | | 5.9 | 1015 | " |
| <i>Abies alba</i> ¶ | " | | 519 | | 6.7 | 1085 | " |
| <i>Picea abies</i> ¶ | " | | 301 | | 8.5 | 982 | " |
| <i>Pinus sylvestris</i> ¶ | " | | 460 | | 9.5 | 961 | " |
| <i>Pinus nigra</i> ¶ | " | | 342 | | 11.0 | 959 | " |
| <i>Quercus ilex</i> ; 45 years¶ | " | | 564 | | 11.8 | 950 | " |
| Temperate deciduous; 66 years§¶ | Willow Creek, WI | 211 | 675 | | 4.8 | 776 | (Curtis <i>et al.</i> 2002) |
| Temperate deciduous; 90 years§¶ | U.M. Biol. Station, MI | 301 | 999 | | 6.2 | 750 | " |
| Temperate deciduous; 60 years§¶ | Harvard Forest, MA | 245 | 670 | | 7.1 | 1066 | " |
| Temperate deciduous; 80 years§¶ | Morgan Monroe, IN | 520 | 994 | | 11.1 | 1012 | " |
| Temperate deciduous; 120 years§¶ | Walker Branch, TN | 188 | 724 | | 13.8 | 1352 | " |
| <i>Nothofagus solandri</i> ; 52 years; subalpine‡§ | Craigieburn Range, NZ | 250 | 389 | 1570 | 5.1 | 1570 | (Benecke & Nordmeyer 1982) |
| <i>P. contorta</i> plant; 23 years; subalpine‡ | " | | 734 | 2919 | " | " | " |
| <i>Nothofagus solandri</i> ; 52 years; montane‡§ | " | 280 | 840 | 3710 | 8.0 | 1447 | " |
| <i>P. contorta</i> plant; 20 years; montane‡ | " | | 1460 | 5560 | " | " | " |
| <i>Pseudotsuga menziesii</i> ; 40 years§ | Charles Pack, WA | 408 | | | 9.4 | 1000 | " |
| <i>Pseudotsuga menziesii</i> ; 40 years§ | " | 191 | | | " | " | " |
| <i>Pseudotsuga menziesii</i> ; 40 years§ | Washington, USA | 312 | | | " | " | " |
| Boreal mixed forest; 45–130 years¶ | Howland Forest, ME | | 595 | | 5.5 | 1000 | (Savage & Davidson 2001) |
| Temperate hardwood; 60–100 years¶ | Harvard Forest, MA | | 529 | | 8.5 | 1050 | " |
| Temperate hardwood; 60–100 years¶ | " | | 498 | | " | " | " |
| Temperate hardwood; 60–100 years¶ | " | | 459 | | " | " | " |
| <i>Fagus sylvatica</i> ; 80 years¶ | Zealand Isl., Denmark | | 365 | | 8.1 | 510 | (Pilegaard <i>et al.</i> 2001) |
| <i>Eucalyptus pauciflora</i> ; 54 years¶ | Brindabella, Australia | | 465 | | 9.0 | 1200 | (Keith, Raison & Jacobsen 1997) |
| <i>Fagus sylvatica</i> ; 30 years¶ | Hesse Forest, France | | 488 | | 9.2 | 820 | (Granier <i>et al.</i> 2000) |
| <i>Quercus</i> and <i>Pinus</i> forest; c. 45 years 2nd growth‡§¶ | Brookhaven, NY | 150 | 338 (314)† | 1206 | 9.8 | 1240 | (Whittaker & Woodwell 1969) |
| <i>Pinus radiata</i> plant; 20 years; C‡¶ | Canberra, Australia | | 1022 (903)† | 2415 | 12.8 | 791 | (Ryan <i>et al.</i> 1996) |
| <i>P. radiata</i> plant; 20 years; I‡ | " | | 1036 | 2531 | " | " | " |
| <i>P. radiata</i> plant; 20 years; I + F‡ | " | | 739 | 3438 | " | " | " |
| <i>Metrosideros polymorpha</i> ; mature¶ | Mauna Loa, HI | | 501 | | 13.0 | 2600 | (Raich 1998) |
| <i>Metrosideros polymorpha</i> ; mature¶ | " | | 417 | | 13.0 | 2600 | " |
| <i>M. polymorpha</i> / <i>Acacia koa</i> ; mature¶ | " | | 595 | | 19.3 | 6000 | " |
| <i>Quercus</i> spp. and <i>Carya ovata</i> ; 55 years‡§¶ | Oak Ridge, TN | 434 | 432 (393)† | 1329 | 13.2 | 1400 | (Malhi, Baldocchi & Jarvis 1999) |
| <i>Liriodendron tulipifera</i> ; c. 50 years‡§¶ | Oak Ridge, TN | 374 | 744 (811)† | 2162 | 13.3 | 1265 | (Harris <i>et al.</i> 1975) |
| Temperate deciduous; 50–100 years¶ | Walker Branch, TN | | 597 | | 13.8 | 1352 | (Hanson <i>et al.</i> 1993) |
| Temperate deciduous; 50–100 years¶ | " | | 642 | | " | " | " |
| Temperate deciduous; 50–100 years¶ | " | | 634 | | " | " | " |
| Temperate deciduous; 50–100 years¶ | " | | 748 | | " | " | " |
| <i>Pinus taeda</i> plant; FACE C; 17 years¶ | Duke Forest, NC | | 731 | | 15.5 | 1140 | (Finzi <i>et al.</i> 2001) |
| § <i>Pinus taeda</i> plant; 16 years§ | Piedmont Region, NC | 566 | | | 15.6 | 1150 | (Kinerson, Ralston & Wells 1977) |
| <i>Pinus taeda</i> plant; 12 years; C‡§¶ | Piedmont Region, NC | 199 | 701 | 1532 | 17.0 | 1210 | (Maier <i>et al.</i> 2004) |
| <i>Pinus taeda</i> plant; 12 years; I‡ | " | | 898 | 1924 | " | " | " |

