

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/225392232>

Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon

Article in *Oecologia* · February 2000

DOI: 10.1007/s004420050044

CITATIONS

282

READS

243

5 authors, including:



Joshua P Schimel

University of California, Santa Barbara

244 PUBLICATIONS **19,250** CITATIONS

[SEE PROFILE](#)



Leandro V. Ferreira

Museu Paraense Emilio Goeldi - MPEG

130 PUBLICATIONS **5,696** CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



National Climate Assessment (3rd) [View project](#)



How environmental changes affect soil biogeochemistry [View project](#)

All content following this page was uploaded by [Leandro V. Ferreira](#) on 23 December 2013.

The user has requested enhancement of the downloaded file.

Jeffrey Q. Chambers · Niro Higuchi
 Joshua P. Schimel · Leandro V. Ferreira
 John M. Melack

Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon

Received: 14 June 1999 / Accepted: 31 August 1999

Abstract Decomposition rate constants were measured for boles of 155 large dead trees (>10 cm diameter) in central Amazon forests. Mortality data from 21 ha of permanent inventory plots, monitored for 10–15 years, were used to select dead trees for sampling. Measured rate constants varied by over 1.5 orders of magnitude ($0.015\text{--}0.67\text{ year}^{-1}$), averaging 0.19 year^{-1} with predicted error of 0.026 year. Wood density and bole diameter were significantly and inversely correlated with rate constants. A tree of average biomass was predicted to decompose at 0.17 year^{-1} . Based on mortality data, an average of 7.0 trees $\text{ha}^{-1}\text{ year}^{-1}$ died producing $3.6\text{ Mg ha}^{-1}\text{ year}^{-1}$ of coarse litter (>10 cm diameter). Mean coarse litter standing-stocks were predicted to be 21 Mg ha^{-1} , with a mean residence time of 5.9 years, and a maximum mean carbon flux to the atmosphere of $1.8\text{ Mg C ha}^{-1}\text{ year}^{-1}$. Total litter is estimated to be partitioned into 16% fine wood, 30% coarse wood, and 54% non-woody litter (e.g., leaves, fruits, flowers). Decomposition rate constants for coarse litter were compiled from 20 globally distributed studies. Rates were highly correlated with mean annual temperature, giving a respiration quotient (Q_{10}) of 2.4 ($10^{\circ\text{C}^{-1}}$).

Key words Wood decomposition · Coarse surface litter · Tree mortality · Carbon cycling models · Global biogeochemistry

J.Q. Chambers · J.P. Schimel · J.M. Melack
 Department of Ecology, Evolution and Marine Biology,
 University of California,
 Santa Barbara, CA 93106, USA

J.Q. Chambers (✉) · N. Higuchi
 Departamento de Silvicultura Tropical,
 Instituto Nacional de Pesquisas da Amazônia (INPA,
 National Institute of Amazon Research), CP-478,
 Manaus, Amazonas, 69011-970, Brazil
 e-mail: jeff@inpa.gov.br

J.Q. Chambers · L.V. Ferreira
 Biological Dynamics of Forest Fragments Project, INPA, CP-478,
 Manaus, Amazonas, 69011-970, Brazil

Introduction

Dead trees play a number of important roles in the structure and function of ecosystems (Franklin et al. 1987). They provide habitat for a large variety of organisms (Harmon et al. 1986), influence the potential for wild-fires (Uhl and Kauffman 1990; Kaufmann et al. 1998), and play important roles in carbon and nutrient cycles (Lambert et al. 1980; Fahey 1983; Krankina and Harmon 1995). Because dead trees decompose relatively slowly, and tree mortality is episodic, few studies have focused on the biogeochemistry of coarse surface litter, and studies are especially lacking in the tropics.

The forests of the world contain about 80% of terrestrial above-ground biomass, and about 40% of all forests are in the Neotropics (Dixon et al. 1994). Tropical forests account for about 35% of global net primary production (Melillo et al. 1993; Potter et al. 1993). Malhi et al. (1998) estimate that Amazon forests process (via gross primary production) an amount equal to all atmospheric CO_2 every 25 years. Tropical forests may also play an important role as a net sink for atmospheric CO_2 (Grace et al. 1995; Malhi et al. 1998; Phillips et al. 1998). To predict how global changes will affect carbon cycling in tropical forests, understanding the behavior of individual components is important. For the coarse litter, basic parameters such as standing stocks, decomposition rates, and factors controlling rates have not been characterized.

Decomposition studies in the tropics generally focus on fine surface litter (e.g., leaves and twigs). Tropical coarse litter decomposition studies include rate estimates of 0.11 year^{-1} for stumps of five tree species in Puerto Rico (Odum 1970), $0.76\text{--}1.23\text{ year}^{-1}$ for logs of one species from West Malaysia (Yoneda et al. 1977), 0.57 year^{-1} for logs of one species from West Sumatra (Yoneda et al. 1990), and 0.46 year^{-1} for trees that died and completely decomposed over a 10-year interval in Panama (Lang and Knight 1979). None of these studies sampled from a representative population of dead trees.

Global and regional carbon cycling models are being employed to predict the behavior of tropical forests un-

der various global change scenarios (Cao and Woodward 1998; Pan et al. 1998; Tian et al. 1998). An important part of model development is predicting carbon pools and fluxes associated with undisturbed forest. The motivation for this study was to provide carbon cycling models with useful parameterization and validation information for coarse litter. The specific goals were (1) to measure decomposition rate constants for boles (the trunk from base to first major branch) of dead trees, (2) to quantify factors controlling decomposition rate constants, (3) to predict standing stocks, production rates, and the mean residence time of coarse litter, and (4) to investigate controls over coarse litter decomposition at the global scale.

Materials and methods

Study sites and dead tree selection

The measurements were carried out over a 2-year period (1996–1997) on permanent plots monitored by the Biological Dynamics of Forest Fragments Project (BDFFP) of the Smithsonian Institution (Lovejoy and Bierregaard 1990; Rankin-De Merona et al. 1992) and the Biomass and Nutrient Experiment (BIONTE) of the National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazônia-INPA). Data from permanent plots included dates when trees died, their diameter and breast height (DBH, i.e., at 1.3 m) and taxonomic information. Plots spanned a 50 × 40 km area (~2°30' S, 60° W) approximately 70 km north of Manaus in the Brazilian Amazon with an elevation of 100–150 m. The vegetation is old-growth dense tropical evergreen forest (*terra firme*, or not seasonally inundated) with some trees living up to 1400 years (Chambers et al. 1998). Mean annual rainfall is about 2200 mm and mean average temperature is 26.7°C, with a distinct dry season from June to September. Soil type varies gradually with elevation comprising Oxisols on plateaus (about 80% clay), Ustisols on slopes, and Spodosols (2–5% clay) in valleys (Bravard and Righi 1989). Nearly 2000 species of vascular plants have been identified in this region (Ribeiro et al. 1994). A survey of BDFFP plots identified about 700 species of trees >10 cm DBH, most of which have abundances of less than 1 individual ha⁻¹ (Rankin-De Merona et al. 1992).

