



## Respiration from coarse wood litter in central Amazon forests

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**Abstract.** Respiration from coarse litter (trunks and large branches > 10 cm diameter) was studied in central Amazon forests. Respiration rates varied over almost two orders of magnitude (1.003–0.014  $\mu\text{g C g}^{-1} \text{ C min}^{-1}$ ,  $n = 61$ ), and were significantly correlated with wood density ( $r_{\text{adj}}^2 = 0.42$ ), and moisture content ( $r_{\text{adj}}^2 = 0.39$ ). Additional samples taken from a nearby pasture indicated that wood moisture content was the most important factor controlling respiration rates across sites ( $r_{\text{adj}}^2 = 0.65$ ). Based on average coarse litter wood density and moisture content, the mean long-term carbon loss rate due to respiration was estimated to be  $0.13 \text{ yr}^{-1}$  (range of 95% prediction interval (PI) =  $0.11\text{--}0.15 \text{ yr}^{-1}$ ). Comparing mean respiration rate with mean mass loss (decomposition) rate from a previous study, respiratory emissions to the atmosphere from coarse litter were predicted to be 76% (95% PI = 65–88%) of total carbon loss, or about  $1.9$  (95% PI =  $1.6\text{--}2.2$ )  $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ . Optimum respiration activity corresponded to about  $2.5 \text{ g H}_2\text{O g}^{-1}$  dry wood, and severely restricted respiration to  $< 0.5 \text{ g H}_2\text{O g}^{-1}$  dry wood. Respiration from coarse litter in central Amazon forests is comparable in magnitude to decomposing fine surface litter (e.g. leaves, twigs) and is an important carbon cycling component when characterizing heterotrophic respiration budgets and net ecosystem exchange (NEE).

### Introduction

Net ecosystem exchange (with the atmosphere) (NEE) is the difference between gross primary production (GPP), and total respiration ( $R_t$  = heterotrophic + autotrophic). Because NEE is the difference between two relatively large fluxes, NEE is typically an order of magnitude less than either GPP or  $R_t$ . Eddy covariance measurements have indicated that Amazon forests are acting as a net carbon sink (negative NEE) on the order of  $1.0\text{--}5.9 \text{ Mg C}$

$\text{ha}^{-1} \text{yr}^{-1}$  (Mahli et al. 1998; Grace et al. 1995; Fan et al. 1990). This measured sink has been corroborated by forest inventory plot data (Phillips et al. 1998). However, given the many potential sources of error in these large-scale measurements (Mahli et al. 1998; Goulden et al. 1996; Keller et al. 1996), a 95% confidence interval about the magnitude of the sink strength for Amazon forests would probably not preclude carbon balance. Independent ground measurements of all significant carbon fluxes (e.g.  $> 0.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ) are important to help evaluate eddy covariance results, and for understanding the factors that control flux variability.

Respiration exerts a strong control over short- and long-term variation in NEE (Goulden 1997). Thus, to more thoroughly evaluate the hypothesis that tropical forests are acting as net carbon sinks, detailed studies for separate respiratory fluxes are required (e.g. soil organic matter, surface litter), along with factors that control flux variability. There are respiration data for fine surface litter, soil, and live wood from tropical regions (e.g., Sampaio et al. 1993; Ryan et al. 1994; Trumbore et al. 1995; Davidson & Trumbore 1995), but investigations of respiration from coarse litter (dead trunks and branches  $> 10 \text{ cm}$  diameter) are lacking. This is a notable deficiency because wood decay is the primary source of carbon flux to the atmosphere from land-use in the Brazilian Amazon, and this flux may largely offset the proposed carbon sink from undisturbed forests (Houghton et al. 2000).

Because eddy covariance results cannot offer insight into the future behavior of carbon balance, data that characterize how individual carbon pools respond to environmental changes are needed to develop predictive models (Amthor 1989). Without data describing controls over carbon pools and fluxes, however, models are often based on parameterizations that may or may not be accurate. In the CASA model, for example, all surface litter losses are as  $\text{CO}_2$  respired to the atmosphere (Potter 1993), whereas in the Century model, a large fraction of wood carbon is incorporated into soil organic matter (Parton 1987, 1988). This study provides important coarse litter data for tropical forests.

Most litter studies focus on leaves, twigs, fruits and other small organic matter components (fine litter). Tree mortality and damage results in the production of coarse litter whose role in carbon cycling is often overlooked, especially in the tropics (Harmon et al. 1986). Central Amazon forests have coarse litter inputs that are at least 30% of total surface litter production, with a average decomposition rate of about  $0.17 \text{ yr}^{-1}$  (Chambers et al. 2000). Also, based on forest inventory data, Chambers (1998) demonstrated that year-to-year variability in tree mortality results in coarse litter stocks with a strong patchy distribution. Thus, decomposition of coarse litter probably results in

a substantial respiratory flux to the atmosphere with considerable spatial and temporal variability.

