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SPECIES, ROTATION, AND LIFE-FORM DIVERSITY EFFECTS ON SOIL CARBON IN EXPERIMENTAL TROPICAL ECOSYSTEMS

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Abstract. Extensive areas of species-rich forests in the tropics have been replaced by tree monocultures over the last two decades, and the impact on biogeochemical cycles is unclear. We characterized effects on soil carbon dynamics of species identity and rotation frequency in experimental plantations containing three native, non-N-fixing tree species, *Hyeronima alchoreoides*, *Cedrela odorata*, and *Cordia alliodora*, grown in monocultures and in polycultures with two monocot species, *Euterpe oleracea* and *Heliconia imbricata*. Over all treatments, change in total soil organic carbon (TSOC, 0–15 cm) after 10 years ranged from a loss of 24% (0.9 mg/ha in 1-yr rotation of *Cedrela*) to an increase of 14% (0.6 mg/ha under *Hyeronima* polycultures). Species differed in their effects on quantities of TSOC ($P = 0.038$), but differences were more pronounced in light particulate organic matter (LPOM; $P = 0.001$), a biologically active, sand-size soil fraction that constituted 6% of TSOC. Effects of rotation frequency were strong; in *Cedrela* and *Cordia*, the 4-yr rotations had higher soil C stocks than did long-term monocultures, where soil C stocks had declined under 10-yr-old trees. Under *Cedrela* and *Cordia*, polycultures had significantly higher stocks of soil C than monocultures, whereas soil C stocks were high under *Hyeronima* in both cultures. In polycultures, *Hyeronima* dominated detrital inputs, contributing 88% of litterfall and fine-root growth, whereas *Cedrela* and *Cordia* contributed <34%. Root C:N ratio and fine-root growth accounted for most of the variability in changes in soil C stocks after 10 years in long-term rotations (partial $R^2 = 0.70$ and 0.14, respectively). These data suggested that roots drove soil C accrual in long-term rotations, and that mechanisms involving root chemistry, and not quantity of detrital inputs, best explained effects of species on soil C sequestration.

Key words: *carbon sequestration;* Cedrela odorata; Cordia alliodora; *detrital quantity and quality;* Hyeronima alchorneoides; *particulate organic matter; plantations; root growth; soil organic matter; species composition; species diversity; tropical ecosystems.*

INTRODUCTION

Plant species differ in their ability to capture resources (e.g., Tilman 1988) and in their impacts on ecosystem processes (e.g., Vitousek et al. 1987, Chapin 1993, Russell et al. 1998). Likewise, different mixes of species affect ecosystem functioning in different ways (e.g., Haggar and Ewel 1997, Tilman et al. 1997, Hooper and Vitousek 1998, Hector et al. 1999, Loreau et al. 2001). Insight into the effects of plant species and species richness on ecosystem processes is especially important in the tropics, where land-use changes involving replacement of natural with managed systems are often accompanied by loss of biodiversity (e.g., O'Brien and Kinnaird 2003). Tree plantation coverage in the tropics more than doubled in the 1990s, from 31 million ha in 1990 (Singh 1993) to over 76 million ha in 2000 (FAO 2001). Of that area, 56% involved conversion of natural, presumably mixed-species forests to monocultures; the remaining 44% of plantations replaced pasture or croplands. Especially in degraded landscapes in the humid tropics, the latter type of conversion can increase soil fertility, carbon storage (Fisher 1995), and biodiversity (Haggar et al. 1997).

Our study of species effects on ecosystem processes focuses on soil organic matter (SOM) dynamics. Soil OM directly influences many ecosystem processes, such as plant productivity, through its effects on soil structure, water-holding capacity, and measures of soil fertility such as cation exchange, nutrient release during decomposition, and available N and P (Young 1976, Brown et al. 1994, Tiessen et al. 1994). Despite the role of soil C in the global carbon cycle (UNFCC 1997, Scholes and Noble 2001), it is unknown whether tropical soils, taken as a whole, are a net sink or a source for atmospheric CO_2.

Soil OM quantity alone, however, does not necessarily correlate well with SOM turnover rate or capacity of the soil to supply nutrients (Sanchez and Miller 1986). Furthermore, the relatively small changes in the large quantities of total SOM induced by species and

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management may not be detectable against background soil variability (Paustien et al. 1997). These modest, shorter term effects can, however, be detected by monitoring biologically active soil C fractions such as the light fraction, light particulate organic matter (LPOM), and potentially mineralizable carbon (Cambardella and Elliott 1992, Christensen 1992, Barrios et al. 1996, 1997, Guggenberger and Zech 1999, Alvarez and Alvarez 2000, Motavalli et al. 2000). The light fraction is defined by density alone, whereas LPOM is defined by both size (sand sized, >53 μm) and density.

Because the ultimate source of SOM is CO_2 fixed by plants, differences among species in traits such as fine-root and aboveground litter production have the potential to influence the quantity of soil C stocks. The chemical and structural nature of the detritus produced affects the rate of decomposition (e.g., Heal et al. 1997), which also influences litter and SOM dynamics, and soil C stocks (Olson 1963, Paustien 1997, Kaye et al. 2000). Thus, important mechanisms by which species can influence the quantity of soil C stocks involve the quantity and chemistry of detrital inputs.

In experimental plantations established in 1991 in lowland Costa Rica, we examined effects of tree species, stand rotation frequency, and life-form diversity on soil C and N quantities in whole soil and size fractions, and soil biological processes related to soil fertility. We measured aboveground detrital production, assayed fine-root growth, and assessed the relative influences of quantity and chemistry of detrital inputs on soil C storage. Whereas most studies of species' effects on soil C compare strongly contrasting species, e.g., N-fixers and non-N-fixers (Barrios et al. 1997, Bashkin and Binkley 1998), different life-forms (Solomon et al. 2002), or conifers and broadleaved trees (Johnson 1992), we compared effects of less contrasting tree species, all non-N-fixing angiosperms. We worked at the low end of the diversity scale, combining the three most common life-forms (trees, palms, perennial herbs) in the local rain forest.

Methods

Study site

The study site is located in the Atlantic lowlands of Costa Rica at La Selva Biological Station (10°26′ N, 83°59′ W, elevation 40 m). Mean (± 1 SE) annual rainfall is 4210 ± 113 mm (n = 40 yr), and mean monthly rainfall is >100 mm. Mean annual temperature is 25.8°C; diurnal average temperatures vary <3°C over the year (Sanford et al. 1994, Matlock and Hartshorn 1999). This research was conducted on plots occupying 8 ha on a peninsula formed by the confluence of the Puerto Viejo and Sarapiquí Rivers. Site preparation in 1991 consisted of felling existing vegetation on an abandoned cocoa plantation, removing trunks of merchantable overstory trees, burning the slash, and immediately establishing the experimental plots (Haggar and Ewel 1995). The study site soil is a fertile, sandy loam composed of Holocene and Pleistocene alluvia of volcanic origin. Soil on the site is uniform enough to be classified within a single soil family, eutric Hapludand (Weitz et al. 1997), characterized by minimum horizon development and high base saturation. Soil erosion is virtually nil. Prior to plot establishment, soil (0–10 cm) pH was 6.5 and contained 34 mg/g soil organic carbon (SOC, as determined by Walkley-Black method), 13.7 μg/g extractable nitrate- and ammonium-nitrogen, and 18.2, 496, 1570, and 245 μg/g extractable P, K, Ca, and Mg, respectively (Haggar and Ewel 1997).

