




What controls variation in carbon use efficiency among Amazonian tropical forests?

Christopher E. Doughty^{1,14} , Gregory R. Goldsmith^{3,4}, Nicolas Raab⁵, Cecile A. J. Girardin⁵, Filio Farfan-Amezquita⁶, Walter Huaraca-Huasco^{5,6}, Javier E. Silva-Espejo⁷, Alejandro Araujo-Murakami⁸, Antonio C. L. da Costa⁹, Wanderley Rocha¹⁰, David Galbraith¹¹, Patrick Meir^{2,12}, Dan B. Metcalfe¹³, and Yadvinder Malhi⁵

¹ School of Informatics, Computing and Cyber systems, Northern Arizona University, Flagstaff, AZ 86011 USA

² Research School of Biology, Australian National University, Canberra, Australia

³ Ecosystem Fluxes Group, Laboratory for Atmospheric Chemistry, Paul Scherrer Institut, 5232 Villigen, Switzerland

⁴ Schmid College of Science and Technology, Chapman University, Orange, CA 92866, USA

⁵ Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

⁶ Universidad Nacional San Antonio Abad del Cusco, Cusco, Peru

⁷ Departamento de Biología, Universidad de La Serena, Casilla 554, La Serena, Chile

⁸ Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia

⁹ Universidade Federal do Pará, Belém, Pará, Brazil

¹⁰ Amazon Environmental Research Institute (IPAM), Canarana, Mato Grosso, Brazil

¹¹ School of Geography, University of Leeds, Leeds, UK

¹² School of Geosciences, University of Edinburgh, Edinburgh, UK

¹³ Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

ABSTRACT

Why do some forests produce biomass more efficiently than others? Variations in Carbon Use Efficiency (CUE: total Net Primary Production (NPP)/ Gross Primary Production (GPP)) may be due to changes in wood residence time (Biomass/NPP_{wood}), temperature, or soil nutrient status. We tested these hypotheses in 14, one ha plots across Amazonian and Andean forests where we measured most key components of net primary production (NPP: wood, fine roots, and leaves) and autotrophic respiration (R_a; wood, rhizosphere, and leaf respiration). We found that lower fertility sites were less efficient at producing biomass and had higher rhizosphere respiration, indicating increased carbon allocation to belowground components. We then compared wood respiration to wood growth and rhizosphere respiration to fine root growth and found that forests with residence times <40 yrs had significantly lower maintenance respiration for both wood and fine roots than forests with residence times >40 yrs. A comparison of rhizosphere respiration to fine root growth showed that rhizosphere growth respiration was significantly greater at low fertility sites. Overall, we found that Amazonian forests produce biomass less efficiently in stands with residence times >40 yrs and in stands with lower fertility, but changes to long-term mean annual temperatures do not impact CUE.

Key words: Amazonia; CUE; GPP; NPP; temperature.

IS GROWTH A CONSTANT FRACTION OF GPP (GROSS PRIMARY PRODUCTION) OR DOES IT VARY AMONG FOREST TYPES? This question has important implications for both global ecology and environmental science. Forests that produce biomass more efficiently remove more carbon from the atmosphere, potentially acting as more efficient and responsive moderators of climate change. For instance, a $\pm 20\%$ uncertainty in current estimates of carbon use efficiency (CUE: total Net Primary Production (NPP)/ Gross Primary Production (GPP)) used in landscape models (*e.g.*, ranging from 0.4 to 0.6) could misrepresent an amount of carbon

equal to total anthropogenic emissions of CO₂ when scaled to the terrestrial biosphere (DeLucia *et al.* 2007). Understanding CUE in forests will improve our understanding of the terrestrial carbon cycle and potential feedbacks on the climate system. However, before we can achieve improvements in ecosystem models simulating CUE, we need to develop the mechanistic underpinnings of observed patterns in CUE.

In particular, CUE is rarely measured in tropical forests due to the difficulty of measuring both GPP and total NPP at the same site. However, data are increasing and Campioli *et al.* (2015) recently provided a global synthesis of CUE with >100 sites worldwide. Total GPP is often quantified from above-canopy eddy covariance flux measurements corrected for estimated

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¹⁴Corresponding author; e-mail: chris.doughty@nau.edu

daytime respiration, which in turn is derived from nighttime flux measurements (Baldocchi 2003). However, calm nights in tropical forests lead to large potential errors in nighttime CO₂ flux measurements (Miller *et al.* 2004). Alternatively, both GPP and CUE can be estimated by the quantification and scaling of the major components of NPP (such as NPP_{fine roots}, NPP_{wood}, NPP_{canopy} and NPP_{branchfall}) and autotrophic respiration (R_a), where $CUE = NPP / (NPP + R_a)$, although this method may generate scaling errors.

What controls the variation in CUE in forests? It has frequently been suggested or assumed that the CUE of forest stands has a fairly invariant value, *ca.* 0.5 (Gifford 1995, Dewar *et al.* 1998, Waring *et al.* 1998, Enquist *et al.* 2007, Van Oijen *et al.* 2010). There is evidence that autotrophic respiration rates are closely linked to supply rates through photosynthesis (Gifford 1995, Dewar *et al.* 1998), at a fixed ratio of photosynthesis ranging between 40 and 50% (Van Oijen *et al.* 2010), and independent of abiotic factors such as climate and soils. However, existing field data question this suggestion, indicating that different forest types may vary substantially in CUE (Meir & Grace 2002). For instance, CUE in tropical forests was initially described as ~0.3 (Chambers *et al.* 2004) compared with ~0.5 for temperate forests (DeLucia *et al.* 2007). It has been hypothesized that variation in CUE can be explained by variation in (1) temperature, (2) wood residence time, and (3) soil fertility.

