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

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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 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 maintainance 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.

Introduction

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 ±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 CO_2 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 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 CO_2 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 $NPP_{fineroot}$, 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),

64 and independent of abiotic factors such as climate and soils. However, existing field data question this
65 suggestion, indicating that different forest types may vary substantially in CUE (Meir & Grace, 2002).
66 For instance, CUE in tropical forests was initially described as ~0.3 (Chambers et al., 2004) compared
67 with ~0.5 for temperate forests (DeLucia et al., 2007). It has been hypothesized that variation in CUE
68 can be explained by variation in 1) temperature, 2) wood residence time, and 3) soil fertility.

69 Temperature: Autotrophic respiration has often been estimated as a simple Q_{10} relationship
70 with temperature (the change in respiration rate over a temperatures increase of 10˚C), thus
71 decoupling ecosystem carbon losses from inputs through photosynthesis (Huntingford et al., 2004).
72 Therefore, a possible explanation for reduced CUE in tropical forests is that warmer temperatures
73 increase total respiration rates.

74 Wood Residence Time (Biomass/NPP_{wood}): Variations in CUE in temperate and boreal forests
75 have also been hypothesized to relate to changes in stand age, with younger forests allocating more
76 carbon to growth and less to respiration than older forests. For instance, two (non-tropical forest)
77 studies have found that less carbon was allocated to growth in older forests (DeLucia et al., 2007;
78 Goulden et al., 2011). Others (Vicca et al., 2012) have suggested that these studies confounded
79 fertility with forest type (DeLucia et al., 2007; Drake et al., 2011). However, in these studies, it is
80 unclear which components of respiration had changed (i.e. maintenance versus growth respiration or
81 wood versus root respiration).

82 Tropical forests tend to have conditions that favour growth (total NPP), with wet, warm
83 conditions that allow for growth year round, raising the possibility that tropical forests could produce
84 excess carbon that is stored as non-structural carbohydrates (NSCs) (Körner 2015). This would imply
85 that carbon uptake is driven by growth dynamics and that carbon investment in plant tissue is
86 mediated via environmental factors that control growth (Dietze et al., 2014; Fatichi et al., 2014). This
87 could, in turn, lead to increased tropical forest respiration rates. Chambers et al. (2004) proposed the
88 concept of "null respiration," hypothesizing that tropical forests produce abundant sugars that are
89 stored as NSCs and that are burned off if not needed (Amthor, 2000; Chambers et al., 2004; Wurth et
90 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-solubilising 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 mycorrhyzal 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 they were greatest in a P-deficient montane rainforest soil (16.6% of the aboveground NPP), but lower in a P-rich montane soil (3.1%) and in the lowland rainforest (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

Field 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 SI Tables 1 and 2). 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; Huasco et al., 2014) at elevations ranging from 1500 m to 3025 m asl. Full site descriptions are in the supplementary online material (SOM). 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 supplementary figures. 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 (Araujo-Murakami et al., 2014; da Costa et al., 2014; del Aguila-Pasquel et al., 2014; Doughty et al., 2014b; Girardin et al., 2014; 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; Doughty et al., 2015b; Doughty et al., 2015a).

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 SOM Table 3 and 4). For NPP, this includes canopy litterfall (NPP_{canopy}) from 25 litterfall traps per plot at bimonthly to monthly intervals, above-ground 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 ($NPP_{branchfall}$), and fine root productivity ($NPP_{fine\ root}$) from ingrowth cores installed and harvested every three months. Total NPP is the summation of these terms (Eq 1) and does not include smaller terms resolved on less than a three monthly basis included in previous studies.

$$\text{Total NPP} = NPP_{fineroot} + NPP_{ACW} + NPP_{canopy} + NPP_{branchfall} \quad \text{Eq 1}$$

Autotrophic respiration includes rhizosphere respiration ($R_{rhizosphere}$), 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). Above-ground 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:

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

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

189 between 9:00-14:00, but see SOM for specific details) by leaf area index (measured monthly using
190 hemispherical photos and analysed using CAN-EYE software). Leaf dark respiration is measured
191 using a gas exchange system (Li-Cor 6400 or Ciras-2) on dark-adapted leaves from cut branches from
192 sunlit and shaded parts of the canopy. Autotrophic respiration, $R_{a,}$ is the summation of these terms
193 (Eq 3) and does not include smaller terms resolved on less than a three monthly basis included in
194 previous studies. Respiration rates were standardized to the plot mean annual temperature.

195 $$R_a = R_{rhizosphere} + R_{wood} + R_{canopy} \quad \text{Eq 3}$$

196

197 Further methodological details are available in SOM and in an online manual
198 (www.gem.tropicalforests.ox.ac.uk). Individual site data and full site-specific methodological details
199 are available in a series of site specific companion papers (Araujo-Murakami et al., 2014; da Costa et
200 al., 2014; del Aguila-Pasquel et al., 2014; Doughty et al., 2014b; Girardin et al., 2014; Huasco et al.,
201 2014; Malhi et al., 2014; Rocha et al., 2014). Each site-specific paper presents both an estimate of
202 spatial and sampling error for each measurement.