Hectare-sized permanent plots were established in the central Amazon during the 1980s to study the effects of various logging practices (BIONTE) and fragmentation (BDFFP) on forest ecology. 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 21-ha-sized plots that were established as controls (at least 100 m from forest edges) in the primary forest were used to select dead trees for sampling. Census intervals allowed establishing the time of mortality to within an average of ±1.2 years.

A total of about 880 trees died in the 21 ha of permanent plots during inventories up to 1992. This population of dead trees was stratified to test for controls over decomposition rates. Wood density and diameter have been shown to control wood decomposition rates in tropical forests (Bultman and Southwell 1976; Harmon et al. 1995), but large trees, and trees representing the extremes of density are relatively rare. In Amazon forests, the largest trees contain a disproportionately large fraction of the forest biomass (Brown et al. 1995). To obtain adequate samples for a number of density and size classes, mortality records were sorted and dead trees were selected randomly. Size classes were large trees (>50 cm DBH), mid-sized trees (20–50 cm DBH), and small trees (10–20 cm DBH). Density classes were <0.45 g cm⁻³ for light-, and >0.85 g cm⁻³ for heavy-wooded species. Mortality was also

stratified by agent and mode of death to test for additional controls over decomposition rates.

Bole sampling

Three cross-sections were cut from each selected dead tree to determine mass loss rate. First, the length of the bole from the base to the first major branch point was measured. The bole was then divided into three equal-length segments and cross-sections (5–10 cm thick) were cut from the center of each section using a chainsaw or, for friable wood, a machete. Cross-sections were weighed on a portable electronic balance and the average thickness was measured. Wedges from each cross-section were removed with a machete, weighed, and returned to the laboratory. Moisture content was determined by drying wood to constant weight at ~70°C in a drying oven.

Estimating decomposition rates

Decomposition rate constants were calculated using a single exponential model that assumes that a constant fraction of the mass is lost per unit time (Olson 1963) given by:

$$k_d = -\ln(M_t/M_o)/t \quad (1)$$

where M_t is the mass at time t and M_o is the original mass of a cross-section, and decomposition rates are given as fractional mass lost per year (year⁻¹). M_t was measured by weighing cross-sections in the field and subtracting moisture content. To estimate M_o , permanent-plot data were used to predict the original mass of an intact cross-section from:

$$M_o = \pi r^2 h \rho \quad (2)$$

where r is the original radius, h is the thickness of the cross-section, and ρ is the oven dry-weight wood density for the species being sampled.

Taxonomic identifications of dead trees enabled us to use wood density values from literature sources in Eq. 2. This presented some difficulties because the availability and quality of botanical data in these species-rich forests varies. Of the potential sample population of dead trees from BDFFP, 73% had been identified to genus and 55% to species. For the BIONTE sites, species identifications were determined by field-workers who often have comprehensive knowledge of forest tree species. When common names were unambiguous to genus, they were cross-referenced to scientific names using Silva et al. (1977) and Higuchi et al. (1985).

Using taxonomic information, wood density values were obtained from literature sources (Le Cointe 1934; IPT 1989; Reyes et al. 1992; Fearnside 1997). However, in most cases, even when species identifications were available, wood density data for a particular species was rarely available. Of all dead trees identified, 6% had wood density values for the species, and 40% for the genus. Despite this limitation, wood densities for dead trees ranged from 0.33 to 0.92 g cm⁻³. This range captures a large portion of the variability in wood density found in these forests. Because many species are rare, and sampling high-density species is difficult, it was not logistically feasible to gather additional data on wood density for the species not found in the literature.

Fragmentation often made estimating original diameters difficult or impossible. To estimate the original radius for use in Eq. 2, a function describing change in diameter with height (i.e., taper) was developed. A tape was placed on boles of recently uprooted trees (without buttresses or irregular stem geometries), and diameters at known distances were measured with tree calipers. Since taper is more extreme at the base of a bole, diameter was measured a number of times up to 1.3 m (DBH), and every meter thereafter.

Errors estimating wood density and original cross-section diameters for use in Eq. 2 had a large effect on estimated rates over short decomposition intervals. For boles that had been decomposed

ing for only a few years, errors estimating the original mass were large compared to mass lost via decomposition. Using estimated error in cross-section diameter and wood density, and a decomposition rate of 0.20 year⁻¹, errors exceeded 25% for decomposition intervals <3 years. Thus, only trees that had been dead for more than 3 years were included in the analyses.

Error in estimating decomposition rate constants was investigated using a simple model. It was assumed that error in bole diameter and wood density were normally distributed, and error in estimating the time of mortality was uniformly distributed within the census interval. Random deviates were drawn from these distributions and decomposition rate constants were recalculated for each bole sampled. Differences between these rates were used to calculate maximum, minimum, and average error in estimating decomposition rate constants.

In some cases, dead trees could not be found in the field. In most instances, we determined that these boles had completely decomposed using inventory maps. If these completely decomposed dead trees were not included in the sampling population, results would have been biased against fast-decomposing wood. To prevent large overestimates when estimating rate constants using the single-exponential model, we assumed that 5% of the original mass remained for completely decomposed boles.

Tests for controls on decomposition rates

The rate of decomposition depends on a number of substrate quality factors including the size and shape of the material, wood density, relative proportions of cellulose, hemicellulose, and lignin, the presence or absence of polyphenolic extractives (e.g., tannins), and other factors. Studies have also shown that a single-exponential model is often an oversimplification, and that the rate of decomposition can vary over time (Mindermann 1968; Harmon et al. 1995). For this study, we used regression analysis to test for size, wood density, and time as controls over decomposition rate constants. We hypothesized that rate constants would be negatively correlated with size and density, and if rates followed first-order kinetics, independent of time. Statistical analyses were done using SAS (version 6.12).

