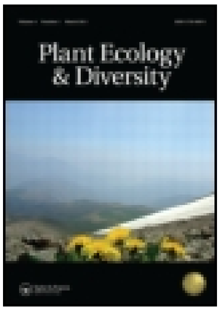

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Assessing above-ground woody debris dynamics along a gradient of elevation in Amazonian cloud forests in Peru: balancing above-ground inputs and respiration outputs

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Assessing above-ground woody debris dynamics along a gradient of elevation in Amazonian cloud forests in Peru: balancing above-ground inputs and respiration outputs

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Background: Dead biomass, including woody debris (WD), is an important component of the carbon cycle in tropical forests.
Aims: This study analyses WD (>2 cm) and other above-ground fluxes in mature tropical forest plots along an elevational gradient (210–3025 m above sea level) in southern Peru.
Methods: This work was based on inventories of fine and coarse WD (FWD and CWD, respectively), above-ground biomass, and field-based and experimental respiration measurements.
Results: Total WD stocks ranged from 6.26 Mg C ha^{-1} at 3025 m to 11.48 Mg C ha^{-1} at 2720 m. WD respiration was significantly correlated with moisture content ($P < 0.001$; $R^2 = 0.25$), temperature ($P < 0.001$; $R^2 = 0.12$) and wood density ($P < 0.001$; $R^2 = 0.16$). Controlled experiments showed that both water content and temperature increased respiration rates of individual WD samples. The full breadth of the temperature sensitivity coefficient, or Q_{10}, estimates, ranging from 1.14–2.13, was low compared to other studies. In addition, temperature sensitivity of WD respiration was greater for higher elevations.
Conclusions: Carbon stocks, mortality and turnover of above-ground biomass varied widely and were not significantly related with elevation or slope. This study demonstrates that some forests may be a carbon source due to legacies of disturbance and increasing temperatures, which may cause additional, short-term carbon efflux from WD. Predictions of tropical forest carbon cycles under future climate should incorporate WD dynamics and related feedback.

Keywords: Amazon Basin; Andes; carbon balance; cloud forest; montane forest; necromass; respiration; temperature sensitivity; tropical forest; turnover

Introduction

Tropical forests play a major role in the global carbon (C) cycle (Malhi and Phillips 2005; Keller et al. 2009) and store a large proportion of global terrestrial C (Dixon et al. 1994; Saatchi et al. 2011). Tropical forests alone account for one-third of all terrestrial net primary productivity (Field et al. 1998; Malhi and Grace 2000; Del Grosso et al. 2008) and about the same proportion of net exchange of C between the atmosphere and terrestrial vegetation (Melillo et al. 1993). Long-term studies of tropical forests and their C cycles are important for quantifying global C budgets (Houghton et al. 2001; Davidson and Artaxo 2004), understanding potential responses and feedback from the C cycle to changes in temperature and rainfall (Lewis et al. 2011), and providing an empirical basis for developing and supporting mechanisms for mitigating global climate change (e.g. Kremen et al. 2000; Laurance 2007). Above-ground biomass (AGB), particularly live AGB (i.e. living trees), represents one of the largest portions of forest C stores and is the most frequently studied pool (Keller et al. 2001; Nascimento and Laurance 2002). However, accurate quantification of C stocks and fluxes is limited by incomplete measurement of all significant components of the C cycle in tropical forests (Brown 2002; Palace et al. 2012).

Necromass is an important portion of the forest C cycle and is an intermediate component between biomass stocks and alternate terrestrial, aquatic and atmospheric C pools (Brown et al. 1992; Malhi et al. 2009). Above-ground necromass includes fine litter (small organic matter, leaves and twigs <2 cm diameter) and woody debris (WD) (sticks and trunks >2 cm diameter) (Harmon et al. 1986). Woody debris (WD) provides habitat for fauna and flora, influences wildfire potential, and plays an important role in nutrient and C cycling (Chambers et al. 2000; Palace et al. 2007).

In tropical forests, the stocks of WD can comprise up to 30% of AGB (Clark et al. 2002) and contribute to ca. 15% of total ecosystem respiration (Palace et al. 2007). Quantifying both C stocks of, and fluxes from, WD can indicate the disturbance history of an ecosystem and shed light on the overall C balance of the ecosystem

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(Baker et al. 2007; Palace et al. 2007). Although old-growth tropical forests are generally considered to be sinks (Cramer et al. 2001; Luyssaert et al. 2008; Pan et al. 2011), C efflux through WD decomposition can significantly increase ecosystem respiration, transforming some tropical forest stands into a net C source to the atmosphere (e.g. Rice et al. 2004; Pyle et al. 2008).

Theoretically, WD pools in old-growth forests are in equilibrium over the long term (i.e. inputs equal outputs) and any changes should be in balance with changes in AGB (Baker et al. 2007). In reality, disturbance from stochastic events (e.g. severe storms and landslides) or anthropogenic activity causes temporary or permanent shifts in this balance (Palace et al. 2007), resulting in altered C emission patterns from WD and the ecosystem as a whole (Rice et al. 2004). Despite its significance, WD can be difficult to measure and is infrequently quantified in tropical forests (Harmon et al. 1995; Chambers et al. 2000; Clark 2002; Rice et al. 2004; Palace et al. 2007). However, a growing body of literature is providing important insights into C storage and cycling of WD in the tropics (e.g. Chambers et al. 2001; Rice et al. 2004; Baker et al. 2007; Palace et al. 2008; Pyle et al. 2008).

Estimates of WD stocks in undisturbed tropical forests vary widely across global and regional scales (see Figure 1 in Baker et al. (2007) for estimates from lowland tropics; Palace et al. 2012). Most studies have measured stocks of fallen, large WD (>10 cm diameter), also known as coarse woody debris (CWD). Of these studies, few measured fine woody debris (FWD) or standing dead tree stocks, even though these pools have been estimated to represent up to 20% and 15%, respectively, of total WD stocks (Palace et al. 2007). As with stocks, decomposition rates vary widely across the tropics (see Table 4 in Baker et al. 2007). WD respiration has been rarely quantified in the tropics even though respiratory emissions to the atmosphere from WD make significant contributions to total ecosystem respiration and may account for up to 75% of total C loss from dead wood (Sampaio et al. 1993; Chambers et al. 2001). Even fewer studies have quantified all significant portions of WD simultaneously (but see Palace et al. 2008; Pyle et al. 2008), nor how WD fluxes would shift with changing global temperature or precipitation.

Transects over elevation gradients are powerful natural experiments that can test ecological and evolutionary hypotheses (Körner 2007) and be used as "natural laboratories for understanding environmental controls on ecosystem function" (Malhi et al. 2010). In fact, with careful selection, temperature can be largely isolated from other geophysical factors (i.e. moisture and seasonal variability) as the key driver of variation in ecological properties along a gradient (Malhi et al. 2010). Forests along such a gradient can be used as an analogue of future climate change by shedding light on the responses of various ecological processes to temperature (e.g. Girardin et al. 2010; Zimmermann et al. 2009). This includes, for example, exploring the sensitivity of carbon biomass dynamics to temperature, a factor known to increase decomposition rates in WD (e.g. Adair et al. 2008; Meier et al. 2010; this study). In addition, the C balance of tropical montane forests can be particularly susceptible to climate change because geophysical factors currently controlling C dynamics at lower elevations (and associated higher temperatures) can shift to higher elevations and temporarily, or permanently, modify various C fluxes and the overall C balance of the ecosystem. Despite the sensitivity of tropical montane forests to changes in climate, there have been no comprehensive analyses of WD in this forest type.

Therefore, the overall aim of this paper was to quantify the C balance and climatic sensitivity of WD along a transect, from lowland Amazon forest to Andean cloud forest, spanning almost 3000 m in elevation and a mean annual temperature range of 14 °C. Specifically, we tested two non-exclusive hypotheses: H1, WD stocks increased with elevation because of reduced decomposition rates (measured as heterotrophic respiration rates) as a response to decreasing saprophyte metabolism due to lower temperatures at higher elevations; H2, WD stocks decreased with elevation because of lower AGB input as a response to decreasing AGB productivity and turnover rates at lower temperatures.

To evaluate the contribution of each above component to the dynamics of WD C stocks observed at each site we further hypothesised that: H3, all sites were in steady state and temporal changes in WD stocks were near zero (i.e. inputs and outputs were balanced); H4, the decrease in heterotrophic respiration at higher elevations (and the resulting decrease in overall efflux from WD) would be followed by a decrease in above-ground WD input (i.e. tree mortality).

Materials and methods

Site description

The five study sites were located along a gradient of elevation on the eastern flank of the Andes in south-eastern Peru (Figure 1). The transect stretched from lowland Amazon rainforest (210 m), through the base of the cloud zone (1500–1800 m) to high montane forest just below the treeline (3025 m). One long-term study plot characterised by mature, tropical forest was surveyed at each of five elevations: 210 m (Tambopata), 1000 m (Tono), 1500 m (San Pedro), 2720 m (Trocha Union) and 3025 m (Wayqecha) (Table 1). Most plots had limited accessibility. Each elevation had unique vegetative features, site characteristics and climatic variables (Table 1). Climate along the gradient was largely aseasonal in temperature but seasonal in precipitation, with a dry season occurring from May to August. Sites in the cloud forest zone (1500–3000 m) were frequently immersed in cloud, not only during the wet season, but also throughout the dry season, and the soil remained saturated year-round (Girardin et al. 2010). Along the gradient, mean annual temperature ranged from 26.4–12.5 °C, and mean annual precipitation ranged from 1706–3087 mm per year.

