

# Lignin and enhanced litter turnover in tree plantations of lowland Costa Rica

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Received 1 October 2006; received in revised form 26 November 2006; accepted 29 November 2006

## Abstract

We quantified the effect of overstory species composition on forest floor dynamics in lowland Costa Rica. Aboveground litter production and forest floor mass were measured over 1 year in 16-year-old single-species plantations established in a randomized complete block design with four blocks. The tree species investigated (=experimental treatments) were *Hyeronima alchorneoides*, *Pentaclethra macroloba*, *Pinus patula* subsp. *tecunumanii*, *Virola koschnyi*, *Vochysia ferruginea*, and *Vochysia guatemalensis*. Organic matter fluxes in litterfall, which averaged 10.1 Mg ha<sup>-1</sup> year<sup>-1</sup>, were similar to those reported from comparable Neotropical plantations, whereas nitrogen fluxes in litterfall (up to 210 kgN ha<sup>-1</sup> year<sup>-1</sup>) were high. Litter production was significantly greater beneath *Hyeronima* and *V. ferruginea* than beneath *Virola*, primarily due to high rates of non-woody litter production by *Hyeronima*, large amounts of twig litter production by *V. ferruginea*, and low production of both fractions by *Virola*. *V. ferruginea* had significantly more branch litter on the ground than did any other species, whereas *Hyeronima* had the largest accumulations of non-woody (mostly leaf) litter. Accumulations of woody litter correlated closely with rates of branchfall: branches  $\leq 1$  cm in diameter persisted on the forest floor for 0.9 year on average, independent of species. Rates of decay of non-woody litter, in contrast, varied significantly among species, with fastest rates (2.8 year<sup>-1</sup>) observed beneath *Pentaclethra* and the slowest decay rates (1.5 year<sup>-1</sup>) in plots of *V. guatemalensis*. Contrary to expectations, litter decay rates increased with increasing lignin contents, paralleling results of a concomitant study that found a significant negative correlation between litter lignin and surface-soil organic matter content. Our results demonstrate that different overstory-tree species generate significantly different forest floors, in terms of mass, composition and dynamics. These differences affect soil restoration, tree regeneration and other ecological processes important to selecting species for tropical plantation establishment and reforestation efforts.

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**Keywords:** Carbon cycling; Decomposition; Forest floor; Litterfall; Nitrogen fluxes; Tropical forest

## 1. Introduction

Reforestation of previously cropped or pastured tropical forest lands offers many potential benefits (Evans and Turnbull, 2004), including enhancement of soil organic matter levels and fertility (Nye and Greenland, 1960). A variety of mechanisms exist whereby trees may affect soil physical and chemical properties in previously deforested sites (Fisher, 1995). These include: gathering nutrients from a large soil volume and concentrating them at the soil surface via aboveground litter production (Alban, 1982); promoting N fixation by symbiotic, root-associated microorganisms (e.g., Pearson and Vitousek,

2001); producing organic detritus that promotes or inhibits the formation of soil organic matter (e.g., Kaye et al., 2000); ameliorating soil microclimatic conditions via development of a leafy canopy and surface litter layers (e.g., Montagnini et al., 1993); influencing the nature of the mycorrhizal associations that mediate soil-to-plant nutrient transfers (Read and Perez-Moreno, 2003) and soil carbon dynamics (e.g., Rillig et al., 2001); and modifying the distribution and abundance of soil invertebrates that consume detritus (e.g., Warren and Zou, 2002). Individual tree species potentially influence each of these processes and, thus, the characteristics of the regenerating forest.

The forest floor, the fine detritus that lies on the soil surface, plays a central role in these processes. It is home to a diversity of fauna, fungi, algae, plants and microbes, and provides food to earthworms and other soil-dwelling organisms. The forest floor

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protects the soil surface from the physical impacts of rain and diminishes evaporative water loss from soils during dry spells. It is where seeds germinate, providing the next generation of trees. It is where many of the organic materials produced aboveground are decomposed, and where the nutrients they contain are mineralized to forms available for plant uptake. Humification of forest floor materials produces soil organic matter, and the compounds produced during decomposition influence soil genesis and chemistry. The forest floor ties together the aboveground and belowground ecosystems: measurements of forest floor dynamics provide insight into the mechanisms by which tree crops maintain, enhance, or deplete soil fertility during stand development.

The depth, mass, and nutrient content of the forest floor are ultimately controlled by additions of fine litter from aboveground and the mineralization of that litter during decomposition. Understanding these two basic processes, litter production and decomposition, thus provides a framework for evaluating the dynamics of the forest floor and its relationship to site and soil properties. Comparative studies have demonstrated that tropical plantations composed of different tree species vary in both litter production and decay rates (Montagnini et al., 1993; Kershner and Montagnini, 1998; Smith et al., 1998a, 2002), and in their effects on surface-soil properties (Fisher, 1995; Bashkin and Binkley, 1998; Cuevas and Lugo, 1998; Smith et al., 1998b, 2002; Stanley and Montagnini, 1999; Kaye et al., 2000; Russell et al., submitted for publication). To evaluate the relative effects of aboveground litter production rate versus litter chemistry on fine litter accumulations in tropical forest plantations, we compared forest floor dynamics in replicated plantations of five native and one non-native tree species in lowland, humid Costa Rica.