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

205 $$\text{CUE} = \text{Total NPP/GPP} = \text{NPP}/(\text{NPP}+R_a) \quad \text{Eq 4}$$

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

212 The second analysis is to directly measure the efficiency of production of wood and roots (Eq
213 5-8). We separate maintenance respiration from growth respiration by finding the linear relationship
214 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.

$R\_main_{fineroots}$ = y intercept of the regression between $R_{rhizosphere}$ and $NPP_{fineroots}$ Eq 5

$R\_growth_{fineroots}$ = The slope of the regression between $R_{rhizosphere}$ and $NPP_{fineroots}$ Eq 6

R_main_{wood} = y intercept of the regression between R_{wood} and NPP_{wood} Eq 7

R_growth_{wood} = The slope of the regression between R_{wood} and NPP_{wood} Eq 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 $mmol_c\ kg^{-1}$ and high fertility sites were defined as cation exchange capacity>25 $mmol_c\ kg^{-1}$. 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 coefficitnets. All VIFs were less than 2.5 and all correlation coefficinents <0.7, indicating minimal likelihood for collinearity to influence our results (Dorman et al. 2012). 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

242 random categorical effect of fertility (low fertility - cation exchange capacity<25 $mmol_c$ kg^{-1} and high
243 fertility - cation exchange capacity>25 $mmol_c$ kg^{-1}). We find no evidence for patterns in the model
244 residuals associated with temporal autocorrelation. Based on model validation, CUE was log-
245 transformed for analysis. To determine whether slopes and intercepts significantly differed between
246 our groups, we use analysis of covariance. All analyses were implemented using R 3.1.2 (R Core
247 Team 2015).

248 **Results**

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

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

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

264 Total plot CUE incorporates many measurements, each with a source of uncertainty and we
265 might more accurately estimate CUE by comparing rhizosphere respiration to fine root growth and
266 wood respiration to wood growth rates to see how organ-specific CUE varies with fertility, wood
267 residence time, and temperature (Table 1 and Figures 3-5). Using this data, we can separate
268 maintenance respiration (i.e. the y intercept of the linear regression) and growth respiration (i.e. the
269 slope of the regression).

270 Both the low and highland sites had similar maintenance rhizosphere respiration (0.24±0.04
271 vs. 0.27±0.12 Mg C ha^{-1} mo^{-1}, a very small, but significant difference $P<0.01$) (Figure 3a). This
272 indicates that maintaining root and mycorrhizae mass requires similar rates of respiration regardless of
273 temperature, and that the maintenance of root and mycorrhizae mass is ~10% of GPP (assuming a

GPP of ~35 Mg C ha^{-1} yr^{-1}). 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^{-1}) to high (cation exchange capacity>25 $mmol_c$ kg^{-1}) fertility sites (Figure 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^{-1} mo^{-1}) 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 (Figure 3c). We find no significant difference in growth respiration between stands with τ_{res} <40 years and stands with τ_{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 τ_{res} >40years (0.40±0.05 Mg C ha^{-1} mo^{-1}) than at stands with τ_{res} <40 years (0.27±0.05 Mg C ha^{-1} mo^{-1}) (Table 1).

Next, we compared efficiency of woody biomass production (stem growth rate) to wood respiration across the sites (Figure 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 versus 0.56±0.06 Mg C ha^{-1} mo^{-1}). 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 versus 0.28± 0.15) (Figure 4a). There were no significant differences between low and high fertility sites for either woody maintainance respiration (0.56±0.06 versus 0.49±0.03 Mg C ha^{-1} mo^{-1}) or wood growth respiration (0.08 ± 0.31 versus 0.52±0.14 unitless) (Figure 4b). Wood maintenance respiratory costs were significantly greater (P<0.01) at stands with τ_{res} >40 years (0.60±0.04 Mg C ha^{-1} mo^{-1}) than at stands with τ_{res} <40 years (0.44±0.03 Mg C ha^{-1} mo^{-1}). Wood

299 growth respiration was not significantly different between stands with different τ_{res} (0.42±0.15 versus
300 0.22±0.22 unitless) (Figure 4c).

301 Mean maintenance respiration for wood was almost double that for roots (0.52±0.05 versus
302 0.28±0.06 Mg C ha^{-1} mo^{-1}) (Figure 5 and Table 1). Growth respiration across all categories averaged
303 0.44 ± 0.12 mol CO_2 per mol C added to structure. This was slightly higher, but within range of
304 growth respiration of crops estimated from biochemical pathway analysis at 0.13 - 0.43 mol CO_2 per
305 mol C added to structure (Amthor, 2000).