Experimental design

To investigate the effects of species, rotation frequency, and life-form diversity on ecosystem processes, three experiments were initiated in 1991 in a split-plot randomized block design. Each experiment was distinguished by its dominant tree species: *Hyeronima alchorneoides* Allemao (Euphorbiaceae), *Cedrela odorata* L. (Meliaceae), or *Cordia alliodora* R. & P. Cham. (Boraginaceae). These native species produce valuable wood, and all of them fall into the broad functional group of dicotyledonous, fast-growing, non-N-fixing trees. They were chosen for the experiments because they differ in phenology, physiognomy, and resource partitioning (Haggar and Ewel 1995, 1997). *Hyeronima* is evergreen, whereas the other two are deciduous. *Cedrela* leaves are pinnately compound, whereas the others are simple. Crown structure in *Hyeronima* is sympodial with orthotropic branching, in *Cordia* it is monopodial with plagiotropic branching, and in *Cedrela* it is monopodial with orthotropic branching. Each dominant tree species was grown under four treatments, three of which were tree monocultures subject to rotations of 1 or 4 yr, or long-term (uncut). The fourth treatment (also uncut) was a polyculture containing one of the dominant trees plus two perennial monocot species, a palm *Euterpe oleracea* Mart (Arecaceae) and *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae). Each experimental plot was replicated three times. Thus, the experimental design consisted of 3 tree species × 4 treatments × 3 blocks, for a total of 36 plots.

The plot for each species was 90 × 40 m and divided into two parts, one part (60 × 40 m) was maintained in monoculture, and the other part (30 × 40 m) was interplanted additively with *Euterpe* and *Heliconia*. For testing effects of complementarity, this additive design was preferable to a replacement design because the same density of tree species could be maintained in both monocultures and polycultures (Snaydon 1991). One consequence of an additive design is that polycultures have higher total plant density than monocultures; higher productivity in the polyculture could simply be the result of higher density. To deduce that higher productivity is instead due to complementarity, the investigator must be convinced that productivity of the

monoculture could not be increased under higher plant density. An integral part of our design was the establishment of tree species at a high enough density so that conclusions regarding complementarity could be reached (Haggar and Ewel 1997). At a spacing of 2 m between trees, density was 2887 trees/ha. *Euterpe* was planted at the time of tree planting, between every other tree in every other row of trees, hence at one-quarter density of the tree species. *Heliconia* was planted a year later, between every tree in the row not planted with *Euterpe*, hence at one-half density of the tree species. Plots were lightly thinned on occasion to maintain stand vigor while still ensuring full use of resources, but the total basal area of trees in polycultures was never reduced below that of conspecific monocultures. Root system closure occurred within a year of planting (Haggar and Ewel 1995), and trenching experiments yielded a significant growth response in *Piper* seedlings transplanted into the understory (Gerwing 1994), indicating reasonably complete use of soil resources. The stands were weeded every 2–3 wk, although this soon became unnecessary in the polycultures and some monocultures.

Detrital inputs

Fine-root growth.—We measured fine-root ingrowth (Cuevas et al. 1991) to provide an assay of fine-root detrital inputs in Year 9 of the experiment, 1999–2000. Root ingrowth cores were constructed of polyethylene tubing, 10 cm tall and 7 cm in diameter, 8-mm^2 mesh, with 2-mm nylon mesh screen for tops and bottoms. Cylinders were filled with sieved, root-free soil, inserted into a hole of the same size, and the litter layer was replaced. To determine the appropriate time interval for ingrowth and to assess root mortality rates, we measured root ingrowth in separate sets of cores that were retrieved after 4, 8, and 11 mo. In the uncut monocultures and polycultures, dead root mass increased from 10% to 18% of total mass from 4- to 8-mo intervals, then declined to 10% after 11 mo. We concluded that a 4-mo ingrowth period was best for assessing ingrowth and would capture seasonal variability. Thus, we installed new cores in all plots (5 cores/plot, 0.5 m from randomly selected trees) in July 1999, November 1999, and March 2000, and retrieved each set ~4 mo after installation. Initial separation of roots from soil was done using a hydropneumatic elutriation system (mesh size of 410 μm; Smucker et al. 1982). In tests using sewing threads as an assay for fine roots (mixed with soil), we recovered 100% of initial mass ($n = 5$ replicates). Roots were separated from detritus by hand, sorted by species and by status (live or dead) based on morphological characteristics, and dried at 65°C.

Aboveground inputs.—Litterfall, sorted by species, was measured once every two weeks using four raised, screen-bottomed litter traps (50 × 173 cm) per plot. Felled trees in the 1- and 4-yr rotations were not removed from the plot, but were left to decompose in situ. Although not typical of forestry operations, this practice prevented confounding the effects of nutrient loss via exported biomass with effects of rotation length in this experiment. This input was estimated using allometric equations developed from harvested trees and relationships between diameter and height, and biomass (Haggar and Ewel 1995).

Tissue chemistry

Tissue chemistry was characterized for each tree species, plus the two monocots, by analyzing live roots and senesced leaves for total C, total N, and fractions of C. One randomly selected block was sampled in this relatively uniform site where block effects were not significant for any variable measured. Three plots were sampled for each species, the three monocultures for tree species, and the three polycultures for *Euterpe* and *Heliconia*. For each species, 15 newly senesced leaf and 15 live root biomass samples were collected in June 1999, just prior to felling in the 1- and 4-yr rotations. For the tree species, samples consisted of 5–30 leaves, and 5 leaves for each of *Euterpe* and *Heliconia*. Root samples of 10 g were collected from randomly selected locations within plots. Samples were dried at 65°C and ground in a Wiley mill. A subsample was ground in a ball mill for analyses of C and N by combustion using a N/C/S elemental analyzer (model NA 1500, Carlo-Erba Strumatazione, Milan, Italy). Ash-free lignin and soluble C plus hemicellulose fractions of C were determined using van Soest's detergent fiber method (van Soest 1994, Vogel et al. 1999).

Soil carbon and nitrogen

We measured soil organic carbon (TSOC) and total nitrogen (TN) in whole soil, and C and N in two physical fractions, light particulate organic matter (LPOM), and the silt–clay separate. Light POM is composed primarily of partially decomposed plant, bacterial, algal, and fungal residues, and in the temperate zone has turnover times of months to decades; it is the fraction most sensitive to oxidative losses resulting from soil disturbance (Cambardella and Elliott 1994, Parton et al. 1994). Soil C associated with the silt- and clay-sized fractions is considered to be more stabilized than LPOM (sand-sized) fractions (as reviewed by Christensen 1992, Woomer et al. 1994). To compare the effects of species and rotation frequency on soil fertility from a biological perspective, we measured potential C and net N mineralization, assays of the soil's capacity to release nutrients, and available P. Potentially mineralizable soil C provides an estimate of ''active'' C, a fraction with daily to annual turnover times, but also includes ''slow'' C fractions with turnover times of months to decades (Paul et al. 2001).

Sampling and processing.—To determine the effect of the felling/planting operation on stocks of TSOC and LPOM, and to ensure that timing of sampling

would not confound results, we sampled soil in all 36 plots four times in the course of 2 yr (1999–2000, when the plots were 8–10 yr old), ~1 mo before and 1 mo after cutting and replanting of the 1-yr rotation. In the 4-yr rotation of *Hyeronima*, we also sampled 1, 2, and 3 wk after tree felling in 1999 to monitor LPOM following tree felling. In each sampling, six soil cores, 3.2 cm in diameter and 15 cm deep, were combined to yield one composite sample per plot. The soil was air-dried, roots were removed, and the soil was sieved (2 mm) and mixed. Subsamples were ground on a roller mill prior to analyses of total C and N, and determination of conversion factors to a dry mass (105°C) basis. Organic C and N in whole soil (TSOC, TN) and in light particulate organic matter (LPOMC, LPOMN) were measured in samples from all four sampling times. Potential C, net N mineralization, and available P were measured for the first set of samples, taken in 1999 before stands were felled.