Each plot was a projected 1-ha quadrat (10,000 m^2) divided into 25 subplots (400 m^2). Slope and aspect were

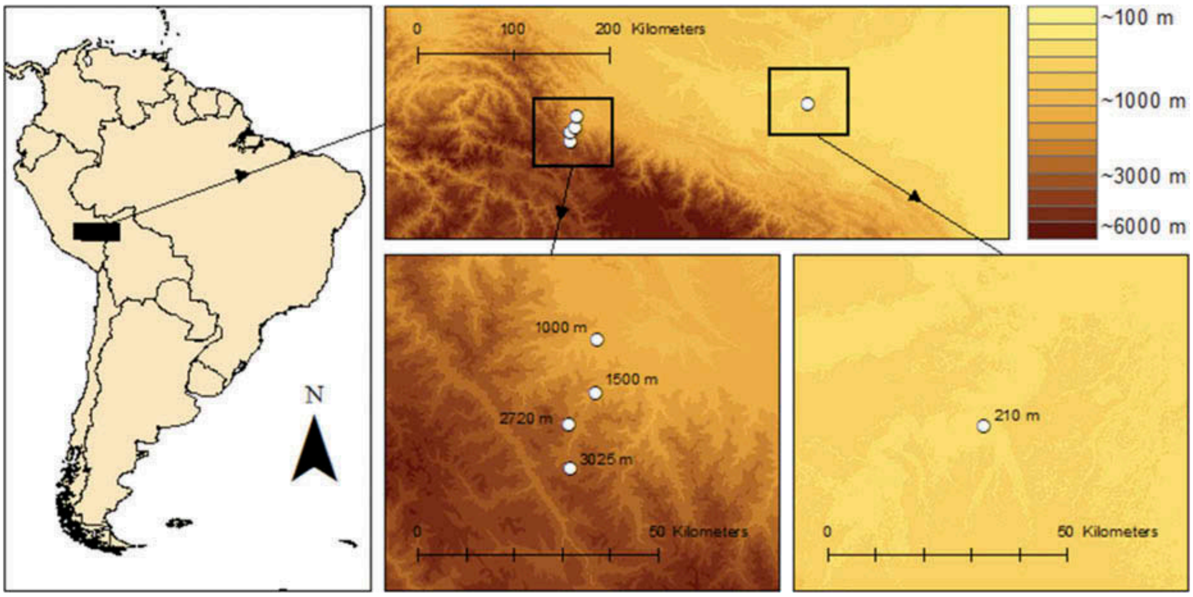

Figure 1. Location of the five permanent rainforest plots considered in this study, spanning an elevation gradient in southern Peru from lowland evergreen Amazonian rain forest to Andean montane forest: 210 m (Tambopata), 1000 m (Tono), 1500 m (San Pedro), 2720 m (Trocha Union), and 3025 m (Wayqecha).

Table 1. Site attributes for five old growth, permanent tropical forest plots along a gradient of elevation in the Peruvian Andes: 210 m (Tambopata), 1000 m (Tono), 1500 m (San Pedro), 2720 m (Trocha Union) and 3025 m (Wayqecha).

	Elevation (m)				
	210	1000	1500	2720	3025
Site (plot number)	Tambopata (3)*	Tono (2)	San Pedro (2)	Trocha Union (4)	Wayqecha (1)
Latitude (degrees)	−12.83	−12.96	−13.05	−13.10	−13.19
Longitude (degrees)	−69.28	−71.56	−71.54	−71.59	−71.59
Mean annual air temperature (°C)	26.4	20.7	18.8	13.5	12.5
Annual precipitation (mm year^{-1})	2200	3087	2631	2318	1706
Geological substrate	Pleistocene alluvial terrace	Alluvial terrace	Granite	Paleozoic shales-slates	Paleozoic shales-slates
Forest type	Amazon terra firme	Andean foothill	Pre-montane forest	Montane forest	Montane forest
Initial census	May 1983	Jul 2004	Sep 2006	Jul 2003	Sep 2003
Predominant aspect direction	n/a	West	West	West	East
Mean slope (°) (± SE)	6.0 (0.53)	9.0 (0.94)	22.7 (1.19)	21.0 (0.71)	18.2 (0.98)
Estimated ground area (ha) (± SE)	1.007 (0.064)	1.017 (0.065)	1.092 (0.070)	1.074 (0.069)	1.057 (0.068)

*Also referred to as “TAM-05” in other studies.

measured with a clinometer and compass from the centre of nine equidistant quadrats in each subplot. Since the bounds of each plot were delineated by projected area, the complete ground-area of each plot was determined trigonometrically by using the angle of incline (i.e. slope, see Table 1) and the projected length as the base length. Each plot- or subplot-based measurement was corrected for the complete, estimated ground-area of each plot (Table 1). Also, all biomass stocks and fluxes are presented in terms of wood C content assuming dry-stem biomass was 47.4% carbon, based on recent studies in Panama, which included volatile carbon compounds that were not captured by conventional dry assessment (Martin et al. 2011).

Woody debris stocks: fine woody debris (FWD) and coarse woody debris (CWD)

At each 1-ha plot along the gradient, the stock of fine woody debris (FWD; WD between 2 and 9.9 cm diameter) and coarse woody debris (CWD; WD ≥10 cm in diameter) was quantified. Data collection for FWD and CWD stocks was conducted during the dry seasons, between June and August of 2007 and 2008. Estimates were calculated at the subplot level, averaged, extrapolated to the ha-level, converted to C content, and (only for CWD) adjusted for plot area.

To inventory FWD stocks, six 3 m × 3 m quadrats (across three subplots with two quadrats in each) were installed at each elevation except 3025 m, where a smaller FWD plot size was used (1 m^2) because of the greater abundance of FWD. At each site, all FWD segments were removed from the quadrats. Samples were measured (i.e. length and diameters at both ends), dried and weighed to determine FWD mass for each quadrat. Density was calculated using mass and volume; the latter was calculated by using the formula for a truncated cone.

The stocks of CWD were sampled at each elevation in five subplots (generally selecting one at each corner and one in the centre) measuring 20 m × 20 m (total of 2000 m^2 per elevation) with the exception of the 210 m elevation site. For 210 m, we used the average CWD stocks published in Baker et al. (2007) that included the plot surveyed in this study and several surrounding plots. All CWD segments were measured and stratified by decay class and by position (i.e. fallen or standing). For each segment, the state of decomposition was classified on a five-point scale (e.g. Keller et al. 2004; Palace et al. 2007), where 1 indicated a solid, recent tree fall and 5 very decomposed material, following criteria adopted from Baker et al. (2007) (Table 2). To estimate CWD density across decay classes, segments were selected at random from each class, cut into the shape of a cuboid and measured to determine volume. Each cuboid was then dried to a constant weight in a drying oven at 80 °C for five days. After drying, each sample was weighed and density was calculated by dividing dry mass by initial volume. Density calculations were then pooled by assigned decay class and averaged to estimate density for each class at each plot.

For fallen CWD, length and diameter at both ends were measured; buttressed trunks of fallen trees were measured just above the buttress. Standing CWD included stumps ($\leq$1.5 m in height) and snags (dead trees $\geq$1.5 m in height). Upper and lower diameter was measured for all stumps. For all standing snags, diameter at breast height (DBH), or diameter above a buttress, was measured. Height and diameters for snags <3 m tall were measured. For snags >3 m, height was estimated to the nearest metre and a taper function was used to calculate the upper diameter (Chambers et al. 2000) (Equation (1))

$$d_h = 1.59(DBH)(h^{-0.091}) \tag{1}$$

where d_h (cm) is the diameter at height h (cm) for a bole of given DBH (cm) (Chambers et al. 2001).

The volume of CWD segments was calculated by using the formula for a truncated cone using the length and diameters at each end. The mass of CWD was calculated for each decay class by multiplying volume and density for each class. The proportion of solid wood space was not used to adjust total volume in this study (c.f. Keller et al. 2004; Baker et al. 2007) because cubes used to determine density were large enough to account for some void space (mean = 56.6 cm^2; $n = 158$; SE = 6.6).

Table 2. Description of woody debris decomposition classes (1–5); adapted from Baker et al. (2007).

Class	Description
1	Solid wood, recently fallen, with intact bark and fine branches still attached
2	Solid wood, but with no fine branches, and bark starting to fall off
3	Non-solid wood, in poorer condition, but where it was still difficult to push a nail into the wood by hand
4	Soft, rotten wood, where a nail could be pushed into the wood easily
5	Soft, rotten wood, which collapsed easily when stepped on

Controls on respiration from woody debris

Respiration was measured in the field and under experimental trials. Respiration of WD was measured using a portable, closed-chamber infrared CO_2 gas analyser system (EGM-4; see PP Systems 2002). Samples were placed into a sealed plastic cylindrical chamber fitted to a metal collar. For each sample, the concentration of CO_2 within the sealed chamber was measured every 5 s over the course of about 120 s. The temperature of each sample was measured with a digital thermometer just before measuring respiration.

After measurement, samples were weighed and oven-dried at 80 °C to a constant weight for 3 to 5 days. After oven-drying, each sample was weighed and volume was measured through volumetric displacement: each sample was tightly wrapped in plastic wrap and placed into a calibrated beaker to estimate dry volume by measuring water displacement to the nearest ml (cm^3).

Field measurements. Efflux of C from WD samples was measured at each site during the dry season in July 2008. Samples of fallen and standing WD were removed from three subplots at each elevation (additional samples were selected from other subplots where WD stocks were low) by removing wedge-shaped pieces. Samples were generally taken from CWD (>10 cm in diameter), although some smaller diameter pieces were also measured. The diameter of each log was measured at the point where the sample was removed. Before measuring respiration of each sample, approximately 2 h was allowed for equilibration of CO_2 concentrations in the wood pore matrix and the atmosphere (Chambers et al. 2001). Samples were measured in the field using an infrared CO_2 gas analyser system (see above).

Respiration experiments. The sensitivity of WD respiration to moisture and temperature was further explored through experimental, field-based trials using a set of samples collected at 210 m in Tambopata. For each respiration reading, sample temperature was measured with a digital thermometer and weight was recorded; water content for each measurement was derived by using sample mass at measurement and dry mass.

Moisture sensitivity was tested by using multiple wetting trials with a set of CWD samples. The initial reading was conducted at field moisture content, and for each subsequent trial samples were sprayed with water until weight increased by ca. 10%. The final reading was conducted after quasi-saturation (i.e. samples were placed in shallow trays of water (ca. 5 mm deep) and sprayed repeatedly). During moisture trials, the range of water content was 0.19–2.28 g H_2O g^{-1} dry wood and temperature was kept within a narrow window of 22.4–26.4 °C.

Sensitivity to temperature was tested by using temperature trials with a set of CWD samples. To minimise the confounding influence of moisture on respiration rate, the sample weight (and moisture content) was kept constant by keeping samples quasi-saturated (i.e. samples were placed in shallow trays of water (ca. 5 mm deep) and sprayed repeatedly). Respiration measurement began before dawn, during the coolest temperatures, and continued until midday when samples were placed in the sun; each sample was measured at least four times. Sample temperatures ranged from 21.8–33.9 °C.

Calculation of CO_2 efflux from WD. For each measurement, a C-based rate of respiration was calculated using WD sample flux and dry weight. The flux (or rate of CO_2 accumulation in the chamber) was calculated by using Equation (2) (modified from PP Systems 2003, 22)

$$r = \left(b \cdot \frac{P}{1000} \cdot \frac{273}{273 + T_c} \cdot \frac{44.01}{22.41} \cdot V \right) \tag{2}$$

where r (mg CO_2 s^{-1}) is CO_2 flux, b (ppm s^{-1}) is the rate of CO_2 accumulation, P (mbar) is the atmospheric pressure, T_C (°C) is the temperature of the chamber and V (m^3) is the volume of the chamber air space. Rate of CO_2 accumulation, b, was calculated using the slope of the relation between CO_2 concentration in the chamber (ppm) and time (s); the first three records for every reading were excluded to allow time for chamber equilibration. P was measured for each record by the EGM-4 gas analyser system and was averaged for each reading. T_C was taken as the temperature of the sample. V was calculated by including the volume of the metal head and the plastic collar minus the wet volume of the WD sample inside the chamber. Due to logistical constraints, it was only possible to measure initial, or wet, volume of WD samples at some elevations. These data were used to calculate wet volume where it could not be measured, based on a linear relation between wet and dry volume ($P < 0.0001$; $n = 103$; $R^2 = 0.88$; see Appendix, Figure A1).