Decomposition can be defined as respiration, fragmentation, and leaching of organic matter which comprise all the processes that result in mass loss (Swift et al. 1979). Respiration from surface litter results in CO<sub>2</sub> emissions to the atmosphere, whereas the other two processes result in organic matter inputs to soil or streams. Most wood decomposition studies quantify rates as either mass loss or density change per unit time, and decomposition is treated as an aggregate process. To characterize ecosystem carbon balance, losses must be partitioned into constituent components (e.g. atmosphere, soil, streams). Studies isolating respiratory losses from coarse litter are few, and are limited to temperate old-growth (Carpenter et al. 1988; Marra & Edmonds 1994) and clear-cut coniferous forest (Marra & Edmonds 1996), and a temperate evergreen oak forest (Yoneda 1985). No coarse litter respiration studies have been published for tropical forests. Also, previous studies used static chamber methods which have been shown to overestimate low flux rates, severely underestimate high flux rates, and are generally less accurate than dynamic chamber methods (Lund et al. 1999).

This study was carried out in central Amazon forests. The objectives were to: (i) develop a methodology for using a dynamic chamber to quantify coarse litter respiration rates; (ii) measure rates from a representative sample of dead trees; (iii) investigate relationships between respiration rate, wood moisture content, and wood density; (iv) estimate the fraction of decomposition as respiratory loss to the atmosphere; and (v) compare the magnitude of coarse litter respiration rates with other heterotrophic sources of CO<sub>2</sub>.

## **Materials and methods**

### *Sites*

Work was carried out on permanent plots established by the Biological Dynamics of Forest Fragments Project (BDFFP) (Lovejoy & Bierregaard 1990), a joint project between Brazil's National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazônia – INPA) and the Smithsonian Institution, and INPA's Biomass and Nutrient Experiment (BIONTE) (Higuchi et al. 1997). Data from permanent plots included dates when trees died, their diameter at breast height (DBH, at 1.3 m), and taxonomic information. Plots are located within a ~1,200 km<sup>2</sup> area (2° 30'S, 60°W) approximately 60 km north of Manaus. Vegetation is closed-canopy old-growth forest, with some of the largest trees living over 1000 years (Chambers et al. 1998). Mean annual rainfall is about 2200 mm and

mean annual temperature is 26.7 °C (National Climatic Data Center). There is a distinct dry season during July, August, and September with usually < 100 mm of rain per month. The terrain is undulating, with soils comprising Oxisols on plateaus, Ultisols on slopes, and Spodosols associated with small streams in valley bottoms (Bravard & Righi 1989). Surface (to 5 cm) clay content decreases from about 75% to 5%, and sand content increases from about 10% to 85%, when moving from plateau to valley (Ferraz et al. 1998). Nearly 1,200 tree species have been identified in nearby forests (Ribeiro et al. 1999), most with densities of less than one individual per hectare (Rankin-De Merona et al. 1992).

Permanent forest inventory plots were established in the central Amazon during the 1980s to study the effects of logging practices (BIONTE, 3 1-ha plots) and fragmentation (BDFFP, 18 1-ha plots) on forest structure and functioning. All trees larger than 10 cm DBH were tagged, measured, and, when possible, identified, and during subsequent inventories, recruitment, growth of surviving trees, and mortality were documented. Mortality records from control plots in the primary forest were used to select dead trees for sampling. Sampled trees had been dead for 3 to 12 years, and in most cases, census intervals allowed establishing the time of death to within  $\pm 1.5$  years.

#### *Field methods*

Boles from 155 dead trees were previously sampled for a coarse litter decomposition study (Chambers et al. 2000). Briefly, these 155 samples were randomly chosen from a larger population of 880 dead trees using mortality data from the BDFFP and BIONTE plots. This population was stratified by DBH, wood density, and time since death, to ensure adequate representation of large trees, low and high wood densities, and decomposition time intervals. Cross-sections (usually 3) were removed from the boles with a chainsaw, or a machete for boles in advanced stages of decomposition. Decomposition (mass loss) rate was estimated using the original mass, the mass at the time of sampling, and the time decomposing, assuming first order decay. Rates were inversely correlated with wood density and bole diameter.