TEMPERATURE.—Autotrophic respiration has often been estimated as a simple Q₁₀ relationship with temperature (the change in respiration rate over a temperature increase of 10°C), thus decoupling ecosystem carbon losses from inputs through photosynthesis (Huntingford *et al.* 2004). Therefore, a possible explanation for reduced CUE in tropical forests is that warmer temperatures increase total respiration rates.

WOOD RESIDENCE TIME (BIOMASS/NPP_{WOOD}).—Variations in CUE in temperate and boreal forests have also been hypothesized to relate to changes in stand age, with younger forests allocating more carbon to growth and less to respiration than older forests. For instance, two (non-tropical forest) studies have found that less carbon was allocated to growth in older forests (DeLucia *et al.* 2007, Goulden *et al.* 2011). Others (Vicca *et al.* 2012) have suggested that these studies confounded fertility with forest type (DeLucia *et al.* 2007, Drake *et al.* 2011). However, in these studies, it remains unclear which components of respiration had changed (*i.e.*, maintenance vs. growth respiration or wood vs. root respiration).

Tropical forests tend to have conditions that favor growth (total NPP), with wet, warm conditions that allow for growth year-round, raising the possibility that tropical forests could produce excess carbon that is stored as non-structural carbohydrates (NSCs) (Korner 2015). This would imply that carbon uptake is driven by growth dynamics and that carbon investment in plant tissue is mediated via environmental factors that control growth (Dietze *et al.* 2014, Fatichi *et al.* 2014). This could, in turn, lead to increased tropical forest respiration rates. Chambers *et al.*

(2004) proposed the concept of ‘null respiration’, hypothesizing that tropical forests produce abundant sugars that are stored as NSCs and that are burned off if not needed (Amthor 2000, Chambers *et al.* 2004, Wurth *et al.* 2005).

SOIL FERTILITY.—Alternatively, studies suggest that variations in CUE are largely attributable to changes in soil nutrient status, with significantly higher CUE in forests with high-nutrient availability compared to forests with low- or medium nutrient availability. For instance, in highly weathered nutrient-depleted soils, plants invest resources in nutrient-solubilizing organic acid root exudates to release nutrients from the soil for uptake (Lambers *et al.* 2008). Based on this process, a recent study that aggregated global CUE data hypothesized that in forests with access to more nutrients, a smaller fraction of GPP is allocated to (often) unmeasured components, such as fungal root symbionts or root exudates used to solubilize soil nutrients from clay’s structure (Vicca *et al.* 2012, Fernandez-Martinez *et al.* 2014). They suggest the term Biomass Production Efficiency (BPE) to refer to the sum of canopy, wood and root biomass components as an alternative to CUE. Specifically, Vicca *et al.* (2012) found that forests with high nutrient availability invest 16 ± 4% more of their photosynthates in biomass production than forests with low-nutrient availability.

Vicca *et al.* (2012) hypothesized that photosynthates were transferred belowground to both mycorrhizal symbionts and root exudates, although these components were not measured in that study. Symbiotic fungi exchange nutrients for carbon (van der Heijden *et al.* 2008, Courty *et al.* 2010) and such symbiotic fungal associations are near universal. Up to 75% of plant phosphorus uptake can be fungal-derived in forests and carbon allocation to ectomycorrhizal fungi could represent up to 30% of the NPP of a tree (Hobbie 2006, Courty *et al.* 2010). Carbon transfers to fungal symbionts are strongly inversely related to nutrient availability (Wallenda & Kottke 1998, Treseder 2004). Much less is known about the carbon uptake of mycorrhizae in tropical forests. However, one study in Sabah, Malaysia directly measured root exudates and found that they were greatest in a P-deficient montane rain forest soil (16.6% of the aboveground NPP), but lower in a P-rich montane soil (3.1%) and in the lowland rain forest (4.7%) (Aoki *et al.* 2012). There is a clear relationship between nutrient status and mycorrhizae, but is the carbon consumed by mycorrhizae sufficient to cause the large shifts in CUE across forest biomes?

The Amazon is an important region to study this question because of its key role in the global carbon cycle (Field *et al.* 1995). If CUE can be explained in the Amazon, then this would contribute to an improved understanding of global carbon cycling trends. A network of long-term forest monitoring plots established throughout the Amazon basin may help answer some of the questions regarding the role of environment in regulating CUE. This plot network measures most major components of NPP and autotrophic respiration, enabling calculation of CUE (Clark *et al.* 2001). We calculate most major components of the carbon cycle, but not volatile organic compounds (VOCs) or carbon allocation to mycorrhizal fungi and root exudates. We can compare rhizosphere respiration (the sum of root respiration and

mycorrhizae respiration) to CUE, fine root growth and soil fertility to partially evaluate the hypothesis of Vicca *et al.* (2012). We can also calculate CUE for individual organs such as wood and roots, as well as separate growth versus maintenance respiration for these components, to improve our understanding of this ecosystem carbon output. Using this dataset, we ask the following questions: (1) In forests with low apparent CUE and low fertility soils, is there an increase in rhizosphere respiration? If so, is this variation in rhizosphere respiration sufficient to explain the apparent variation in CUE among our plots? (2) If variation in rhizosphere respiration is insufficient to explain the shifts in CUE, can variations in either forest residence time or temperature across the plot network contribute to explaining the observed differences in CUE?