This flux (r) was transformed to a C-based measure (r_t, μg C_R min^{-1}) and then converted to a mass-based respiration rate using the formula (Equation (3))

$$R = \frac{r_t}{W} \tag{3}$$

where R (μg C_R g $C_W{}^{-1}$ min^{-1}) is the C flux from the C in WD and W (g C_W) is the weight of the WD sample expressed in carbon content (see above; 0.474 g C_W g^{-1} dry wood; Martin et al. 2011). Moisture content for each sample was calculated gravimetrically as g H_2O g^{-1} dry wood.

Decay classes were assigned to each sample measured for respiration based on ranges of density determined from the decay class density estimation scheme used to calculate CWD stocks. A density range for each class was determined by dividing intervals between density class means at their midpoints. Respiration measurements for each site were then pooled by decay class to calculate the mean respiration rate for each decay class at each site.

Other above-ground C stocks and fluxes

AGB, stem productivity and stem mortality. Since plot establishment, the oldest plot at 210 m has been censused several times while the upper montane sites have been censused two or three times (Table 1). For all sites, AGB, stem productivity (the sum of growth and recruitment) and mortality were calculated based on a repeated census of trees >10 cm DBH. Biomass was calculated by using an allometric equation to estimate AGB (Mg) of all trees (>10 cm DBH) in each plot, using the moist forest equation (Equation (4)) from Chave et al. (2005)

$$AGB = \frac{0.0509(\rho D^2 h)}{1000} \tag{4}$$

where ρ is wood density (g cm^{-3}), D is diameter (cm) and h is total tree height.

Branch fall and branch productivity. Because mortality data only account for inputs associated with larger stem mortality, WD inputs from mortality alone are an incomplete mortality estimate and do not account for the input of branch turnover and small stems. Palace et al. (2008) suggested that using mortality rates could underestimate WD production by up to 45%. Branch fall was surveyed at three elevations: 210, 1500 and 3025 m. At these sites, branches >2 cm diameter fallen from live trees were surveyed every three months between December 2008 and August 2009. All woody material >2 cm diameter that had accumulated along four 1 m × 80 m transects per plot (previously cleared of all woody material) was collected, dried at 70 °C to constant mass and weighed. Branch fall was added to mortality calculations to estimate total above-ground WD input. Due to lack of data, branch fall at 1000 and 2720 m was taken to be equivalent to sites at proximate elevations (i.e. the same as at 1500 and 3025 m, respectively). Assuming equilibrium conditions, branch productivity, or growth, was assumed to be equivalent to branch fall.

Annual WD efflux. To estimate the annual efflux of C (Mg C ha^{-1} year^{-1}) from WD (i.e. FWD plus CWD), respiration rates across decay classes at each plot were averaged, adjusted for mean annual temperature (see Equation (9) in Results) and multiplied by total WD stock. Respiration was averaged because decay class-specific rates were highly variable and did not show clear trends.

Balancing above-ground C stocks and fluxes

Fluxes of C were conceptualised by using a simple compartmental model (adapted from Palace et al. 2008; see Figure 2). Annual net C flux in AGB to the atmosphere was estimated by subtracting total C efflux (based on WD stocks' respiration) from total C uptake (including branch productivity and stem productivity (i.e. growth and recruitment)). This estimate did not consider other forms of carbon efflux from WD (e.g. transport of WD into soil and/or water). Turnover, or residence time, of WD was calculated at each elevation in three ways, dividing total WD stocks by (1) WD inputs (i.e. mortality and branch fall), (2) WD outputs (i.e. CWD respiration) and (3) the average of WD inputs and WD outputs. Under the assumption of steady-state conditions, inputs and outputs to WD stock should be equivalent, and so should be resulting calculations of turnover. However, where input and output vary, turnover can also vary depending on how it is calculated.

A measure of the change in respiration or decay constant associated with a change in temperature of 10 K, known as a temperature sensitivity coefficient or Q_{10} (first developed by van't Hoff (1898), as cited in Lloyd and Taylor (1994)), was estimated using four distinct methods throughout this study. The first was calculated using a set of decay rates approximated from the reciprocal of turnover times for each plot (following Salinas et al. in review). Decay rates were then plotted against mean annual temperature of each plot and fitted with exponential regressions to estimate Q_{10} using the function (Equation (5))

$$f(x) = a * e^{(k*x)} \tag{5}$$

where $f(x)$ is a function of x, and a and k are both constants. The formula for Q_{10} for the exponential regression was simplified using algebra and the quotient of powers (Equation (6))

$$Q_{10} = \frac{f(x_2)}{f(x_1)} = \exp(k * 10) \tag{6}$$

where k is the constant from Equation (5), and $f(x_1)$ and $f(x_2)$ are both functions of x_1 and x_2, respectively (where x_2 minus x_1 is 10 °C). Three other methods for estimating Q_{10} are mentioned below.

Biomass stocks and fluxes. Plot-based measurements of FWD and CWD stocks were extrapolated to a 1-ha area. Ratios of various stocks and fluxes to AGB and total WD were calculated to explore relative patterns of C dynamics. Multiple linear regressions were used to test the influence of independent variables (i.e. temperature, mean slope and precipitation) on several dependent variables (FWD, CWD (fallen/standing), total WD, AGB, stem productivity, stem mortality, branch fall, total mortality, average sample flux, WD efflux, the proportion of all these stocks to AGB, and the proportion of various WD stock to total WD and CWD). Elevation was not used as an independent variable because it was highly correlated with temperature along this transect. Density of debris in various decay classes was compared across sites. The relation between decay-class densities at different plots was examined by using a two-way analysis of variance.

Controls on woody debris respiration. Data collected in the field were analysed independently from that collected during experimental trials. For data collected in the field, the influence of four variables (i.e. wood moisture content, wood density, sample diameter and temperature) on respiration was investigated using multiple linear regressions. The influence of all significant variables from the previous dataset on respiration was determined by a multiple analysis of variance (MANOVA). Respiration rates for samples removed from the same segments were used to determine variation of intra-log respiration using multiple analysis of covariance (MANCOVA). A second estimate for Q_{10} was calculated for samples collected along the elevation gradient, using the exponential relation between sample respiration and temperature (Equations (5) and (6)).

The influence of experimental trials (temperature and moisture) on the respiration of each sample was analysed by using a two-way analysis of covariance. A third Q_{10} was calculated based on temperature trials using the mean of a series of Q_{10} values calculated by using the highest and lowest temperature at which respiration was measured for each sample (c.f. Zheng et al. 2009) (Equation (7))

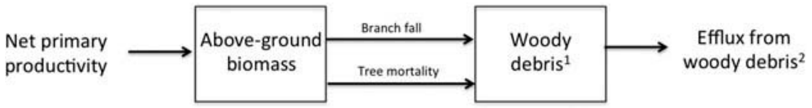

Figure 2. Simple compartmental model of carbon fluxes in above-ground, woody (>2 cm diameter) biomass (adapted from Palace et al. 2008). *Could be further stratified by decay class, size (e.g. FWD, CWD), or position (e.g. standing, fallen); †carbon loss from WD is largely attributed to efflux (i.e. heterotrophic respiration) but also includes C inputs into soils and water.

$$Q_{10} = \left[\frac{R_2}{R_1}\right]^{\left[\frac{10}{T_2 - T_1}\right]} \tag{7}$$

where R_1 is rate of respiration at one temperature (T_1) and R_2 is the rate of respiration at another temperature (T_2). The influence of temperature on respiration was compared between field and experimental observations by using Q_{10} values.

Warming and efflux

A simple model was developed for respiration rate, using a MANOVA, based on all significant variables (temperature, moisture and density). For each site, respiration and mean annual air temperature were entered into the equation, and a constant was determined for density and moisture content terms. The change caused by increases in temperature in increments of 2, 5 and 10 °C was then predicted for each site, assuming moisture and density remained constant. Based on current and modelled increases in annual efflux, a fourth and final set of Q_{10} values was calculated (Equation (7)) for each increment at each site. All statistics were run in JMP statistical package version 5.1.2 (SAS Institute Inc., Cary, NC, USA).

Results

Woody debris stocks (FWD and CWD)

In total, 412 pieces of FWD and 415 segments of CWD were inventoried for stock estimation; a subset of 140 CWD segments was sampled to estimate density of each decay class. Mean density was inversely related to decay class at each plot ($P < 0.001$) and, although density estimates indicated potential plot differences (Figure 3), the measurements for all sites were pooled to create a larger sample size to estimate density for each decay class (Tables 3–5).

Total stock and distribution of WD across standing, fallen and decay classes along the elevation gradient were variable (Table 3). In most cases, stock of CWD across different decomposition classes resembled a normal distribution (i.e. more CWD at intermediate decomposition classes). Stocks of WD and CWD were not significantly correlated with elevation (see Appendix, Table A1).

The proportion of WD stocks to total AGB ranged from 8% to 19% across sites (see Appendix, Table A2). The proportion of FWD to total WD stocks ranged from 6% at the lowest elevation site to 42% at the highest elevation site; excluding 3025 m, FWD comprised no more than 11% of total WD stocks.

Controls on respiration from woody debris

Field measurements. A total of 322 samples were measured across all sites and respiration rates ranged from 0.07–3.42 $\mu\text{g C}_\text{R}\ \text{g C}_\text{W}^{-1}\ \text{min}^{-1}$ (where C_R is carbon respired and C_W is carbon content of the dry sample).

