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What Controls Variation in Carbon Use Efficiency Among Amazonian Tropical Forests?

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1 What controls variation in carbon use efficiency among 2 Amazonian tropical forests? 3

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23 **Abstract**

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

38 **Introduction**

39 Is growth a constant fraction of GPP (Gross Primary Production) or does it vary among forest
40 types? This question has important implications for both global ecology and environmental science.
41 Forests that produce biomass more efficiently remove more carbon from the atmosphere, potentially
42 acting as more efficient and responsive moderators of climate change. For instance, a $\pm 20\%$
43 uncertainty in current estimates of carbon use efficiency (CUE: total Net Primary Production (NPP)/
44 Gross Primary Production (GPP)) used in landscape models (e.g. ranging from 0.4 to 0.6) could
45 misrepresent an amount of carbon equal to total anthropogenic emissions of CO₂ when scaled to the
46 terrestrial biosphere (DeLucia et al., 2007). Understanding CUE in forests will improve our
47 understanding of the terrestrial carbon cycle and potential feedbacks on the climate system. However,
48 before we can achieve improvements in ecosystem models simulating CUE, we need to develop the
49 mechanistic underpinnings of observed patterns in CUE.

50 In particular, CUE is rarely measured in tropical forests due to the difficulty of measuring
51 both GPP and total NPP at the same site. However, data are increasing and Campioli et al., (2015)
52 recently provided a global synthesis of CUE with >100 sites worldwide. Total GPP is often quantified
53 from above-canopy eddy covariance flux measurements corrected for estimated daytime respiration,
54 which in turn is derived from nighttime flux measurements (Baldocchi, 2003). However, calm nights
55 in tropical forests lead to large potential errors in nighttime CO₂ flux measurements (Miller et al.,
56 2004). Alternatively, both GPP and CUE can be estimated by the quantification and scaling of the
57 major components of NPP (such as NPP_{fineroot} , NPP_{wood} , NPP_{canopy} and $NPP_{\text{branchfall}}$) and autotrophic
58 respiration (R_a), where $CUE = NPP / (NPP + R_a)$, although this method may generate scaling errors.

59 What controls the variation in CUE in forests? It has frequently been suggested or assumed
60 that the CUE of forest stands has a fairly invariant value, ca. 0.5 (Gifford, 1995; Dewar et al., 1998;
61 Waring et al., 1998; Enquist et al., 2007; Van Oijen et al., 2010). There is evidence that autotrophic
62 respiration rates are closely linked to supply rates through photosynthesis (Gifford, 1995; Dewar et
63 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 temperature 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 ($\text{Biomass}/\text{NPP}_{\text{wood}}$): 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).

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

103 Vicca et al., (2012) hypothesized that photosynthates were transferred belowground to both
104 mycorrhizal symbionts and root exudates, although these components were not measured in that
105 study. Symbiotic fungi exchange nutrients for carbon (van der Heijden et al., 2008; Courty et al.,
106 2010) and such symbiotic fungal associations are near universal. Up to 75% of plant phosphorus
107 uptake can be fungal-derived in forests and carbon allocation to ectomycorrhizal fungi could represent
108 up to 30% of the NPP of a tree (Hobbie, 2006; Courty et al., 2010). Carbon transfers to fungal
109 symbionts are strongly inversely related to nutrient availability (Wallenda & Kottke, 1998; Treseder,
110 2004). Much less is known about the carbon uptake of mycorrhizae in tropical forests. However, one
111 study in Sabah, Malaysia directly measured root exudates and found they were greatest in a P-
112 deficient montane rainforest soil (16.6% of the aboveground NPP), but lower in a P-rich montane soil
113 (3.1%) and in the lowland rainforest (4.7%) (Aoki et al., 2012). There is a clear relationship between
114 nutrient status and mycorrhizae, but is the carbon consumed by mycorrhizae sufficient to cause the
115 large shifts in CUE across forest biomes?