Table 1 *Continued*

| Dominant vegetation | Location | BNPP* | TBCF* | GPP* | MAT (°C) | MAP (mm) | Reference |
|--|----------------------|-------|--------------|------|----------|----------|--|
| <i>Pinus taeda</i> plant; 12 years; F‡ | " | | 686 | 2382 | " | " | " |
| <i>Pinus taeda</i> plant; 12 years; I + F‡ | " | | 668 | 2587 | " | " | " |
| <i>Pinus elliottii</i> plant; 7–9 years‡§¶ | Bradford, FL | 244 | 778 (671)† | 1407 | 19.6 | 1320 | (Gholz, Hendry & Cropper 1986; Ewel, Cropper & Gholz 1987) |
| <i>Pinus elliottii</i> plant; 26–29 years‡§¶ | " | 307 | 1136 (1050)† | 2482 | " | " | " |
| Tropical dry forest; mature¶ | Ka`upulehu, HI | | 912 | | 20.0 | 732 | (Litton <i>et al.</i> 2008) |
| Tropical dry forest; mature¶ | " | | 1275 | | " | 1189 | " |
| <i>Eucalyptus saligna</i> ; 2 years plant; C; 1 × 1 m‡ | Pepeekeo, HI | | 2353 | 5057 | 21.0 | 4000 | (Ryan <i>et al.</i> 2004) |
| <i>Eucalyptus saligna</i> ; 6 years plant; C; 1 × 1 m‡ | " | | 1185 | 2369 | " | " | " |
| <i>Eucalyptus saligna</i> ; 2 years plant; C; 3 × 3 m‡ | " | | 1843 | 4413 | " | " | " |
| <i>Eucalyptus saligna</i> ; 6 years plant; C; 3 × 3 m‡ | " | | 1448 | 2930 | " | " | " |
| <i>Eucalyptus saligna</i> ; 2 years plant; F; 1 × 1 m‡ | " | | 1900 | 5561 | " | " | " |
| <i>Eucalyptus saligna</i> ; 6 years plant; F; 1 × 1 m‡ | " | | 1740 | 3919 | " | " | " |
| <i>Eucalyptus saligna</i> ; 2 years plant; F; 3 × 3 m‡ | " | | 1580 | 4955 | " | " | " |
| <i>Eucalyptus saligna</i> ; 6 years plant; F; 3 × 3 m‡ | " | | 1442 | 3486 | " | " | " |
| Tropical evergreen broadleaf; old growth¶ | La Selva, Costa Rica | | 721 | | 25.0 | 4375 | (Davidson <i>et al.</i> 2002) |
| Tropical evergreen broadleaf; old growth¶ | " | | 1005 | | " | " | " |
| Tropical evergreen broadleaf; old growth¶ | Paragominas, Brazil | | 1520 | | 26.0 | 1750 | (Davidson <i>et al.</i> 2000) |
| Tropical evergreen broadleaf; 20 years¶ | " | | 1325 | | " | " | " |
| Tropical evergreen broadleaf; old growth‡§¶ | Manaus, Brazil | 690 | 950 | 2620 | 26.6 | 2200 | (Malhi <i>et al.</i> 1999) |
| Tropical evergreen broadleaf; old growth‡¶ | Manaus, Brazil | | 810 | 2860 | 26.7 | 2300 | (Chambers <i>et al.</i> 2004) |

*All units are in g C m⁻² year⁻¹; BNPP, Below-ground Net Primary Production; TBCF, Total Below-ground Carbon Flux; GPP, Gross Primary Production.

†For the analyses in Fig. 4, TBCF was calculated as soil-surface CO₂ efflux minus litterfall to standardize methodology across sites.