Respiration of WD was weakly, positively correlated with wood water content ($P < 0.001$; $R^2 = 0.25$; Figure 4(a)) and sample temperature ($P < 0.001$; $R^2 = 0.12$; Figure 4(b)), and weakly negatively correlated with the natural log of wood density ($P < 0.001$; $R^2 = 0.16$; Figure 4(c)). A regression indicated that sample respiration was not influenced by the diameter of the deriving log ($P = 0.54$). A logarithmic trend line indicated that water content was negatively correlated with the natural log of wood density ($P < 0.001$; $R^2 = 0.38$; Figure 4(d)). Small improvements in these relations were observed when samples were stratified by elevation (see Appendix, Figure A2). Q_{10} was estimated to be 1.66 based on the linear relation between respiration measurements and sample temperature, following Equation (8) (Figure 4(b); $P < 0.001$; $R^2 = 0.12$)

$$R_{WD} = 0.0395911 + [0.033 \cdot T] \tag{8}$$

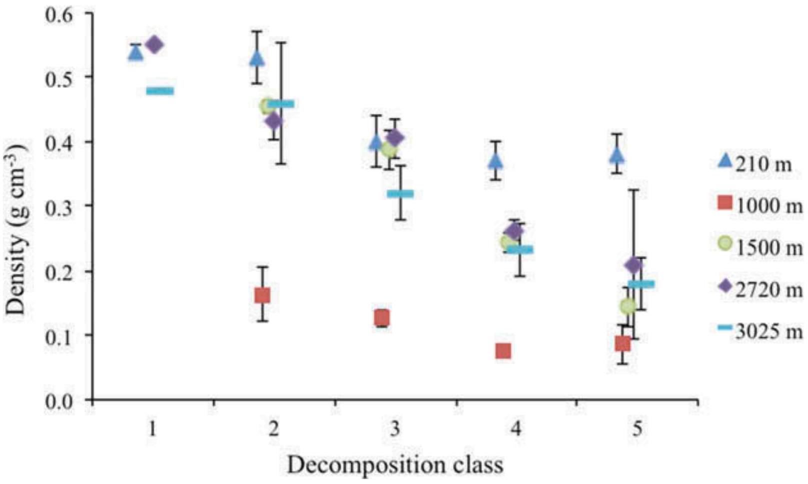

Figure 3. Average density of woody debris decomposition classes from plots along a gradient of elevation (210–3250 m a.s.l.), Peru. Mean density for each decomposition class is pooled from all sites when calculating mass, excluding 210 m (see Table 5). *Data for 210 m published in Baker et al. (2007).

Table 3. Mass (Mg C ha^{-1}) of fine woody debris (FWD), coarse woody debris (CWD) and woody debris (WD = FWD + CWD) measured at five sites along an elevation gradient in the Peruvian Andes. CWD is further stratified by volume (m^3 ha^{-1}), decay class and standing or fallen.

			Total		Standing		Fallen	
		Decay class	Mass (SE)	Volume (SE)	Mass (SE)	Volume (SE)	Mass (SE)	Volume (SE)
210 m*								
	FWD		0.54 (0.06)					
	CWD		8.39 (1.15)	44.06 (9.66)	1.98 (0.45)	10.58 (3.55)	6.42 (0.99)	33.47 (8.41)
		1	0.83 (0.14)	3.33 (1.12)	0.15 (0.05)	0.59 (0.21)	0.68 (0.15)	2.74 (1.08)
		2	1.46 (0.19)	5.96 (1.24)	0.29 (0.14)	1.18 (0.69)	1.17 (0.16)	4.78 (0.99)
		3	2.13 (0.34)	11.58 (2.48)	0.51 (0.12)	2.76 (0.78)	1.62 (0.28)	8.82 (2.01)
		4	1.81 (0.21)	10.77 (1.43)	0.54 (0.11)	3.20 (0.84)	1.27 (0.18)	7.57 (1.34)
		5	2.18 (0.37)	12.42 (3.39)	0.50 (0.13)	2.85 (1.03)	1.68 (0.33)	9.57 (2.99)
	Total WD		8.94 (1.21)					
1000 m								
	FWD		1.05 (0.18)					
	CWD		8.73 (3.04)	58.83 (18.63)	2.45 (0.95)	14.61 (5.62)	6.28 (3.04)	44.22 (18.53)
		1	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)
		2	0.84 (0.41)	4.40 (1.95)	0.46 (0.34)	2.43 (1.56)	0.38 (0.22)	1.97 (0.94)
		3	6.20 (2.66)	37.77 (15.90)	1.96 (1.09)	11.93 (6.39)	4.24 (2.83)	25.83 (16.97)
		4	1.40 (0.44)	12.97 (3.64)	0.03 (0.08)	0.25 (0.32)	1.37 (0.44)	12.72 (3.61)
		5	0.29 (0.22)	3.70 (2.21)	0.00 (n/a)	0.00 (n/a)	0.29 (0.22)	3.70 (2.21)
	Total WD		9.77 (3.22)					
1500 m								
	FWD		0.83 (0.11)					
	CWD		6.81 (1.79)	48.09 (9.64)	2.10 (1.40)	12.89 (7.22)	4.71 (1.23)	35.20 (7.29)
		1	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)	0.00 (n/a)
		2	1.54 (1.29)	8.06 (6.51)	1.33 (1.14)	6.98 (5.75)	0.21 (0.21)	1.08 (0.87)
		3	3.24 (1.12)	19.74 (6.56)	0.41 (0.41)	2.47 (2.18)	2.84 (1.18)	17.27 (6.92)
		4	1.61 (0.47)	14.91 (3.91)	0.35 (0.35)	3.27 (2.77)	1.26 (0.28)	11.65 (2.09)
		5	0.42 (0.24)	5.38 (2.35)	0.01 (0.07)	0.17 (0.24)	0.41 (0.24)	5.21 (2.36)
	Total WD		7.64 (1.90)					
2720 m								
	FWD		1.06 (0.40)					
	CWD		10.42 (1.36)	68.21 (7.60)	4.72 (1.81)	31.40 (11.29)	5.70 (0.72)	36.81 (5.04)
		1	0.27 (0.23)	1.15 (0.77)	0.10 (0.16)	0.42 (0.49)	0.17 (0.19)	0.73 (0.63)
		2	1.41 (0.84)	7.37 (4.18)	0.62 (0.68)	3.27 (3.34)	0.78 (0.40)	4.10 (1.84)
		3	6.81 (1.15)	41.49 (6.72)	2.94 (1.28)	17.89 (7.53)	3.88 (0.69)	23.60 (3.93)
		4	1.84 (0.59)	17.05 (5.01)	1.06 (0.77)	9.82 (6.65)	0.78 (0.33)	7.23 (2.57)
		5	0.09 (0.10)	1.15 (0.64)	0.00 (n/a)	0.00 (n/a)	0.09 (0.10)	1.15 (0.64)
	Total WD		11.48 (1.75)					
3025 m								
	FWD		2.68 (0.45)					
	CWD		3.58 (1.16)	22.44 (6.98)	1.17 (0.65)	7.40 (3.85)	2.40 (1.18)	15.04 (6.42)
		1	0.66 (0.72)	2.76 (2.83)	0.00 (n/a)	0.00 (n/a)	0.66 (0.72)	2.76 (2.83)
		2	0.32 (0.20)	1.67 (0.83)	0.24 (0.19)	1.26 (0.77)	0.08 (0.11)	0.42 (0.35)
		3	2.04 (0.79)	12.45 (4.51)	0.82 (0.65)	4.99 (3.65)	1.22 (0.71)	7.46 (4.05)
		4	0.44 (0.27)	4.08 (2.07)	0.09 (0.12)	0.80 (0.62)	0.35 (0.28)	3.28 (2.09)
		5	0.12 (0.11)	1.47 (0.76)	0.03 (0.07)	0.35 (0.28)	0.09 (0.10)	1.12 (0.68)
	Total WD		6.26 (1.61)					

*Values for plot-based CWD mass and volume published in Baker et al. (2007). Based on several long-term plots in the Tambopata area and not adjusted for area. However, influence of topography is negligible.

Table 4. Average fine woody debris density (g cm^{-3}) at five sites along an elevation gradient in the Peruvian Andes.

Elevation (m)	Mean (SE)
200	0.28 (0.05)
1000	0.21 (0.06)
1500	0.14 (0.09)
2720	0.33 (0.13)
3025	0.43 (0.13)

Table 5. Average coarse woody debris density (g cm^{-3}) measured at four elevations (1000, 1500, 2720, and 3025 m) in the Peruvian Andes.

Decay class	Mean (SE)	*n*
1	0.50 (0.02)	3
2	0.40 (0.04)	14
3	0.33 (0.02)	47
4	0.22 (0.01)	73
5	0.16 (0.03)	21

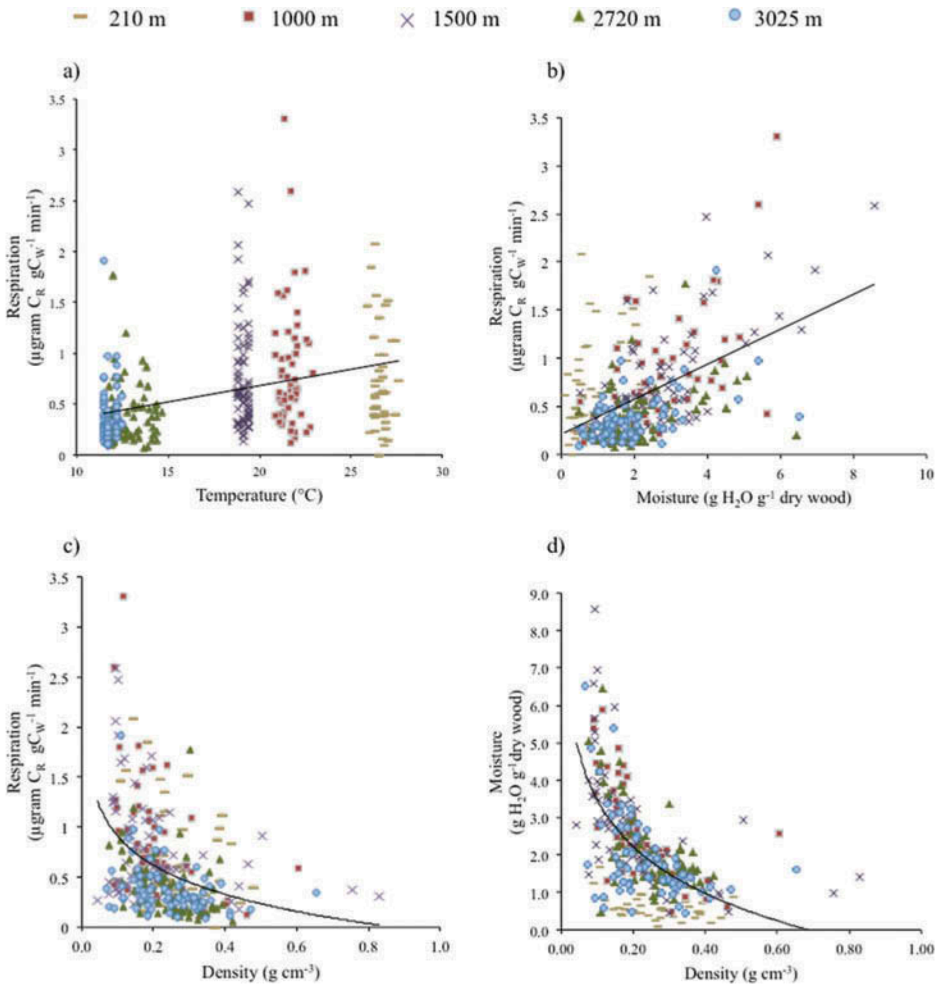

Figure 4. Relationships for data collected in the field at five sites along a gradient of elevation (210–3250 m a.s.l.) Peru. Bivariate regressions between woody debris respiration in the field and: (a) moisture content (linear; $P < 0.001$; $R^2 = 0.25$); (b) temperature (linear; $P < 0.001$; $R^2 = 0.12$); (c) wood density (logarithmic; $P < 0.001$; $R^2 = 0.16$). (d) The relationship between moisture content and wood density was also compared (logarithmic; $P < 0.001$; $R^2 = 0.38$).

where R_{WD} is sample respiration (μg C_R g $C_W{}^{-1}$ min^{-1}) and T is temperature (°C).