For this study, two additional cross-sections were removed from 61 of the previously sampled boles at least 1 m from previous cuts. A wedge was removed from the cross-sections using a machete. The sample was placed in a plastic container (3.8 L, Rubbermaid) and the seal was coated with a small amount of high-vacuum grease (Dow Corning) to minimize leaking. The change in chamber headspace CO<sub>2</sub> concentration was measured as ppm CO<sub>2</sub> s<sup>-1</sup> (or mmol CO<sub>2</sub> mol<sup>-1</sup> air s<sup>-1</sup>,  $\Delta$ CO<sub>2</sub>) using an infra-red gas analyzer (IRGA, LiCor 6200). The chamber was modified to create an air-tight seal with the IRGA sensor head. Measurement of  $\Delta$ CO<sub>2</sub> began once the chamber

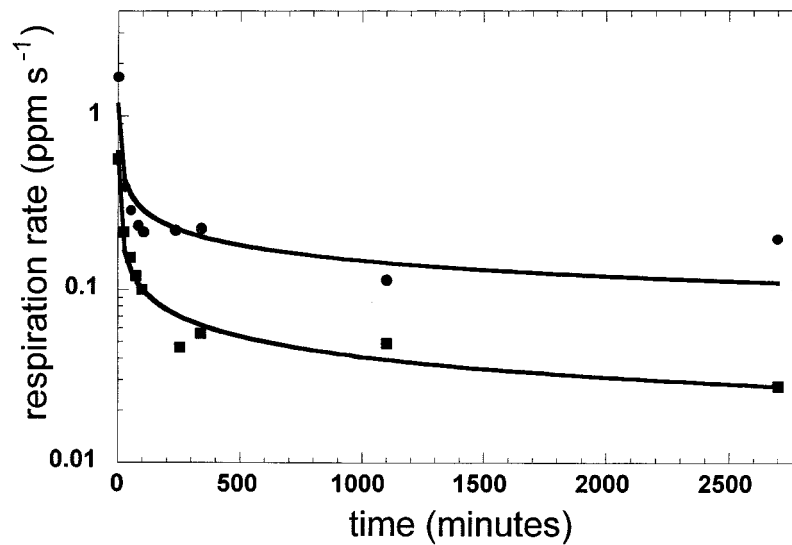


Figure 1. CO<sub>2</sub> emission rates from coarse litter samples removed from boles and immediately placed in the measurement chamber. Respiration rates initially declined rapidly, and then leveled off, as high CO<sub>2</sub> concentrations in the wood pore matrix equilibrated with the atmosphere. After approximately 3 hours, there was no significant decline in CO<sub>2</sub> emissions rate over time, suggesting partial pressure equilibrium with the atmosphere.

humidity stabilized (about 1 minute), and the measurement interval spanned 1–2 minutes. Since coarse litter is not actively transpiring, a correction (flow through the desiccant) for a rise in chamber humidity during the measurement interval was not required. The leak rate of the chamber was determined by creating a CO<sub>2</sub> partial pressure gradient using a soda lime scrubber, and was orders of magnitude lower than typical respiration rates. The volume of the wood sample was estimated (water displacement) to correct the chamber volume, and to determine wood density.

To explore how carbon emissions vary with large changes in environmental conditions, wood samples were also cut from 10 boles located in an approximately 15 year old pasture (one cross-section per log). Respiration rates, wood density and moisture for these samples were calculated as described above.

#### *Atmospheric equilibration*

Initially, samples were placed in the chamber immediately after cutting. Rates of  $\Delta\text{CO}_2$  were very high and declined rapidly (Figure 1). We assumed that this sharp decline was caused by CO<sub>2</sub> partial pressure equilibration between high CO<sub>2</sub> concentrations in the wood pore matrix and the atmo-

sphere. Thacker and Good (1952), For example, found that CO<sub>2</sub> concentration was typically > 10% (vol.) in boles of decomposing sugar maple. To avoid the steepest portion of the decline curve when measuring the initial rate (Figure 1), we allowed samples to equilibrate for 5–10 minutes before placing them in the chamber.

To estimate the average time required for pore matrix CO<sub>2</sub> to equilibrate with the atmosphere, ΔCO<sub>2</sub> rates for 41 samples, representing a wide range of moisture contents and wood densities, were measured a minimum of 4 times after the sample was removed from the log. Since the initial absolute rates varied from 3.59–0.0004 ppm s<sup>-1</sup>, relative rates were calculated as the fraction of the initial rate for each sample. A regression of relative rates vs. time demonstrated that after about 3 hours, there was no significant decline in ΔCO<sub>2</sub> over time. Based on this analysis, the respiration rate for each wedge was estimated by averaging all ΔCO<sub>2</sub> measurements taken ~180 minutes after the sample was removed. At this point, the respiration rate averaged 65% of the initial rate. For some samples in the forest (n = 10), it was only possible to measure the initial rate, and in these cases, respiration rates were estimated as 0.65 of the initial rate.