Soil organic C and total N in whole soil and in LPOM were measured by combustion using a Carlo-Erba NA 1500 N/C/S elemental analyzer. Initial TSOC for the site was determined by Walkley-Black method (WB) using the average of samples taken from three soil pits. To compare our TSOC measurements with initial values, we analyzed all 36 samples from our first sample time by both WB and Carlo-Erba combustion (CE) methods, using 1.724 as the conversion for OM to OC by Walkley-Black (Nelson and Sommers 1996). The relationship between SOC (%) by the two methods was $CE = 0.322 + 0.964 \times WB$ ($r^2 = 0.94$, $P < 0.0001$).

Soil C storage was calculated as the product of bulk density (BD), soil thickness (15 cm), and soil C concentration. Bulk density was measured annually in all plots by soil core method (Blake and Hartge 1986), by sampling a 7.4 cm diameter core over two depths, 0–7.2 cm (in 1999 and 2000) and 7.2–14.4 cm (in 1999), for a total of 108 samples. To circumvent bias due to treatment differences in BD, we used mean BD (0.80 g/cm^3) over all plots (0–14.4 cm depth) in our storage calculations for the top 15 cm (Ellert et al. 2001).

Soil C size fractions.—Light particulate organic matter (LPOM) was quantified according the method of Cambardella and Elliott (1992) and Gale and Cambardella (2000) with the following modifications. Six 5-g samples per plot were first dispersed for 18 h by shaking in 30 ml of 5 g/L sodium metaphosphate. Sonication at an energy level of 17.4 J/s for 90 s in 100 mL water was needed to further disperse samples. In an initial study, we determined that this level of sonication did not fracture LPOM; verification was by visual examination with a dissecting microscope, and by comparing C:N ratios along a continuum of size fractions: <20, 20–53, 53–250, 250–500, and >500 μm. This pilot study also revealed that these soils did not contain LPOM in the 20–53 μm size range; hence LPOM could be defined as the 53–500 μm separate, and the silt + clay fraction as the separate <53 μm. Samples were rinsed thoroughly on a 53-μm sieve and the material retained (LPOM + sand) was backwashed onto a 20-μm filter. A vacuum was applied to remove excess water. The sample was allowed to separate overnight in sodium polytungstate (1.85 g/cm^3), and the part that floated, LPOM, was aspirated, dried at 55°C, ground, and analyzed for TOC and TN. Scanning electron microscopy revealed that the separate that sank contained some undispersed aggregates composed of silt- and clay-sized particles, in addition to sand. That silt–clay fraction was analyzed separately for the first sample time only. The silt–clay C fraction was calculated as the difference between TSOC and LPOM. Charcoal, present in all fractions of these samples, was not quantifiable, but was estimated by microscopy to constitute ~1% of the volume.

Soil organic matter decomposition

C mineralization.—Potentially mineralizable soil C was measured during extended laboratory incubations at 23°C (Paul et al. 2001). A sieved (2 mm), 10-g air-dried soil sample from each of the 36 plots (sampled before tree felling in 1999) was mixed with acid-washed sand (on a 1:1 mass ratio basis) and placed in a 260-mL Erlenmeyer flask (Haddas et al. 1998). The mixture was brought to 60% water-filled pore space using deionized water that contained 2 mL of inoculant that had been prepared by homogenizing 5 g field-moist soil from the respective treatment with 50 mL distilled water. Rate of CO_2-C released was measured periodically over 180 d (before CO_2 concentrations reached 4%) by flushing the flask headspace through an infrared gas analyzer (model 880A, Rosemount Analytical, Incorporated, Orrville, Ohio, USA).

Net N mineralization and available P.—Potential net N mineralization was calculated as the difference between the final and initial quantities of nitrate- and ammonium-N in the incubated soils described above. We extracted 9 g of soil with 2 mol/L KCl in a 1:5 soil : solution ratio. The soil solution was shaken for 30 min and allowed to settle for 30 min, and the filtrate was analyzed colorimetrically for NO_3-N and NH_4-N using an automated ion analyzer (QuickChem 4100, Lachat Instruments Division, Zellweger Analytics, Incorporated, Milwaukee, Wisconsin, USA). Subsamples were dried at 105°C to determine moist-to-dry-mass conversion factors. Available P was extracted by Mehlich III method (Mehlich 1984), and then analyzed using inductively coupled plasma atomic emission spectrometry (model 61-E spectrometer, Thermo Jarrell Ash Corporation, Franklin, Massachusetts, USA; Kuo 1996).

Statistical analyses

In the split-plot randomized block design for this experiment, the main treatment was tree species and the sub-treatment was treatment (rotation frequency and life-form diversity), with all effects treated as fixed

TABLE 1. Fine-root ingrowth and aboveground detrital inputs (means ± 1 SE in parentheses) under different species, rotation frequencies, and life-form diversity in plantations at La Selva, Costa Rica.

	Species‡								
	Hyeronima			*Cedrela*			*Cordia*		
		Significance			Significance			Significance	
Variable and treatment†	Mean (SE)	Trees	All species	Mean (SE)	Trees	All species	Mean (SE)	Trees	All species
Fine-root growth, Year 9 ($g \cdot m^{-2} \cdot yr^{-1}$)									
1-yr rotation monoculture	51 (17)	a	A	38 (12)	a	AB	29 (13)	a	A
4-yr rotation monoculture	23 (4)	a	A	23 (2)	a	A	21 (5)	a	A
Long-term monoculture	196 (41)	b*	B*	80 (8)	b	BC	74 (4)	b	AB
Polyculture, total	455 (40)		C*	121 (29)		C	146 (32)		B
Polyculture, tree only	404 (27)	c*		25 (16)	a		53 (17)	b	
Polyculture, *Euterpe*	47 (15)			72 (11)			89 (38)		
Polyculture, *Heliconia*	4 (1)			24 (3)			4 (1)		
Leaf litterfall, Year 9 ($g \cdot m^{-2} \cdot yr^{-1}$)									
1-yr rotation monoculture	33 (4)	a	A	29 (5)	a	A	49 (15)	a	A
4-yr rotation monoculture	81 (9)	b	B	80 (4)	b	B	105 (21)	b	B
Long-term monoculture	679 (57)	c	C	573 (23)	d	C	449 (43)	c	C
Polyculture, total	722 (31)		C	539 (48)		C	451 (38)		C
Polyculture, tree only	635 (25)	c*		196 (23)	c		138 (8)	b	
Polyculture, *Euterpe*	48 (13)			335 (75)			303 (31)		
Polyculture, *Heliconia*	39 (12)			8 (5)			10 (4)		
Leaf litterfall, mean of Years 5–8 ($g \cdot m^{-2} \cdot yr^{-1}$)									
1-yr rotation monoculture	20 (3)	a	A	41 (8)	a*	A*	11 (2)	a	A
4-yr rotation monoculture	484 (28)	b	B	455 (24)	bc	B	475 (13)	c	B
Long-term monoculture	736 (35)	b	B*	614 (18)	c	B*	467 (15)	c	B
Polyculture, total	697 (30)		B	565 (37)		B	553 (63)		B
Polyculture, tree only	665 (28)	b*		335 (9)	b		218 (23)	b	
Branch litterfall, mean of Years 5–8, tree species ($g \cdot m^{-2} \cdot yr^{-1}$)									
1-yr rotation monoculture	0 (0)	a		0 (0)	a		0 (0)	a	
4-yr rotation monoculture	50 (11)	b*		6 (4)	b		122 (30)	b*	
Long-term monoculture	124 (8)	c*		47 (11)	c		96 (13)	b	
Long-term polyculture	108 (6)	c		47 (13)	c		42 (11)	b	
Leaf biomass, Year 8 (g/m^2)									
1-yr rotation monoculture	90 (9)	a*		34 (6)	a		7 (2)	a	
4-yr rotation monoculture	193 (14)	b		206 (3)	b		309 (16)	b*	
Stem biomass, Year 8 (g/m^2)									
1-yr rotation monoculture	156 (18)	a*		106 (28)	a		9 (3)	a	
4-yr rotation monoculture	3006 (137)	b		2701 (35)	b		3441 (198)	b*	