## 2. Materials and methods

### 2.1. Study site and species

This study was conducted in experimental tree plantations established on the western annex of the Organization for Tropical Studies' La Selva Biological Station (10.5°N, 84.5°W), in the Caribbean lowlands of Costa Rica. La Selva has a mean annual rainfall of about 4000 mm and a mean air temperature of 25.8 °C (Sanford et al., 1994). Soils in the study sites are Typic Tropohumults in the Matabuey consociation; they are highly weathered acidic soils with low base saturation but relatively high organic matter contents (Sollins et al., 1994; Fisher, 1995). Topography of the study area was hilly, with elevations ranging from 51 to 84 m. These soils naturally support diverse mixed-species evergreen tropical rain forest in which *Pentaclethra macroloba* comprises >35% of the tree basal area (Lieberman and Lieberman, 1994) and understory palms are very abundant.

The study sites were planted in late 1988 to early 1989 in formerly grazed pasture that was >30 years old. Four experimental blocks were established, each containing twelve 50-m × 50-m plots. Eleven plots in each block were planted at 3 m × 3 m spacing to a single randomly assigned tree species,

six of which remain and were used in our study: *Hyeronima alchorneoides* Allemão, *Pentaclethra macroloba* (Willd.) Kuntze, *Pinus patula* subsp. *tecunumanii* (Eguiluz & J.P. Perry) Styles (= *Pinus tecunumanii* Eguiluz & J.P. Perry), *Virola koschnyi* Warb., *Vochysia ferruginea* Mart., and *Vochysia guatemalensis* Donn. Sm. *Pinus patula* was the only exotic; the other five species occur naturally in surrounding forests. Early tree growth, soil properties, management activities and vegetation characteristics of these plots were described by González and Fisher (1994), Fisher (1995), Powers et al. (1997) and Haggar et al. (1997, 1998). At the time of this study the plots had overstory stem densities that averaged 200–500 stems ha<sup>-1</sup>, basal areas that averaged 15–40 m<sup>2</sup> ha<sup>-1</sup>, and mean overstory-tree diameters of 22–37 cm.

### 2.2. Litter production and forest floor mass

Each of the 24 plots (4 blocks × 6 species) was sub-divided into four quadrants to allow for stratified random sampling. A single litter trap measuring 1.3 m × 0.4 m and supporting 2-mm nylon-mesh screen was randomly located within each quadrant of each plot, and the litter that fell into each trap was collected every 15 days; branches >1 cm diameter were discarded. The litter collected from each trap was weighed fresh, and was then combined within plots before being sorted into overstory leaves, other leaves, branches ≤1 cm diameter, and other materials. These fractions were oven-dried at 65 °C and weighed. Materials collected from each plot were combined within each month and finely ground prior to chemical analysis. Carbon and nitrogen fluxes in litterfall were determined by multiplying elemental concentrations and mass fluxes for each plot on a monthly basis. Fluxes measured through time were cumulated to determine annual litter production rates and element fluxes for each of the 24 study plots. We mathematically combined data from all materials other than branches into a single category, non-woody litterfall, to parallel measurements of forest floor materials. We herein present litterfall data from 30 December 2003 to 29 December 2004 (365 days). The plantations at that time were in their 16th year of growth post-planting.

The mass of all surface litter present in the plots was measured three times: November 2003, March 2004, and July 2004. At each sampling time a single sample of all detritus above the surface of the mineral soil, but excluding standing dead plants, was collected from a single random location within each quadrant of each of the 24 sample plots (total  $n = 96$ ). At each location all material within a 0.11-m<sup>2</sup> square frame was collected, all branches and woody debris >1 cm diameter and all soil were discarded, and the fresh litter was carefully hand-sorted into woody (≤1 cm diameter, including bark) and non-woody fractions. All samples were oven-dried at 65 °C and weighed. Samples were composited within plots and finely ground prior to chemical analysis. For comparative purposes we twice measured surface fine litter in nearby mature forest, on the same soil type, using identical sampling protocols. Forest data were not included in statistical analyses because they were not part of the experimental design.

*In situ* fine litter decay rates, i.e.,  $k$  values (units = year<sup>-1</sup>), were determined via mass balance by dividing annual fine litter production by mean annual forest floor mass (Olson, 1963; Schlesinger, 1997). These differ from decay rates calculated from litterbag decomposition experiments, which typically are derived for a single material, such as the leaves of one species, enclosed within mesh bags. We independently determined decay constants for branches  $\leq 1$  cm in diameter and for all non-woody litter.