The effect of time was tested by regressing rate constants against the decomposition time interval. Mass loss fraction is another important variable because variability in decomposition rates may be more dependent on the extent of decomposition than on the absolute time decomposing. However, because decomposition time was limited to 3 and ~12 years, the fraction of mass lost was not independent of wood density. Fast-decomposing wood with little mass loss, and slow-decomposing wood with substantial mass loss were not adequately represented in the sampled population. For this reason, fractional mass loss effects could not be investigated.

One of the assumptions of standard linear regression is that the independent variable is measured without error. Error in the independent variable (x_e) always acts to flatten the slope of the regression. Because wood density was often estimated using the average from the genus, the regression of decomposition rate constant against wood density was biased. The extent of this bias was estimated using the pooled variance of the error in the independent variable (s_e^2) and the variance of the independent variable (s_x^2) to calculate a "reliability ratio" (κ) as: $\kappa = s_e^2 / (s_e^2 + s_x^2)$ (Snedecor and Cochran 1989, p. 173). To estimate s_e^2 , the variances of wood density were pooled (Zar 1996) for 99 genera of Neotropical trees (Reyes et al. 1992; Fearnside 1997) where at least two species per genus were represented. Wood density regression coefficients were corrected using κ .

Preliminary analysis showed a large amount of unexplained variability in decomposition rates. Since mortality is not necessarily coincident with the onset of decomposition, using the death of a tree as time zero could have biased results. Some trees die slowly and may already be in an advanced state of decomposition at the time of death, whereas others are relatively intact. To account for this, mortality was stratified by trees that were downed by other

treefalls, with the expectation that trees that died suddenly would, on average, be more intact than trees that died from other causes (e.g., windthrow, died standing). The spatial orientation of mortality (e.g., standing vs downed) can also affect decomposition activity (Harmon et al. 1986). In some cases, forest inventory data also provided information on the orientation of the tree when it died.

Results

Taper function

A total of 33 trees (DBH 10–60 cm) were sampled for taper. An exponential model provided the best fit for regressions of taper against height (r^2 0.87–0.99) giving the function:

$$d_h = 1.59 \text{DBH}(h^{-0.091}) \quad (3)$$

where d_h is the diameter at height h for a bole of given DBH. Variability in the exponential parameter resulted in errors estimating cross-sectional diameters that averaged 5.0% (SE 0.2%). To test model generality, we compared Eqn. (3) with a taper model based on a sample of over 335 trees (Ribeiro 1996). Differences between model predictions averaged ~4%, indicating that our simple taper model was robust.

Controls over decomposition rates

Decomposition rate constants for 155 boles decomposing >3 years were quantified (38 had completely decomposed). All sampled dead trees were identified to genus (54 genera from 23 families), and 106 were identified to 69 species. Sample sizes for DBH classes were 67 for small trees (10–20 cm), 73 for mid-sized trees (20–50 cm), and 15 for large trees (>50 cm). Sample sizes for density classes were 11 for low (<0.45 g cm⁻³), 133 for mid-range (0.45–0.85 g cm⁻³), and 11 for high (>0.85 g cm⁻³) wood density. Decomposition rate constants varied by over 1.5 orders of magnitude (0.015–0.67 year⁻¹). A square-root transformation of rate constants significantly increased the probability of a normal distribution, with a transformed mean of 0.19 year⁻¹. Error analysis showed that combined error from wood density, taper, and the decomposition time interval introduced potential error in rate constant estimates from 0.000 to 0.397 year⁻¹, and averaged 0.026 year⁻¹ (SE 0.004 year⁻¹).

A square-root transformation of decomposition rate constants resulted in evenly distributed residuals about the regression lines. Of the factors tested, wood density exerted the strongest control over decomposition rates (Fig. 1a). The correlation between wood density and decomposition rates for the known-to-species group was considerably higher than for the known-to-genus group (compare slopes in Fig. 1a). The reliability ratio correction for known-to-genus wood density samples increased the slope by 71% ($\kappa=0.585$). Log-transformed DBH was significantly correlated with decomposition rate constants, although the amount of variability accounted for