‡Studies used in Fig. 3 that estimated GPP and the partitioning of GPP to TBCF.

§Studies used in Fig. 4 that estimated BNPP.

¶Studies used in Fig. 4 that estimated TBCF, or the components of TBCF (soil-surface CO₂ efflux and litterfall).

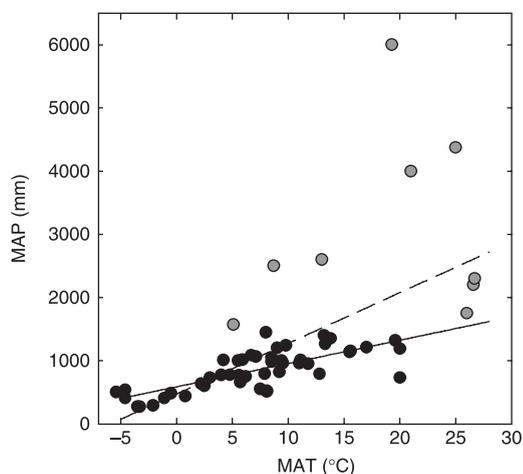


Fig. 2. Across a global forest data base, MAP increased linearly with MAT (dashed line; $n = 56$; $r^2 = 0.40$; 80 mm increase in MAP for each 1°C increase in MAT). Excluding sites with MAP > 1500 mm (grey fill), MAP increased by 37 mm for each 1°C increase in MAT (solid line; $n = 47$; $r^2 = 0.56$).

MAP strongly influenced the relationship, resulting in biased residuals. Eliminating sites > 1500 mm from the analysis resulted in a much smaller increase in MAP (37 mm) for every 1°C increase in MAT and a better fit to the data ($n = 47$; $P < 0.01$; $r^2 = 0.56$; $Y = 587 + 36.9 \times X$). There is strong ecological reason, in addition to the biased residuals, to justify the elimination of sites receiving > 1500 mm MAP from the MAT vs. MAP analysis. At these high MAPs, precipitation is no longer a good predictor of plant available water because actual evapotranspiration remains almost constant beyond annual precipitation sums of 1500 mm (Schulze, Beck & Müller-Hohenstein 2005). Luysaert *et al.* (2007), for example, found that GPP increases linearly with MAP initially but that the response saturates at *c.* 1500 mm MAP.

We conclude that the global patterns in below-ground processes outlined here are primarily, although not exclusively, a response to MAT because: (i) plant available water should be similar across the MAT gradient as increased temperature will increase evapotranspiration, and MAP only increases by 37 mm for every 1°C increase in MAT at sites receiving < 1500 mm MAP; and (ii) MAT was always identified as the most important predictor of below-ground C flux and partitioning

in our data set when MAT, MAP and $\text{MAT} \times \text{MAP}$ were included in multiple regression analyses. For all data sets except the GPP data, both MAP and the $\text{MAT} \times \text{MAP}$ interaction term were removed during multiple regression analyses as they provided no additional explanatory power. In the GPP data set, all three climate variables were equally important. MAP clearly covaries with MAT and is useful in explaining observed patterns, particularly exceptions to general trends, but MAT alone explains the majority of the variation in below-ground C flux and partitioning in our global forest data set. Importantly, differences in MAP and nutrient availability, along with other factors such as species composition and stand age, are likely important in explaining variability in below-ground processes at a given MAT.

GPP AND TBCF : GPP VS. MAT

GPP was positively and linearly related to MAT across a broad and diverse range of forests spanning a global range of MATs (Fig. 3a; $n = 34$; $P < 0.01$; $r^2 = 0.34$; $Y = 1311 + 91.9 \times X$), increasing from a low of $677 \text{ g C m}^{-2} \text{ year}^{-1}$ at -4.6°C MAT to $> 5500 \text{ g C m}^{-2} \text{ year}^{-1}$ at MATs over 20°C . Available studies with the highest estimates of GPP were primarily plantations, where increased resource supply and improved genetics often support higher productivity than found in native forests at comparable MATs. In addition, several studies reported a wide range of GPP values for a single MAT, and these represent treatment manipulations of resource availability for plantations of a given site and species. For example, there are eight data points at 21°C with GPP values ranging from 2369 to $5561 \text{ g C m}^{-2} \text{ year}^{-1}$ that represent 2 and 6 year-old stands that varied in density and nutrient supply treatments for a single species planted at the same site (*Eucalyptus saligna* plantations in Hawaii; Ryan *et al.* 2004). As a result, when only plantation forests were analyzed separately there was no significant relationship between GPP and MAT ($P = 0.75$). When only natural forests were included in the analysis, GPP was positively and linearly related to MAT ($n = 15$; $P < 0.01$; $r^2 = 0.69$; $Y = 1046 + 63.0 \times X$). The slope for natural forests was lower than that for the entire data set (63 ± 18 for natural forests vs. 92 ± 23 for the entire data set; mean \pm SE), but regression coefficients for natural forests fell within the 95% CIs for the regression coefficients from the entire data set.