### 2.3. Tissue chemistry

Overstory leaf chemistry was determined on samples of entire, newly senesced, fallen leaves collected from the ground beneath each plot in March 2004. Leaves were determined to be freshly senesced based on their color and integrity. *Hyeronima* leaves were of various colors including yellow, red and orange; *Pentaclethra* leaves had pinnae that were yellow or yellow and green; *Pinus* needles were straw-colored, in contrast to older, brown needles; *Virola* leaves were blotched yellow and green; *Vochysia* spp. leaves were bright yellow. A minimum of 20 entire leaves (fascicles of *Pinus*) were collected from each species in each plot, and these were combined and dried at 65 °C and finely ground prior to chemical analysis ( $n = 1$  per plot).

Carbon and nitrogen contents of all organic materials were determined with a Flash EA1112 CN analyzer (Carlo Erba Strumatazione, Milan, Italy) using atropine as a standard, and are presented on a 65 °C dry-weight basis. Carbon chemistry of newly senesced leaves was determined with the forage fiber analysis procedure (van Soest, 1994) using an automated fiber analyzer (Ankom Technology, Macedon, New York, USA) in a batch process (Vogel et al., 1999). Senesced-leaf P and Ca concentrations were determined via inductively coupled plasma optical emission spectroscopy (ICP-OES) after microwave digestion of finely ground materials in concentrated nitric acid (Method 3051, U.S. EPA, 2004).

### 2.4. Statistical analyses

Our basic statistical model for testing variables that were measured independently within each plot was ANOVA with treatment (i.e., overstory species) and block as main factors and plots being the experimental units (total model  $n = 24$ ). To identify seasonal variations in surface litter we applied a repeated measures ANOVA, with treatment, block, date, and treatment  $\times$  date being the main effects, and treatment  $\times$  block treated as a random effect. Litter-mass data were natural-log transformed prior to statistical analysis to improve normality of their distributions, but this had no effect on our findings. The

Table 1  
Fine litter production rates and elemental compositions in 16-year-old plantations of six tree species planted in replicated single-species plantations at La Selva, Costa Rica

Species	Total litterfall (Mg ha <sup>-1</sup> year <sup>-1</sup> )	Non-woody litterfall (Mg ha <sup>-1</sup> year <sup>-1</sup> )	Twig litterfall (Mg ha <sup>-1</sup> year <sup>-1</sup> )
<b>Organic matter</b>			
<i>Hyeronima alchorneoides</i>	11.7 (0.6) A	9.9 (0.5) A	1.8 (0.2) BC
<i>Pentaclethra macroleoba</i>	10.3 (0.6)	8.9 (0.6)	1.5 (0.2) BC
<i>Pinus patula</i>	10.0 (0.7)	8.4 (0.4)	1.6 (0.3) BC
<i>Virola koschnyi</i>	7.4 (0.5) B	6.3 (0.5) B	1.0 (0.2) C
<i>Vochysia ferruginea</i>	11.4 (1.4) A	8.4 (1.2)	3.0 (0.2) A
<i>V. guatemalensis</i>	10.1 (0.4)	7.6 (0.4)	2.5 (0.2) AB
Species	Total litterfall (Mg ha <sup>-1</sup> year <sup>-1</sup> )	Non-woody litterfall (mg g <sup>-1</sup> )	Twig litterfall (mg g <sup>-1</sup> )
<b>Carbon</b>			
<i>Hyeronima alchorneoides</i>	5.9 (0.3) A	505 (2) AB	494 (2) A
<i>Pentaclethra macroleoba</i>	5.3 (0.3)	516 (3) A	501 (3) A
<i>Pinus patula</i>	5.0 (0.3)	503 (5) AB	500 (6) A
<i>Virola koschnyi</i>	3.8 (0.3) B	513 (3) A	494 (4) A
<i>Vochysia ferruginea</i>	5.6 (0.7)	490 (3) B	487 (2) A
<i>V. guatemalensis</i>	4.5 (0.2)	442 (3) C	465 (3) B
Species	Total litterfall (kg ha <sup>-1</sup> year <sup>-1</sup> )	Non-woody litterfall (mg g <sup>-1</sup> )	Twig litterfall (mg g <sup>-1</sup> )
<b>Nitrogen</b>			
<i>Hyeronima alchorneoides</i>	169 (16)	15.4 (1.0) BC	9.2 (0.6) CD
<i>Pentaclethra macroleoba</i>	208 (13) A	21.1 (0.9) A	14.2 (0.4) A
<i>Pinus patula</i>	137 (12) B	14.2 (0.5) C	10.9 (0.8) BCD
<i>Virola koschnyi</i>	122 (6) B	17.4 (0.5) B	11.9 (0.9) AB
<i>Vochysia ferruginea</i>	147 (19)	14.5 (0.3) C	8.7 (0.3) D
<i>V. guatemalensis</i>	162 (8)	17.5 (0.5) B	11.5 (0.5) BC

Values are annual means (S.E.);  $n = 4$ . Letters denote significant differences among species as determined with the Tukey–Kramer HSD test at  $\alpha = 0.05$ . Twigs were  $\leq 1$  cm in diameter including bark; larger woody debris was discarded.