The combined influence of temperature, density and water content on WD respiration was significant (Equation (9))

$$R_{WD} = [0.038 \cdot T] - [0.078 \cdot \ln(\rho)] + [0.188 \cdot m] - 0.576 \quad (9)$$

where R_{WD} is sample respiration (μg C_R g $C_W{}^{-1}$ min^{-1}), T is temperature (°C), $\ln(\rho)$ is the natural log of density (g dry wood cm^{-3}) and m is moisture content (g H_2O g^{-1} dry wood) (MANCOVA, $P < 0.001$, $R^2 = 0.42$).

Based on multiple samples measured from the same WD segment, respiration was significantly related to moisture and the segment that it was removed from (MANCOVA, $P < 0.001$, $R^2 = 0.90$). For samples taken from the same segment, respiration was not significantly influenced by density or temperature.

A one-way ANOVA, followed by a Tukey post hoc test showed that there was a significant difference ($P <$ 0.0001) among mean respiration rates across decomposition classes (Table 6). However, the relations between and amongst decomposition classes at each site were not all significant.

Respiration experiments. During moisture trials, the range of respiration achieved was 0.069 to 2.601 μg C_R g $C_W{}^{-1}$ min^{-1}. Elevated moisture content positively influenced respiration of each sample (two-way ANCOVA, $P < 0.0001$, $R^2 = 0.93$). During temperature trials, the highest respiration rate achieved was 5.886 μg C_R g $C_W{}^{-1}$ min^{-1} for a sample at 31 °C. Elevated temperature positively influenced respiration of each sample (two-way ANCOVA, $P < 0.0001$, $R^2 = 0.93$). The average Q_{10} of samples in temperature experiments was 1.77 (SE = 0.11).

Other above-ground C stocks and fluxes

Few definitive patterns of woody above-ground stocks or fluxes (i.e. FWD stocks, CWD stocks (fallen/standing), WD stocks, AGB stocks, stem productivity, stem mortality, branch fall and branch productivity) were observed across

Table 6. Mean rates of respiration, standard error and number of samples measured at five sites along an altitudinal gradient in the Peruvian Andes.

Elevation (m)				Mean	SE	*n*	Difference
210							
	Mean (all samples)			0.75	0.07	43	–
		Decay class					
			1	0.41	–	1	ab
			2	0.78	0.14	6	ab
			3	0.31	0.07	5	b
			4	0.74	0.09	21	ab
			5	1.02	0.22	10	a
	Mean (decay classes)			0.65	0.15	5	–
1000							
	Mean (all samples)			0.86	0.08	56	–
		Decay class	1	0.37	0.24	2	a
			2	0.26	0.02	2	a
			3	0.53	0.21	4	a
			4	0.71	0.08	24	a
			5	1.14	0.15	24	a
	Mean (decay classes)			0.60	0.18	5	–
1500							
	Mean (all samples)			0.77	0.06	74	–
		Decay class	1	0.56	0.14	4	A
			2	0.28	0.07	3	a
			3	0.32	0.10	5	a
			4	0.67	0.06	25	a
			5	0.96	0.10	37	a
	Mean (decay classes)			0.56	0.16	5	–
2720							
	Mean (all samples)			0.41	0.03	76	–
		Decay class	1	–	–	–	–
			2	0.30	0.13	4	ab
			3	0.32	0.09	18	b
			4	0.37	0.03	33	ab
			5	0.58	0.06	20	a
	Mean (decay classes)			0.39	0.06	5	–
3025							
	Mean (all samples)			0.39	0.03	73	–
		Decay class	1	0.27	0.08	2	a
			2	0.25	0.10	3	a
			3	0.30	0.03	16	a
			4	0.40	0.04	27	a
			5	0.48	0.07	25	a
	Mean (decay classes)			0.34	0.05	5	–
Pooled from all sites							
	Mean (all samples)			0.62	0.03	322	–
		Decay class	1	0.44	0.08	9	abc
			2	0.44	0.08	18	ba
			3	0.33	0.04	48	a
			4	0.57	0.03	131	b
			5	0.84	0.06	116	c
	Mean (decay classes)			0.53	0.11	5	–

Mean, mean rates of respiration (μg C_R g C_W^{-1} min^{-1}); SE, standard error; *n* number of samples. The relationship of density class means is represented by letters (a–c) independently for each elevation, where mean values not joined by the same letter significantly differ from one another.

the five plots (see Appendix, Tables A1, A2). Although insignificant, both AGB and net WD efflux increased with higher temperature (i.e. inversely related with elevation), and fallen CWD stock decreased. The pattern for net WD efflux was observed regardless of total WD stocks. Also insignificant, the proportion of fallen CWD to total CWD and WD stocks increased while the proportion of standing CWD to total CWD stock decreased with temperature.

Balancing above-ground C stocks and fluxes

Balancing above-ground inputs and outputs indicated that some sites were net carbon sources while others were net carbon sinks (Figure 5). Estimates of WD turnover varied among and between sites depending on how it was calculated (Table 7). Estimates for Q_{10} ranged from 1.14 to 1.48 (Table 7).

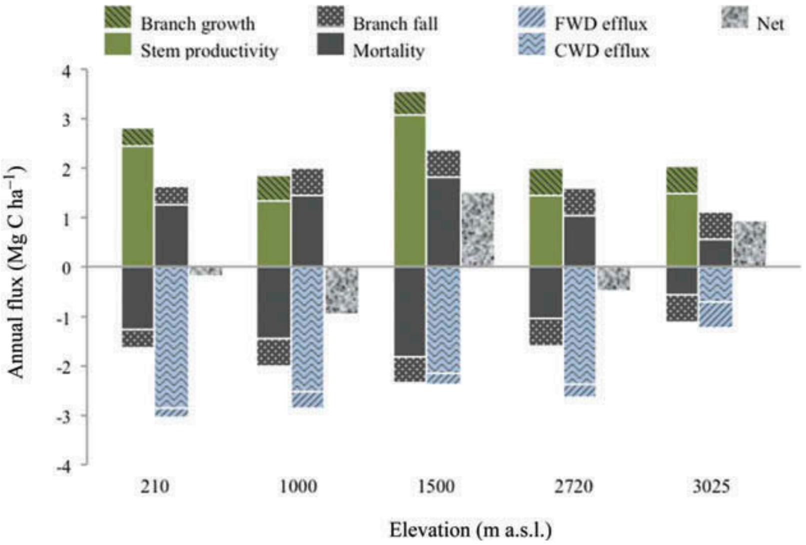

Figure 5. Annual carbon fluxes (Mg C ha^{-1}) of living and dead above-ground biomass from five permanent rainforest plots along an elevation gradient in southern Peru (210–3250 m a.s.l.), Peru; living (branch and stem productivity vs. branch fall and stem mortality), dead (branch fall and stem mortality vs. woody debris efflux), and net flux (indicating amount and direction of C flux from above-ground biomass).

Table 7. Turnover of woody debris (or residence time), decay rate (k) and estimated temperature sensitivity coefficients (Q_{10}) at five elevations, Peruvian Andes.

		Elevation (m)						
		210	1000	1500	2720	3025	R^2	Q_{10}
Turnover								
	(a)	5.42	4.82	3.03	6.81	5.49		
	(b)	2.95	3.37	3.49	4.53	5.22		
	(c)	3.82	3.97	3.24	5.44	5.35		
Decay rate (k)								
	(a)	0.18	0.21	0.33	0.15	0.18	0.06	1.14
	(b)	0.34	0.30	0.29	0.22	0.19	0.92	1.48
	(c)	0.26	0.25	0.31	0.18	0.19	0.52	1.33

Turnover (in years) was calculated for all sites in three ways: dividing total woody debris (WD) stocks by (a) WD inputs (i.e. mortality and branch fall), (b) WD outputs (i.e. coarse woody debris respiration) and (c) the average of WD inputs (a) and WD outputs (b). An exponential regression of decay rate (1/residence time) and temperature was used to calculate R^2 and Q_{10} (Equation (8)).

Table 8. Estimated annual efflux (i.e. respiration from woody debris) at present, and predicted increases with increasing temperature for efflux and respiration coefficients (Q_{10}) at each of five elevations in the Peruvian Andes.

	Elevation (m)				
	210	1000	1500	2720	3025
Current mean annual T (°C)	26.4	20.7	18.8	13.5	12.5
Current efflux (Mg C ha^{-1} year^{-1})	3.03	2.90	2.19	2.53	1.20
Predictions for increases in T (°C)					
+2					
Efflux	3.20	3.13	2.38	2.86	1.38
Q_{10}	1.32	1.46	1.51	1.85	2.05
+5					
Efflux	3.73	3.70	2.83	3.53	1.75
Q_{10}	1.51	1.63	1.66	1.95	2.13
+10					
Efflux	4.60	4.65	3.57	4.65	2.36
Q_{10}	1.51	1.60	1.63	1.84	1.97

Warming and efflux

Estimates indicated that increased temperature would increase annual respiration rates for all sites (Table 8). Values for Q_{10} ranged from 1.32–2.05 for a projection of a 2 °C increase in temperature, and from 1.51–1.97 for a projection of an increase of 10 °C (Table 8). Values of Q_{10} were highest for a 5 °C increase in temperature, ranging from 1.51–2.13 (Table 8). Estimates for Q_{10} were consistently greater for higher elevations (i.e. cooler mean annual temperatures).

Discussion

Woody debris stocks (FWD and CWD)

In comparison to WD estimates for lowland Amazonian tropical forests (see Baker et al. 2007) and estimates from around the world (see Palace et al. 2012), total WD stocks in this study were low. Contrary to the proposed hypotheses (H1 and H2), no clear trends of WD stocks were observed along the elevation gradient. Excluding the highest elevation, the proportion of CWD to FWD was fairly consistent along the gradient and agreed with other studies across the Amazon Basin that estimated FWD to comprise 12% to 21% of total fallen WD (Rice et al. 2004; Palace et al. 2007). High FWD stock at 3025 m may be related to different C dynamics and is a possible indicator of recent disturbance. Estimates for the proportion of WD stocks to coarse AGB in this study were relatively low in comparison to, or at some site even lower than, other estimates for the Amazon Basin where WD comprised from 10% to 26% of coarse AGB (Rice et al. 2004; Palace et al. 2007; Chao et al. 2009; Appendix, Table A2).