### *Calculations*

A mass based respiration rate (μg C g<sup>-1</sup> C min<sup>-1</sup>) was calculated using the rate of CO<sub>2</sub> accumulation in the chamber, and the chamber volume. Mass was determined by drying the sample at 70 °C to a constant weight. Carbon content was measured for samples from 70 boles from the decomposition study (Chambers et al. 2000) with a Fisons C/N auto-analyzer, and averaged 49%. Moisture content was expressed gravimetrically (g H<sub>2</sub>O g<sup>-1</sup> dry wood). Wood density was calculated from oven dry weight and water displacement volume. To compare respiration rates with long-term decomposition rates (Chambers et al. 2000), ΔC was also calculated as an annual carbon loss rate assuming that a constant fraction of material is lost per unit time (Olson 1963) from  $k_c = -\ln((m_c - \Delta C)/m_c)$  (Eqn. 1), where ΔC is in units of g C yr<sup>-1</sup>,  $m_c$  is the mass of carbon in the wood, and  $k_c$  is the carbon loss rate (fraction yr<sup>-1</sup>).

### *Statistical analyses*

Statistics were performed using SAS (v. 6.12). Relationships between wood moisture content, wood density, and respiration rates were investigated using multiple linear regression. The  $x$  and  $y$  variables were transformed to calculate best-fit regressions with residuals exhibiting no curvilinearity (homoscedasticity). The site effect (forest vs. pasture) was examined using

*Table 1.* Comparison of wood density and moisture content for coarse litter from two separate studies at the same sites as described in the text. Using single-factor ANOVAs, no significant differences were detected between the two studies. For the test, to increase normality, moisture values were  $\log_{10}$  transformed. Combined average wood moisture and density were 0.96 (1.05–0.87 = 95% C.I.,  $n = 149$ )  $\text{g H}_2\text{O g}^{-1}$  dry wood, and 0.51 (0.48–0.54 = 95% C.I.,  $n = 105$ )  $\text{g cm}^{-3}$ . Combined moisture content was higher than either study separately because some boles were sampled twice, and these were averaged

Variable	Study	n	Average	95% C.I.	min	max	P-value
moisture	respiration	61	0.89	0.80–1.00	0.245	2.291	0.659
	decomposition	137	0.93	0.84–1.02	0.266	5.000	
density	respiration	61	0.53	0.50–0.56	0.272	1.054	0.297
	decomposition	64	0.49	0.47–0.52	0.196	0.993	

site as an indicator variable (Neter et al. 1996, p. 455). Transformations to increase the probability of a normal distribution were performed on variables that exhibited skewed distributions when performing ANOVAs.

#### *Large-scale fluxes*

To assess whether coarse litter respiration relationships were applicable over larger temporal and spatial scales, we had to determine if the range in wood density and moisture content were representative of larger spatial and temporal scales. This study took place during the transition from wet to dry season of 1997 (June–August), whereas sampling from the decomposition study (Chambers et al. 2000) was carried out during both the dry and wet seasons of 1996–97, and covered a larger area. Single-factor ANOVAs showed no significant differences in wood moisture content (log-transformed) or wood density between the two studies (Table 1). Despite being carried out in the dry season, high rainfall often coincided with sampling days during this study, and may explain why the moisture regime of coarse litter was not significantly drier than for sampling that took place during both wet and dry seasons.

Average hectare-scale fluxes were predicted using a mean coarse litter respiration rate, and standing stocks. Average wood density and moisture (Table 1) were used to predict an average coarse litter respiration rate based on regression relationships. Error was expressed as a 95% prediction interval (PI) for the mean response from regression relationships. Because there is also error associated with estimates for average coarse litter moisture and

wood density, a 95% PI was also estimated for error in these predictor variables.

## Results

Coarse litter respiration rates for the forest varied by almost two orders of magnitude ( $1.003\text{--}0.014 \mu\text{g C g}^{-1} \text{ C min}^{-1}$ ,  $n = 61$ ), and varied to a lesser extent in the pasture ( $0.213\text{--}0.004 \mu\text{g C g}^{-1} \text{ C min}^{-1}$ ,  $n = 10$ ). Respiration rates exhibited a strongly skewed distribution, and log-transformations significantly increased the probability of a normal distribution. Averages from log-transformed data were  $0.192 \mu\text{g C g}^{-1} \text{ C min}^{-1}$  for the forest and  $0.023 \mu\text{g C g}^{-1} \text{ C min}^{-1}$  for the pasture. Respiration rates were almost an order of magnitude lower in the pasture, and this difference was highly significant (ANOVA,  $p < 0.0001$ ).