Tukey–Kramer HSD test was applied post-hoc to distinguish significant differences among effects at  $\alpha = 0.05$ .

The null hypothesis that litter decay rates were similar among species leads to the prediction that litter mass across all species increases linearly with increasing litter production. We quantified this effect using least-squares linear regression of the plot-level data ( $n = 24$ ). Relationships between measured senesced-leaf variables and litter decay rates were quantified by calculating Pearson's product-moment correlations, again with  $n = 24$ . All statistics were performed using JMP Version 5.1.2 (SAS Institute, Inc.).

### 3. Results

#### 3.1. Litterfall

Across all species, litterfall averaged  $10.1 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ; previously reported litterfall rates in mature forests of La Selva range from  $7.8$  to  $10.9 \text{ Mg ha}^{-1} \text{ year}^{-1}$  (Parker, 1994; Davidson et al., 2002). Leaves of the planted overstory species comprised  $>50\%$  of the total fine litter production beneath all species in our study. Total leaves comprised  $>67\%$  of fine litterfall (Table 1), which is typical among tropical forests (Proctor, 1983). Averaged across all species, litterfall was maximal in March with a secondary maximum in October and minima in April and December (Fig. 1). Total annual fine litterfall varied significantly among species ( $P < 0.04$ ), but not among blocks ( $P > 0.9$ ). Fine litter production was significantly greater beneath *Hyeronima* and *V. ferruginea* than beneath *Virola* (Table 1). These differences were primarily due to high rates of non-woody litter production by *Hyeronima*, large amounts of twig litter production by *V. ferruginea*, and relatively low production of both fractions by *Virola* (Table 1).

These differences among species changed somewhat when litterfall was expressed in terms of C or N fluxes (Table 1). Carbon concentrations in litterfall beneath *V. guatemalensis* were significantly lower than those beneath any other species tested. Litterfall N concentrations were significantly lowest in *V. ferruginea* and were highest in *Pentaclethra*, the only

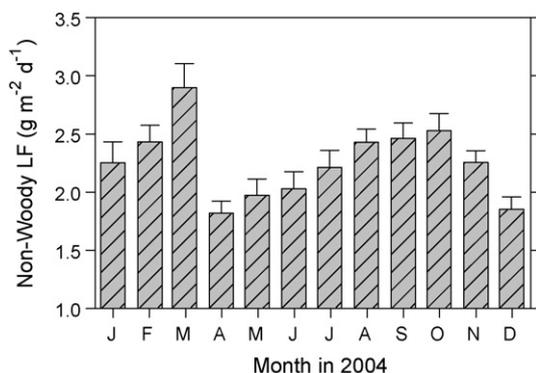


Fig. 1. Mean monthly litterfall (LF) within 16-year-old plantations in lowland Costa Rica. Shown are means across all six species studied; twig litterfall had no distinct seasonal trend and is excluded from this figure. S.E. bars are based on  $n = 24$ .

N-fixing tree species studied. *Virola* had the lowest rates of litter production in terms of organic matter, C and N (Table 1).

#### 3.2. Litter mass

Total fine surface litter and non-woody litter mass both varied significantly among sampling dates (ANOVA,  $P < 0.008$ ): there was more litter on the ground in July 2004 than in November 2003 (Fig. 2). These temporal variations did not coincide closely with temporal trends in litter production (Fig. 1), although litterfall was low at the end of the year in 2004. Temporal variability in litter mass apparently is typical among plantations at La Selva (e.g., Byard et al., 1996; Kershner and Montagnini, 1998; Horn and Montagnini, 1999). Among all plots and dates, total fine surface litter accumulations averaged  $5.8 \text{ Mg ha}^{-1}$ , which is similar to litter accumulations in adjacent, undisturbed forest ( $5.9 \pm 0.4 \text{ Mg ha}^{-1}$ , based on two sampling dates). Mean annual total, twig and non-woody litter accumulations varied significantly among species (ANOVA,  $P < 0.007$ , Table 2), but not among blocks ( $P > 0.09$ ). *Vochysia ferruginea*, whose local name is botarrama (branch-tosser), had significantly more branch litter than did any other species, whereas *Virola* had the least. *Hyeronima* had the largest accumulations of non-woody (mostly leaf) litter whereas *Virola* had the least. Total litter accumulations