† Treatment means ($n = 3$ blocks) within the columns (species) followed by the same letter are not significantly different ($\alpha = 0.05$). Lowercase letters represent comparisons of tree species only; capital letters represent comparisons using total of all species in polycultures.

‡ Species means within rows (i.e., treatments) that are significantly higher are denoted by an asterisk (*$P < 0.05$).

(Littell et al. 1991). We tested for homogeneity of variances, normal distribution, and spatial correlation. Root ingrowth and litterfall data had unequal variances; analyses were performed on natural log-transformed data that did fit the assumptions. We found no significant spatial correlations. For the response variables TSOC, TN, LPOMC, and LPOMN, ANOVA was first conducted using a repeated-measures design to test for differences among the four sampling times. None of the variables varied in any consistent way over time, so subsequent ANOVAs were conducted on means over four sample times within species, treatment, and block. For ANOVA of tissue chemistry, the model contained two factors (tissue type, species). Bonferroni multiple comparison tests were used to compare differences among treatments and species with an experiment-wise error rate of $\alpha = 0.05$. Step-wise multiple regression was used to evaluate importance of quantity and tissue chemistry of inputs (SAS Institute 1988).

RESULTS

Species' effects in long-term monoculture

Detrital inputs differed significantly among species in long-term monocultures of this study. Leaf and branch litterfall were higher in *Hyeronima*, significantly so over Years 5–8, but not in Year 9 (Table 1, Fig. 1A). Fine-root ingrowth and tissue chemistry, measured only in Year 9, also differed significantly among species (Tables 1 and 2, Fig. 1B, C). Over all treatments and sampling times, dead roots constituted only 8% of total fine-root ingrowth; only totals are

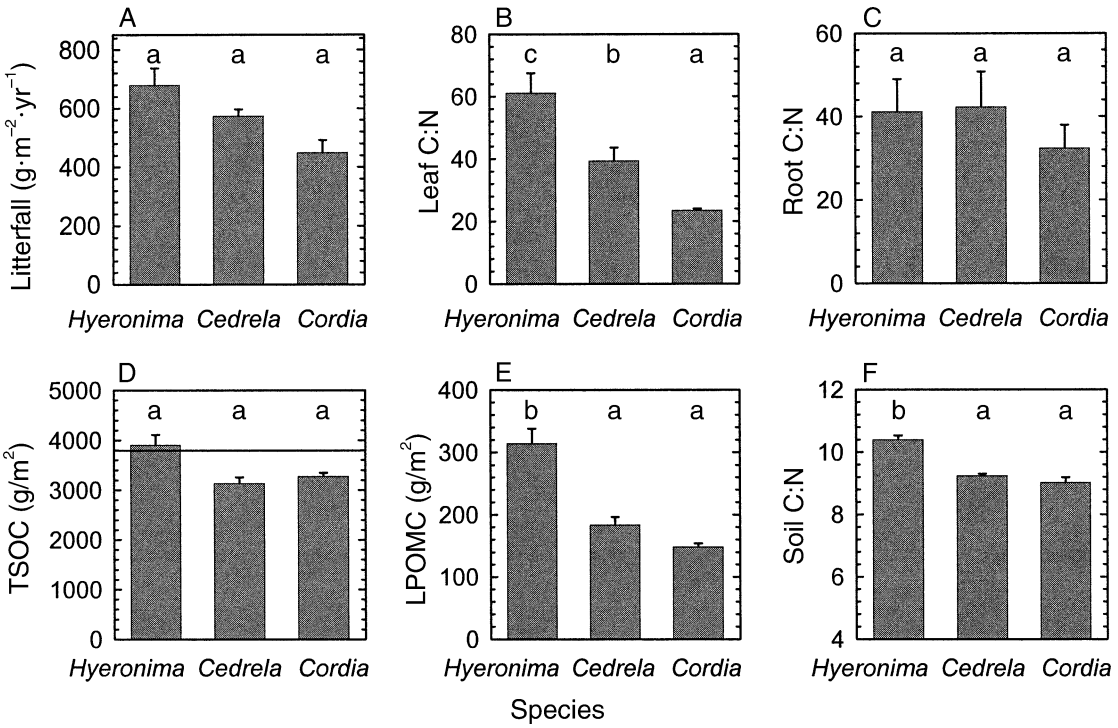

FIG. 1. Species effects in 9-yr-old monocultures at La Selva, Costa Rica: (A) leaf litterfall in Year 9, (B) newly senesced leaf C:N ratio, (C) live root C:N ratio, (D) total soil organic C (TSOC), (E) light particulate organic matter (LPOM) C, and (F) whole soil C:N ratio. Means (+1 SE) with the same lowercase letters are not significantly different ($\alpha = 0.05$). Soil C means are based on four measurements over Years 8–10 in three blocks. Initial TSOC in panel D (Year 1) is denoted by the horizontal line.

TABLE 2. Tissue chemistry (means, with 1 SE in parentheses) of species in plantations at La Selva, Costa Rica.

Variable	Species†	Tissue type	
		Senesced leaves	Live roots
C (%)	*Heliconia*	40.30 (2.19) a	44.63 (2.70) a
	Euterpe	45.47 (1.11) ab	48.50 (1.07) ab
	Cordia	45.91 (0.59) ab	45.61 (1.46) ab
	Cedrela	48.77 (1.29) b	47.82 (1.14) b
	Hyeronima	50.39 (1.40) b	47.42 (1.38) b
N (%)	*Euterpe*	0.46 (0.03) a	0.79 (0.05) a
	Heliconia	0.73 (0.01) a	0.60 (0.05) a
	Hyeronima	0.84 (0.10) ab	1.22 (0.18) a
	Cedrela	1.27 (0.15) b	1.23 (0.25) a
	Cordia	1.96 (0.05) c	1.50 (0.28) a
Lignin (%)	*Heliconia*	12.28 (0.53) a	13.11 (0.17) a
	Euterpe	15.13 (0.60) ab	20.91 (0.28) ab
	Cedrela	19.82 (4.80) bc	27.04 (3.77) bc
	Cordia	21.16 (0.41) bc	24.25 (3.28) bc
	Hyeronima	25.61 (1.93) c	31.30 (4.59) c
Hemicellulose‡ (%)	*Euterpe*	41.55 (2.18) a	41.11 (0.86) a
	Heliconia	46.45 (0.60) ab	55.38 (0.76) a
	Hyeronima	53.90 (2.67) ab	42.32 (6.23) a
	Cordia	58.18 (0.36) ab	41.01 (1.31) a
	Cedrela	58.39 (6.52) b	40.90 (0.74) a

† Means within columns (species, $n = 3$) followed by the same letter are not significantly different ($\alpha = 0.05$).