The proportion of standing CWD stock to total WD stock of 41% at 2720 m was higher than other studies that presented proportions ranging from 10–30% (Clark et al. 2002; Rice et al. 2004; Palace et al. 2007; Pyle et al. 2008). Although the ratio of fallen CWD to total WD seemed to decrease with increasing elevation, no strong trend was observed for standing and fallen CWD stock along the gradient. This could be a result of high stochastic variability of these stocks. For this reason, Pyle et al. (2008) suggested that the proportion of standing dead wood was not a good indicator of site-specific WD dynamics.

The stock of CWD across the five decay classes was in agreement with other studies (Keller et al. 2004; Palace et al. 2007), where the central decay classes, specifically number 3, comprised a high proportion of total CWD stocks. However, some legacies of disturbance could be inferred. Lacking CWD for the least decomposed decay class for 1000 and 1500 m indicated a lack of recent disturbance. In contrast, a higher proportion of CWD in the least decomposed decay class at 3025 m could indicate a recent disturbance, which corroborates our inferences based on high FWD. High stock of CWD in the most decomposed decay class at 210 m perhaps indicates an old disturbance event. Overall, the variability of proportions in various decay classes is a function of the stochastic nature of disturbance and WD inputs (e.g. blowdowns, fire, landsides).

As expected, the density of CWD in more advanced stages of decomposition was progressively lower across all sites. Palace et al. (2008) suggested that specific density estimates for a decay class can be applied across wide areas with similar vegetation types, while cautioning that this may not always be true based on other conflicting variables. Although density estimates were pooled from all plots to provide a more robust sample size, density estimates indicated slight variation among plots. In addition, a review of the literature following a similar description protocol for tropical decay class densities indicates that this caution is warranted (Rice et al. 2004; Baker et al. 2007; Palace et al. 2007). In areas where WD density varies spatially, the use of site-specific density estimates may be most appropriate (Chao et al. 2008).

Controls on respiration from woody debris

In agreement with previous work (Chambers et al. 2001), WD moisture content, density and temperature significantly influenced respiration rates. Field samples showed that mean rates of respiration were higher for more decomposed WD. However, this relation was not statistically significant for all sites, indicating high variability of respiration within decay classes. Wood density was negatively correlated with moisture content both in the field and after saturation, showing that actual water absorption and water absorption potential are both a function of wood density or decay class. In addition, the response of respiration (by microorganisms and fungi) to water content is variable for wood with similar moisture contents but at varying stages of decomposition (Dix 1985). Field data and experimentation showed that temperature strongly influenced respiration rates (e.g. Figure 4).

Other above-ground C stocks and fluxes

A wide range of biotic and abiotic factors that operate across varying local and regional spatial scales influence above-ground stocks and fluxes. AGB, often the best-studied component, is influenced by variability in climate, topography, soil chemistry, and stand-level basal area and wood density (Keller et al. 2001; Baker et al. 2004; Malhi et al. 2006; Anderson et al. 2009). These factors also operate across various scales (c.f. Clark and Clark 2000). Our work suggests a possible, positive relation between temperature and AGB. Work along the same transect of elevation (Girardin et al. 2010; including all sites in this study plus others) indicated that AGB decreased for higher elevations (i.e. increased with higher temperature), primarily because tree stature declined with elevation. Our results also suggest a possible, negative relation between slope and AGB, which contrasts with the findings of Alves et al. (2010). Although our estimates for net primary productivity (NPP) across sites showed no trend with elevation, Girardin et al. (2010) reported a decline in NPP along this same gradient. In addition, although not statistically significant, the best indicator for stem mortality was annual precipitation. Estimates of total WD respiration along the gradient showed that gross fluxes increased with temperature as a result of accelerated decomposer activity (Figure 5; Appendix, Table A1).

Balancing above-ground C stocks and fluxes

Without considering C efflux from WD, all but one of the forest plots along the gradient would be considered net sinks of above-ground C due to accumulation in woody growth. However, upon consideration of WD efflux, estimated net storage of C indicates that three plots are a net source of C. This is in agreement with other studies that have found some tropical forest stands to be net sources of C (Rice et al. 2004; Pyle et al. 2008). Considering that estimates of net flux are above and below the zero benchmark, the estimates appear not to be skewed and are likely to be a reflection of the overall direction of C flux over the time period presented.

Under the assumption of steady-state conditions, net flux should be zero or minimal. In addition, necromass inputs and outputs should be equal and resulting calculations of turnover should be the same. However, our estimates illustrate that necromass outputs and inputs are not equal and these sites are not in equilibrium. Along the gradient, WD plays a role in ecosystem C dynamics and is an indicator of site differences (Pyle et al. 2008). In fact, due to rapid C accumulation at 1500 m, it is possible this site is recovering from a disturbance event. Relatively low stocks of WD suggest that the disturbance either happened some time ago or woody biomass was removed from the site (e.g. fire, landslide, anthropogenic activity).

Warming and efflux

The full breadth of Q_{10} estimates, calculated by using four distinct methods (one short-term and three long-term), ranged from 1.14–2.13. Short-term Q_{10} based on experimentation was estimated to be 1.77 and in close agreement with a long-term Q_{10} estimate of 1.66 based on the relation between field respiration measurements and sample temperature. All estimates were low and contrasted with the results of two other studies conducted along the same transect. The first found a Q_{10} of around 3.9 based on a fungal decay experiment on a common substrate across a gradient (Meier et al. 2010). The second, a fine wood translocation experiment along an elevation transect, found a Q_{10} of 3.1 (Salinas et al. in review). Although no difference was found between long- and short-term Q_{10} in this study, these earlier studies indicate that long-term Q_{10} could be larger than short-term Q_{10}. In the short term, the microbial community should not change much in size or composition but the metabolism of individual microbes or fungi can change rapidly in response to environmental factors. In the long term, however, the community population size and composition should change in response to changes in temperature.

This study also demonstrated that woody debris pools at lower temperatures (i.e. higher elevations) are more sensitive to changes in temperature, based on Q_{10} estimates calculated by using predicted changes in respiration. This is in agreement with studies estimating the sensitivity of soil respiration, which suggest that areas where temperatures are low may be more sensitive to fluctuations in temperature and have higher values for Q_{10} (Lloyd and Taylor 1994; Zheng et al. 2009; Zhou et al. 2009). This includes a soil translocation experiment conducted along our transect (Zimmermann et al. 2009), which showed that values for Q_{10} decreased with increasing temperature (i.e. decreasing elevation).

Limitations and uncertainties

Due to the spatially and temporally episodic nature of WD input, sampling area and protocol could affect estimated WD volume. For example, small-scale studies may be located within or away from large tree falls (Condit 1997) that could result in overestimation or underestimation of WD stocks. In addition, analyses were conducted at the single-plot level, and we recognise the need to survey additional plots at each elevation to build the strength of the observed relations and robustness of results.

The stocks of WD could be misrepresented because density estimates might not be representative of each WD category at each site. Additional error could be a result of density variability within logs: along the log and between inner and outer sections (c.f. Larjavaara and Muller-Landau 2010). There are also limitations in scaling individual measurements of sample respiration to annual respiration. Firstly, estimates of WD respiration could be skewed by increased surface-to-volume ratio after removing a sample from a log despite equilibration with the atmosphere. In addition, annual respiration estimates could be affected by variability in moisture and density within sampled logs, variables that both affect sample respiration. Lastly, the annual estimates presented in this work are based on measurements during the dry season. However, temperature is aseasonal along the gradient, with shifts in precipitation throughout the year. Although no significant relation between mean WD moisture and mean annual precipitation was observed across sites, this might be due to dry-season sampling. Ultimately, estimates of efflux might actually be higher if WD moisture (and respiration from WD) is higher during the wet season.

Although branch fall data are not available for all plots, estimates are important for each plot to avoid underestimating WD inputs. In fact, Palace et al. (2008) suggested that mortality rates alone could underestimate WD production by up to 45%. However, it is likely that the specific contribution that large branches (≥10 cm) make to total FWD and CWD input is variable at each site. The same is true for the contribution of branch growth to NPP, which was estimated to be equal to (or in equilibrium) with branch fall.

Conclusions

Stocks of WD and estimated fluxes of AGB indicated disequilibria between ecosystem C inputs and outputs and suggested potential legacies and timelines of disturbance. Stocks of WD did not show clear patterns with regard to temperature nor other C stocks, indicating variability and complex factors influencing WD stock. Respiration of WD was most influenced by moisture and temperature. In addition, some sites displayed an annual efflux of C from the WD pool, resulting in a net loss of C from AGB storage. Similar patterns were observed for other studies (Rice et al. 2004; Pyle et al. 2008).

Changes in atmospheric and climatic conditions could result in the alteration of WD decomposition and cycling, in addition to influencing other C pools. In warmer climatic conditions, existing WD pools along the Andean tropics, and other high elevation regions, are susceptible to increased C efflux as a result of increased rates of decay. As a result, a temperature increase could cause a temporary efflux of C from the AGB of a stand, specifically from existing WD stocks. This may be accompanied by increased mortality rates and faster turnover (Phillips and Gentry 1994; Phillips et al. 2004). However, a significant increase in C efflux would only proceed until new equilibrium conditions were reached – a process that could operate through various mechanisms and on varying timescales. In addition, it appeared that sites with cooler annual temperatures at higher elevations were more sensitive to equivalent increases in temperature.

Given the appropriate conditions, the C dynamics of a site could be altered substantially by increasing temperature, first resulting in an efflux of C from the WD pool followed by various feedbacks between above- and below-ground C fluxes. Ultimately, increased temperatures and a changing global climate will increase C emissions from WD temporarily and potentially alter patterns of WD dynamics permanently. This has implications not only for the C balance of these sites, but also for the ecosystems that they represent and frame.

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References

Adair EC, Parton WJ, Del Grosso SJ, Silver WL, Harmon ME, Hall SA, Burke IC, Hart SC. 2008. Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. Global Change Biology 14:2636–2660.

Alves LF, Vieira SA, Scaranello MA, Camargo PB, Santos FAM, Joly CA, Martinelli LA. 2010. Forest structure and live above-ground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). Forest Ecology and Management 260:679–691.