Comparing relationships across sites, respiration rates were highly correlated with both wood density (Figure 2(b)) and wood moisture content (Figure 2(c)). There was also a strong relationship between wood density and moisture content (Figure 2(a)). The relationship between respiration rate and wood density, and between moisture content and wood density, showed a significant site effect. There was no site effect for the relationship between respiration rate and moisture content. Analysis of the forest data alone indicated outliers ( $n = 2$ ) when regressing respiration rates vs. wood density. The outliers were two snags (standing dead trees) that had much lower moisture, and respiration rates, than for downed boles with similar wood density. The mean and range in annual respiration rate (Eqn. 1) was  $0.110 (0.887\text{--}0.007) \text{ yr}^{-1}$  for the forest, and  $0.012 (0.119\text{--}0.002) \text{ yr}^{-1}$  for the pasture.

95% prediction intervals (PIs) were calculated using both error in the predictor variable (i.e. wood density and moisture content), and error in the coefficients from the regression equations (Figure 2, Eqns. (4) & (5)). Using the average coarse litter moisture and 95% CI (Table 1), the average respiration rate (Figure 2, Eqn. (5)) and 95% PI was  $0.12 (0.11\text{--}0.14) \text{ yr}^{-1}$ . Using average coarse litter wood density and 95% CI (Table 1), the average respiration rate (Figure 2, Eqn. (4)) and 95% PI was also  $0.12 (0.11\text{--}0.14) \text{ yr}^{-1}$ . For comparison, Summers (1998) measured average coarse litter wood density of  $0.46 \pm 0.03 (95\% \text{ CI}) \text{ g cm}^{-3}$ , which gave an average respiration rate (Figure 2, Eqn. (4)) and 95% PI of  $0.15 (0.13\text{--}0.18) \text{ yr}^{-1}$ . Analysis of error associated with the predicted coefficients of the regression equations gave similar results. Average respiration rates and 95% PIs for average wood density, moisture content, and Summers (1998) average wood density were  $0.12 (0.11\text{--}0.14) \text{ yr}^{-1}$ ,  $0.12 (0.11\text{--}0.14) \text{ yr}^{-1}$ , and  $0.15 (0.13\text{--}0.17)$