MATERIALS AND METHODS

STUDY SITES.—We collected data on CUE for between 2–4 years (generally starting in January 2009) from 14 plots in the Global Ecosystems Monitoring (GEM) network, spanning contrasting rainfall and soil regimes in Amazonia and the Andes (edaphic and climatic properties in Tables S1 and S2). The plots showed wide environmental variability. In western Amazonia, on relatively fertile soils, they range from those with a moderate dry season in SE Peru (Malhi *et al.* 2014) to an ecotone in Bolivia between humid Amazon forest and *chiquitano* dry forest with a strong dry season (Araujo-Murakami *et al.* 2014). In eastern Amazonia, on infertile soils, they ranged from humid forest in NE Amazonia (da Costa *et al.* 2014, Doughty *et al.* 2014b) to dry forest in SE Amazonia, close to the dry forest-savanna ecotone (Rocha *et al.* 2014). We also include four montane cloud forest plots located in the Andes Mountains (Girardin *et al.* 2014, Huaraca-Huasco *et al.* 2014) at elevations ranging from 1500 m to 3025 m asl. Full site descriptions are in the online Supporting Information (SI). Western Amazonian soils generally have weaker physical structure (*i.e.*, limited rooting depth, poor drainage, low water holding capacity), which may also affect forest mortality rates and turnover times (Quesada *et al.* 2012). We have tried to maximize our sample size by including a 1 ha fire experiment plot (Rocha *et al.* 2014) and a drought plot (da Costa *et al.* 2014); the results without these plots are qualitatively similar and we show them in the Supporting Information. The other plots show little evidence of anthropogenic disturbance of forest community structure, hosting mixed-age tree communities. Detailed descriptions of the carbon cycle of each plot are given in individual site papers (del Aguila-Pasquel *et al.* 2014, Araujo-Murakami *et al.* 2014, da Costa *et al.* 2014, Doughty *et al.* 2014b, Girardin *et al.* 2014, Huaraca-Huasco *et al.* 2014, Malhi *et al.* 2014, Rocha *et al.* 2014). Spatial gradients in this carbon cycle are described in Malhi *et al.* (2015), and temporal responses to carbon allocation, seasonality, and drought events are explored in (Doughty *et al.* 2014a, 2015a,b).

MEASUREMENTS.—The GEM (global ecosystem monitoring) plot carbon monitoring protocol measures and sums all major components of NPP and autotrophic respiration on monthly or seasonal

timescales in each one ha forest plot between 2009–2010 or 2012 (for specific dates for each plot and measurement see Tables S3 and S4). For NPP, this includes canopy litterfall (NPP_{canopy}) from 25 litterfall traps per plot at bimonthly to monthly intervals, aboveground coarse woody productivity (NPP_{ACW}) of all medium-large (≥ 10 cm DBH) trees in the plot via dendrometers at 1–3 month intervals, the turnover of branches on live trees by conducting transect censuses every three months of freshly fallen branch material from live trees ($NPP_{\text{branchfall}}$), and fine root productivity ($NPP_{\text{fine root}}$) from ingrowth cores installed and harvested every three months. Total NPP is the summation of these terms (equation 1) and does not include smaller terms resolved on less than a three monthly basis included in previous studies.

$$\text{Total NPP} = NPP_{\text{fine root}} + NPP_{\text{ACW}} + NPP_{\text{canopy}} + NPP_{\text{branchfall}} \quad (1)$$

Autotrophic respiration includes rhizosphere respiration ($R_{\text{rhizosphere}}$), which is estimated by subtracting surface collars that capture soil heterotrophic respiration, fine root respiration, and mycorrhizae respiration ($N = 12$ per plot) from collars that capture only soil heterotrophic respiration (the collars allow water to drain, but neither fine roots nor mycorrhizae to enter). We use these data to calculate a ratio of autotrophic soil respiration to total soil respiration and multiply this ratio by 25 collars per plot measuring total soil respiration. We corrected for the impact of cutting the roots with a disturbance experiment ($N = 10$ per plot, described in SOM). Aboveground woody respiration is estimated by measuring stem respiration on 20–25 trees per plot on a monthly timescale and scaling to the stand level by estimating stem surface area (SA) using the following equation:

$$\log(\text{SA}) = -0.105 - 0.686\log(\text{DBH}) + 2.208\log(\text{DBH})^2 - 0.627\log(\text{DBH})^3 \quad (2)$$

where DBH (diameter at breast height) is bole diameter at 1.3 m height (Chambers *et al.* 2004). Canopy respiration (R_{canopy}) is estimated by multiplying leaf dark respiration (generally measured 1–2 times per plot on 3–4 leaves per branch, 2 branches per tree on 20–25 large trees per plot generally between 9:00–14:00, but see SOM for specific details) by leaf area index (measured monthly using hemispherical photos and analysed using CAN-EYE software). Leaf dark respiration is measured using a gas exchange system (Li-Cor 6400 or Ciras-2) on dark-adapted leaves from cut branches from sunlit and shaded parts of the canopy. Autotrophic respiration, R_a , is the summation of these terms (equation 3) and does not include smaller terms resolved on less than a three monthly basis included in previous studies. Respiration rates were standardized to the plot mean annual temperature.

$$R_a = R_{\text{rhizosphere}} + R_{\text{wood}} + R_{\text{canopy}} \quad (3)$$

Further methodological details are available in SOM and in an online manual (www.gem.tropicalforests.ox.ac.uk). Individual

site data and full site-specific methodological details are available in a series of site specific companion papers (del Aguila-Pasquel *et al.* 2014, Araujo-Murakami *et al.* 2014, da Costa *et al.* 2014, Doughty *et al.* 2014b, Girardin *et al.* 2014, Huaraca-Huasco *et al.* 2014, Malhi *et al.* 2014, Rocha *et al.* 2014). Each site-specific paper presents both an estimate of spatial and sampling error for each measurement.

In this study, we focus specifically on presenting two novel analyses. The first analysis is comparing CUE (equation 4), rhizosphere respiration and soil fertility.

$$\text{CUE} = \text{Total NPP/GPP} = \text{NPP}/(\text{NPP} + \text{Ra}) \quad (4)$$

Vicca *et al.* (2012) hypothesized that low CUE is due to forests increasing root exudate transfer to mycorrhizae in exchange for nutrients at low fertility sites. We do not directly measure root exudates in our study, but we do measure rhizosphere respiration which combines fine root and mycorrhizae respiration. It is well-documented that root exudate carbon is transferred to mycorrhizae in exchange for nutrients (van der Heijden *et al.* 2008, Courty *et al.* 2010) and that these exudates are therefore correlated with metabolic processes and mycorrhizal respiration.