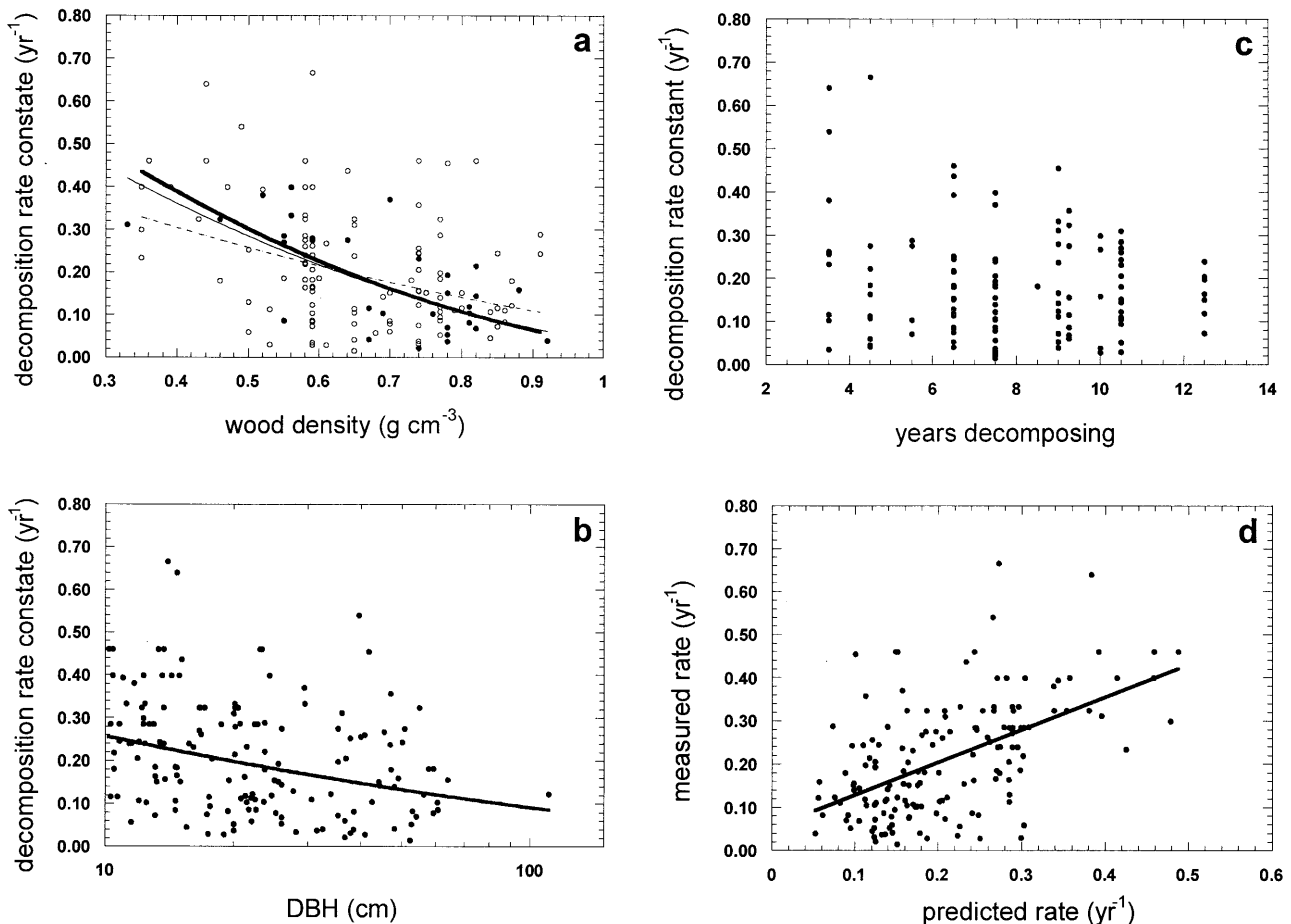


Fig. 1 **a** Decomposition rate as a function of wood density for boles of dead trees known to species (*thin solid line*) [$k_d = (0.871 - 0.676p)^2$, $r^2_{adj} = 0.43$, $n = 32$, $P < 0.0001$], and to genus (*broken line*) [$k_d = (0.728 - 0.441p)^2$, $r^2_{adj} = 0.14$, $n = 32$, $P < 0.0001$]. Error in wood density introduced by using the average for the genus caused a downward bias in the slope that was corrected as described in the text [*thick solid line*; $k_d = (0.918 - 0.738p)^2$, $n = 155$]. **b** Bole decomposition rate as a function of diameter [$k_d = (0.711 - 0.204 \log DBH)^2$, $r^2_{adj} = 0.10$, $n = 155$, $P < 0.0001$]. **c** There was no correlation between time decomposing and decomposition rate constants ($n = 155$, $P = 0.96$), although the variance was non-constant. **d** The relationship between estimated bole decomposition rates and those predicted from a multiple regression with wood density and diameter as the predictor variables ($y = 0.0565 + 0.757x$, $r^2_{adj} = 0.25$, $n = 155$, $P < 0.0001$). The slope for wood density was corrected for bias as described in the text [$k_d = (1.104 - 0.670p - 0.163 \log DBH)^2$]

was small (Fig. 1b). The slope of the relationship between the decomposition time interval and decomposition rate constants was not significantly different from zero (Fig. 1c). However, since error was dependent on the time decomposing, and rate constants for completely decomposed boles were probably underestimated, the variance was non-constant. Both wood density and log-DBH terms were significant in the multiple-regression analysis. Interaction of the predictor variables was not significant ($P = 0.18$). Predicted and measured decomposition rate constants were moderately correlated (Fig. 1d). Importantly, analysis of residuals showed that pre-

dicted decomposition rate constants were unbiased, and the slope of measured versus predicted rates (0.76; Fig. 1d) demonstrates that the multiple regression accounted for most of the range in measured decomposition rates (Fig. 1d).

Of the 155 boles sampled, reliable information on the mode of death was available for 65 dead trees (40 uprooted and 25 died standing). A one-way ANOVA showed that the mode-of-death effect did not have a significant effect on decomposition rate constants ($P = 0.91$). For agent of death, a one-way ANOVA comparing rate constants for trees that were killed by falling trees ($n = 68$), and by other means ($n = 41$) were significantly different ($P < 0.05$). Unexpectedly, decomposition rate constants for trees killed by other falling trees were higher. This occurred because trees killed by treefalls were on average smaller than trees that died from other causes (Fig. 2), and smaller boles decay faster (Fig. 1c). After statistically adjusting for size differences among groups (ANCOVA), rates were not significantly different.

Discussion

As expected, both wood density and DBH were significantly correlated with decomposition rate constants. However, the amount of total variability explained by these two factors was relatively small (Fig. 1d). Part of

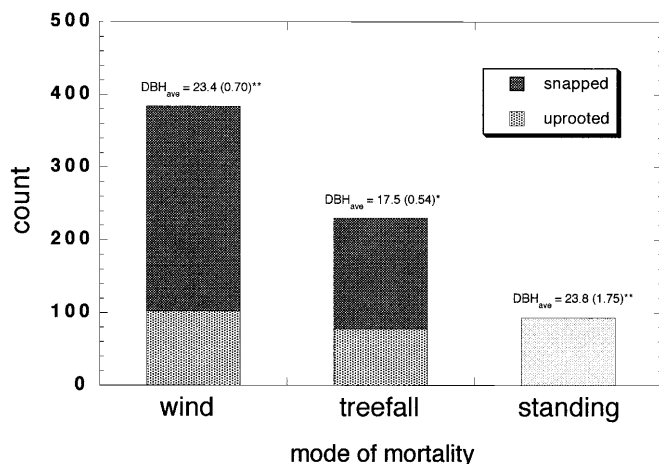


Fig. 2 Mode and agent of mortality for 707 trees that died at the BDFFP sites for the inventories considered. The average DBH of all mortality (21.1 cm) is not significantly different from the average living tree (20.8 cm, $n > 10,000$, $P = 0.41$), indicating no size-specific differences in mortality. However, the average DBH for the wind ($n = 384$) and standing ($n = 93$) categories are significantly higher (**), and for treefall ($n = 230$) significantly lower (*), than for live trees ($P < 0.0001$)

this weak correlation is attributed to errors estimating wood density. The slope bias introduced by this error was corrected by calculating a reliability ratio. A correlation coefficient could not be calculated for the corrected regression equations. However, using only the samples where wood density was known to species suggests that the amount of decomposition rate variability accounted for by wood density and DBH was probably higher than that shown in Fig. 1d [for known-to-species samples: $k_d = (1.130 - 0.601p - 0.220 \log DBH)^2$, $r^2_{adj} = 0.48$, $n = 32$, $P < 0.0001$].