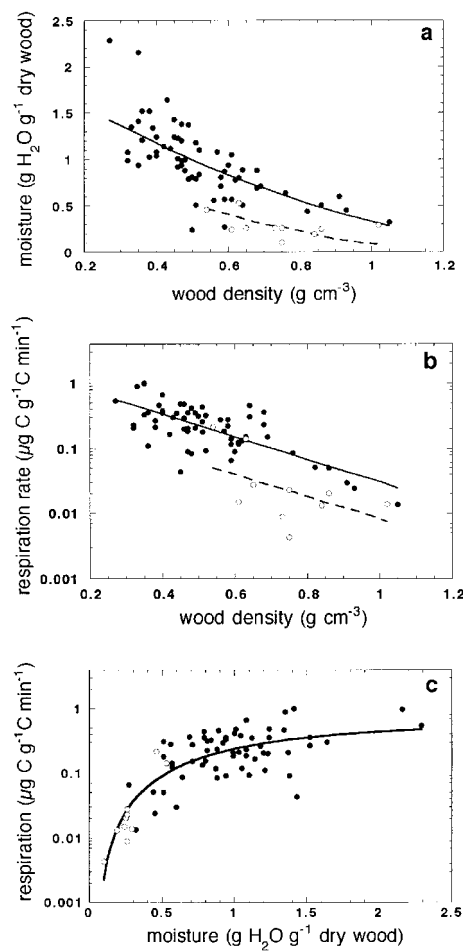


Figure 2. Relationships between wood moisture ( $M$ , g H<sub>2</sub>O g<sup>-1</sup> dry wood), wood density, ( $\rho$ , g dry weight cm<sup>-3</sup>), and respiration rate ( $k_r$ , μg C g<sup>-1</sup> wood C min<sup>-1</sup>). The curves are best-fit regressions with residuals exhibiting homoscedasticity (SAS v. 6.12) giving statistically unbiased estimates. Open circles represent wood sampled in pastures and solid circles in forest. (a)  $M$  and  $\rho$  were highly correlated with a significant site effect (multiple regression and ANOVA,  $\sqrt{M} = 1.14 + 0.268[\text{site} = \text{forest}] - 0.841\rho$ ,  $p < 0.0001$ ,  $r_{\text{adj}}^2 = 0.67$ )(1). (b) In predicting respiration rates, there was a significant site effect for  $\rho$  ( $\text{Log}[k_r] = -0.379 + 0.562[\text{site} = \text{forest}] - 1.71\rho$ ,  $p < 0.0001$ ,  $r_{\text{adj}}^2 = 0.62$ ) (2), with pasture logs respiring at lower rates. (c) However, with respect to  $M$ , there was no site effect, and moisture alone was a good predictor of respiration rates for both pasture and forest sites ( $\text{Log}[k_r] = -0.650 + 1.592\text{Log}[M]$ ,  $p < 0.0001$ ,  $r_{\text{adj}}^2 = 0.65$ )(3). Predicting annual carbon loss rates ( $k_c$ , see text), regression analysis of the forest data alone gave  $\text{Log}[k_c] = -1.788\rho$ , ( $r_{\text{adj}}^2 = 0.42$ , y-intercept not significant,  $p = 0.91$ )(4), for density, and  $\text{Log}[k_c] = -0.889 + 1.42\text{Log}[M]$ , ( $r_{\text{adj}}^2 = 0.39$ )(5), for moisture. An annual loss rate for both forest and pasture was given by  $\text{Log}[k_c] = -0.886 + 1.66\text{Log}[M]$ , ( $r_{\text{adj}}^2 = 0.64$ ) (6).

yr<sup>-1</sup>, respectively. Thus, error analysis showed similar PIs (error bars) when calculated for both the  $x$  (predictor) and  $y$  (response) variables.

We estimated an average coarse litter respiration rate and PI of 0.13 (0.11–0.15) yr<sup>-1</sup> by averaging error in the wood density and moisture error estimates. Chambers et al. (2000) estimated an average decomposition (mass loss) rate of 0.17 yr<sup>-1</sup> for the same sites studied here. Thus, we estimate that 76% (95% PI = 65–88%) of carbon mass loss from coarse litter decomposition is respiratory. Mean standing-stocks of coarse litter in 3 ha of central Amazon forests ranged from 5.7–26.3 Mg C ha<sup>-1</sup>, and averaged 14.9 Mg C ha<sup>-1</sup> (Summers 1998). Thus, as a first approximation, using the average coarse litter respiration rate and 95% PI estimated here, the mean flux of carbon to the atmosphere is estimated to be 1.9 (1.6–2.2) Mg C ha<sup>-1</sup> yr<sup>-1</sup>.

## Discussion

### *Methodological considerations*

The time required for a sample removed from a decomposing bole to reach CO<sub>2</sub> atmospheric equilibrium was about three hours. An important question is whether the rate measured after three hours is indicative of the actual respiration rate when the sample was located within the intact bole. Two factors that can influence the activity of fungi are CO<sub>2</sub> and O<sub>2</sub> concentrations. The interior of decaying boles are characterized by high CO<sub>2</sub> and low O<sub>2</sub> pressures (Thacker and Good 1952) that may restrict the growth of fungi. Removing a sample from the bole may enhance respiration rates by reducing CO<sub>2</sub>, and increasing O<sub>2</sub>, concentrations.

A number of studies have shown, however, that fungal growth is not inhibited by CO<sub>2</sub> concentrations as high as 15% (vol.) (Thacker & Good 1952), and is not markedly reduced until O<sub>2</sub> concentrations fall below about 1.5% (vol.) (Scheffer 1986). The highest CO<sub>2</sub> concentrations found in the heartwood of dead sugar maple trees was about 17%, and O<sub>2</sub> concentrations ranged from 1–14% (Thacker and Good 1952). O<sub>2</sub> concentration above 5% (vol.) have little effect on increasing fungal growth rates (Scheffer 1986). With respect to high CO<sub>2</sub> concentrations, growth of some wood-decay fungi can be slightly stimulated above 10% (vol.) CO<sub>2</sub>, and most show no metabolic decline with high CO<sub>2</sub> (Dix and Webster 1995). This suggests that changes in CO<sub>2</sub> and O<sub>2</sub> concentrations caused by removing samples from decaying boles will not significantly alter fungal metabolism rates. However, these studies were carried out in environments very different from tropical forests, and additional studies are needed to determine the sensitivity of fungal activity to the sampling methodology used here.

Another important consideration is the timing of CO<sub>2</sub> equilibration with the atmosphere. When a wood sample is removed from a decaying bole, the surface area exposed to the atmosphere increases, and a large amount of trapped CO<sub>2</sub> can escape. As this high concentration equilibrates with the atmosphere, there is a large pulse of CO<sub>2</sub>. Regression analysis indicated that about three hours were required until there was no significant decline in CO<sub>2</sub> emission rate. We assumed that this stable rate was respiratory activity. Although not directly comparable, Sampaio et al. (1993) found that about 90% of fine litter losses in a humid tropical forest were respiratory. In combination with our results, it appears that a large fraction of litter decomposition mass loss is respiratory.