The second analysis is to directly measure the efficiency of production of wood and roots (equations 5-8). We separate maintenance respiration from growth respiration by finding the linear relationship between NPP and autotrophic respiration. The y intercept in this relationship is, by definition, the maintenance respiration and the slope is the growth respiration (Penning de Vries 1975). We use this methodology to separate out growth and maintenance respiration for both wood and roots.

$$R_{\text{main}_{\text{fine roots}}} = y \text{ intercept of the regression between } R_{\text{rhizosphere}} \text{ and } \text{NPP}_{\text{fine roots}} \quad (5)$$

$$R_{\text{growth}_{\text{fine roots}}} = \text{The slope of the regression between } R_{\text{rhizosphere}} \text{ and } \text{NPP}_{\text{fine roots}} \quad (6)$$

$$R_{\text{main}_{\text{wood}}} = y \text{ intercept of the regression between } R_{\text{wood}} \text{ and } \text{NPP}_{\text{wood}} \quad (7)$$

$$R_{\text{growth}_{\text{wood}}} = \text{The slope of the regression between } R_{\text{wood}} \text{ and } \text{NPP}_{\text{wood}} \quad (8)$$

We compare estimates of CUE, maintenance respiration and growth respiration to site-specific data on wood residence time, soil fertility, and temperature. We determine wood residence time (τ_{res}) by dividing aboveground woody biomass by aboveground wood production (Galbraith *et al.* 2013). This refers to wood residence time and not stand age, which refers to the time since disturbance (all our measured plots are effectively old growth forests). We determine mean annual temperatures using meteorological stations situated near each of our plots. We determine soil fertility using cation exchange capacity (collected from the mineral

layer) as a proxy for soil fertility (Quesada *et al.* 2010). Low fertility sites were defined as cation exchange capacity < 25 mmol_c/kg and high fertility sites were defined as cation exchange capacity > 25 mmol_c/kg. This threshold was chosen to give an approximate even distribution between low and high fertility plots.

To determine whether CUE varied as a function of τ_{res} , cation exchange capacity and temperature, we use ordinary least squares regression. Due to the limited sample sizes, we do not pursue multiple regression approaches. To test for multicollinearity among these predictors, we calculated variance inflation factors (VIF) and pairwise correlation coefficients. All VIFs were less than 2.5 and all correlation coefficients < 0.7, indicating minimal likelihood for collinearity to influence our results (Dormann *et al.* 2013). To determine whether plot-averaged monthly values of CUE varied as a function of rhizosphere respiration, we use a linear mixed-effects model with a random categorical effect of fertility (low fertility - cation exchange capacity < 25 mmol_c/kg and high fertility - cation exchange capacity > 25 mmol_c/kg). We find no evidence for patterns in the model residuals associated with temporal autocorrelation. Based on model validation, CUE was log-transformed for analysis. To determine whether slopes and intercepts significantly differed between our groups, we use analysis of covariance. All analyses were implemented using R 3.1.2 (R Core Team 2015).

RESULTS

In the lowland sites, mean CUE was 0.37 ± 0.01 (this error is the standard error between monthly measurements, for full propagated error see site-specific papers). The lowest CUE sites were the two plots at Caxiuanã in the Eastern Amazon and the highest were in the southern Amazon in Bolivia.

We compared τ_{res} , temperature, and base cation saturation of cation exchange capacity (Quesada *et al.* 2010) to plot averaged values of CUE (Fig. 1). CUE did not vary significantly as a function of temperature or τ_{res} ($P > 0.1$, Fig. 1A and B). However, CUE generally increased in stands with $\tau_{\text{res}} < 40$, as would be expected by theory, and the non-significant result may be due to small sample size. There was a significant increase in plot averaged CUE as a function of increasing soil fertility ($P = 0.02$; Fig. 1C).

We then used our dataset to explore the relationship between CUE and soil fertility (cation exchange capacity) as a function of rhizosphere respiration (Fig. 2). We compared plot-averaged monthly values of CUE for all our sites (14, one ha plots) to rhizosphere respiration rates for the same sites and time periods and binned these data according to fertility rates of the soil (cation exchange capacity). The lower fertility sites had higher rhizosphere respiration and lower CUE.

Total plot CUE incorporates many measurements, each with a source of uncertainty and we might more accurately estimate CUE by comparing rhizosphere respiration to fine root growth and wood respiration to wood growth rates to see how organ-specific CUE varies with fertility, wood residence time, and temperature (Table 1 and Figs. 3–5). Using this data, we

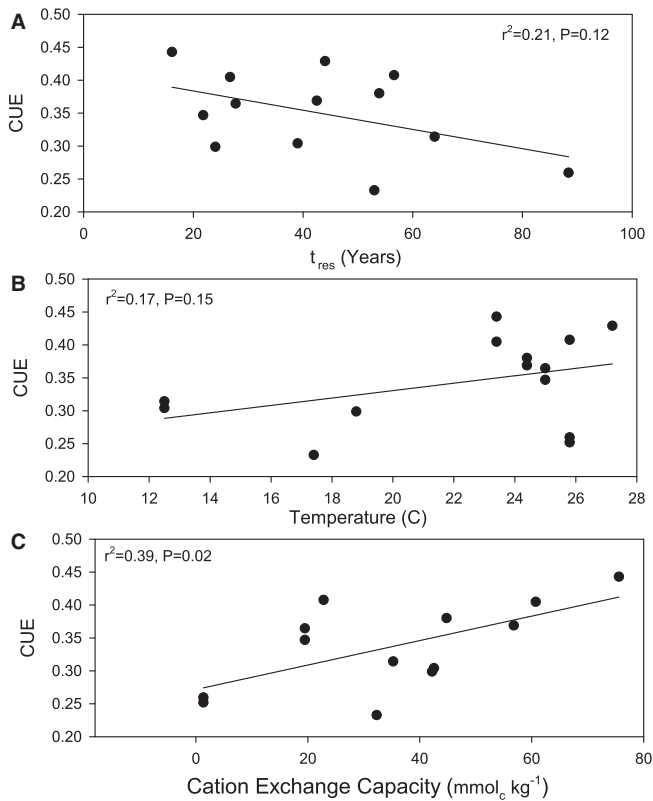


FIGURE 1. A comparison of carbon use efficiency ($NPP/NPP+R_d$) as a function of (A) wood residence time, (B) mean annual temperature, and (C) cation exchange capacity for 14 plots averaged over the length of each plot's dataset (between 2–4 years).