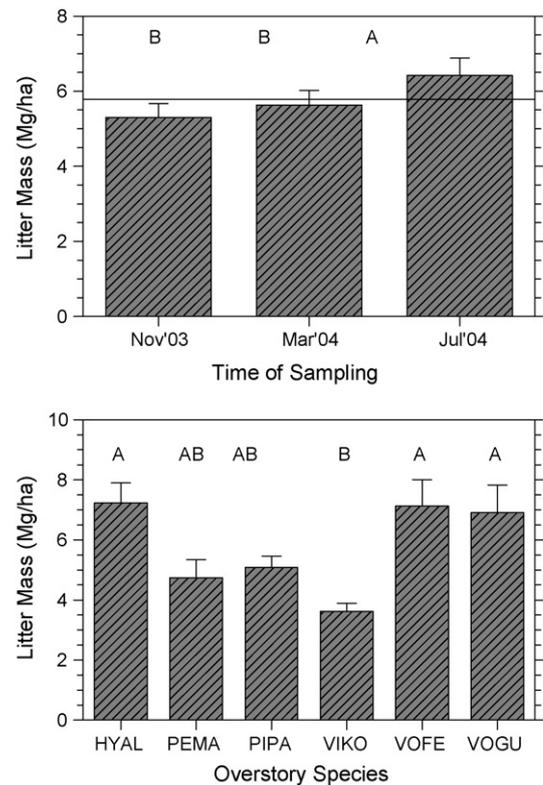


Fig. 2. Mean total surface litter mass (+S.E.) varied among sampling dates (upper) and among plantations of different species (lower) in lowland Costa Rica. In the upper figure the solid horizontal line shows the mean value of all plots across the three sampling times. In the lower figure the species are identified by the first two letters of their genus and species. Capital letters above each bar show significant differences among treatments as determined with the Tukey HSD test at  $\alpha = 0.05$ .

Table 2  
Surface fine litter accumulations and element concentrations in 16-year-old plantations of six tree species planted in replicated single-species plantations at La Selva, Costa Rica

	Total litter (Mg ha <sup>-1</sup> )	Non-woody litter (Mg ha <sup>-1</sup> )	Twig litter (Mg ha <sup>-1</sup> )
<b>Litter mass</b>			
<i>Hyeronima alchorneoides</i>	7.2 (0.7) A	5.9 (0.6) A	1.3 (0.1) BC
<i>Pentaclethra macroloba</i>	4.7 (0.6)	3.4 (0.5) B	1.4 (0.2) BC
<i>Pinus patula</i>	5.1 (0.4)	3.8 (0.3)	1.3 (0.1) BC
<i>Virola koschnyi</i>	3.6 (0.3) B	2.9 (0.2) B	0.7 (<0.1) C
<i>Vochysia ferruginea</i>	7.1 (0.9) A	3.9 (0.5)	3.2 (0.4) A
<i>V. guatemalensis</i>	6.9 (0.9) A	5.1 (0.7)	1.9 (0.3) B
Mature forest	5.9 (0.4)	4.8 (0.4)	1.1 (0.2)
	Total litter (Mg ha <sup>-1</sup> )	Non-woody litter (mg g <sup>-1</sup> )	Twig litter (mg g <sup>-1</sup> )
<b>Litter carbon</b>			
<i>Hyeronima alchorneoides</i>	3.5 (0.3) A	482 (8) A	488 (3) AB
<i>Pentaclethra macroloba</i>	2.3 (0.3)	473 (5) AB	496 (4) A
<i>Pinus patula</i>	2.4 (0.2)	472 (8) AB	489 (2) AB
<i>Virola koschnyi</i>	1.7 (0.2) B	463 (1) AB	478 (8) ABC
<i>Vochysia ferruginea</i>	3.3 (0.4) A	447 (5) B	476 (4) BC
<i>V. guatemalensis</i>	2.8 (0.4)	392 (01) C	462 (2) C
Mature forest	2.8 (0.2)	473 (3)	471 (6)
	Total litter (kg ha <sup>-1</sup> )	Non-woody litter (mg g <sup>-1</sup> )	Twig litter (mg g <sup>-1</sup> )
<b>Litter nitrogen</b>			
<i>Hyeronima alchorneoides</i>	98.0 (6.3)	14.7 (0.9) BC	9.7 (0.6) C
<i>Pentaclethra macroloba</i>	78.4 (7.6)	17.7 (0.8) A	14.7 (0.3) A
<i>Pinus patula</i>	63.4 (4.0) B	13.4 (0.6) C	10.0 (0.4) C
<i>Virola koschnyi</i>	58.6 (4.9) B	17.1 (0.4) AB	12.5 (0.3) B
<i>Vochysia ferruginea</i>	92.0 (10.7)	15.5 (0.3)	9.9 (0.8) C
<i>V. guatemalensis</i>	109.1 (14.6) A	17.6 (0.2) A	11.3 (0.3) BC
Mature forest	92.2 (11.8)	16.0 (1.3)	13.3 (0.8)

Values are means (S.E.);  $n = 4$ . Letters denote significant differences among species as determined with the Tukey–Kramer HSD test at  $\alpha = 0.05$ . Twigs were  $\leq 1$  cm in diameter including bark; larger woody debris was discarded. Data from the mature forest, collected with the same techniques on two dates, are included for comparison; they were not included in any statistical analyses.

were significantly greater beneath *Hyeronima*, *V. ferruginea* and *V. guatemalensis* than they were in *Virola* (Fig. 2).