Time was not significantly correlated with decomposition rate constants. However, because decomposition rates vary considerably, time spent decomposing is not a good indicator of the extent of decomposition. The fraction of the initial mass remaining is probably a better indicator of decomposition state. However, because the decomposition time was limited to between 3 and ~12 years, fractional mass loss was not independent of wood density, and changes in decomposition rate with decomposition state (e.g., fraction mass lost) could not be tested. To examine if decomposition rates are dependent on time, or the extent of decomposition, require “chronosequence” studies that track individual boles over time.

Both mode and agent of mortality were not significantly correlated with decomposition rate constants. This suggests that other factors are more important in determining mass loss rates than simple correlates with the decomposition environment (e.g., downed vs standing), and the onset of decomposition processes (e.g., how rapidly a tree died). For example, the relationship between wood density and chemical constituents (e.g., lignin and polyphenolics) is not straightforward. *Swartzia reticulata*, has dense wood (0.91 g cm^{-3}) that decomposed quickly (0.36 year^{-1} , $n = 2$), and the light-colored wood

suggests that secondary compounds are not abundant. Conversely, white-rot is common in these forests (J. Chambers, personal observation), suggesting that in many cases, chemical barriers to decomposition are not effective. Because substrate quality is complex in these species-rich forests, wood density alone fails to incorporate all of the components determining substrate quality. Nevertheless, we believe that decomposition models based on easily obtained parameters (e.g., diameter, wood density) are more pragmatic for describing large-scale carbon cycling dynamics than models based on detailed characterizations of wood chemistry.

Wood decomposition and carbon cycling

Wood density of the taxa sampled for this study varied from 0.33 g cm^{-3} for *Jacaranda copaia* (Leguminosae) to 0.92 g cm^{-3} for *Brosimum rubescens* (Moraceae). Wood density for 268 Amazon tree species varied from 0.14 to 1.21 g cm^{-3} (Fearnside 1997), and the extremes in wood density are rare. DBH in this study varied from 10 to 110 cm compared to 10–160 cm of over 10,000 trees measured on 18 ha distributed across a 60-km transect at BDFFP, and trees over 100 cm DBH are rare (about $0.5 \text{ individuals ha}^{-1}$). Sampled tree mortality was reasonably representative of large-scale forest structure, and the models developed here are appropriate for exploring the role of coarse litter in large-scale carbon cycling.

The average wood density in tropical forests of Amazonia is about 0.69 g cm^{-3} (Fearnside 1997). Using DBH data from ~800 tree deaths, and an allometric equation based on over 300 destructively sampled trees ($\text{biomass} = 0.135 \text{ DBH}^{2.546}$; Santos 1996), the average dry-weight mass of a dying tree is about 600 kg. Solving the allometric equation for diameter, a 600-kg tree has an equivalent DBH of 27.1 cm. This is larger than the average DBH of trees $> 10 \text{ cm DBH}$ (21.1 cm) because biomass scales to the radius squared. Employing the regression equation from Fig. 1d, the average dead tree decomposes at 0.17 year^{-1} , and 95% of its mass is lost in 18 years. This estimate compares with the average decomposition rate of all the dead trees sampled ($n = 155$, 0.19 year^{-1}).

From the mortality data used in this study, 7.0 trees $\text{ha}^{-1} \text{ year}^{-1}$ died, producing an average of $4.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$ of wood litter. Based on the destructive sampling of 29 trees (N. Higuchi, unpublished data) about 85% of the mass of a tree is $> 10 \text{ cm}$ in diameter, resulting in a coarse litter production rate of $3.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$. Assuming a large-scale steady-state of coarse-litter dynamics, the standing stock is given by production divided by the decomposition rate constant (Olson 1963), or 21 Mg ha^{-1} , with a mean residence time of 5.9 years. Since wood is about 50% carbon, coarse litter releases a maximum of $1.8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ to the atmosphere. An individual-based simulation model tracking the fate of live and dead trees predicted that stocks are probably higher

(~30 Mg ha⁻¹) than estimated here using averaging assumptions (J.Q. Chambers, unpublished data). Supporting the higher estimate, a recent exhaustive study at the BIONTE sites measured 29.7±12.2 Mg ha⁻¹ in 3 ha of undisturbed forest (Summers 1998). Coarse-litter standing stocks provide an important ecosystem attribute for validating carbon cycling models.

Other estimates of coarse-litter standing stocks for terra firme forests include 42.3 Mg ha⁻¹ for the eastern Amazon (Uhl and Kauffman 1990) and 7.6 Mg ha⁻¹ for the Venezuelan Amazon (Kauffman et al. 1988). Delaney et al. (1998) estimated standing stocks for tropical evergreen forests in Venezuela of 33.3 Mg ha⁻¹. The range in estimates for standing stocks compiled from dense terra firme forests from the central Amazon is 10.5–21.2 Mg ha⁻¹ (Martius 1997). These estimates are broadly consistent with our result. Because tree mortality exhibits a large degree of spatial and temporal variability, and the substrate quality of wood varies greatly, calculating the appropriate spatial scale to estimate average coarse-litter standing stocks is difficult. J. Q. Chambers (unpublished data) estimated that a plot of at least 10 ha is required to representatively sample local variability in tree mortality.

Based on four separate studies in dense terra firme forests in the central Amazon, fine-surface-litter production averages 7.8 Mg ha⁻¹year⁻¹, and 1.3 Mg ha⁻¹year⁻¹ (17%) of this litter is fine wood litter (Klinge and Rodrigues 1968; Franken et al. 1979; Luizão and Schubart 1987; Luizão 1995). Using the calculations above for wood litter production from tree mortality, surface litter production consists of about 16% fine wood, 30% coarse wood, and 54% non-woody litter (e.g., leaves, fruits, flowers). Because only a small fraction of above-ground biomass is non-woody (1–2%), annual variation in the quality of surface litter production is primarily due to

differences in tree mortality rates. This potential variability in surface litter production is important for models that aim to predict changes in annual carbon fluxes to the atmosphere. Large-scale models that aggregate all soil carbon into a single pool (e.g., Tian et al. 1998) cannot account for annual variability in litter quality. Given that net fluxes on the order of 1 Mg ha⁻¹ year⁻¹ are globally important when extrapolated across the entire Amazon (e.g., Grace et al. 1995), the details, not just the aggregate behavior, of carbon cycling models need to be validated.