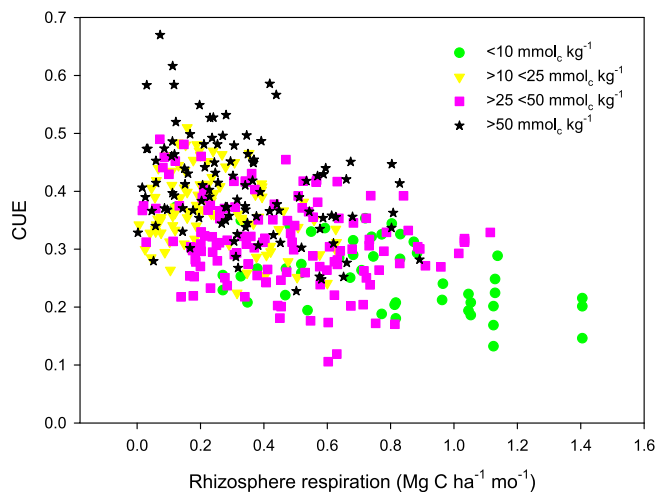


FIGURE 2. Monthly, plot-averaged values of CUE ($NPP/NPP+R_d$) as a function of rhizosphere respiration from 14, one ha lowland tropical forest plots. Color codes are mean soil total cation exchange capacity ($mmol_c/kg$).

can separate maintenance respiration (*i.e.*, the y intercept of the linear regression) and growth respiration (*i.e.*, the slope of the regression).

TABLE 1. A summation of the y -intercepts, slopes and p -values of the linear relationships of organ growth (x -axis) versus organ respiration (y -axis) (from Figs. 3–4) for the various categories.

Categories	Intercept (Mg C/ha/mo)	Slope (unitless)
Low fertile roots	0.24 ± 0.06	$0.72 \pm 0.24^*$
High fertile roots	0.39 ± 0.05	$0.00 \pm 0.21^*$
Low fertile wood	0.56 ± 0.06	0.08 ± 0.31
High fertile wood	0.49 ± 0.03	0.52 ± 0.14
Low elevation roots	$0.24 \pm 0.04^{**}$	0.52 ± 0.13
High elevation roots	$0.27 \pm 0.12^{**}$	1.47 ± 0.97
Low elevation wood	$0.52 \pm 0.03^{**}$	0.28 ± 0.15
High elevation wood	$0.56 \pm 0.06^{**}$	0.45 ± 0.32
Low τ_{res} roots	$0.27 \pm 0.05^{***}$	0.30 ± 0.23
High τ_{res} roots	$0.40 \pm 0.05^{***}$	0.15 ± 0.17
Low τ_{res} wood	$0.44 \pm 0.03^{**}$	0.42 ± 0.15
High τ_{res} wood	$0.60 \pm 0.04^{**}$	0.22 ± 0.22

Stars indicate significant differences in intercept between categories (*i.e.*, low vs. high elevation root intercept), or in slope between categories (*i.e.*, low vs. high elevation root slope) based on ANCOVAs with $^* < 0.05$, $^{**} < 0.01$ and $^{***} < 0.001$. NPP was a significant predictor of respiration in all six models.

Both the low and highland sites had similar maintenance rhizosphere respiration (0.24 ± 0.04 vs. 0.27 ± 0.12 Mg C/ha/mo, a very small, but significant difference $P < 0.01$) (Fig. 3A). This indicates that maintaining root and mycorrhizae mass requires similar rates of respiration regardless of temperature, and that the maintenance of root and mycorrhizae mass is $\sim 10\%$ of GPP (assuming a GPP of ~ 35 Mg C/ha/yr). Growth rhizosphere respiration (*i.e.*, the slope) differs, but not significantly ($P > 0.05$), between the low and highland sites (0.52 ± 0.13 and 1.47 ± 0.97 unitless).

We then compared how soil fertility affects growth and maintenance respiration of roots, comparing low (cation exchange capacity < 25 $mmol_c/kg$) to high (cation exchange capacity > 25 $mmol_c/kg$) fertility sites (Fig. 3B), a threshold chosen to give an approximately even balance of plots. There was no significant difference ($P > 0.05$) in maintenance respiration (0.24 ± 0.06 and 0.39 ± 0.05 Mg C/ha/mo) between low and high fertility soils. However, there was a significant ($P < 0.05$) difference in slopes (0.72 ± 0.24 and 0.00 ± 0.21 unitless), with increased growth rhizosphere respiration at less fertile sites (Table 1).

We then compared belowground CUE to τ_{res} of the forests to explore how efficiently forests of different residence times grow fine roots (Fig. 3C). We find no significant difference in growth respiration between stands with $\tau_{res} < 40$ years and stands with $\tau_{res} > 40$ years (0.30 ± 0.23 and 0.15 ± 0.17 unitless). However, root maintenance respiratory costs were significantly ($P < 0.001$) greater at stands with $\tau_{res} > 40$ years (0.40 ± 0.05 Mg C/ha/mo) than at stands with $\tau_{res} < 40$ years (0.27 ± 0.05 Mg C/ha/mo) (Table 1).