Carbon and nitrogen concentrations in surface litter also varied significantly among species (ANOVA,  $P < 0.001$ ). In general, *Pentaclethra*, *Virola* and *V. guatemalensis* had relatively N-rich litter, whereas *Pinus* plots had relatively N-poor litter (Table 2). Total forest-floor carbon accumulations were significantly greater ( $P < 0.006$ ) in *Hyeronima* and *V. ferruginea* stands than beneath *Virola*, whereas total forest-floor nitrogen was significantly greater in *V. guatemalensis* than in either *Pinus* or *Virola* (Table 2).

### 3.3. Litter decay (turnover) rates

Decay rates of non-woody litter varied significantly among plots of different species ( $P < 0.031$ ), but those of small-branch litter did not ( $P > 0.34$ ). Non-woody litter was comprised mostly of leaves of the overstory species, which contributed an average of 70% of the non-woody litter production in our plots. Non-woody litter disappeared significantly faster (2.8 year<sup>-1</sup>) in *Pentaclethra* plots than in *V. guatemalensis* (1.5 year<sup>-1</sup>). Similar results were obtained when data were expressed in

terms of carbon, but litter-C decay rates generally were 0.1–0.2 year<sup>-1</sup> faster than were those calculated for organic matter.

Total fine litter mass, non-woody litter mass and twig litter mass all correlated significantly and positively with their corresponding litterfall rates (linear regressions,  $n = 24$ ,  $P < 0.004$ ). The  $R^2$ -values of these relationships, i.e., 0.47, 0.33 and 0.64 year, respectively, provide estimates of the proportion of the observed variability in litter mass that was due to differences in litter production among plots. The remaining variance presumably is attributable, in part, to differences among species in litter chemistry.

### 3.4. Overstory leaf chemistry

Senesced-leaf chemistry (Table 3) varied significantly among species for all measured variables (ANOVA,  $P < 0.0001$ ), with no significant block effects ( $P > 0.27$ ). Lignin contents, lignin:N, cellulose:lignin and foliar  $P$  varied by 3 $\times$  among species, whereas senesced-leaf N and hemicellulose concentrations and C:N varied by factors of  $>2$ . *Pinus patula*, the only conifer (and exotic) species planted, had the lowest concentrations of cell solubles, P, Ca and N, the

Table 3

Chemical characteristics of newly senesced leaves of six tree species established in plantations in lowland Costa Rica

Variable	<i>Hyeronima alchorneoides</i>	<i>Pentaclethra macroloba</i>	<i>Pinus patula</i>	<i>Virola koschnyi</i>	<i>Vochysia ferruginea</i>	<i>Vochysia guatemalensis</i>
Nitrogen (mg g <sup>-1</sup> )	11.4 (0.6) C	19.7 (0.4) A	8.8 (0.6) D	14.8 (0.4) B	11.1 (0.4) C	13.7 (0.2) B
C:N	45 (2) B	27 (1) C	61 (5) A	36 (1) BC	44 (1) B	31 (<1) C
Phosphorus (mg g <sup>-1</sup> )	0.62 (0.09) A	0.50 (0.02) AB	0.22 (0.03) C	0.61 (0.04) A	0.41 (0.02) BC	0.66 (0.03) A
Calcium (mg g <sup>-1</sup> )	6.7 (0.9) BC	3.5 (0.5) CD	2.3 (0.1) D	11.5 (1.1) A	5.3 (0.4) CD	9.2 (0.7) AB
Lignin (mg g <sup>-1</sup> )	140 (10) BC	252 (10) A	175 (6) B	283 (14) A	131 (3) C	83 (2) D
Cell Solubles (mg g <sup>-1</sup> )	631 (17) A	479 (12) B	456 (10) B	473 (12) B	618 (9) A	646 (4) A
Hemicellulose (mg g <sup>-1</sup> )	74 (2) C	101 (3) B	125 (3) A	59 (4) D	91 (2) B	92 (<1) B
Cellulose (mg g <sup>-1</sup> )	150 (5) C	163 (4) BC	234 (4) A	179 (2) B	156 (3) C	178 (2) B

Shown are means ( $\pm$ S.E.) based on four replicated plots of each species, with  $\geq 20$  leaves collected per species per plot. Letters within rows denote significant differences among species as determined with the Tukey–Kramer HSD test at  $\alpha = 0.05$ .

highest contents of hemicellulose and cellulose, and the highest C:N and lignin:N. *Pentaclethra macroloba*, the only N-fixing species studied, had the highest senesced-leaf concentrations of C and N, and the lowest foliar C:N (Table 3).