116 The Amazon is an important region to study this question because of its key role in the global
117 carbon cycle (Field et al., 1995). If CUE can be explained in the Amazon, then this would contribute

118 to an improved understanding of global carbon cycling trends. A network of long-term forest
119 monitoring plots established throughout the Amazon basin may help answer some of the questions
120 regarding the role of environment in regulating CUE. This plot network measures most major
121 components of NPP and autotrophic respiration, enabling calculation of CUE (Clark et al., 2001). We
122 calculate most major components of the carbon cycle, but not volatile organic compounds (VOCs) or
123 carbon allocation to mycorrhizal fungi and root exudates. We can compare rhizosphere respiration
124 (the sum of root respiration and mycorrhizae respiration) to CUE, fine root growth and soil fertility to
125 partially evaluate the hypothesis of Vicca et al. (2012). We can also calculate CUE for individual
126 organs such as wood and roots, as well as separate growth versus maintenance respiration for these
127 components, to improve our understanding of this ecosystem carbon output. Using this dataset, we
128 ask the following questions:

129

130 1. In forests with low apparent CUE and low fertility soils, is there an increase in rhizosphere
131 respiration? If so, is this variation in rhizosphere respiration sufficient to explain the apparent
132 variation in CUE among our plots?

133 2. If variation in rhizosphere respiration is insufficient to explain the shifts in CUE, can variations in
134 either forest residence time or temperature across the plot network contribute to explaining the
135 observed differences in CUE?

136 **Materials and methods**

137 **Field sites**

138 We collected data on CUE for between 2-4 years (generally starting in January 2009) from 14
139 plots in the Global Ecosystems Monitoring (GEM) network, spanning contrasting rainfall and soil
140 regimes in Amazonia and the Andes (edaphic and climatic properties in SI Tables 1 and 2). The plots
141 showed wide environmental variability. In western Amazonia, on relatively fertile soils, they range
142 from those with a moderate dry season in SE Peru (Malhi et al., 2014) to an ecotone in Bolivia
143 between humid Amazon forest and chiquitano dry forest with a strong dry season (Araujo-Murakami
144 et al., 2014). In eastern Amazonia, on infertile soils, they ranged from humid forest in NE Amazonia
145 (da Costa et al., 2014; Doughty et al., 2014b) to dry forest in SE Amazonia, close to the dry forest-
146 savanna ecotone (Rocha et al., 2014). We also include four montane cloud forest plots located in the
147 Andes Mountains (Girardin et al., 2014; Huasco et al., 2014) at elevations ranging from 1500 m to
148 3025 m asl. Full site descriptions are in the supplementary online material (SOM). Western
149 Amazonian soils generally have weaker physical structure (i.e. limited rooting depth, poor drainage,
150 low water holding capacity), which may also affect forest mortality rates and turnover times (Quesada
151 et al., 2012). We have tried to maximize our sample size by including a 1 ha fire experiment plot
152 (Rocha et al., 2014) and a drought plot (da Costa et al., 2014); the results without these plots are
153 qualitatively similar and we show them in the supplementary figures. The other plots show little
154 evidence of anthropogenic disturbance of forest community structure, hosting mixed-age tree
155 communities. Detailed descriptions of the carbon cycle of each plot are given in individual site papers
156 (Araujo-Murakami et al., 2014; da Costa et al., 2014; del Aguila-Pasquel et al., 2014; Doughty et al.,
157 2014b; Girardin et al., 2014; Huasco et al., 2014; Malhi et al., 2014; Rocha et al., 2014). Spatial
158 gradients in this carbon cycle are described in Malhi et al. (2015), and temporal responses to carbon
159 allocation, seasonality and drought events are explored in (Doughty et al., 2014a; Doughty et al.,
160 2015b; Doughty et al., 2015a).