Comparisons with other studies

Awareness of the importance of coarse litter has increased in recent years and decomposition studies have been carried out in a variety of ecosystems (Table 1). These studies sought to quantify large-scale decomposition dynamics, and employed roughly comparable methods. Studies in tropical evergreen forests, however, were lacking from this global summary. A literature search, however, discovered two tropical studies where rates of coarse-litter production and standing stocks allowed estimates of steady-state turnover rates of 0.19 year⁻¹ (Kira 1976) and 0.20 year⁻¹ (Yoneda et al. 1990). Turnover rates are comparable to an average decomposition rate constant.

With rate data on coarse-litter decomposition spanning the major global forested ecosystems, we tested for controls using mean annual precipitation and temperature. Precipitation was not correlated with rate constants ($P=0.49$). Mean annual temperature, however, was highly correlated with rate constants (Fig. 3). More complex multiple-regression models, including transformations of precipitation and interaction effects, were not significant.

Table 1 Large wood decomposition studies from a number of globally distributed ecosystems. Decomposition rate constants (k , year⁻¹) were characterized in each study using comparable methods (MAT mean annual temperature in °C)

Ecosystem	Location	MAT	k	Source
Southern taiga	Northwestern Russia	3.7	0.040	Krankina and Harmon (1995)
Temperate coniferous	Canadian Rocky Mountains	1.9	0.011	Johnson and Greene (1991)
Temperate coniferous	Central Oregon, near LaPine	11.4	0.027	Busse (1994)
Temperate coniferous	Olympic National Park	10.5	0.011	Graham and Cromack (1982)
Temperate coniferous	Sequoia National Park	8.9	0.050	Harmon et al. (1987)
Temperate coniferous	Pacific northwest	11.7	0.028	Sollins (1981)
Temperate coniferous	Cascade Head, Oregon	10.1	0.012	Grier (1978)
Temperate coniferous	H.J. Andrews Forest	6.5	0.006	Means et al. (1985)
Temperate coniferous	Wyoming, near Laramie	5.9	0.016	Fahey (1983)
Temperate coniferous	New Hampshire, Mt Moosilauke	3.4	0.030	Lambert et al. (1980)
Temperate coniferous	New Hampshire, White Mountains	3.4	0.030	Foster and Lang (1982)
Temperate mixed	Northern Wisconsin and Michigan	5.7	0.021	Tyrell and Crow (1994)
Temperate mixed	North central Minnesota	2.0	0.062	Alban and Pastor (1993)
Temperate mixed	Southern Appalachians	12.6	0.080	Mattson et al. (1987)
Temperate deciduous	Hubbard Brook, New Hampshire	3.4	0.096	Arthur et al. (1992)
Temperate deciduous	Lawrence County, Indiana	11.8	0.024	MacMillan (1988)
Temperate deciduous	Nashville, Tenn.; Radnor Lake	15.6	0.086	Onega and Eikmeier (1991)
Mediterranean	Western Australia	16.2	0.132	Brown et al. (1996)
Dry tropical	Yucatan peninsula, Mexico	25.0	0.197	Harmon et al. (1995)
Tropical evergreen	Manaus, Brazil	26.7	0.167	This study

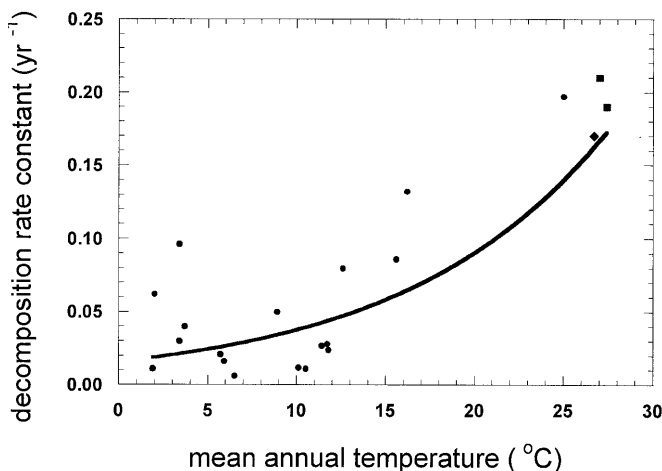


Fig. 3 Decomposition rate as a function of mean annual temperature for the studies listed in Table 1 (*diamond* this study). Coarse-litter turnover rates for two additional tropical forest sites (*squares*) were derived from data in literature sources as described in the text. This relationship, $k_d = 0.0157e^{0.0875T}$, predicts a global Q_{10} of 2.4 (10°C^{-1})

The presence of forests requires adequate moisture; however, forests occur over a broad range of temperatures. This probably explains why temperature alone, and not precipitation, is a good predictor of differences in decomposition rates. Interestingly, the lowest decomposition rate constant measured for this study (0.015 year^{-1}), is comparable to the lowest global rates from Table 1.

The temperature dependence of biological processes is often expressed as an exponential Q_{10} function that describes how metabolic rates respond to a 10°C increase in temperature (Kirschbaum 1993). An exponential model provided the best fit of wood decomposition rate versus mean annual temperature (Fig. 3), resulting in a global-scale coarse-litter decomposition Q_{10} estimate of 2.4 (10°C^{-1}). Given global warming scenarios indicating a $3\text{--}5^\circ\text{C}$ rise in mean annual temperature (Kattenberg et al. 1996), this relationship predicts an increase in average wood decomposition rates at the global scale of about 70–120%, with much of this organic matter lost as CO_2 to the atmosphere (J.Q. Chambers, J.P. Schimel, A.D. Nobre, unpublished data). There are probably more complicated phenomenon associated with global warming that can influence litter decomposition rates including changes in litter production rates, leaf area, and soil temperature. However, these effects have not been well characterized, especially for tropical forests.

Coarse litter and global changes

Additional research is needed to determine the role of coarse litter in response to local and global environmental changes. Variation in tree mortality, for example, can affect the quantity and quality of inputs, and the spatial and temporal variation in decomposition dynamics. Nelson et al. (1994) have identified large blow-downs in the

Amazon basin that can raze $>1000 \text{ ha}$ of primary forest. Smaller treefall gaps are associated with large quantities of coarse litter at $<1000 \text{ m}^2$. The Amazon basin is also subject to droughts associated with El Niño events, and droughts can increase tree mortality rates (Condit et al. 1995). Given reports of Amazon forests potentially acting as a large carbon sink (Grace et al. 1995; Malhi et al. 1998), perhaps in response to CO_2 fertilization, short-term variability must be distinguished from long-term trends (Keller et al. 1996; Malhi et al. 1998). Site disturbance history, and the decomposition dynamics of coarse litter, can play an important role in determining whether a given tract of forest acts as a net source or sink for atmospheric carbon.