#### 4. Discussion

Fine litter production among the species we studied averaged 7.4–11.7 Mg ha<sup>-1</sup> year<sup>-1</sup>, including 120–210 kg ha<sup>-1</sup> year<sup>-1</sup> of nitrogen. Also at La Selva, but in younger plantations on alluvial soils, litter production among four native tree species averaged 8.2–12.6 Mg ha<sup>-1</sup> year<sup>-1</sup>, with 70–130 kg ha<sup>-1</sup> year<sup>-1</sup> of N (Montagnini et al., 1993). In 23–26-year-old plantations in Puerto Rico, fine litterfall among 10 species ranged from 8.1 to

14.3 Mg ha<sup>-1</sup> year<sup>-1</sup> with 50–150 kg ha<sup>-1</sup> year<sup>-1</sup> of N (Cuevas and Lugo, 1998). In eastern Pará, Brazil, litterfall in 23–37-year-old plantations averaged 8.0–10.3 Mg ha<sup>-1</sup> year<sup>-1</sup> and contained 40–130 kg ha<sup>-1</sup> year<sup>-1</sup> of N (Smith et al., 1998a). These data demonstrate that species vary in their litter production rates even when grown under similar conditions, and also that litterfall N fluxes at our site were large in comparison to those in other Neotropical plantations.

Across all study plots, litter production correlated positively with forest floor mass, as would be expected. Indeed, most of the observed variability in small-branch litter accumulations among our experimental plots could be explained by differences in small-branch litter production (Fig. 3). Small branches persisted on the forest floor for an average of 0.9 year,

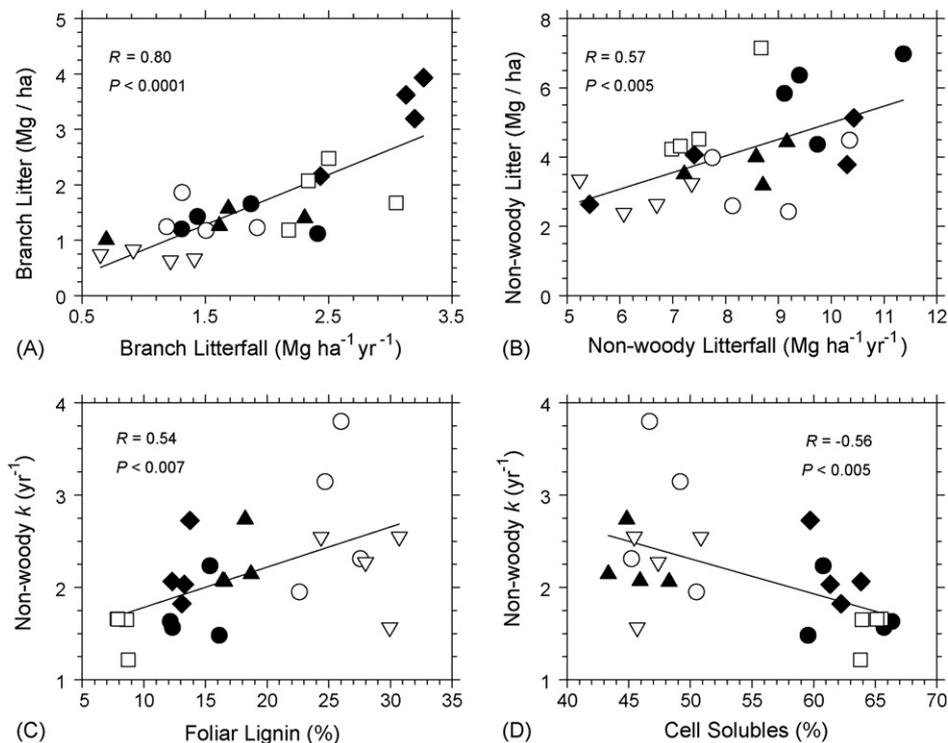


Fig. 3. Relationships between forest-floor mass and related variables in 16-year-old experimental plantations in lowland Costa Rica. (A) The mass of small-branch litter present increased with increasing rates of small-branch litter production. (B) The mass of non-woody litter correlated positively with non-woody litter production. (C) Non-woody litter decay rates ( $k$  values) increased with increasing leaf lignin content, but (D) decreased with increasing cell soluble content. Symbols: ● = *Hyeronima alchorneoides*, ○ = *Pentaclethra macroloba*, ▲ = *Pinus patula*, ▽ = *Virola koschnyi*, ◆ = *Vochysia ferruginea*, and □ = *Vochysia guatemalensis*.

regardless of overstory species. In contrast, non-woody litter turnover rates varied significantly among plantations of different species, indicating that factors other than litter production rate influenced the accumulated mass of non-woody litter on the forest floor.