161 **Measurements**

162 The GEM (global ecosystem monitoring) plot carbon monitoring protocol measures and sums
163 all major components of NPP and autotrophic respiration on monthly or seasonal timescales in each
164 one ha forest plot between 2009-2010 or 2012 (for specific dates for each plot and measurement see
165 SOM Table 3 and 4). For NPP, this includes canopy litterfall (NPP_{canopy}) from 25 litterfall traps per
166 plot at bimonthly to monthly intervals, above-ground coarse woody productivity (NPP_{ACW}) of all
167 medium-large (≥ 10 cm DBH) trees in the plot via dendrometers at 1-3 month intervals, the turnover of
168 branches on live trees by conducting transect censuses every three months of freshly fallen branch
169 material from live trees ($NPP_{\text{branchfall}}$), and fine root productivity ($NPP_{\text{fine root}}$) from ingrowth cores
170 installed and harvested every three months. Total NPP is the summation of these terms (Eq 1) and
171 does not include smaller terms resolved on less than a three monthly basis included in previous
172 studies.

173

$$174 \text{ Total NPP} = NPP_{\text{fineroot}} + NPP_{\text{ACW}} + NPP_{\text{canopy}} + NPP_{\text{branchfall}} \quad \text{Eq 1}$$

175

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

$$185 \log(\text{SA}) = -0.105 - 0.686 \log(\text{DBH}) + 2.208 \log(\text{DBH})^2 - 0.627 \log(\text{DBH})^3 \quad \text{Eq 2}$$

186 where DBH (diameter at breast height) is bole diameter at 1.3 m height (Chambers et al., 2004).

187 Canopy respiration (R_{canopy}) is estimated by multiplying leaf dark respiration (generally measured 1-2
188 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.

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

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.

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

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

215 maintenance respiration and the slope is the growth respiration (Penning de Vries, 1975). We use
216 this methodology to separate out growth and maintenance respiration for both wood and roots.

217 $R_{\text{main}_{\text{fineroots}}} = y$ intercept of the regression between $R_{\text{rhizosphere}}$ and $NPP_{\text{fineroots}}$ Eq 5

218

219 $R_{\text{growth}_{\text{fineroots}}} =$ The slope of the regression between $R_{\text{rhizosphere}}$ and $NPP_{\text{fineroots}}$ Eq 6

220

221 $R_{\text{main}_{\text{wood}}} = y$ intercept of the regression between R_{wood} and NPP_{wood} Eq 7

222

223 $R_{\text{growth}_{\text{wood}}} =$ The slope of the regression between R_{wood} and NPP_{wood} Eq 8

224

225 We compare estimates of CUE, maintenance respiration and growth respiration to site-
226 specific data on wood residence time, soil fertility, and temperature. We determine wood residence
227 time (τ_{res}) by dividing aboveground woody biomass by aboveground wood production (Galbraith et
228 al., 2013). This refers to wood residence time and not stand age, which refers to the time since
229 disturbance (all our measured plots are effectively old growth forests). We determine mean annual
230 temperatures using meteorological stations situated near each of our plots. We determine soil fertility
231 using cation exchange capacity (collected from the mineral layer) as a proxy for soil fertility (Quesada
232 et al., 2010). Low fertility sites were defined as cation exchange capacity $< 25 \text{ mmol}_c \text{ kg}^{-1}$ and high
233 fertility sites were defined as cation exchange capacity $> 25 \text{ mmol}_c \text{ kg}^{-1}$. This threshold was chosen to
234 give an approximate even distribution between low and high fertility plots.

235 To determine whether CUE varied as a function of τ_{res} , cation exchange capacity and
236 temperature, we use ordinary least squares regression. Due to the limited sample sizes, we do not
237 pursue multiple regression approaches. To test for multicollinearity among these predictors, we
238 calculated variance inflation factors (VIF) and pairwise correlation coefficients. All VIFs were less
239 than 2.5 and all correlation coefficients < 0.7 , indicating minimal likelihood for collinearity to
240 influence our results (Dorman et al. 2012). To determine whether plot-averaged monthly values of
241 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 Caxiuana 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 $\tau_{\text{res}} < 40$, 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. $0.27 \pm 0.12 \text{ Mg C ha}^{-1} \text{ mo}^{-1}$, 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 $\sim 10\%$ of GPP (assuming a

274 GPP of $\sim 35 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). Growth rhizosphere respiration (i.e. the slope) differs, but not
275 significantly ($P > 0.05$), between the low and highland sites (0.52 ± 0.13 and 1.47 ± 0.97 unitless).