#### *Controls over respiration rates*

This study showed that moisture alone accounted for a large part of the variation in coarse litter respiration rates (Figure 2(c)). This relationship appeared to hold for coarse litter decomposing in both the forest and pasture. Wood density was also highly correlated with respiration rates, although this relationship appears to have been ultimately controlled by the relationship between wood moisture and wood density (Figure 2(a), 2(b)). Wood density changes slowly over time, whereas wood moisture can rapidly respond to temporal changes in precipitation. Low density wood that experiences dry conditions, for example, will exhibit relatively low respiration rates, but when wet-up by precipitation, will probably experience a rapid increase in rates (Figure 2(c)).

Fungi do not respond to moisture content but to water potential, and the water potential of decayed wood is higher than intact wood at the same moisture content (Dix and Webster 1995). As wood decays, cell wall polymers are hydrolyzed, and the matrix potential at a given water content rises, increasing the availability of moisture to microbial communities (Dix 1985). At very low moisture contents, the water potential for decayed wood can be > 5 times higher than intact wood at the same moisture content (Dix 1985). Fungi can also actively regulate wood moisture content, creating a more favorable decay environment (Rayner and Boddy, 1988). Fungi responsible for wood decay respond rapidly to changes in water potential, and growth is severely limited below -4.0 Mpa (Boddy 1983a; Dix 1984).

Optimal water potential values are at least -1.0 Mpa, and probably higher in many cases (Boddy 1983a). Averaging the regression relationships between moisture content (g H<sub>2</sub>O g<sup>-1</sup> dry wood) and water potential Dix (1985) predicts that decayed wood moisture contents of 2.5 and 0.5 g H<sub>2</sub>O g<sup>-1</sup> dry wood should correspond to optimal (-1.0 Mpa) and severely limited (-4.0 MPa) fungal growth rates, respectively. These limits coincide well with the

relationship found between wood moisture and respiration rates in this study (Figure 2(c)). Wood-decay fungi are affected by relatively small changes in moisture content (Dix and Webster 1995, and references therein), and a strong relationship between moisture content and respiration rate is expected. Due to the relationships between wood density, moisture content, and respiration rates found in this study (Figure 2), there appears to be a non-linear response, with respiration rates continuously increasing as decomposition proceeds, wood density declines, and water potential increases. Moisture contents above  $2 \text{ g H}_2\text{O g}^{-1}$ , for example, were associated with low wood densities and high respiration rates (Figure 2). From these relationships, a simple model can be developed to explore the time course of respiratory carbon losses from coarse litter.

If we assume that fungal hyphae colonize a log from the periphery and move inward toward the core at a constant rate ( $k_h$ ), then the volumetric fraction of the log that is colonized is given by:  $f_c = 2k_h t/r - k_h^2 t^2/r^2$  (Eqn. 2), where  $t$  is the time since initial colonization and  $r$  is the radius of the log. Assuming a linear relationship between  $k_h$  and wood density ( $\rho$ ) (high density wood is colonized more slowly), and employing the regression equations for moisture content vs. wood density, respiration rate vs. moisture content, we can simulate how respiration rates would vary with time.

The resulting time-series predict that the course of decomposition should differ between density classes. High density wood exhibits a relatively long colonization phase (Figure 3(d)), whereas low density wood follows first-order decay (single-exponential) more closely (Figure 3(a)). In support of this model, Harmon et al. (1995) found that decomposing wood from four tropical trees species exhibited time-series curves similar to Figure 3, with the high density species exhibiting a longer colonization phase (M. Harmon, personal communication). Most studies assume first-order decay and use a single-exponential model when calculating organic matter decomposition rates (Wieder and Lang 1982). Deviations from the single-exponential model are important for determining the timing of respiratory losses. However, when estimating long-term rates, a single-exponential model makes reasonable predictions (i.e., the curves in Figure 3 converge over time).

The relationships described above concern downed coarse litter in the forest interior. These relationships may change in contrasting environments. High mortality on the edges of forest fragments, for example, result in dramatically increased coarse litter production rates (Laurance et al. 1997). Also, in pastures, coarse litter moisture contents and respiration rates were significantly lower for the same wood density values (Figure 2(a)). Snags (standing dead trees) also exhibited lower moisture contents ( $0.245$  and  $0.270 \text{ g H}_2\text{O g}^{-1}$  dry wood,  $n = 2$ ) and respiration rates ( $0.008$  and  $0.036 \text{ yr}^{-1}$ ),