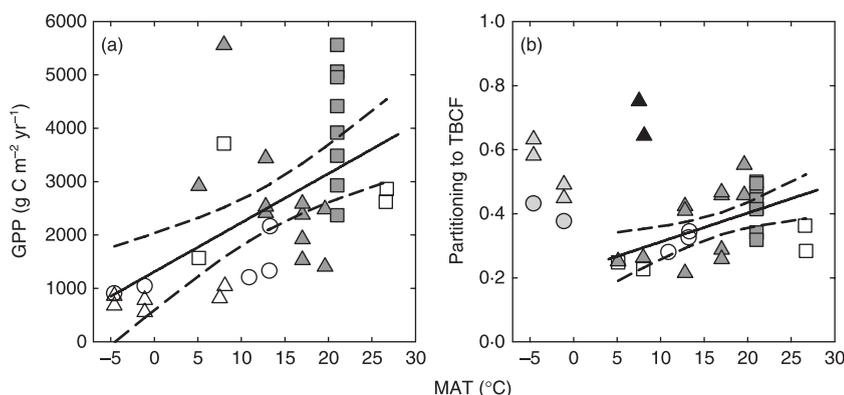


Fig. 3. Across a wide range of forests that included both plantations (dark grey fill) and natural forests (open fill): (a) GPP increased linearly with MAT (regression fit \pm 95% CIs), and (b) partitioning to TBCF increased linearly with MAT for temperate and tropical forests (regression fit \pm 95% CIs). Partitioning to TBCF was higher (0.64–0.75) in semi-arid *Pinus ponderosa* woodlands (black fill) and decreased with MAT for boreal ecosystems (light grey fill), but available data were limited. Triangles are needleleaf evergreen, circles are deciduous, and squares are broadleaf evergreen forests.

Critically, while the inclusion of plantation forests in the data set did increase the variability and slope of the MAT vs. GPP relationship, the relationships between GPP and MAT for natural forests alone and the entire data set showed similar trends of increasing GPP with MAT.

These results agree with Luyssaert *et al.* (2007) but contradict those of Valentini *et al.* (2000), who found no relationship between GPP and latitude for EUROFLUX sites where GPP was estimated with eddy covariance measurements and MAT varied from 4.1 to 15.3 °C. This discrepancy can perhaps best be explained by the fact that for the latitudinal MAT gradient in Valentini *et al.* (2000), and in contrast to our study, warmer sites were also drier. Importantly, the EUROFLUX study highlighted that decreasing C uptake with increasing latitude could not be explained by decreased GPP, but instead by increased ecosystem respiration. While non-steady state increases in heterotrophic respiration may explain reduced net ecosystem exchange (NEE) across high latitudes (Valentini *et al.* 2000), autotrophic respiration is unlikely to have increased with latitude and the strong correlation between GPP and MAT that we found is not likely the result of the temperature dependence of autotrophic respiration. First, the fraction of GPP used for plant respiration appears to be strongly conservative across ecosystems, with little variation attributable to stand age, resource availability, above-ground biomass or competition (see Litton *et al.* 2007). For the studies included in our MAT analysis that estimated total autotrophic respiration ($n = 23$), respiration accounted for a constant fraction of GPP (0.57 ± 0.02 ; mean \pm SE) and did not vary with MAT (Fig. 5; $r^2 = 0.12$; $P = 0.11$; $Y = 0.59 - 0.003 \times X$). Second, partitioning of GPP to respiration shows either ephemeral or no response to experimentally manipulated temperatures (Gifford 1994, 1995; Tjoelker *et al.* 1999; Atkin *et al.* 2007), and these trends appear to hold across broad plant functional types (Campbell *et al.* 2007), with rare exceptions for plants grown well outside of their natural temperature range (Atkin *et al.* 2007; Campbell *et al.* 2007). Overall, increased respiration in response to experimentally manipulated temperatures acclimates rapidly and appears to be a short term response (see King *et al.* 2006).

Our results are in line with evidence that ANPP and TBCF (Giardina *et al.* 2005; Raich *et al.* 2006), net ecosystem production (NEP; Tian *et al.* 1999; Curtis *et al.* 2002) and GPP (Luyssaert *et al.* 2007) all increase with MAT. These positive relationships are not surprising, however, because many components of forest C budgets show strong linear and positive relationships to MAT (Giardina *et al.* 2005; Raich *et al.* 2006), and all components of the forest C budget are strongly and positively related to GPP (Litton *et al.* 2007).