276 We then compared how soil fertility affects growth and maintenance respiration of roots,
277 comparing low (cation exchange capacity $< 25 \text{ mmol}_c \text{ kg}^{-1}$) to high (cation exchange capacity > 25
278 $\text{mmol}_c \text{ kg}^{-1}$) fertility sites (Figure 3b), a threshold chosen to give an approximately even balance of
279 plots. There was no significant difference ($P > 0.05$) in maintenance respiration (0.24 ± 0.06 and
280 $0.39 \pm 0.05 \text{ Mg C ha}^{-1} \text{ mo}^{-1}$) between low and high fertility soils. However, there was a significant
281 ($P < 0.05$) difference in slopes (0.72 ± 0.24 and 0.00 ± 0.21 unitless), with increased growth rhizosphere
282 respiration at less fertile sites (Table 1).

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

289 Next, we compared efficiency of woody biomass production (stem growth rate) to wood
290 respiration across the sites (Figure 4). There was very small, but significant ($P < 0.01$) differences in
291 maintenance respiration of wood between low and highland sites (0.52 ± 0.03 versus $0.56 \pm 0.06 \text{ Mg C}$
292 $\text{ha}^{-1} \text{ mo}^{-1}$). A few particularly high values at a lowland site (Kenia B) and particularly low values at a
293 highland site (Esperanza) obscure this difference. There was no difference in wood growth respiration
294 (0.45 ± 0.32 versus 0.28 ± 0.15) (Figure 4a). There were no significant differences between low and
295 high fertility sites for either woody maintenance respiration (0.56 ± 0.06 versus $0.49 \pm 0.03 \text{ Mg C ha}^{-1}$
296 mo^{-1}) or wood growth respiration (0.08 ± 0.31 versus 0.52 ± 0.14 unitless) (Figure 4b). Wood
297 maintenance respiratory costs were significantly greater ($P < 0.01$) at stands with $\tau_{\text{res}} > 40$ years
298 ($0.60 \pm 0.04 \text{ Mg C ha}^{-1} \text{ mo}^{-1}$) than at stands with $\tau_{\text{res}} < 40$ years ($0.44 \pm 0.03 \text{ Mg C ha}^{-1} \text{ mo}^{-1}$). 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 CO₂ 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 CO₂ per
305 mol C added to structure (Amthor, 2000).

306

307 **Discussion**

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

310 Soil fertility

311 There was a significant relationship ($P < 0.05$, Figure 1) between plot averaged CEC and CUE,
312 and this appears to be associated with increased rhizosphere respiration (root plus mycorrhizal
313 respiration) at the least fertile sites (Figure 2). These results are congruent with the recent study by
314 Vicca et al. (2012), which found a statistically significant effect of nutrient status, but not climate
315 zone, forest type or stand age ($P > 0.1$). Previous studies found stand age to be important in
316 explaining CUE (DeLucia et al., 2007; Goulden et al., 2011), but Vicca et al. (2014) raised the
317 possibility that there was an uneven distribution of forests with high nutrient availability across the
318 globe that may have confounded these conclusions.

319 However, because the total CUE measured by our plot network includes all components, it is
320 difficult to understand which organ (leaves, fine roots, or wood) may be driving these results. For this
321 reason, we also present organ-level CUE, which can give us a more specific understanding of the
322 forest. Root growth versus rhizosphere respiration shows no significant difference in maintenance
323 respiration ($P > 0.05$, figure 3b), but growth respiration is significantly higher at less fertile sites than
324 more fertile sites ($P < 0.05$, figure 5). We hypothesize that root growth requires more carbon at low
325 fertility sites because more carbon is allocated to mycorrhizae to search for nutrients. Averaged over
326 a year, the increase in rhizosphere growth respiration at low fertility sites over high fertility sites sums
327 to $\sim 2.4 \pm 1.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (assuming a total GPP of $\sim 35 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Malhi et al., 2015) or 7% of
328 total GPP) (Figure 3b). We do not directly measure mycorrhizal respiration, mycorrhizal biomass or
329 root exudates; therefore, this number is a very rough estimate (but possibly within our error estimate
330 of 3-11%) of carbon potentially transferred to these non-plant components. This compares with Vicca
331 et al. 2012 that found an increase of $16 \pm 4\%$ of photosynthates towards biomass production between
332 the low and high fertile site and Aoki et al 2012 that found an increase of 13.5% of aboveground NPP

333 towards root exudates between the low and high fertility sites. The relationship between mycorrhizal
334 growth and respiration is complicated, Bidartondo et al., (2001) found that carbon allocated into
335 symbionts was mostly used as energy to acquire nutrients instead of for mycorrhizal growth.