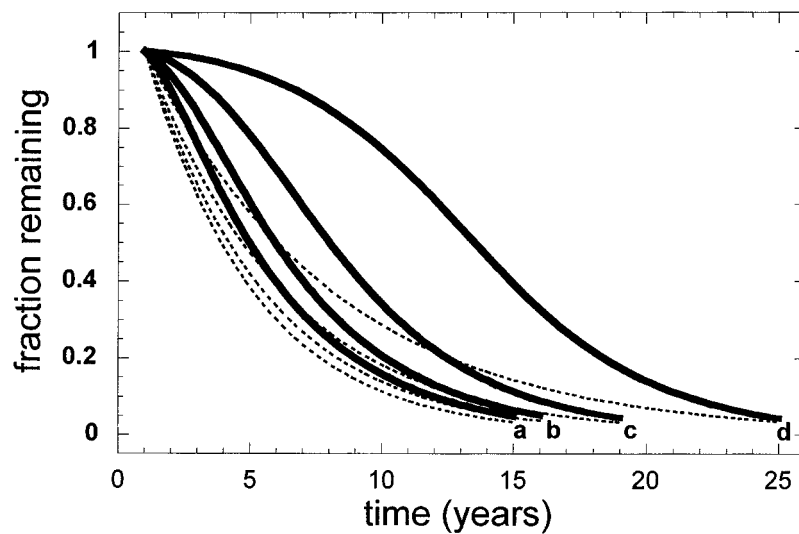


Figure 3. Simulated timing of mass loss due to respiration for increasing values of initial wood density ( $\rho$ ,  $\text{g cm}^{-3}$ ). The qualitative model used to generate these curves assumes that the rate of fungal penetration ( $k_h$ ,  $\text{cm yr}^{-1}$ ) is an inverse linear function of wood density, with higher density wood being colonized more slowly ( $\rho$  and  $k_h$  varying from 0.90–0.30 and 2.0–8.0, a–d, respectively). High density wood is predicted to experience a lag-time in respiration corresponding to a colonization phase. Non-linear mass loss curves (solid line) are compared with those predicted using a single-exponential model (dotted line).

and were identified as outliers in the regression analysis of the forest data. Coarse litter that is exposed to increased solar radiation will be drier than coarse litter in the forest interior, and will also experience larger fluctuations in moisture content (Boddy 1983b; Dix and Webster 1995). This is an important area for further research because coarse litter in disturbed areas has been identified as the main contributor of the land-use flux of carbon to the atmosphere for the Brazilian Amazon (Houghton et al. 2000).

#### *Large-scale carbon fluxes*

The loss of carbon from decomposing wood must either enter the atmosphere as  $\text{CO}_2$  or be redistributed within the ecosystem (e.g. soils, streams). In this study we estimated that about 76% of carbon is lost to the atmosphere ( $1.9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ), and 24% is redistributed. In comparison, fluxes to the atmosphere from soil respiration (surface fine litter and soil, including root respiration) in forests in the vicinity of the BIONTE plots were  $26.0 \pm 6.8$  (95% C.I.)  $\text{Mg C ha}^{-1} \text{ yr}^{-1}$  (Sotta 1998). For a drier evergreen forest in the eastern Amazon, soil surface fluxes were estimated to be  $1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$

for fine surface litter, and  $6.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  for soil organic matter to 5 m depth (Trumbore et al. 1995). Total soil carbon flux in the eastern Amazon, including root respiration, was estimated to be  $23.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ . If soil carbon fluxes in the central Amazon are partitioned similarly to forests in the eastern Amazon, the magnitude of the carbon flux from coarse litter is comparable to that from fine surface litter.

When calculating NEE, net primary production (NPP) is balanced against total heterotrophic respiration ( $R_h$ ). Over large spatial scales, NEE fluxes as small as  $0.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ , can have important implications for the global carbon cycle (Law et al. 1999; Goulden et al. 1996). A number of studies have indicated that tropical forests are acting as net carbon sinks (Malhi et al. 1998; Phillips et al. 1998; Grace et al. 1995; Fan et al. 1990). When simply scaled over the entire Amazon basin ( $\sim 5.0 \times 10^8 \text{ ha}$ ) these proposed sinks ( $0.5\text{--}3.0 \text{ Pg yr}^{-1}$ ) represent a sizable portion of emissions from fossil fuels ( $5.7 \text{ Pg yr}^{-1}$ ) and deforestation ( $2 \text{ Pg yr}^{-1}$ ) (Houghton 1991). Thus, independent measures of source pools fluxes are important to help assess the accuracy of eddy covariance results. Also, understanding the biological and physical controls over the source and magnitude of respiratory fluxes are important for developing predictive models. We have demonstrated that respiration from coarse litter is a significant carbon flux, and that wood moisture content explains a large portion of flux variability both in forests and pastures.

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