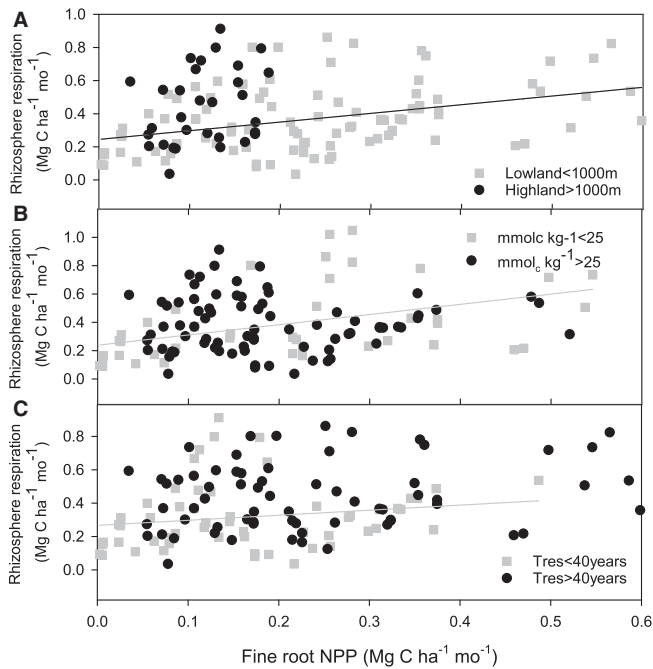


FIGURE 3. Plot mean fine root NPP ($\text{Mg C}/\text{ha}/\text{mo}$) from every third month versus rhizosphere respiration for (A) lowland (gray) versus highland (black), for (B) low fertility (gray) and high fertility (black) and (C) <40 yr residence times (gray) and >40 yr residence times (black) in a series of 1 ha tropical forest plots. Statistics are shown in Table 1. Elevation is a proxy for temperature.

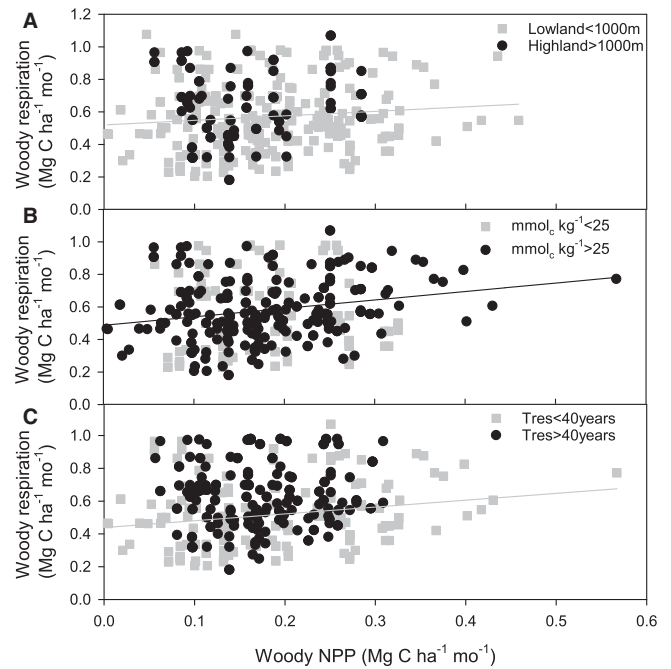


FIGURE 4. Plot mean monthly woody NPP ($\text{Mg C}/\text{ha}/\text{mo}$) versus wood respiration ($\text{Mg C}/\text{ha}/\text{mo}$) for (A) lowland (gray) versus highland (black), for (B) low fertility sites (gray) and high fertility sites (black), and (C) <40 yr residence time (gray) versus >40 yr residence time (black). Statistics are shown in Table 1. Elevation is a proxy for temperature.

Next, we compared efficiency of woody biomass production (stem growth rate) to wood respiration across the sites (Fig. 4). There was very small, but significant ($P < 0.01$) differences in maintenance respiration of wood between low and highland sites (0.52 ± 0.03 vs. 0.56 ± 0.06 $\text{Mg C}/\text{ha}/\text{mo}$). A few particularly high values at a lowland site (Kenia B) and particularly low values at a highland site (Esperanza) obscure this difference. There was no difference in wood growth respiration (0.45 ± 0.32 vs. 0.28 ± 0.15) (Fig. 4A). There were no significant differences between low and high fertility sites for either woody maintenance respiration (0.56 ± 0.06 vs. 0.49 ± 0.03 $\text{Mg C}/\text{ha}/\text{mo}$) or wood growth respiration (0.08 ± 0.31 vs. 0.52 ± 0.14 unitless) (Fig. 4B). Wood maintenance respiratory costs were significantly greater ($P < 0.01$) at stands with $\tau_{\text{res}} > 40$ years (0.60 ± 0.04 $\text{Mg C}/\text{ha}/\text{mo}$) than at stands with $\tau_{\text{res}} < 40$ years (0.44 ± 0.03 $\text{Mg C}/\text{ha}/\text{mo}$). Wood growth respiration was not significantly different between stands with different τ_{res} (0.42 ± 0.15 vs. 0.22 ± 0.22 unitless) (Fig. 4c).

Mean maintenance respiration for wood was almost double that for roots (0.52 ± 0.05 vs. 0.28 ± 0.06 $\text{Mg C}/\text{ha}/\text{mo}$) (Fig. 5 and Table 1). Growth respiration across all categories averaged 0.44 ± 0.12 mol CO_2 per mol C added to structure. This was slightly higher, but within the range of growth respiration of crops estimated from biochemical pathway analysis at 0.13 – 0.43 mol CO_2 per mol C added to structure (Amthor 2000).

DISCUSSION

Which factors are the most important in controlling the variation in CUE at our sites: soil fertility, temperature, or wood residence time?