336

337 Temperature

338 There was no significant trend between temperature and CUE at the plot scale ($P > 0.05$,
339 Figure 1b) and only very small differences at the organ scale (Figure 5a and b). Therefore,
340 temperature does not appear to explain variation in CUE in our plot network. This indicates that
341 forest respiration rates in the tropics acclimate to mean temperature and that the simple Q_{10}
342 temperature relationship may not apply to long-term changes in mean biome temperatures (Amthor,
343 2000; Galbraith et al., 2010).) This does not mean that climate warming in tropical forests is not an
344 important issue (Doughty and Goulden 2008; Clark et al., 2013) and this study does not address the
345 question of whether hotter years at these sites impact carbon cycling.

346

347 Wood Residence Time

348 There was no significant relationship ($P > 0.05$, Figure 1a) between plot averaged τ_{res} and CUE.
349 However, a slightly more complex story emerges when looking at the organ level comparisons. The
350 cost of maintaining both wood and roots was significantly ($P < 0.001$) greater at stands with $\tau_{\text{res}} > 40$
351 years versus stands with $\tau_{\text{res}} < 40$ years. If we scale these effects over a year (averaging seasonal
352 variation and assuming a total GPP of $\sim 35 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ which is the average GPP from our seven
353 humid lowland plots (35.44 ± 3.57) Doughty et al 2015b), roots require $1.6 \pm 0.36 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and
354 wood requires $1.9 \pm 0.42 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ more carbon for maintenance at stands with $\tau_{\text{res}} > 40$ years than
355 at stands with $\tau_{\text{res}} < 40$ years (Figures 3c and 4c) for a total sum of $3.5 \pm 0.78 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$.

356 The observed changes in wood maintenance respiration between the different τ_{res} sites cannot
357 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 $\tau_{\text{res}} < 40$ years is $14,990 \pm 2,260 \text{ m}^2 \text{ ha}^{-1}$ and for stands with $\tau_{\text{res}} > 40$ years is $18,680 \pm 2,380 \text{ m}^2 \text{ ha}^{-1}$, an increase of $\sim 25\%$ while the increase in wood maintenance respiration is $> 50\%$. One possible explanation is that tropical forests with $\tau_{\text{res}} < 40$ 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 $\sim 5.7 \pm 2.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, 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.

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

408

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435

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 ($\text{NPP} / \text{NPP} + \text{R}_a$) 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 ($\text{NPP} / \text{NPP} + \text{R}_a$) 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 ($\text{Mg C ha}^{-1} \text{ mo}^{-1}$) 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) < 40 yr 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 ($\text{Mg C ha}^{-1} \text{ mo}^{-1}$) versus wood respiration ($\text{Mg C ha}^{-1} \text{ mo}^{-1}$)
459 ¹) for (a) lowland (grey) versus highland (black), for (b) low fertility sites (grey) and high fertility
460 sites (black), and (c) < 40 yr 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 ($\text{Mg C ha}^{-1} \text{ mo}^{-1}$) based on the y intercepts and error bars
464 from figure 3, (b) wood maintenance respiration ($\text{Mg C ha}^{-1} \text{ mo}^{-1}$) 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),

467 high fertile sites (black square), low elevation (red circle), high elevation (black circle), low residence
468 time (red triangle), high residence time (black triangle). Stars indicate significant differences based
469 on ANCOVAs with $* < 0.05$, $** < 0.01$ and $*** < 0.001$. Elevation is a proxy for temperature.

470

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472

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