Variation was high across the MAT gradient for partitioning of GPP to TBCF (Fig. 3b) and there was no relationship between TBCF : GPP and MAT for all sites combined ($n = 34$; $P = 0.25$; $r^2 = 0.04$; $Y = 0.44 - 0.003 \times X$). However, much of the variation was driven by three sites examined in two different studies – *Picea mariana*, *Pinus banksiana* and *Populus tremuloides* dominated boreal forests (Gower *et al.* 1997; Ryan, Lavigne & Gower 1997) and semi-arid *Pinus*

ponderosa dominated woodland (Law *et al.* 2001). When these sites were excluded from the analysis, TBCF : GPP was positively and linearly related to MAT (Fig. 3b; $n = 26$; $P < 0.01$; $r^2 = 0.28$; $Y = 0.22 + 0.01 \times X$), which supports our first hypothesis.

Based on data presented in Giardina *et al.* (2005), partitioning of GPP to TBCF should increase with MAT. In this earlier global synthesis, both ANPP and TBCF increased linearly with MAT, but the slope was steeper for TBCF. Assuming that above-ground autotrophic respiration can be estimated from ANPP as $0.96 \times \text{ANPP}$ (Litton *et al.* 2007), then GPP and partitioning to TBCF can be calculated across a MAT gradient. In the hypothesized relationship that results from this analysis, which we caution includes several important assumptions, partitioning to TBCF increases with MAT. However, this hypothesized relationship varies from that presented in Fig. 3b in two ways: (i) the hypothesized relationship is nonlinear and best described by a power function ($Y = 0.42 \times X^{0.033}$); and (ii) TBCF : GPP in the hypothesized relationship increases more slowly with increasing MAT than that documented here for temperate and tropical ecosystems.

There is compelling ecological evidence for why GPP and partitioning of GPP to TBCF should be strongly linked (Fig. 3), and we contend that the response of above-ground processes to environmental change can be used to predict potential changes in below-ground C flux and partitioning in response to a changing climate. First, there is an increasing body of evidence that points to a strong role of current photosynthates in driving below-ground C cycling (Ekblad & Höglberg 2001; Höglberg & Read 2001, 2006; Giardina *et al.* 2004). Second, all components of forest ecosystem C budgets are tightly linked to GPP and, therefore, to each other – an increase in GPP increases all component fluxes (Litton *et al.* 2007).

Increased flux and partitioning of GPP to below-ground with rising temperature is particularly important because the strongest impact of climate change on below-ground C cycling may be increased heterotrophic activity that could lead to decreases in soil C (Pendall *et al.* 2004). Thus, even if rising temperatures reduce soil C storage by increasing microbial activity, increased flux and partitioning of C to below-ground may at least partially offset this potentially important positive feedback on atmospheric CO₂ concentrations.

Are there compelling reasons for why the boreal forest and *P. ponderosa* woodland sites do not fit broader patterns of TBCF : GPP? While these sites were exceptions in our data set, boreal forests and water-limited forest ecosystems are clearly important ecosystems globally. These data points could provide valuable insight into the TBCF : GPP relationship if underlying mechanisms for the differences can be identified. The boreal sites appeared to show a pattern of decreased partitioning to TBCF with MAT (Fig. 3b), although the relationship was not significant. This is in line with evidence presented in Giardina *et al.* (2005), who found that most forest types, including *Pinus* dominated forests, show a strong positive relationship between above- and below-ground productivity. However, spruce (*Picea*) and fir (*Abies* and *Pseudotsuga*) forests showed negative relationships between

ANPP and BNPP. Moreover, Vogel *et al.* (2008) documented a similar pattern of reduced partitioning to below-ground with increasing MAT in boreal forests. The apparent decrease in partitioning of GPP to TBCF with increasing MAT in boreal sites may relate to increased nutrient supply that accompanies increased MAT (Vogel *et al.* 2008), because increased resource supply reduces the fraction of GPP partitioned to below-ground (Litton *et al.* 2007).

The *P. ponderosa* woodland exhibited TBCF : GPP values almost double that found in any other temperate ecosystem. Partitioning of GPP to TBCF has been shown to increase as water availability decreases (Litton *et al.* 2007). The *P. ponderosa* site has the lowest MAP (*c.* 550 mm) of any of the sites in the data base at this MAT, and MAP there is strongly seasonal with cool, wet winters and warm, dry summers (Law *et al.* 2001). In addition, understorey grasses and shrubs represented up to 50% of stand leaf area index and 42% of above-ground production and respiration in younger stands, and these plant functional types may differ from trees in how they allocate C to above- and below-ground (Litton, Sandquist & Cordell 2008). Taken together, partitioning to TBCF may be high at this site in response to strongly limiting below-ground resources and, for the young stands, a large component of grass and shrub vegetation.