Carbon cycling of coarse litter is also important for understanding ecosystem response to land use. Amazon forests are being converted to other purposes at a rate of about $1.5 \times 10^6 \text{ ha}^{-1} \text{ year}^{-1}$ (Skole and Tucker 1993). In secondary and logged forests, species compositions, size class structures, and mortality rates differ from the primary forest. In logged forests, for example, standing stocks of coarse litter are much larger than in primary forests (Uhl and Kauffman 1990). Along the edges of forest fragments, tree mortality rates are two to four times as high as in primary forests, resulting in a large shift of carbon from live trees to coarse litter (Laurance et al. 1997, 1998). In pastures, a large fraction of the above-ground carbon remains as coarse litter (Kauffman et al. 1998). In each of these environments, wood decomposition rates may vary, and can influence the magnitude and timing of carbon released to the atmosphere. However, no studies have considered the details of coarse-litter decomposition and the release of carbon in contrasting land use categories for tropical forests. Given the importance of ecosystem response to land use in determining net fluxes of carbon to the atmosphere (Houghton 1994; Kaufmann et al. 1995; Trumbore et al. 1995; Fearnside and Guimaraes 1996), additional studies on the dynamics of coarse litter in disturbed ecosystems are needed to assess regional and global-scale carbon budgets.

Acknowledgements We would like to thank Allan Stewart-Oaten for discussions on analytical methods and Mark Harmon, Sandra Brown, Jochen Schenk, Michael Keller, and an anonymous reviewer for comments on previous versions of this manuscript. Aluizio Ferenades de Conceicao, Jose Ribamar Marques de Oliveira, Alaercio Marajo dos Reis, and Antonio Martins provided vast forest knowledge and invaluable help in the field. We are grateful for the logistics and technical support of the BIONTE and BDFFP projects. The work was supported in part by Lawrence Livermore National Laboratory's Laboratory Directed Research and Development program (95-DI-005) under the auspices of the U.S. Department of Energy subordinate to Contract no. W-7405-Eng-48 with the University of California, and by the NASA Terrestrial Ecology Program.

References

- Alban DH, Pastor J (1993) Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. *Can J For Res* 23:1744–1749
- Arthur MA, Tritton LM, Fahey TJ (1992) Dead bole mass and nutrients remaining 23 years after clear-felling of a northern hardwood forest. *Can J For Res* 23:1298–1305
- Bravard S, Righi D (1989) Geochemical differences in an Oxisol-Spodisol toposequence of Amazonia, Brazil. *Geoderma* 44:29–42
- Brown IF, Martinelli LA, Thomas WW, Moreira MZ, Cid Ferreira CA, Victoria RA (1995) Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. *For Ecol Manage* 75:175–189
- Brown S, Mo J, McPherson JK, Bell DT (1996) Decomposition of woody debris in western Australian forests. *Can J For Res* 26:954–966
- Bultman JD, Southwell CR (1976) Natural resistance of tropical American woods to terrestrial wood-destroying organisms. *Biotropica* 8:71–95
- Busse MD (1994) Downed bole-wood decomposition in lodgepole pine forests of central Oregon. *Soil Sci Soc Am J* 58:221–227
- Cao M, Woodward FI (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* 393:249–251
- Chambers J, Higuchi N, Schimel JP (1998) Ancient trees in Amazonia. *Nature* 391:135–136
- Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 Neotropical tree and shrub species and the impact of severe drought. *Ecol Monogr* 65:419–439
- Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica* 30:2–11
- 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
- Fahey TJ (1983) Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecol Monogr* 53:51–72
- Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *For Ecol Manage* 90:59–87
- Fearnside PM, Guimaraes WM (1996) Carbon uptake by secondary forests in Brazilian Amazonia. *For Ecol Manage* 80:35–46
- Foster JR, Lang GE (1982) Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Can J For Res* 12:617–626
- Franken M, Imler U, Klinge H (1979) Litterfall in inundation, riverine and terra firme forests of central Amazonia. *Trop Ecol* 20:225–235
- Franklin JF, Shugart HH, Harmon ME (1987) Tree death as an ecological process. *BioScience* 37:550–556
- Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS, Nobre C, Moncrieff J, Massheder J, Malhi Y, Wright I, Gash J (1995) Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992–1993. *Science* 270:778–780
- Graham RL, Cromack K (1982) Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Can J For Res* 12:511–520
- Grier CC (1978) A *Tsuga heterophylla*-*Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balance of fallen logs. *Can J For Res* 8:198–206
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Latting JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. In: Macfadyen A, Ford ED (eds) *Ecology of coarse woody debris in temperate ecosystems*. Academic Press, London, pp 133–302
- Harmon ME, Cromack K, Smith BG (1987) Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. *Can J For Res* 17:1265–1272
- Harmon ME, Whigham DF, Sexton J, Olmsted I (1995) Decomposition and mass of dead wood in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. *Biotropica* 27:305–316
- Higuchi N, Jardim CSF, Santos J dos, Barbosa AP, Wood TWW (1985) Bacia 3 – inventário florestal comercial. *Acta Amazon* 15:327–369
- Houghton RA (1994) The worldwide extent of land-use change. *BioScience* 44:305–313
- IPT (1989) Fichas de Características das Madeiras Brasileiras. Instituto de Pesquisas Tecnológicas, São Paulo, Brazil
- Johnson EA, Greene DF (1991) A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia*-*Picea engelmannii* forests. *J Veg Sci* 2:523–530
- Kattenberg A, Giorgi F, Grassl H, Meehl GA, Mitchell JFB, Stouffer RJ, Tokioka T, Weaver AJ, Wigley TML (1996) Climate models projections of future climate. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) *Climate models projections of future climate*. Cambridge University Press, Cambridge, UK, pp 285–357
- Kauffman JB, Uhl C, Cummings DL (1988) Fire in the Venezuelan Amazon. 1. Fuel biomass and fire chemistry in the evergreen rainforest of Venezuela. *Oikos* 53:167–175
- Kauffman JB, Cummings DL, Ward DE, Babbitt R (1995) Fire in the Brazilian Amazon. 1. Biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* 104:397–408
- Kaufmann JB, Cummings DL, Ward DE (1998) Fire in the Brazilian Amazon. 2. Biomass, nutrient pools and losses in cattle pasture. *Oecologia* 113:415–427
- Keller M, Clark DA, Clark DB, Weitz AM, Veldkamp E (1996) If a tree falls in the forest... *Science* 273:201
- Kira T (1976) Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. In: Tomlinson PB, Zimmermann MH (eds) *Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia*. Cambridge University Press, Cambridge, pp 561–590
- Kirschbaum MUF (1993) A modelling study of the effects of changes in atmospheric CO₂ concentration, temperature, and atmospheric nitrogen input on soil organic carbon storage. *Tellus* 45B
- Klinge H, Rodrigues WA (1968) Litter production in an area of Amazonian terra firme forests. *Amazoniana* 1:287–301
- Krankina ON, Harmon ME (1995) Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. *Water Air Soil Pollut* 82:227–238
- Lambert RL, Lang GE, Reiners WA (1980) Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61:1460–1473
- Lang GE, Knight DH (1979) Decay rates for boles of tropical trees in Panama. *Biotropica* 11:316–317
- Laurance WF, Laurance SG, Ferreira LV, Rankin-de Merona JM, Gascon C, Lovejoy TE (1997) Biomass collapse in Amazonian forest fragments. *Science* 278:1117–1118
- Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG (1998) Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79:2032–2040
- Le Cointe P (1934) A Amazonia Brasileira. III. Árvores e Plantas Uteis. *Livaria Classica*, Belem, Para, Brazil
- Lovejoy T, Bierregaard R (1990) Central Amazonian forests and the Minimum Critical Size of Ecosystem Project. In: Gentry A (eds) *Central Amazonian forests and the Minimum Critical Size of Ecosystem Project*. Yale University Press, New Haven, pp 60–71
- Luizão FJ (1995) Ecological studies in contrasting forest types in central Amazonia. PhD thesis, University of Stirling
- Luizão FJ, Schubart HOR (1987) Litter production and decomposition in a terra firme forest of central Amazonia. *Experiencia* 43:259–265