SOIL FERTILITY.—There was a significant relationship ($P < 0.05$, Fig. 1) between plot averaged CEC and CUE, and this appears to be associated with increased rhizosphere respiration (root plus mycorrhizal respiration) at the least fertile sites (Fig. 2). These results are congruent with the recent study by Vicca *et al.* (2012), which found a statistically significant effect of nutrient status, but not climate zone, forest type, or stand age ($P > 0.1$). Previous studies found stand age to be important in explaining CUE (DeLucia *et al.* 2007, Goulden *et al.* 2011), but Vicca *et al.* (2012) raised the possibility that there was an uneven distribution of forests with high nutrient availability across the globe that may have confounded these conclusions.

However, because the total CUE measured by our plot network includes all components, it is difficult to understand which organ (leaves, fine roots, or wood) may be driving these results. For this reason, we also present organ-level CUE, which can give us a more specific understanding of the forest. Root growth versus rhizosphere respiration shows no significant difference in maintenance respiration ($P > 0.05$, Fig. 3B), but growth respiration is significantly higher at less fertile sites than more fertile sites ($P < 0.05$, Fig. 5). We hypothesize that root growth requires

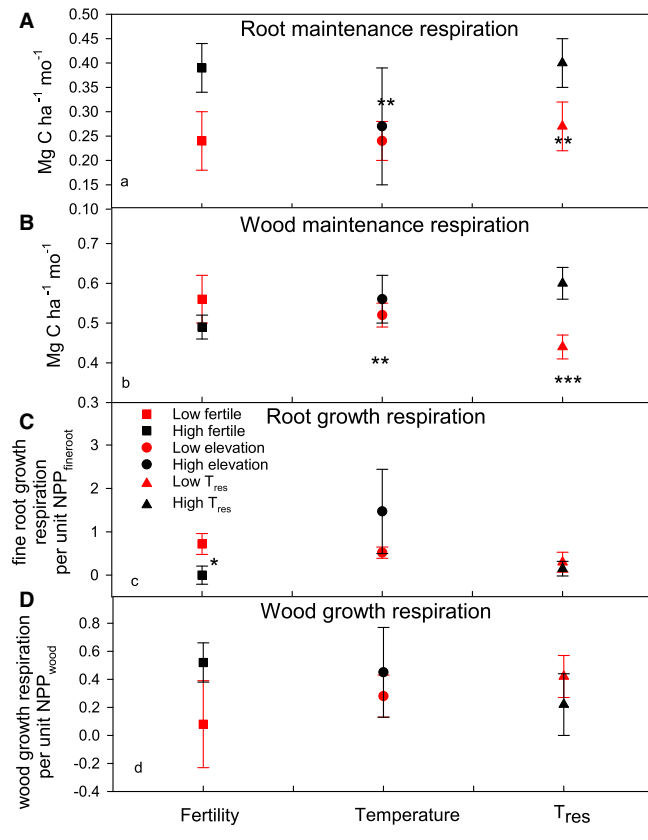


FIGURE 5. (A) Root maintenance respiration (Mg C/ha/mo) based on the y intercepts and error bars from Fig. 3, (B) wood maintenance respiration (Mg C/ha/mo) based on the y intercepts and error bars from Fig. 4, (C) root growth respiration based on the slope and error bars from Fig. 3, (D) wood growth respiration based on the slope and error bars from Fig. 4 for low fertile sites (red square), high fertile sites (black square), low elevation (red circle), high elevation (black circle), low residence time (red triangle), high residence time (black triangle). Stars indicate significant differences based on ANCOVAs with * <0.05 , ** <0.01 and *** <0.001 . Elevation is a proxy for temperature.

more carbon at low fertility sites because more carbon is allocated to mycorrhizae to search for nutrients. Averaged over a year, the increase in rhizosphere growth respiration at low fertility sites over high fertility sites sums to $\sim 2.4 \pm 1.4$ Mg C/ha/yr (assuming a total GPP of ~ 35 Mg C/ha/yr (Malhi *et al.* 2015), or 7% of total GPP) (Fig. 3B). We do not directly measure mycorrhizal respiration, mycorrhizal biomass or root exudates; therefore, this number is a very rough estimate (but possibly within our error estimate of 3–11%) of carbon potentially transferred to these non-plant components. This compares with Vicca *et al.* (2012), who found an increase of $16 \pm 4\%$ of photosynthates toward biomass production between the low and high fertile site and Aoki *et al.* (2012), who found an increase of 13.5% of above-ground NPP toward root exudates between low and high fertility sites. The relationship between mycorrhizal growth and respiration is complicated, Bidartondo *et al.* (2001) found that carbon allocated into symbionts was mostly used as energy to acquire nutrients instead of for mycorrhizal growth.

TEMPERATURE.—There was no significant trend between temperature and CUE at the plot scale ($P > 0.05$, Fig. 1B) and only very small differences at the organ scale (Fig. 5A and B). Therefore, temperature does not appear to explain variation in CUE in our plot network. This indicates that forest respiration rates in the tropics acclimate to mean temperature and that the simple Q_{10} temperature relationship may not apply to long-term changes in mean biome temperatures (Amthor 2000, Galbraith *et al.* 2010). This does not mean that climate warming in tropical forests is not an important issue (Doughty & Goulde 2008, Clark *et al.* 2013) and this study does not address the question of whether hotter years at these sites impact carbon cycling.

WOOD RESIDENCE TIME.—There was no significant relationship ($P > 0.05$, Fig. 1A) between plot averaged τ_{res} and CUE. However, a slightly more complex story emerges when looking at the organ level comparisons. The cost of maintaining both wood and roots was significantly ($P < 0.001$) greater at stands with $\tau_{res} > 40$ years vs. stands with $\tau_{res} < 40$ years. If we scale these effects over a year (averaging seasonal variation and assuming a total GPP of ~ 35 Mg C/ha/yr which is the average GPP from our seven humid lowland plots (35.44 ± 3.57) Doughty *et al.* (2015b)), roots require 1.6 ± 0.36 Mg C/ha/yr and wood requires 1.9 ± 0.42 Mg C/ha/yr more carbon for maintenance at stands with $\tau_{res} > 40$ years than at stands with $\tau_{res} < 40$ years (Figs. 3C and 4C) for a total sum of 3.5 ± 0.78 Mg C/ha/yr.