BNPP, TBCF AND BNPP : TBCF VS. MAT

BNPP was positively and linearly related to MAT (Fig. 4a; $n = 43$; $P < 0.01$; $r^2 = 0.57$; $Y = 145.9 + 14.4 \times X$). As with BNPP, TBCF was also positively and linearly related to MAT (Fig. 4a; $n = 63$; $P < 0.01$; $r^2 = 0.41$; $Y = 404.3 + 23.1 \times X$). Both below-ground C fluxes varied by more than an order of magnitude over a similar MAT gradient – BNPP ranged from 42 to 690 $\text{g C m}^{-2} \text{ year}^{-1}$, and TBCF from 186 to 1520 $\text{g C m}^{-2} \text{ year}^{-1}$. Variability in the data sets was moderate, with MAT explaining 57% and 41% of the variation in BNPP and TBCF, respectively. Still, these relationships are remarkable

given that data were taken from studies that varied with respect to methodology, species, soil type, resource availability, climate, stand age and stand history.

The linear models suggest that BNPP approaches zero at -10° while TBCF approaches zero at -18°C . These zero flux interception points are very plausible as the flux of C to below-ground appears to approach zero as MAT drops below -10°C and ecosystems become dominated by non-forest vegetation (Shaver & Jonasson 2001). Hence, the relationships between TBCF or BNPP and MAT lead to estimates of zero below-ground C process rates that are in line with ecological observations of vegetation types that fall outside of the MAT range of our data set.

Estimating BNPP is labour intensive and methodologically difficult, while estimating TBCF is more straightforward. Thus, large-scale relationships between BNPP and TBCF could be used to estimate BNPP across large regions. Moreover, the primary fluxes used to estimate TBCF (soil-surface CO_2 efflux and litterfall) are commonly measured in ecosystem studies, making a relationship between TBCF and BNPP valuable for modelling stand level process rates and total C inputs to soils (BNPP plus above-ground litterfall) across landscapes.

Based on the TBCF and BNPP relationships with MAT (Fig. 4a), our analysis indicates that partitioning of TBCF to BNPP increases nonlinearly with MAT (Fig. 4b). We estimated that BNPP : TBCF varies from 0.26 to 0.53 across the entire MAT gradient, but centers around *c.* 0.50 (range of 0.42 to 0.53) for MATs corresponding to temperate and tropical ecosystems ($5\text{--}30^\circ \text{C}$). This finding supports our second hypothesis that BNPP : TBCF would be *c.* 0.50 across the range of MAT examined, but also highlights that the fraction of TBCF that is BNPP appears to increase with temperature, and this increase is particularly noticeable at the lower end of the MAT gradient. To our knowledge, this synthesis across diverse forests is the first to directly quantify the fraction of TBCF that is partitioned to BNPP for such a large data set. Nadelhoffer & Raich (1992) calculated that *c.* 33% of TBCF

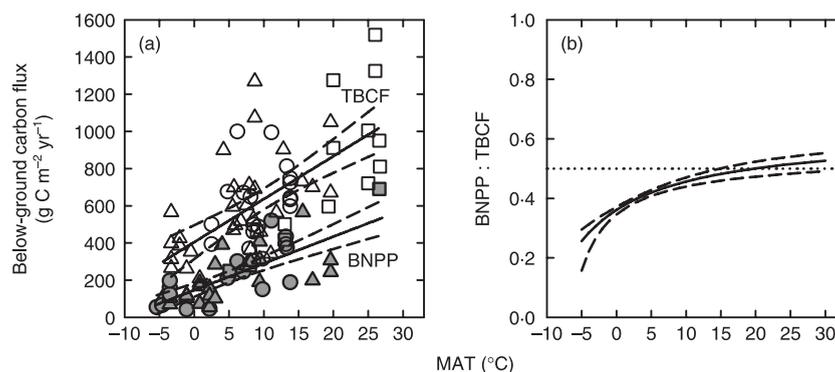


Fig. 4. (a) Below-ground C flux increased with MAT across a wide range of forest ecosystems for both BNPP (grey fill) and TBCF (open fill). Solid lines are regression fits and dashed lines 95% CIs. (b) These relationships were used to predict the ratio of BNPP : TBCF ($\pm 95\%$ CIs) at 1°C increments across the same range of MATs. The fraction of TBCF that goes to BNPP was variable across the MAT gradient, increasing from 0.26 at -5°C to 0.53 at 30°C . However, variability in BNPP : TBCF was smaller for MATs of $5\text{--}30^\circ \text{C}$ (0.42–0.53), which correspond to temperate and tropical forests. The horizontal dotted line in (b) refers to a BNPP : TBCF of 0.50, an assumption in some terrestrial ecosystem models and ecosystem studies of stand carbon use efficiency. Triangles are needleleaf evergreen, circles are deciduous, and squares are broadleaf evergreen forests.