- MacMillan PC (1988) Decomposition of coarse woody debris in an old-growth Indiana forest. *Can J For Res* 18:1353–1362
- Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf A, Scott S (1998) Carbon dioxide transfer over a central Amazonian rain forest. *J Geophys Res-Atmos* 103:31593–31612
- Martius C (1997) Decomposition of wood. In: Junk WJ (eds) *Decomposition of wood*. Springer, Berlin Heidelberg New York, pp 267–276
- Mattson KG, Swank WT, Waide JB (1987) Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. *Can J For Res* 17:712–721
- Means JE, Cromack K, MacMillan PC (1985) Comparison of decomposition models using wood density of Douglas-fir logs. *Can J For Res* 1985:1092–1098
- Mellilo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary productivity. *Nature* 363:234–240
- Mindermann G (1968) Addition, decomposition and accumulation of organic matter in forests. *J Ecol* 56:355–362
- Nelson BW, Kapos V, Adams JB, Oliveira WJ, Braun OPG, Amaral IL do (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* 75:853–858
- Odum HT (1970) Forest metabolism and energy flow. In: Odum HT, Pigeon RF (eds) *Forest metabolism and energy flow*. US-AEC Technical Information Center, Oak Ridge, Tenn, pp 1220–1245
- Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322–331
- Onega TI, Eickmeier WG (1991) Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. *Bull Torr Bot Club* 118:52–57
- Pan YD, Melillo JM, McGuire AD, Kicklighter DW, Pitelka LF, Hibbard K, Pierce LL, Running SW, Ojima DS, Parton WJ, Schimel DS (1998) Modeled responses of terrestrial ecosystems to elevated atmospheric CO₂: a comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia* 114:389–404
- Phillips OL, Malhi Y, Higuchi N, Laurance WF, Núñez PV, Vázquez RM, Laurance SG, Ferreira LV, Stern M, Brown S, Grace J (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442
- Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, Klooster SA (1993) Terrestrial ecosystem production: a process model based on global satellite and surface data. *Glob Biogeochem Cycl* 7:811–841
- Rankin-De Merona JM, Prance GTH, Hutchings RW, Silva MFD, Rodrigues WA, Uehling ME (1992) Preliminary results of a large-scale tree inventory of upland rain forest in the central Amazon. *Acta Amazon* 22:493–534
- Reyes G, Brown S, Chapman J, Lugo AE (1992) Wood densities of tropical tree species. *Gen Tech Rep SO-88*. USDA Forest Service, New Orleans
- Ribeiro JELS, Nelson BW, Silva MFD, Martins LSS, Hopkins M (1994) Ducke forest reserve: diversity and composition of the vascular flora. *Acta Amazon* 24:19–30
- Ribeiro RJ (1996) Estudo de função de forme para espécies florestais de terra-firme de Amazonia central. MS thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil
- Santos JD (1996) Analize de modelos de regressão para estimar a fitomass de floresta tropical umida de terra-firme da Amazônia Brasileira. PhD thesis, Universidade Federal de Viçosa, Minas Gerais, Brazil
- Silva MFD, Lisbôa PLB, Lisbôa RCL (1977) Nomes vulgares de plantas Amazônicas. Instituto Nacional de Pesquisas da Amazônia, Belém, Brazil
- Skole D, Tucker C (1993) Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260:1905–1910
- Snedecor GW, Cochran WG (1989) *Statistical methods*, 8th edn. Iowa State University Press, Ames
- Sollins P (1981) Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can J For Res* 12:18–28
- Summers PM (1998) Estoque, decomposição, e nutrientes da liteira grossa em floresta de terra-firme, na Amazônia central. MS thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
- Tian H, Mellilo JM, Kicklighter DW, McGuire AD, Heifrich JVKI, Moore BI, Vörösmarty CJ (1998) Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* 396:664–667
- Trumbore SE, Davidson EA, Barbosa de Carmago P, Nepstad DC, Martinelli LA (1995) Belowground cycling of carbon in forests and pastures of eastern Amazonia. *Glob Biogeochem Cycl* 9:515–528
- Tyrrell LE, Crow TR (1994) Dynamics of dead wood in old-growth hemlock-hardwood forests of northern Wisconsin and northern Michigan. *Can J For Res* 24:1672–1683
- Uhl C, Kauffman JB (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71:437–449
- Yoneda T, Yoda K, Kira T (1977) Accumulation and decomposition of big wood litter in Pasoh Forest, West Malaysia. *Jpn J Ecol* 27:53–63
- Yoneda T, Tamin R, Ogino K (1990) Dynamics of aboveground big woody organs in a foothill dipterocarp forest, West Sumatra, Indonesia. *Ecol Res* 5:111–130
- Zar JH (1996) *Biostatistical analysis*, 3rd edn. Prentice Hall, Upper Saddle River, NJ