The observed changes in wood maintenance respiration between the different τ_{res} sites cannot be explained by differences in forest sapwood volume alone (Doughty *et al.* 2015b, Malhi *et al.* 2015). The estimated mean woody surface area (which can be taken as an estimate of active area of sapwood) for stands with $\tau_{res} < 40$ years is $14,990 \pm 2,260$ m²/ha and for stands with $\tau_{res} > 40$ years is $18,680 \pm 2,380$ m²/ha, an increase of $\sim 25\%$ while the increase in wood maintenance respiration is $>50\%$. One possible explanation is that tropical forests with $\tau_{res} < 40$ years have tree communities dominated by faster-growing species that prioritize growth over defence and thus have lower biomass and maintenance respiration costs (Malhi *et al.* 2015). More conservative, defensive strategies found in older, less dynamic tropical forests may carry high respiration costs associated with the production and maintenance of defence compounds (Coley *et al.* 1985). This may also help explain why tropical forests appear to have lower CUE than many temperate forests (DeLucia *et al.* 2007), because temperate forests are often recovering following disturbance or management and prioritizing rapid growth over defence.

If wood residence time is driving much of the changes in CUE through an increase in maintenance respiration, what is causing the changes to wood residence time across our plot network, where all stands are effectively ‘closed canopy old-growth’ but have different dynamics? Forests have low τ_{res} because they have higher mortality, not because they are unproductive (Malhi *et al.* 2015). The causes for higher mortality in these plots remains unresolved, but has been linked to soil physical/structural properties (*e.g.*, topography, soil depth), to seasonal drought

stress frequency, and to other disturbance factors (Quesada *et al.* 2012).

If we combine the increased maintenance costs of forests with higher residence time with the increased rhizosphere respiration at low fertility sites, there is a total potential increased respiratory cost of $\sim 5.7 \pm 2.2$ Mg C/ha/yr, with $\sim 60\%$ of the effect from wood residence time and $\sim 40\%$ due to low fertility soils. This difference is exemplified by comparing the control site of the Caxiuana drought experiment (da Costa *et al.* 2014) with low CEC and high τ_{res} (GPP = 39.18, NPP = 11.20, CUE = 0.29) to Kenia wet (Araujo-Murakami *et al.* 2014) with high CEC and low τ_{res} (GPP = 34.14, NPP = 15.50, CUE = 0.45). This difference is sufficient to explain much of the variation in CUE observed across our sites, but this ratio (60/40%) is a simple estimate based on our plots and may not be applicable to other regions under different conditions.

The mechanisms driving whole plant respiration remain poorly understood and quantified compared to those driving photosynthesis. Currently, most carbon cycling models do not account for either root exudates or increased respiration in older stands. Typically, terrestrial biosphere models partition autotrophic respiration (R_a) into maintenance (R_m) and growth (R_g) terms. Whereas maintenance respiration is calculated separately for each plant tissue, growth respiration is typically calculated as a bulk term and is usually a fixed fraction of ($GPP - R_m$). In contrast, global biogeochemical models have recently incorporated nutrient limitation into their framework, whereby forests with a medium- or low-nutrient availability class have a greater fraction of GPP partitioned to unaccounted NPP components such as root exudates (Buendia *et al.* 2014). Our data indicate that this is an improvement, but that wood residence time is slightly more important as a determinant of CUE. This suggests a need for reanalysis in other biomes of what is driving these trends and eventually, following further data analysis, a reorganization of autotrophic respiration in carbon cycling models.

CONCLUSIONS

Overall, our results correlate τ_{res} with changes in CUE, but also provide evidence for an increase in carbon allocated belowground in lower fertility sites. Our analysis, breaking down CUE into its component parts, was not available for the other studies analysed in Vicca *et al.* (2012). However, it would be valuable to assemble a similar dataset for boreal and temperate forests in order to compare and contrast with the trends that we have observed in our tropical sites. We also note that most current models do not account for these trends in autotrophic respiration and suggest that their modification could potentially improve prediction of carbon cycling responses to future environmental change.

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AUTHOR CONTRIBUTIONS

CED, YM, and DBM designed and implemented the study. CED, CAJG, FFA, DG, WHH, JES, AA, ACLC, TF, AM, WR, and OP collected the data. CED and GRG performed the analysis. CED wrote the paper with contributions from NR, GRG, YM, PM, and DBM.

DATA AVAILABILITY

Data available from the Dryad Repository: <https://doi.org/10.5061/dryad.2hv6c> (Doughty *et al.* 2017), and www.gem.tropicalforests.ox.ac.uk and as part of Supporting Information.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Site descriptions of plots.

FIGURE S1. Monthly averaged cation exchange capacity and residence time (bottom) versus CUE.

FIGURE S2. Same as Fig. 2 but without data from the

Caxuiana drought experiment or the Tanguro burning experiment.

FIGURE S3. Same as Fig. 2 but excluding R_{thizo} from the CUE calculation.

FIGURE S4. Same as Fig. 2 but without data from the Caxuiana drought experiment or the Tanguro burning experiment.

FIGURE S5. Same as Fig. 3 but without data from the Caxuiana drought experiment or the Tanguro burning experiment.

TABLE S1. *Table of main plot characteristics for the lowland sites.*

TABLE S2. *Table of main plot characteristics for the highland sites.*

TABLE S3. *Methods for intensive studying of carbon dynamics.*

TABLE S4. *Data analysis techniques for intensive studying of carbon dynamics.*

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