‡ Includes soluble C.

TABLE 3. Soil characteristics (means, with 1 SE in parentheses) under different species, rotation frequencies, and life-form diversity in plantations at La Selva, Costa Rica.

Variable and treatment†	Species‡		
	Hyeronima	*Cedrela*	*Cordia*
Total soil organic C (mg/g)			
1-yr rotation monoculture	25.61 (1.93) a	24.51 (2.09) a	25.27 (0.90) a
4-yr rotation monoculture	32.01 (1.35) b	29.63 (1.79) bc	33.15 (0.49) b
Long-term monoculture	32.55 (1.73) b	26.13 (1.04) ab	27.33 (0.57) a
Long-term polyculture	36.96 (1.95) b	33.36 (0.81) c	34.14 (0.64) b
Light particulate organic matter C (mg/g)			
1-yr rotation monoculture	0.84 (0.16) a	0.92 (0.17) a	0.87 (0.13) a
4-yr rotation monoculture	2.65 (0.28) b	1.80 (0.03) b	2.34 (0.20) bc
Long-term monoculture	2.62 (0.20) b*	1.53 (0.11) ab	1.24 (0.05) ab
Long-term polyculture	2.90 (0.28) b	2.99 (0.22) c	3.13 (0.40) c
CO_2-C released, cumulative over 180-d laboratory incubations (mg/g)			
1-yr rotation monoculture	1.03 (0.08) a	0.92 (0.07) a	1.11 (0.12) a
4-yr rotation monoculture	1.36 (0.09) ab	1.24 (0.07) b	1.39 (0.11) a
Long-term monoculture	1.44 (0.02) b	1.13 (0.04) ab	1.21 (0.09) a
Long-term polyculture	1.32 (0.08) ab	1.71 (0.01) c*	1.53 (0.03) a
Total soil N (mg/g)			
1-yr rotation monoculture	2.91 (0.21) a	2.80 (0.20) a	2.88 (0.03) a
4-yr rotation monoculture	3.15 (0.13) ab	3.17 (0.20) ab	3.57 (0.03) b
Long-term monoculture	3.13 (0.15) ab	2.83 (0.09) a	3.02 (0.02) a
Long-term polyculture	3.55 (0.19) b	3.33 (0.09) b	3.51 (0.07) b
Light particulate organic matter N			
1-yr rotation monoculture	0.04 (0.01) a	0.04 (0.01) a	0.05 (0.01) a
4-yr rotation monoculture	0.11 (0.02) b	0.09 (0.01) b	0.16 (0.01) bc
Long-term monoculture	0.11 (0.01) b*	0.08 (0.01) ab	0.08 (0.01) ab
Long-term polyculture	0.13 (0.01) b	0.15 (0.01) c	0.19 (0.03) c
Potential net N mineralization over 180 d in incubated soil ($\mu g \cdot g^{-1} \cdot d^{-1}$)			
1-yr rotation monoculture	0.46 (0.05) a	0.40 (0.05) a	0.39 (0.06) a
4-yr rotation monoculture	0.55 (0.12) a	0.44 (0.04) ab	0.63 (0.06) ab
Long-term monoculture	0.56 (0.05) a	0.35 (0.10) a	0.46 (0.07) ab
Long-term polyculture	0.56 (0.11) a	0.66 (0.01) b	0.72 (0.04) b
Available P ($\mu g/g$)			
1-yr rotation monoculture	25 (1) a	29 (3) a	30 (2) ab
4-yr rotation monoculture	34 (4) a	40 (9) ab	33 (2) b
Long-term monoculture	31 (1) a	20 (4) a	22 (1) a
Long-term polyculture	30 (3) a	84 (21) b	26 (1) ab
Bulk density, 0–14.4 cm depth (Mg/m^3)			
1-yr rotation monoculture	0.90 (0.02) c	0.93 (0.02) c	0.89 (0.02) c
4-yr rotation monoculture	0.75 (0.02) b	0.75 (0.04) b	0.79 (0.03) b
Long-term monoculture	0.78 (0.01) ab	0.81 (0.01) ab	0.83 (0.03) ab
Long-term polyculture	0.73 (0.03) a	0.69 (0.04) a	0.72 (0.05) a

† Treatment means ($n = 3$ blocks) within columns (species) followed by the same letter are not significantly different ($\alpha = 0.05$).

‡ Species means within rows (i.e., treatments) that are significantly higher are denoted by an asterisk ($*P < 0.05$).

reported, and are referred to as ''root growth.'' Root growth was significantly higher in *Hyeronima* (Table 1). *Hyeronima* and *Euterpe* had higher concentrations of lignin and/or higher C:N and lignin:N, whereas *Cordia*, *Cedrela*, and *Heliconia* had higher concentrations of hemicellulose and lower C:N and lignin:N (Table 2).

Differences in these species traits did not result in significant differences in most soil properties. Although total soil organic carbon (TSOC), silt–clay fraction C, potential C mineralization, total N (TN), potential net N mineralization, and available P were higher under *Hyeronima*, variability was high enough that the differences were not significant (Table 3, Fig. 1D). Light particulate organic matter (LPOM) C and N stocks (Table 3, Fig. 1E) and soil C:N ratio (Fig. 1F), however, were significantly higher under *Hyeronima*. Compared to initial values for the site, soil C stocks after 10 years were slightly higher under *Hyeronima* and lower under the other two species (Fig. 1D).

The three tree species differed in their responses to rotation frequency and increased life-form diversity, as evidenced by significant Species × Treatment interactions ($\alpha < 0.05$) for leaf litterfall (Year 9, all species combined in polyculture, and mean of Years 5–8 for all species and trees only) and root growth (Year 9, all

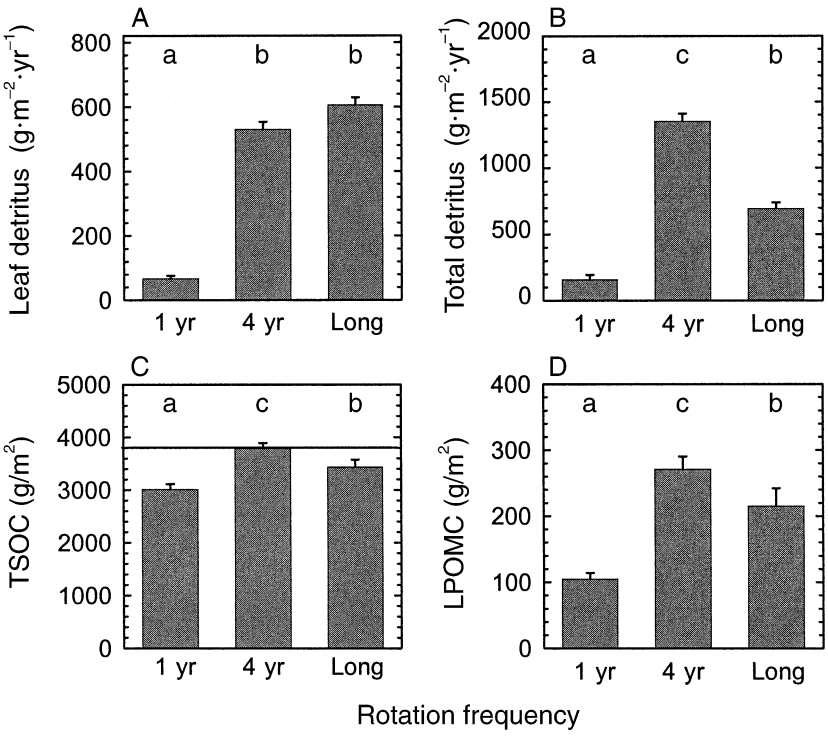

FIG. 2. Rotation-frequency effects in 9-yr-old monocultures under 1-yr, 4-yr, and long-term rotations at La Selva, Costa Rica: (A) leaf detritus consists of leaf and flower inputs from litterfall and felled biomass; (B) total detritus includes all aboveground inputs from litterfall and felled biomass (leaves, branches, and flowers); (C) total soil organic C (TSOC); and (D) light particulate organic matter C (LPOMC). Means (+1 SE) with the same lowercase letters are not significantly different ($\alpha = 0.05$). Detrital means are based on data from Years 5–8 of the experiment. Initial TSOC in panel C (Year 1) is denoted by the horizontal line.