Similar findings are often attributed to differences in substrate quality or chemistry (e.g., Gholz et al., 2000). This possibility is supported by our data: virtually every leaf variable that we measured varied significantly among species (Table 3). Correlation of measured senesced-leaf characteristics with non-woody litter decay rates supported several observations. First, many measured leaf characteristics co-varied significantly with one another: this prevents the unambiguous assignment of cause (of altered decay rate) to any individual variable, and may explain why so many different leaf-level variables are significantly correlated to litter decay rate in at least one study. Second, leaf lignin ( $r = 0.54$ ) and cell soluble-C contents ( $r = -0.56$ ) correlated particularly strongly ( $P < 0.01$ ) with litter decay rates in our experiment—but in the wrong ways! Litter decay was significantly faster beneath species with higher lignin contents (Fig. 3), contrary to expectations (e.g., Meentemeyer, 1978; Melillo et al., 1982), and decay was significantly slower in plantations with more cell solubles (Fig. 3), also contrary to expectations (Moorhead et al., 1999; Allison and Vitousek, 2005). Third, species-related factors were approximately as important ( $R^2 \sim 0.3$ ) in determining non-woody forest floor mass as was litterfall rate ( $R^2 = 0.33$ ). Finally, there were no significant correlations between litter decay rates and senesced-leaf P or Ca concentrations ( $r = -0.2$ ,  $P > 0.37$ ), despite evidence that these soils, in mature forests at La Selva, have potentially limiting concentrations of available P and base cations (Denslow et al., 1987; Vitousek and Denslow, 1987).

Litter decomposition rates are influenced by at least three general factors: the composition and activity of the decomposer community (O, organisms), the quality of the detritus (Q) and the physicochemical environment, P (Anderson and Swift, 1983). Overstory-tree species identity potentially influences all three of these factors. Under our experimental design, climate, land-use history and soil type were all similar among treatments; the differences in litter turnover that we observed among species can be attributed directly to the planted species. However, the plant traits (Table 3) constitute an observational study: species varied from one another in multiple ways. Therefore, we cannot infer causation from the correlations we found between litter decay rates and senesced-leaf chemistry (Fig. 3). This is generally true of all decomposition studies; experimental studies in which individual biochemicals can be tested singly, under controlled conditions, are needed.

Contrary to previous studies, we found a highly significant, positive correlation between lignin contents and decay rates (Fig. 3C). This finding is supported by measurements of soil organic matter contents in the same sites (Russell et al., submitted for publication), which correlated negatively with foliar lignin contents ( $n = 24$ ,  $r = -0.52$ ,  $P < 0.01$ ). It would appear that the decomposer organisms in our sites did not just tolerate lignin, they preferred it. Perhaps organisms can trump

chemistry in controlling litter decomposition in tropical rain forests (Anderson and Swift, 1983; Lavelle et al., 1993). Regardless, this result contradicts models that predict that lignin depresses litter turnover rates (e.g., Meentemeyer, 1978) and highlights the potential problem that exists when individual factors are presumed to control the rate of a process that is under multivariate control.

An alternative explanation is that lignin had no effect on decay rates, but correlated with another factor that did. One possible such factor is soluble-C content, which correlated negatively with both foliar lignin contents ( $r = -0.83$ ,  $P < 0.0001$ ) and litter decay rates (Fig. 3D). Cell solubles, as determined with the forage-fiber technique, generally include easily and rapidly metabolized compounds (van Soest, 1994). It is possible that the species we investigated contained high concentrations of soluble tannins, which have been linked to slower decomposition rates (see Maie et al., 2003), but additional measurements would be needed to test this hypothesis. Our results do demonstrate unambiguously that overstory-tree species identity significantly influences the amounts, composition, and dynamics of surface litter in tropical forest plantations. Although the underlying causal mechanisms remain imperfectly understood, the central role of the forest floor in connecting the above- and belowground ecosystems suggests that these differences describe one way by which individual species alter the trajectory of ecosystem development after tropical reforestation.

## Acknowledgements

We thank Dr. Eugenio González for his assistance with project management; Dennes Chavarría, Roger Gómez, Marlon Hernández, and Marvin, Eduardo, and Bernal Paniagua for their assistance in Costa Rica; Elizabeth Easton and Oscar Valverde-Barrantes for their assistance with C and N analyses; and Trish Patrick for conducting the carbon-chemistry analyses. Funding was provided by U.S. National Science Foundation grant DEB-0236502.

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