Anderson LO, Malhi Y, Ladle RJ, Aragão LEOC, Shimabukuro Y, Phillips OL, Baker T, Costa ACL, Espejo JS, Higuchi N, et al. 2009. Influence of landscape heterogeneity on spatial patterns of wood productivity, wood specific density and above ground biomass in Amazonia. Biogeosciences 6:1883–1902.

Baker TR, Honorio EN, Phillips OL, Martin J, van der Heijden GMF, Garcia M, Espejo JS. 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. Oecologia 152:495–504.

Baker TR, Phillips OL, Malhi Y, Almeda S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF, et al. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10:545–562.

Brown S. 2002. Measuring carbon in forests: current status and future challenges. Environmental Pollution 116:363–72.

Brown S, Lugo AE, Iverson LR. 1992. Processes and lands for sequestering carbon in the tropical forest landscape. Water, Air, and Soil Pollution 64:139–155.

Chambers JQ, Higuchi N, Schimel JP, Ferreira LV, Melack JM. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia 122:380–388.

Chambers JQ, Schimel JP, Nobre AD. 2001. Respiration from coarse wood litter in central Amazon forests. Biogeochemistry 52:115–131.

Chao KJ, Phillips OL, Baker TR, Peacock J, Lopez-Gonzalez G, Vásquez Martínez R, Monteagudo A, Torres-Lezama A. 2009. After trees die: quantities and determinants of necromass across Amazonia. Biogeosciences 6(8):1615–1626.

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99.

Clark DB, Clark DA. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. Forest Ecology and Management 137:185–198.

Clark DB, Clark DA, Brown S, Oberbauer SF, Veldkamp E. 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. Forest Ecology and Management 164:237–248.

Chao KJ, Phillips OL, Baker TR. 2008.Wood density and stocks of coarse woody debris in a northwestern Amazonian landscape. Canadian Journal of Forest Research 38:795–805.

Condit, R. 1997. Forest turnover, diversity and CO_2. Trends in Ecology & Evolution 12:249–250.

Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, et al. 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Global Change Biology 7:357–373.

Davidson EA, Artaxo P. 2004. Globally significant changes in biological processes of the Amazon Basin: results of the Large-scale Biosphere & Atmosphere Experiment. Global Change Biology 10:519–529.

Del Grosso S, Parton W, Stohlgren T, Zheng D, Bachelet D, Prince S, Hibbard K, Olson R. 2008. Global potential net primary production predicted from vegetative class, precipitation, and temperature. Ecology 89:2117–2126.

Dix NJ. 1985. Changes in relationship between water content and water potential after decay and its significance for fungal succession. Transactions of the British Mycological Society 85:649–653.

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J. 1994. Carbon pools and flux of global forest ecosystems. Science 263:185–190.

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281:237–240.

Girardin CAJ, Malhi Y, Aragão LEOC, Mamani M, Huaraca Huasco W, Durand L, Feeley KJ, Rapp J, Silva-Espejo JE, Silman M, et al. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. Global Change Biology 16: 3176–3192.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Harmon ME, Whigham DF, Sexton J. 1995. Decomposition and mass of woody detritus in the dry tropical forest of the Northeastern Yucatan Peninsula, Mexico. Biotropica 27:305–316.

Hoff, van't JH. 1898. Lectures on theoretical and physical chemistry. Part I. Chemical dynamics. Lehfeldt, RA translator. London (UK): Edward Arnold. p. 224–229.

Houghton J, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA, editors. 2001. Climate change 2001: the scientific basis (contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge (UK): Cambridge University Press.

Keller M, Bustamante M, Gash J, Silva Dias P, editors. 2009. Amazonia and global change (Geophysical Monograph Series; Vol. 186). Washington (DC): AGU). doi:10.1029/GM186.

Keller M, Palace M, Asner GP, Pereira R, Silva JNM. 2004. Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. Global Change Biology 10:784–795.

Keller M, Palace M, Hurtt G. 2001. Biomass in the Tapajos National Forest, Brazil: examination of sampling and allometric uncertainties. Forest Ecology and Management 154:371–382.

Körner C. 2007. The use of ''altitude'' in ecological research. Trends in Ecology & Evolution 22:569–574.

Kremen C, Niles JO, Dalton MG, Daily GC, Ehrlich PR, Fay JP, Grewal D, Guillery RP. 2000. Economic incentives for rain forest conservation across scales. Science 288:1828–1832.

Laurance WF. 2007. A new initiative to use carbon trading for tropical forest conservation. Biotropica 39:20–24.

Larjavaara M, Muller-Landau HC. 2010. Rethinking the value of high wood density. Functional Ecology 24:701–705.

Lewis SL, Brando PM, Phillips OL, van der Heijden GMF, Nepstad D. 2011. The 2010 Amazon drought. Science 331:554.

Lloyd J, Taylor JA. 1994. On the temperature dependence of soil respiration. Functional Ecology 8:315–323.

Luyssaert S, Schulze E -D, Borner A, Knohl A, Hessenmoller D, Law BE, Ciais P, Grace J. 2008. Old-growth forests as global carbon sinks. Nature 455:213–215.

Malhi Y, Grace J. 2000. Tropical forests and atmospheric carbon dioxide. Trends in Ecology & Evolution 15:332–337.

Malhi Y, Phillips OL, editors. 2005. Tropical forests and global atmospheric change. Oxford (UK): Oxford University Press.

Malhi Y, Saatchi S, Girardin CAJ, Aragão LEOC. 2009. The production, storage, and flow of carbon in Amazonian forests, p. 355–372. In: Keller, M., Bustamante, M., Gash, J. and P. Silva Dias, editors. Amazonia and Global Change (Geophysical Monographs Series; Vol. 186). Washington (DC): AGU.

Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S. 2010. Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Global Change Biology 16:3171–3175.

Malhi Y, Wood D, Baker TR, Wright JA, Phillips OL, Cochrane T, Meir P, Chave J, Almeida S, Arroyo L, et al. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. Global Change Biology 12:1107–1138.

Martin AR, Thomas SC. 2011. A reassessment of carbon content in tropical trees. PLoS ONE 6:e23533. doi:10.1371/journal.pone.0023533.

Meier CL, Rapp J, Bowers RM, Silman M, Fierer N. 2010. Fungal growth on a common wood substrate across a tropical elevation gradient: temperature sensitivity, community composition, and potential for above-ground decomposition. Soil Biology and Biochemistry. doi:10.1016/j.soilbio.2010.03.005.

Melillo J, McGuire DA, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL. 1993. Global climate change and terrestrial net primary production. Nature 363:234–240.

Nascimento HEM, Laurance WL. 2002. Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. Forest Ecology and Management 168:311–321.

Palace M, Keller M, Asner GP, Silva JNM, Carlos P. 2007. Necromass in undisturbed and logged forests in the Brazilian Amazon. Forest Ecology and Management 238:309–318.

Palace M, Keller M, Frolking S, Hurtt H. 2012. A review of above ground necromass in tropical forests. In: Sudarshana P, Nageswara-Rao M, Soneji JR, editors. Tropical forests. Rijeka (Croatia): InTech.

Palace M, Keller M, Silva H. 2008. Necromass production: studies in undisturbed and logged Amazon forests. Ecological Applications 18:873–884.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, et al. 2011. A large and persistent carbon sink in the world's forests. Science 333:988–993.

Phillips OL, Baker TR, Arroyo L, Higuchi N, Killeen TJ, Laurance WF, Lewis SL, Lloyd J, Malhi Y, Monteagudo A, et al. 2004. Pattern and process in Amazon tree turnover, 1976–2001. Philosophical Transactions of the Royal Society of London Series B–Biological Sciences 359: 381–407.

Phillips OL, Gentry AH. 1994. Increasing turnover through time in tropical forests. Science 263:954–958.

PP Systems. 2002. Operator's manual, Version 1.00. EGM-4 environmental gas monitor for CO_2. Hitchin (Hertfordshire): PP Systems Inc.

PP Systems. 2003. Operator's manual, Version 3.30.SRC-1/CPY-2 closed system chambers (for use with all EGMs (1/2/3/4) and CIRAS-1). Hitchin (Hertfordshire): PP Systems Inc.

Pyle EH, Santoni GW, Nascimento HEM, Hutyra LR, Vieira S, Curran DJ, van Haren J, Saleska SR, Chow VY, Carmago PB, et al. 2008. Dynamics of carbon, biomass, and structure in two Amazonian forests. Journal of Geophysical Research–Biogeosciences 113:G0B008. doi:10.1029/2007JG00059.

Rice AH, Pyle EH, Saleska SR, Hutyra L, Camargo PB, Portilho K, Marques DF, Palace M, Keller M, and Wofsy SC. 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecological Applications 14: s55–71.

Saatchi SS, Harris NL, Brown S, Lefsky M, Mitchard ETA, Salas W, Zutta BR, Buermann W, Lewis SL, Hagen S, et al. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. Proceedings of the National Academy of Sciences of the United States of America 108: 9899–9904.

Salinas N, Malhi Y, Aragão LEO, Meir P, Silman M, Roman Cuesta R, Huaman J, Salinas D, Huaman V, Gibaja A, et al. In Review. High sensitivity of fine wood decomposition to temperature along a tropical forest elevation transect. New Phytologist, in review.

Sampaio EVSB, Dall'Olio A, Nunes KS, Lemos EEP. 1993. A model of litterfall, litter layer losses and mass transfer in a humid tropical forest at Pernambuco, Brazil. Journal of Tropical Ecology 9:291–301.

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana A. 2009. Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000m tropical forest altitudinal gradient. European Journal of Soil Science 60:895–906.

Zheng Z-M, Yu G-R, Fu Y-L, Wang Y-S, Sun X-M, Wang Y-H. 2009. Temperature sensitivity of soil respiration is affected by prevailing climatic conditions and soil organic carbon content: a trans-China based case study. Soil Biology and Biochemistry 41:1531–1540.

Zhou T, Shi P, Hui D, Luo Y. 2009. Global pattern of temperature sensitivity of soil heterotrophic respiration (Q_{10}) and its implications for carbon-climate feedback. Journal of Geophysical Research 114:1–9.