species combined and trees only). Effects on soil characteristics of the tree species also depended on the treatment, with Species × Treatment interactions significant for TSOC, TN, LPOMC, LPOMN, potentially mineralizable C, and silt–clay-size separates.

Rotation-frequency effects

Rotation frequency had a large influence on aboveground detrital inputs (Fig. 2A, B). Quantities of leaf detrital inputs (from litterfall and felling) in the 4-yr rotation were substantial, to the extent that the average over the 4-yr cycle equaled litterfall inputs in the long-term monoculture (Table 1). With stems included in the aboveground detrital amounts, inputs in the 4-yr rotation exceeded those in the long-term rotation (Table 1, Fig. 2B).

Within each combination of rotation and species, there were no significant differences in TSOC, TN, LPOMC, or LPOMN concentrations among the four sampling times (before and after felling in Years 8–10; Fig. 3). Hence, means within treatment and species over those four sample times were used in the following ANOVAs. Soil C stocks differed significantly among rotation frequencies; over all species, both TSOC and LPOMC stocks were highest under the 4-yr rotation (Table 3, Fig. 2C, D). Soil C storage peaked in the 4-yr rotation under *Cedrela* and *Cordia* and declined in the long-term monoculture, but remained high even after 10 years under *Hyeronima* (Table 3). The 1-yr rotation had a dramatic influence on soil C stocks over the 10-yr experiment, such that soil C and LPOM stocks declined under all species (Fig. 2C, D). Trends were similar even for the silt–clay C fraction (derived by subtraction of LPOMC from TSOC values; Table 3). For *Cedrela* and *Cordia*, potential C mineralization, net N mineralization, and available P were highest in the 4-yr rotation, although not always significantly higher; in *Hyeronima*, the long-term rotation tended to have the highest values (Table 3).

Even in the detailed study in which soil was sampled at weekly intervals for one month following felling/replanting in the 4-yr rotation of *Hyeronima*, there were no significant differences among sampling times in LPOMC concentration, the property most likely to be influenced by disturbance (data not shown). Because LPOM and soil C did not decline following felling, differences in disturbance regimes did not explain differences in soil C stocks among rotation frequencies. Observed differences were thus attributed to differences in detrital inputs that had occurred over the 10-yr course of the experiment.

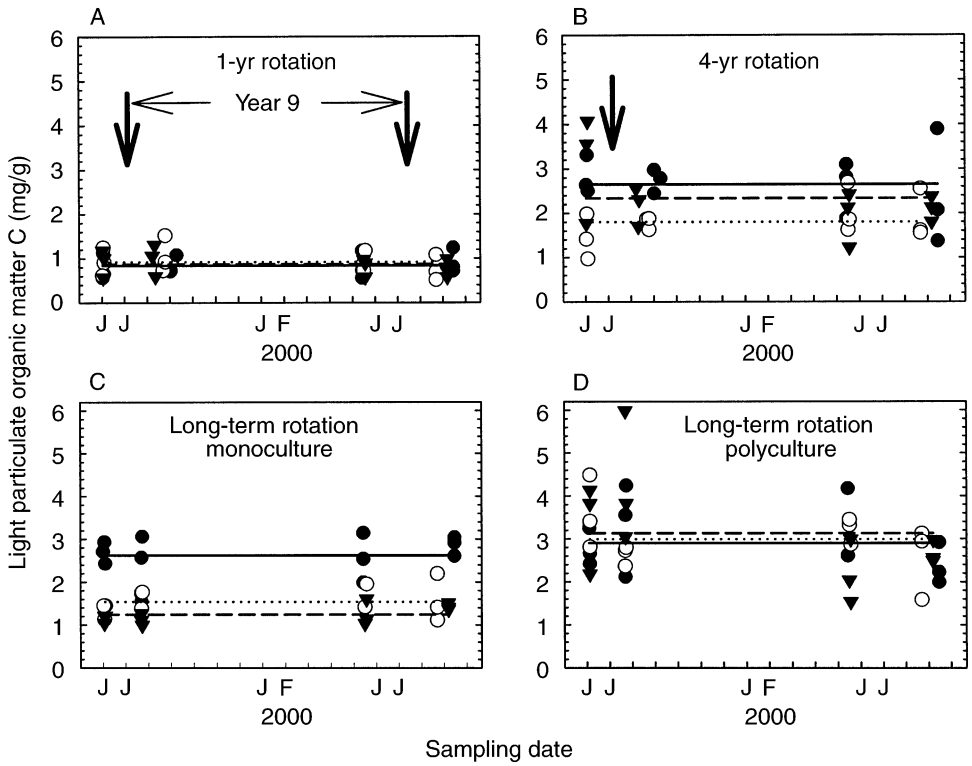

FIG. 3. Light particulate organic matter C concentrations over four sampling times, under four treatments and three tree species in plantations at La Selva, Costa Rica. Vertical arrows indicate timing of first tree felling and replanting for that year, relative to timing of soil sampling. Symbols represent data from each of four sampling times in three blocks for each species; lines denote the mean over all four sample times within each species and treatment. Symbols denote the following species: *Hyeronima,* solid circles and solid lines; *Cedrela,* open circles and dotted lines; and *Cordia,* solid triangles and dashed lines.

Comparisons of long-term monocultures with polycultures

In general, total litterfall in 9-yr-old polycultures was not higher than in monocultures of the same age (Fig. 4A), but root growth increased in polycultures, suggesting higher total detrital inputs in polycultures than in monocultures (Fig. 4B). Individual species fared differently in polyculture; however, *Hyeronima* maintained the same litterfall rates, whereas *Cedrela* and *Cordia* litterfall rates declined (Table 1, Fig. 4A, B). The most striking response of *Hyeronima* when grown in polyculture was a doubling of root growth, and a change in allocation pattern: the ratio of fine-root growth to leaf litterfall increased from 0.29 in monoculture to 0.64 in polyculture. In contrast, this ratio remained nearly constant in *Cedrela* (0.14 in mono- and 0.13 in polyculture), as both root growth and leaf litterfall declined. The ratio increased somewhat in *Cordia,* from 0.16 in monoculture to 0.38 in polyculture, where root growth was not as negatively influenced by the additional species as was litterfall production. Tree species accounted for the following respective root growth and litterfall in polycultures: *Hyeronima,* 89% and 88%; *Cordia,* 38% and 31%; and *Cedrela,* 22% and 36% (Table 1). *Hyeronima* differed from the other two species in its response in polyculture, especially in terms of its dominance of root growth and detrital production, and its capacity to increase its allocation to root growth.