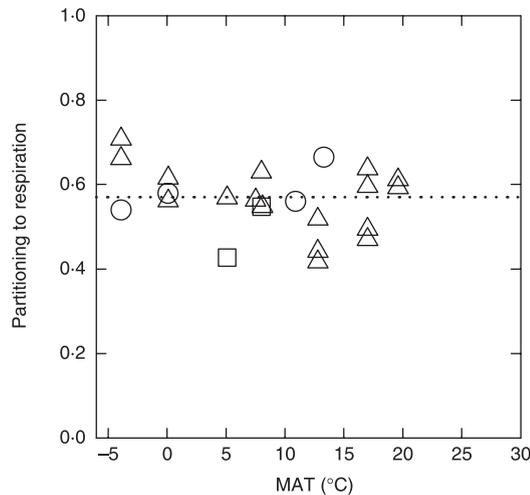


Fig. 5. Partitioning of gross primary production to total autotrophic respiration (Respiration/GPP) did not vary with mean annual temperature across a broad range of forests. The dotted line represents the mean value for partitioning to respiration across the entire temperature gradient (0.57). Triangles are needleleaf evergreen, circles are deciduous, and squares are broadleaf evergreen forests.

goes to fine root production for deciduous and coniferous forests from Wisconsin and Massachusetts (MATs of *c.* 7–9 °C). Based on our analysis, BNPP : TBCF for this MAT range should be *c.* 0.46. This higher estimate is at least in part explained by the fact that our BNPP estimates included both fine and coarse root production.

The variation in BNPP : TBCF with temperature (Fig. 4b) indicates that below-ground CUE ranges from a low of 0.26 at –5 °C to a more constant value of *c.* 0.50 at MATs > 5 °C. This pattern in below-ground CUE differs from that found for total ecosystem CUE, which was constant across the entire MAT gradient (0.43; Fig. 5). In order for below-ground CUE to decrease at low temperatures while total ecosystem CUE stays constant, above-ground CUE would have to increase proportional to the decrease in below-ground CUE. In fact, Ryan *et al.* (1997) found that above-ground CUE (Mean = 0.47) was considerably higher than below-ground CUE (Mean = 0.30) for four out of six boreal stands growing at MATs of –4.6 to –1.1 °C. In addition, Litton *et al.* (2007) calculated that above-ground CUE was, on average, *c.* 25% higher than below-ground CUE across a range of forests. The differences in estimates of above- vs. below-ground CUE documented in these prior studies closely match the patterns found here, and this suggests that the observed variation in BNPP : TBCF with temperature is robust.

Because BNPP is a component of TBCF, there is a strong ecological explanation for why TBCF exceeds BNPP and why these two fluxes are correlated across large gradients. The similar slopes of the BNPP and TBCF relationships with MAT (14.4 ± 2.0 and 23.1 ± 3.6 , respectively; mean \pm SE) likely reflect the similar levels of control that MAT has on ecosystem productivity and below-ground processes (Fitter *et al.* 1999; Giardina *et al.* 2005). The similar relationships also support

the notion that components of stand C budgets scale together across broad gradients (Litton *et al.* 2007). Critically, the two relationships were developed with largely independent data sets, so the relationship is not the simple result of plotting a measured component of TBCF against TBCF measured in the same study (i.e. statistical autocorrelation).

Several studies presented in Litton *et al.* (2007) estimated BNPP and TBCF independently within the same study, allowing us to examine BNPP : TBCF at individual sites (Note: as with all studies in the BNPP : TBCF analysis, we recalculated TBCF as soil-surface CO₂ efflux minus litterfall where necessary; see Methods and materials). Most of these studies were conducted in *Pinus* plantations (Gholz & Fisher 1982; Ryan *et al.* 1996; Maier *et al.* 2004), and one study was conducted in a series of temperate deciduous forests (Curtis *et al.* 2002). BNPP : TBCF for these studies, which fell in the range of 5–20 °C MAT, averaged 0.40 (\pm 0.05, SE) across all studies and treatments, which is slightly lower than but in general agreement with BNPP : TBCF presented here for this same MAT range (Fig. 4b; 0.42–0.50).

Two of the *Pinus* studies also manipulated resource availability (Ryan *et al.* 1996; Maier *et al.* 2004), and resource supply appears to strongly impact BNPP : TBCF. For *P. radiata*, BNPP : TBCF increased from 0.34 to 0.97 from control to irrigated and fertilized plots, and for *P. taeda* increased from 0.28 to 0.43 across a similar gradient of resource supply. Both TBCF and the partitioning of GPP to TBCF declined with increasing resource supply in these studies (Litton *et al.* 2007). It is unlikely that BNPP can account for as much as 97% of TBCF as suggested above, as BNPP calculations exclude important components of TBCF (e.g. root respiration, root exudates and mycorrhizae) and these can be large fractions of TBCF (e.g. Hobbie 2006). These two studies do, however, suggest that as below-ground resource supply increases, a larger proportion of TBCF is used for BNPP.