Appendix

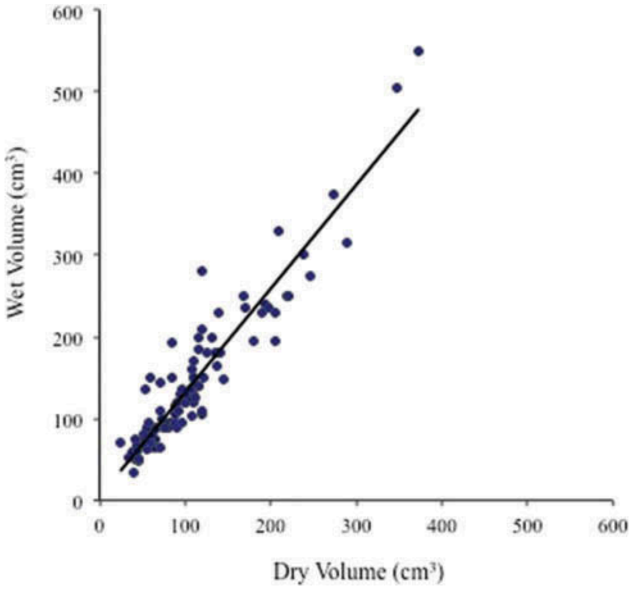


Figure A1. Relation between wet and dry volume as measured for a subset of WD samples ($n = 103$) collected at 210, 2720, and 3025 m. The best-fit linear relation ($P < 0.0001$; $R^2 = 0.88$) was used to estimate initial volume for samples where only dry volume was measured: $V_W = (1.27 \cdot V_D) + 5.15$, where V_D is the measured dry volume in cubic centimetres and V_w is the estimated wet volume in cubic centimetres.

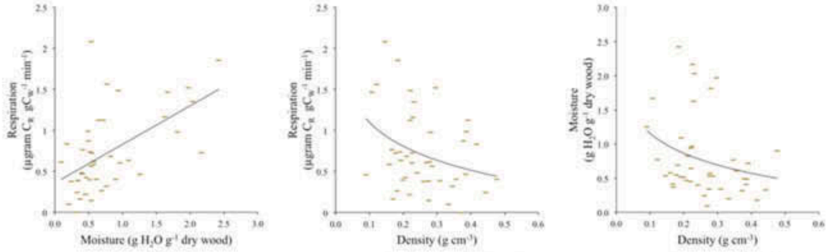
Table A1. Relations between environmental variables and AGB data derived for five permanent rainforest plots along an elevation gradient in southern Peru. Matrix showing relations (i.e. correlation coefficient, R^2, and p-value) between three independent variables (i.e. elevation, mean slope and mean annual precipitation) and several dependent variables ($n = 5$).

		Independent variable								
		Temperature			Mean slope			Mean annual precipitation		
Dependent variable		Correlation	R^2	p-value	Correlation	R^2	p-value	Correlation	R^2	p-value
Stock (Mg C ha^{-1})										
FWD		−0.73	0.53	0.16	0.31	0.10	0.61	−0.63	0.39	0.26
CWD		0.32	0.10	0.60	−0.21	0.04	0.74	0.57	0.32	0.32
CWD (standing)		−0.25	0.06	0.69	0.28	0.08	0.65	0.26	0.07	0.67
CWD (fallen)		0.70	0.49	0.19	−0.55	0.30	0.34	0.67	0.45	0.21
WD (FWD+CWD)		0.10	0.01	0.87	−0.14	0.02	0.83	0.47	0.22	0.43
AGB		0.76	0.57	0.14	−0.85	0.73	0.07	−0.22	0.05	0.73
Flux (MgC ha^{-1} yr^{-1})										
Stem productivity		0.47	0.22	0.43	0.15	0.02	0.81	0.05	0.00	0.94
Stem mortality		0.57	0.32	0.32	−0.04	0.00	0.94	0.80	0.63	0.11
Branch fall		−0.81	0.65	0.10	0.59	0.35	0.30	0.17	0.03	0.79
Total mortality		0.45	0.20	0.45	0.05	0.00	0.94	0.84	0.70	0.08
Average sample flux (1–5)		0.96	0.92	0.01	−0.67	0.45	0.22	0.62	0.39	0.26
WD efflux		0.76	0.57	0.14	−0.61	0.37	0.28	0.66	0.43	0.23
Proportions										
FWD	AGB	−0.85	0.73	0.07	0.48	0.24	0.41	−0.58	0.34	0.30
CWD	AGB	−0.18	0.03	0.77	0.31	0.10	0.61	0.49	0.24	0.41
CWD (standing)	AGB	−0.41	0.17	0.49	0.46	0.22	0.43	0.21	0.05	0.73
CWD (fallen)	AGB	0.09	0.01	0.89	0.12	0.01	0.85	0.72	0.52	0.17
WD (FWD + CWD)	AGB	−0.40	0.16	0.51	0.45	0.20	0.45	0.37	0.14	0.54
FWD	WD	−0.64	0.41	0.25	0.28	0.08	0.65	−0.67	0.45	0.21
CWD	WD	0.64	0.41	0.25	−0.28	0.08	0.65	0.67	0.45	0.21
CWD (standing)	WD	−0.33	0.11	0.59	0.46	0.21	0.44	0.25	0.06	0.69
CWD (fallen)	WD	0.95	0.90	0.01	−0.62	0.39	0.26	0.62	0.38	0.27
FWD	CWD	−0.62	0.38	0.27	0.26	0.07	0.68	−0.70	0.49	0.19
CWD (standing)	CWD	−0.79	0.63	0.11	0.71	0.51	0.18	−0.17	0.03	0.78
CWD (fallen)	CWD	0.80	0.64	0.10	−0.71	0.51	0.18	0.18	0.03	0.77
Stem productivity	AGB	0.03	0.00	0.96	0.60	0.36	0.29	0.18	0.03	0.78
Stem mortality	AGB	0.13	0.02	0.83	0.39	0.15	0.51	0.72	0.52	0.17
Branch fall	AGB	−0.79	0.63	0.11	0.82	0.67	0.09	0.20	0.04	0.75
Total mortality	AGB	−0.06	0.00	0.92	0.53	0.28	0.36	0.68	0.46	0.21

Table A2. Matrix showing proportions of various carbon stock and fluxes to carbon stocks (i.e. AGB, WD, CWD) at five elevations along a gradient of elevation in Peru.

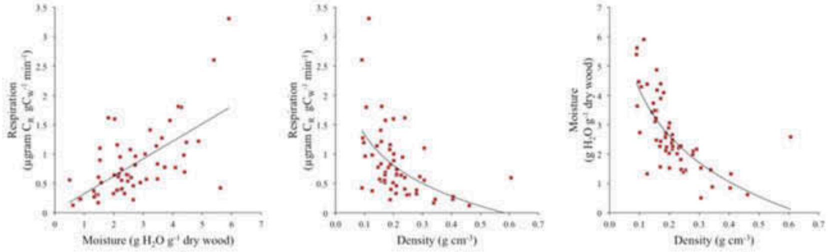
		Elevation (m)				
Proportions		210	1000	1500	2720	3025
FWD	AGB	0.005	0.013	0.013	0.017	0.034
CWD	AGB	0.075	0.112	0.105	0.170	0.045
CWD (standing)	AGB	0.018	0.031	0.032	0.077	0.015
CWD (fallen)	AGB	0.058	0.080	0.073	0.093	0.030
WD (FWD + CWD)	AGB	0.080	0.125	0.118	0.187	0.079
FWD	WD	0.061	0.107	0.109	0.092	0.429
CWD	WD	0.939	0.894	0.891	0.908	0.572
CWD (standing)	WD	0.221	0.251	0.275	0.411	0.187
CWD (fallen)	WD	0.718	0.643	0.616	0.497	0.383
FWD	CWD	0.065	0.120	0.123	0.101	0.750
CWD (standing)	CWD	0.235	0.281	0.308	0.453	0.327
CWD (fallen)	CWD	0.765	0.719	0.692	0.547	0.670
Stem productivity	AGB	0.022	0.017	0.047	0.024	0.019
Stem mortality	AGB	0.011	0.019	0.028	0.017	0.007
Branch fall	AGB	0.003	0.007	0.008	0.009	0.007
Total mortality	AGB	0.015	0.025	0.036	0.026	0.014

210 m



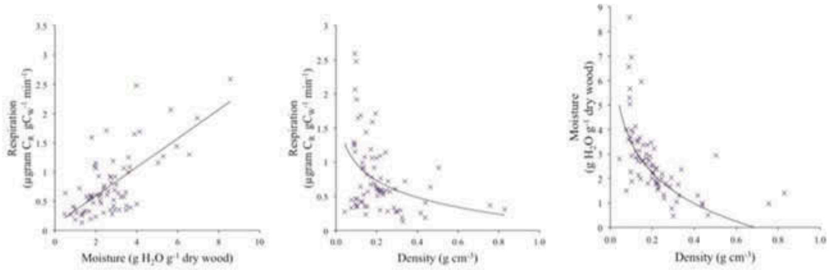
a. ($P<0.001$; $R^2=0.314$) b. ($P<0.033$; $R^2=0.106$) c. ($P<0.075$; $R^2=0.075$)

1000 m



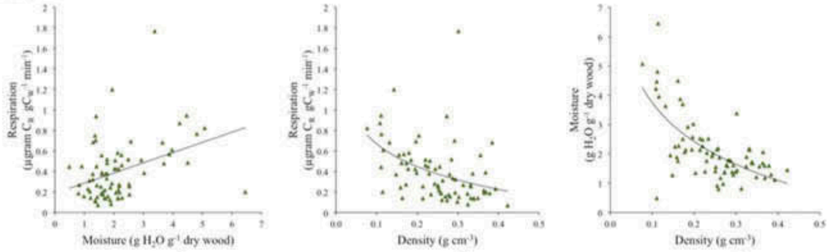
a. ($P<0.001$; $R^2=0.395$) b. ($P<0.001$; $R^2=0.267$) c. ($P<0.001$; $R^2=0.539$)

1500 m



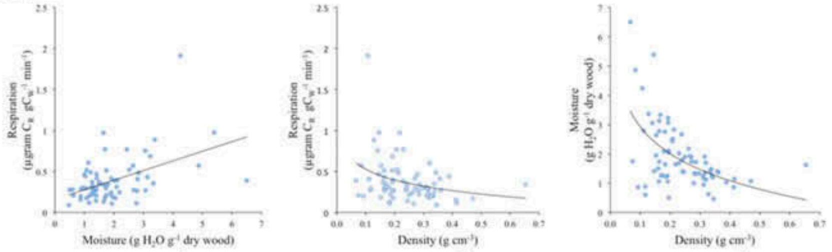
a. ($P<0.001$; $R^2=0.481$) b. ($P<0.001$; $R^2=0.138$) c. ($P<0.001$; $R^2=0.406$)

2720 m



a. ($P<0.001$; $R^2=0.143$) b. ($P<0.001$; $R^2=0.178$) c. ($P<0.001$; $R^2=0.440$)

3000 m



a. ($P<0.001$; $R^2=0.231$) b. ($P<0.001$; $R^2=0.097$) c. ($P<0.001$; $R^2=0.287$)

Figure A2. Relations for data collected in the field at five sites along a gradient of elevation (210–3250 m a.s.l., Peru), here stratified by elevation (see Figure 4 for unstratified results). Bivariate regressions between WD respiration in the field and (a) moisture (linear); (b) wood density (logarithmic). (c) The relation between moisture and wood density was also compared (logarithmic).