On average (over all three species), stocks of TSOC and LPOMC in the upper 15 cm were higher in polycultures (Table 3, Fig. 4C, D). This general result did not apply to *Hyeronima*, however, as soil C stocks were high in monoculture and did not increase significantly with the addition of two life-forms. Potential C and net N mineralization and available P in polycultures were significantly higher than in monocultures of *Cedrela*. Trends were the same for *Cordia*, but were not significantly different. Under *Hyeronima*, mineralization rates and available P concentration were similarly high in both the mono- and polyculture.

DISCUSSION

In this study, in which climate and initial soil conditions were similar for all treatments, soil C stocks and biological processes that affect soil fertility were influenced by species, rotation frequency, and life-form diversity. We related our results to other studies and evaluated the relative influence of various plant traits on soil C dynamics, focusing on quantity and quality of detrital inputs.

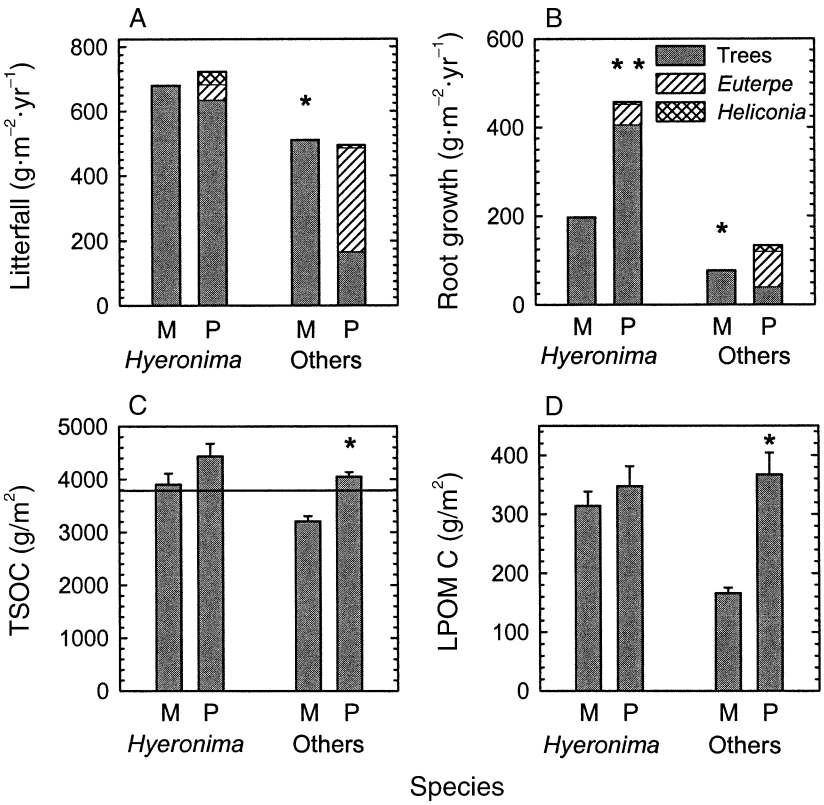

FIG. 4. Life-form diversity effects in 9-yr-old, long-term plantations at La Selva, Costa Rica: (A) leaf litterfall in Year 9 of experiment, (B) fine-root growth in Year 9 of experiment, (C) total soil organic C (TSOC; means + 1 SE), and (D) light particulate organic matter C (LPOMC; means + 1 SE). Significant differences ($P < 0.05$) between monocultures (M) and polycultures (P) within tree species are denoted by an asterisk. Two asterisks denote significance for both tree species alone and all species combined in polyculture. Initial TSOC in panel C is denoted by the horizontal line.

Effects of species, rotation frequency, and life-form diversity

Nitrogen-fixing trees tend to stimulate soil C accumulation (Johnson 1992, Resh et al. 2002), but the effects of non-N-fixers, and the interspecific differences among tropical species are not as well studied. In short-term (3–5 year) comparisons in forest plantations, Montagnini (2000) found relatively few differences in TSOC content under eight native tree species. In contrast, Fisher (1995) found significantly higher TSOC under 3 of 11 species. Gleason and Ewel (2002) found that soil C content differed under three mangrove species, and that these differences were related to root growth, decomposition rates, and tissue chemistry. In our study, 10-year trends in TSOC were unclear because of high variation relative to differences among means. We suggest that LPOMC stocks might provide a better indicator of species effects than TSOC because LPOMC has a smaller variance; hence smaller mean separations are needed to detect statistically significant differences.

We found that rotation frequency had a greater influence on soil C than did species composition or addition of two life-forms. As found in most studies of TSOC (Fox 2000), the tree-felling operation itself had little impact, although some studies demonstrate large losses and others show net gains in soil C storage (as reviewed by Johnson 1992). Other management factors, especially cultivation, fertilization, and intense prescribed fire (Johnson 1992) have measurable impacts on total soil C over periods of <12 years.

In comparisons of monocultures and mixtures with *Eucalyptus*, Kaye et al. (2000) found that soil C increased linearly with increasing percentage of *Albizzia*, an N-fixing tree. Loss of species richness, as in removal of the understory in slash pine plantations in Florida, resulted in reduction of soil C stocks by 33%, primarily as a result of reduced fine-root inputs (Shan et al. 2001). The addition of functional groups of species did not necessarily decrease leaching losses (Hooper and Vitousek 1998) or increase soil C stocks (Russell 2002); in those studies, differences between monocultures and polycultures depended on the identity of the functional groups in the comparison. In this study, all 10-year-old polycultures had net gains in soil C stocks (Fig. 4C), and higher available P and potential mineralization rates of C and N compared to monocultures (Table 3). *Hyeronima* differed from the other two species in