The separation of soil-surface CO₂ efflux ('soil respiration') into autotrophic and heterotrophic sources (Hanson *et al.* 2000) and estimates of the contribution of autotrophic respiration to soil-surface CO₂ efflux (Bond-Lamberty, Wang & Gower 2004a,b) have received more attention than partitioning of TBCF to BNPP. Respiration derived from heterotrophic sources represents C that has entered the detrital C cycle while autotrophic CO₂ represents C that was released directly from plant roots and the rhizosphere as CO₂. Despite the important contributions to our understanding of below-ground processes in forests, these efforts provide only limited information for understanding BNPP on annual time steps. First, the heterotrophic component of soil-surface CO₂ efflux includes C sources that are derived from organic C with ecosystem residence times that range from days to millennia. Second, information on autotrophic vs. heterotrophic sources of soil-surface CO₂ efflux is difficult to scale back to BNPP. Specifically, it is exceedingly difficult to estimate the fraction of the heterotrophic or autotrophic C flux that is derived from the current year's supply of C (Giardina *et al.* 2004). For this reason, we suggest that the focus of future below-ground studies be on the partitioning of TBCF to BNPP.

The data presented here provide critical pieces of information for quantifying below-ground processes across global gradients in temperature – the size of below-ground fluxes, the fraction of GPP partitioned to TBCF, and the fraction of TBCF partitioned to BNPP. Our results highlight the potential role that quantification of TBCF can play in constraining BNPP estimates in stand, regional and global level C studies. They also confirm the assumptions previously made that BNPP is *c.* 50% of TBCF, at least for MATs that correspond to temperate and tropical ecosystems. However, BNPP estimates examined here did not include mycorrhizal production or exudation, the inclusion of which would increase estimates of BNPP : TBCF (see Hobbie 2006). In turn, TBCF estimates do not include coarse root increment, the inclusion of which would decrease estimates of BNPP : TBCF. We suspect that BNPP is more strongly under-estimated than TBCF, and so real BNPP : TBCF estimates may be slightly higher across forests. However, before estimates of BNPP : TBCF can be further refined, methodological and semantic constraints need to be addressed (Pendall *et al.* 2004; Giardina *et al.* 2005). For example, should mycorrhizal respiration be defined as a heterotrophic or autotrophic C flux? Taxonomic considerations would lead to defining this C flux as heterotrophic, but functionally, mycorrhizae act as an extension of the plant and so this flux might better be described as autotrophic. A similar argument can be made for root C exudates and rhizosphere respiration. While clearly a component of BNPP, functionally most of this C is quickly respired in the rhizosphere (Giardina *et al.* 2004). On a stand scale or on annual time steps, this CO₂ flux is indistinguishable from CO₂ derived from autotrophic respiration within the root. In contrast, fine root production is a ‘measurable’ component of BNPP, and it is also distinguishable from other below-ground autotrophic C fluxes (Gower *et al.* 2001; Matamala *et al.* 2003; Norby *et al.* 2004).

The relationships outlined here are notable given that data were collected using diverse methodologies and from sites that varied with respect to species, soil type, resource availability, climate, stand age and stand history. We anticipate that these global patterns will be useful in understanding how C fluxes and partitioning at individual sites respond to the temperature increases that are expected over the next century. Litton *et al.* (2007) demonstrated that global patterns of C partitioning in response to resource availability held within sites where resource availability was varied through fertilization and irrigation. Typically, the magnitude of change in C partitioning within a site was smaller than across sites, but the direction of change was consistent. Still, care should be taken in applying global relationships in below-ground C cycling to individual sites (see Davidson *et al.* 2002). Critically, the temperature response of below-ground C cycling at a given site may be strongly mediated by feedbacks and interactions with variables other than temperature including CO₂ concentration, and nutrient and water availability (Pendall *et al.* 2004). Further, the indirect effects of warming on ecosystems, such as changes in natural disturbance regimes, may exert a larger influence than the direct effects of climate on stand and landscape scale C storage and process rates (Bond-Lamberty *et al.* 2007).

In summary, our results point to global patterns in below-ground C flux and partitioning in forests across a global scale gradient in MAT. This information should be valuable to modelling efforts and ecosystem-level C cycling studies. Three points are particularly informative: (i) GPP and C flux to TBCF and BNPP all increase with increasing MAT; (ii) partitioning of GPP to TBCF increases with increasing MAT for MATs corresponding to temperate and tropical forests; and (iii) partitioning of TBCF to BNPP centres around 0.50 at MATs > 5 °C. These results at least partially confirm existing assumptions about below-ground C cycling, but we caution that clear exceptions to the general patterns exist and there are no known mechanisms to explain these discrepancies. Future efforts to understand below-ground C cycling and its response to climate will necessarily rely on new methodological advances. Critically, no field study has examined how below-ground C flux and partitioning vary in response to MAT for a single species at sites where soils, topography, resource availability and other climate variables are held constant.

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