306

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 ($P<0.05$, Figure 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 (Figure 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. (2014) 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 ($P>0.05$, figure 3b), but growth respiration is significantly higher at less fertile sites than more fertile sites ($P<0.05$, figure 5). We hypothesize that root growth requires 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 ~2.4 ± 1.4 Mg C ha^{-1} yr^{-1} (assuming a total GPP of ~35 Mg C ha^{-1} yr^{-1} (Malhi et al., 2015) or 7% of total GPP) (Figure 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 that found an increase of 16 ± 4% of photosynthates towards biomass production between the low and high fertile site and Aoki et al 2012 that found an increase of 13.5% of aboveground NPP

towards root exudates between the 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 aquire nutrients instead of for mycorrhizal growth.

Temperature

There was no significant trend between temperature and CUE at the plot scale ($P>0.05$, Figure 1b) and only very small differences at the organ scale (Figure 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 and Goulden 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 ($P>0.05$, Figure 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 τ_{res} >40 years versus stands with τ_{res} <40 years. If we scale these effects over a year (averaging seasonal variation and assuming a total GPP of ~35 Mg C ha^{-1} yr^{-1}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^{-1} yr^{-1} and wood requires 1.9 ±0.42 Mg C ha^{-1} yr^{-1} more carbon for maintenance at stands with τ_{res} >40 years than at stands with τ_{res} <40 years (Figures 3c and 4c) for a total sum of 3.5±0.78 Mg C ha^{-1} yr^{-1}.

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 and 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 τ_{res} <40 years is 14,990 ± 2,260 m^2 ha^{-1} and for stands with τ_{res} >40 years is 18,680 ± 2,380 m^2 ha^{-1}, an increase of ~25% while the increase in wood maintenance respiration is >50%. One possible explanation is that tropical forests with τ_{res} <40 years have tree communities dominated by faster-growing species that prioritise 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 prioritising 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 ~5.7±2.2 Mg C ha^{-1} yr^{-1}, with ~60% of the effect from wood residence time and ~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.

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

397

398 Conclusions

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

407

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436 **Table 1** - A summation of the y-intercepts, slopes and p-values of the linear relationships of organ
437 growth (x-axis) versus organ respiration (y-axis) (from figures 3-4) for the various categories. Stars
438 indicate significant differences in intercept between categories (i.e. low versus high elevation root
439 intercept) or in slope between categories (i.e. low versus high elevation root slope) based on
440 ANCOVAs with *<0.05, **<0.01 and ***<0.001. NPP was a significant predictor of respiration in all
441 six models.

Categories	**Intercept (Mg C ha^{-1} mo^{-1})**	**Slope (unitless)**
Low fertile roots	0.24±0.06	0.72±0.24*
High fertile roots	0.39±0.05	0.00±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±0.04**	0.52±0.13
High elevation roots	0.27±0.12**	1.47±0.97
Low elevation wood	0.52±0.03**	0.28±0.15
High elevation wood	0.56±0.06**	0.45±0.32
Low τ_{res} roots	0.27±0.05***	0.30±0.23
High τ_{res} roots	0.40±0.05***	0.15±0.17
Low τ_{res} wood	0.44± 0.03**	0.42±0.15
High τ_{res} wood	0.60±0.04**	0.22±0.22

442

443 **Figures**

444

445 **Figure 1 –** A comparison of carbon use efficiency (NPP/ NPP+R_a) as a function of (a) wood
446 residence time, (b) mean annual temperature, and (c) cation exchange capacity for 14 plots averaged
447 over the length of each plot's dataset (between 2-4 years).

448

449 **Figure 2 -** Monthly, plot-averaged values of CUE (NPP/ NPP+R_a) as a function of rhizosphere
450 respiration from 14, one ha lowland tropical forest plots. Color codes are mean soil total cation
451 exchange capacity (mmolc kg^{-1}).

452

453 **Figure 3** – Plot mean fine root NPP (Mg C ha^{-1} mo^{-1}) from every third month versus rhizosphere
454 respiration for (a) lowland (grey) versus highland (black), for (b) low fertility (grey) and high fertility
455 (black) and (c) < 40yr residence times (grey) and > 40 yr residence times (black) in a series of 1 ha
456 tropical forest plots. Statistics are shown in Table 1. Elevation is a proxy for temperature.

457

458 **Figure 4** – Plot mean monthly woody NPP (Mg C ha^{-1} mo^{-1}) versus wood respiration (Mg C ha^{-1} mo^{-1}) for (a) lowland (grey) versus highland (black), for (b) low fertility sites (grey) and high fertility
460 sites (black), and (c) <40yr residence time (grey) vs > 40 yr residence time (black). Statistics are
461 shown in Table 1. Elevation is a proxy for temperature.

462

463 **Figure 5** – (a) Root maintenance respiration (Mg C ha^{-1} mo^{-1}) based on the y intercepts and error bars
464 from figure 3, (b) wood maintenance respiration (Mg C ha^{-1} mo^{-1}) based on the y intercepts and error
465 bars from figure 4, (c) root growth respiration based on the slope and error bars from figure 3, (d) root
466 growth respiration based on the slope and error bars from figure 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.

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