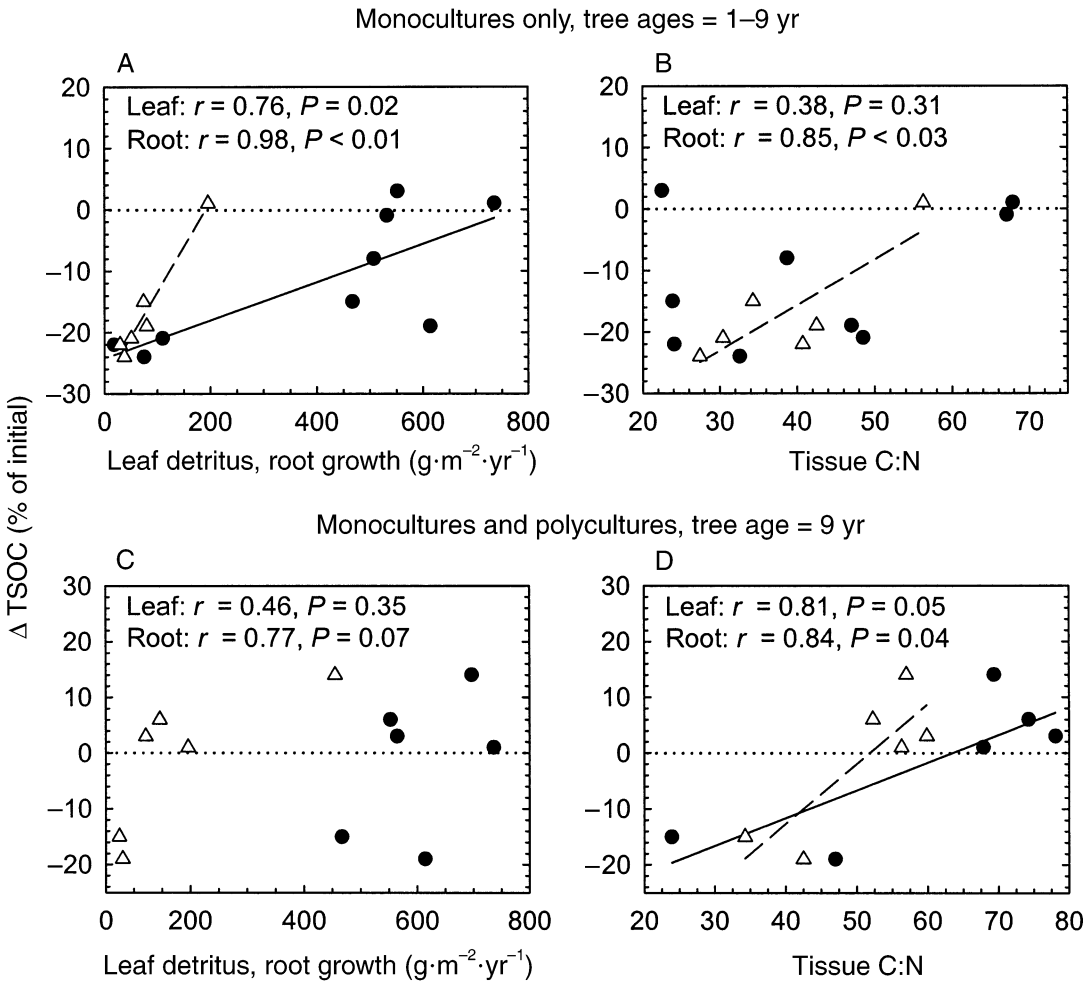

FIG. 5. Change in total soil organic C (TSOC) after 10 years and its correlations with quantity and quality of organic matter inputs in plantations at La Selva, Costa Rica: (A, B) data from monocultures in 1-yr, 4-yr, and long-term rotations; and (C, D) data from long-term monocultures and polycultures. Correlation analyses were conducted separately for leaf litterfall, fine-root growth, C:N ratio of senesced leaves, and C:N ratio of live roots. Solid and dashed regression lines correspond to leaf (solid circles) and root (open triangles) traits, respectively. Dotted horizontal lines represent zero change in TSOC. Each point represents an average of four sampling times and three blocks.

that soil C stocks and measures of soil fertility were high in the monoculture, such that the increase in polyculture was insignificantly small. The implication for the design of forestry systems is that monocultures of ''super'' species can be as productive as polycultures and thereby increase soil C storage. Nevertheless, polycultures of two out of three species had higher soil C stocks and indices of fertility than did monocultures in our site. We examined two main mechanisms underlying these results.

Quantity and chemistry of detrital inputs

Higher detrital production should result in higher soil C, when other factors are equal. We sought, however, to characterize: (1) the extent to which above- and belowground production differed in their influence on soil C stocks, and (2) the relative importance of quantity and quality of inputs. We conducted two sets of correlation analyses, the first of which involved a wide range of detrital inputs by including all possible rotations of the tree species. Change in TSOC over 10 years was significantly correlated with quantity of leaf detrital inputs ($n = 9$ monocultures; Fig. 5A). In the six monocultures for which we could adequately characterize root growth (1-yr and long-term rotations only), change in TSOC was significantly correlated with root growth (Fig. 5A) and live root C:N (Fig. 5B).

The second set of correlation analyses involved 9-year-old plants only. Among the long-term monocultures and polycultures, leaf detrital inputs varied relatively less, by 47%, compared to 194% in the comparison that included 1- and 9-year-old trees. Thus, by nine years of age, species differed relatively less in quantity of aboveground inputs, and that quantity was not significantly correlated with changes in TSOC after 10 years (Fig. 5C). Root growth, however, did vary

more among species, by 144%, only slightly less than in comparisons of Fig. 5A, where it varied by 148%. Changes in soil C stocks in the long-term cultures were correlated with quantity of root growth at only $\alpha = 0.07$ (Fig. 5C). In contrast, changes in soil C were significantly correlated with C:N of both leaves and roots (Fig. 5D). This was consistent with expected trends in litter decomposition, based on relationships between tissue chemistry and decomposability (as reviewed by Heal et al. 1997). In step-wise regression, root C:N, root growth, leaf litterfall, and leaf C:N had decreasingly significant effects on changes in soil C, as indicated by their respective partial r^2 values: 0.70, 0.14, 0.08, and 0.07. Once a critical mass of detrital inputs had been reached, root traits were more important in driving soil C accrual than were senesced-leaf traits, and plant traits involving tissue chemistry were relatively more important than quantities of inputs.

Soil C dynamics

Soil C accumulations can be surprisingly fast in tropical secondary forests on degraded agricultural lands (Lugo et al. 1986, Lugo and Brown 1993). Rates of soil C sequestration in the tropics range from 0.5 to 2.0 $mg \cdot ha^{-1} \cdot yr^{-1}$ in secondary forests (Brown and Lugo 1990, Rhoades et al. 2000) and from 0 to 1.1 $mg \cdot ha^{-1} \cdot yr^{-1}$ in 10–13-year-old tree plantations in Hawaii and Puerto Rico (Bashkin and Binkley 1998, Resh et al. 2002). Previous land use at our study site (cocoa plantation) had not degraded soil C stocks to the extent reported for other agricultural uses (Detwiler 1986). Nevertheless, 10 years into this experiment, soil C storage in the 0–15 cm depth interval had increased up to 14% or 0.6 $mg \cdot ha^{-1} \cdot yr^{-1}$ in *Hyeronima* polycultures. In contrast, soil C stocks decreased by as much as 24% or 0.9 $mg \cdot ha^{-1} \cdot yr^{-1}$ (*Cedrela* in 1-yr rotation). Although this site was not tilled, losses of soil C surpassed rates of inputs, even under some long-term monocultures. These losses suggested that soil C sequestration was limited in this warm, wet climate by rapid SOC turnover rates (e.g., Richter et al. 1999); high SOC decay rates would be expected at this site, given the generally observed relationship between temperature and SOC turnover rate (Trumbore 1997, Holland et al. 2000).

In our site, LPOM accounted for a relatively small proportion of total soil C: 4–9% over all treatments, within the range of reported light-fraction values at La Selva (Sollins et al. 1984). Tropical soils can contain substantially larger proportions of light-fraction C, depending on mineralogy (Motavalli et al. 1994). Most of soil C in our site, 91–97% over all treatments, was in the silt–clay fraction, considered to be less labile than LPOM (sand-sized) fractions (as reviewed by Christensen 1992). We found, however, that changes in TSOC over 10 years were significantly correlated with both LPOM ($r = 0.95$, $P < 0.0001$) and silt–clay size fractions ($r = 0.99$, $P < 0.0001$). The proportion of the silt–clay fraction that was resistant to sonication, 13% over all treatments, was moderately labile and subject to changes in land use. Similarly, Solomon et al. (2002) found that the silt-size separates in other tropical soils (Paleudalfs) were moderately labile. These findings suggest that soils containing low proportions of LPOM are not necessarily less vulnerable to soil C losses caused by management practices.

We conclude that in this site where abiotic conditions are optimal, relatively fast turnover rates of soil C make decisions regarding selection of species, rotation frequency, and life-form diversity even more critical if the soil resource is to be managed as a carbon sink. Our results indicate that on average, polycultures accrue more soil C. Nevertheless, soil C stocks can also increase under monocultures of trees, depending on the species. Our data suggest that above a certain threshold of detrital production, chemistry of detrital inputs, especially of roots, is the plant trait that drives soil C sequestration.

Acknowledgments

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