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Tree Species Effects on Soil Properties in Experimental Plantations in Tropical Moist Forest

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ABSTRACT

We resampled one of the earliest replicated experimental sites used to investigate the impacts of native tropical tree species on soil properties, to examine longer term effects to 1-m depth. The mono-dominant stands, established in abandoned pasture in 1988 at La Selva Biological Station, Costa Rica, contained six species, including one exotic, *Pinus patula* ssp. *tecunumanii* (Eguiluz & J.P. Perry) Styles, and five native species: *Pentaclethra macroloba* (Willd.) Ktze (N_2-fixing); *Hyeronima alchorneoides* Allemao; *Virola koschnyi* Warb.; *Vochysia ferruginea* Mart.; and *Vochysia guatemalensis* J.D. Smith. Soil organic carbon (SOC) differed significantly among species in the surface (0–15-cm) layer, ranging from 44.5 to 55.1 g kg^{-1}, compared with 46.6 and 50.3 g kg^{-1} in abandoned pasture and mature forest, respectively. The change in surface SOC over 15 yr ranged from –0.03 to 0.66 Mg C ha^{-1} yr^{-1}. The species differed in the quantity and chemical composition of their detrital production. Soil organic C was significantly correlated with fine-root growth, but not with aboveground detrital inputs. Soil organic C increased with potential C mineralization on a grams of C basis, indicating that species influenced both the quality and quantity of SOC. Contrary to expectations, SOC declined with increasing fine-root lignin concentrations, indicating that lignin-derived C did not dominate refractory SOC pools. We hypothesize that differences among species in the capacity to increase SOC stocks involved fine-root traits that promoted soil microbial turnover and, thus, greater production of recalcitrant, microbial-derived C fractions.

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Abbreviations: SOC, soil organic carbon.

Forest soil properties, including the quantity and quality of SOC stocks, are influenced by the complex interactions of climate, soil type, management, and tree species (Lal, 2005). A growing body of evidence has demonstrated that tree species can differ in their influence on soil properties. In particular, differences between N_2-fixing and non-N_2-fixing species, between gymnosperms and angiosperms, and between native and exotic species are often highlighted (Vitousek et al., 1987; Binkley and Ryan, 1998; Binkley et al., 2000; Giardina et al., 2001; Rhoades et al., 2001; Kaye et al., 2002). Even species within a functional group such as broad-leaved evergreen tropical trees can differ in their short-term effects on soil (Fisher, 1995; Albrecht and Kandji, 2003; Russell et al., 2004). A better understanding of the extent to which species within a functional group differ, and the mechanisms by which they influence soil properties, will improve our ability to predict the effects of species on ecosystems. An enhanced predictive capacity has many applications, including the restoration of degraded landscapes, management of invasive species, design of sustainable agroforestry systems, selection of species for C sequestration in managed systems, and improvement of biogeochemical models.

Species may differ in a variety of traits, including production of detritus (Montagnini et al., 1993), partitioning of production between above- and belowground tissues (Cuevas

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et al., 1991), depth distribution of roots (Carvalheiro and Nepstad, 1996), chemical and physical attributes of tissues (Challinor, 1968), effects on microclimate (Montagnini et al., 1993), capacity to redistribute nutrients (Alban, 1982), promotion of N_2 fixation (Roggy et al., 1999), and effects on soil N mineralization (Ewel, 2006) and soil invertebrate populations (Warren and Zou, 2002; Hobbie et al., 2006). Any trait that influences the quantity, location, or decomposability of detrital inputs can influence soil properties by affecting the quantity and turnover of SOC. Because SOC influences soil fertility via effects on soil nutrient supply and soil physical and chemical properties, effects of species on SOC can have important feedbacks to the ecosystem.

In a replicated experimental site in which climate, soil type, and management were similar, Fisher (1995) investigated four mechanisms by which trees might ameliorate degraded soil: (i) increase the amount of soil N, particularly if the species fix N_2; (ii) alter the quantity and quality of soil organic matter and associated soil properties; (iii) enrich surface soil nutrients, particularly in deep-rooted species; and (iv) alter the microclimate by reducing temperature and moisture extremes. In this site, situated on abandoned pasture at La Selva Biological Station, Costa Rica, the 11 tree species differed in a variety of traits (González and Fisher, 1994), and 3 yr after the plantations were established, significant changes in soil properties had occurred, with the species differing in their effects (Fisher, 1995). Could these differences be expected to persist beyond the early, rapid-growth phase of the trees? The present study was undertaken 15 yr after the initiation of this experiment, by which time six species had survived. The objectives were to determine the extent to which the six remaining species differed in their effects on soil properties, and to evaluate several plant traits that could drive the observed differences in SOC, including the quantity, location, and chemistry of inputs. This study addressed four broad hypotheses related to the patterns and mechanisms of species effects on soil:

1. Species effects of trees on soil properties persist beyond the early rapid-growth phase following plantation initiation. Long-term studies in temperate-zone forests support this hypothesis (Binkley and Valentine, 1991; Augusto et al., 2002), but tropical data are scarcer and rarely involve native species (Kaye et al., 2002).
2. Differences among species in soil properties are confined to the surface soil. Evidence from other sites demonstrates that trees can influence deep soil by various mechanisms, including organic acid production and pumping of nutrients from deep soil (e.g., Dijkstra and Smits, 2002).
3. Species differ in their effects on the quantity of SOC as a result of differences in detrital production. Other experimental studies have indicated that fine-root growth contributes relatively more to SOC stocks than do aboveground detrital inputs (Norby et al., 2004; Russell et al., 2004). Thus, we hypothesized that SOC is more highly correlated with detrital inputs from fine roots.
4. Species differ in their effects on soil C quality as well as quantity. Species are expected to differ in their detrital chemistry, and this in turn influences its decomposability (e.g., Heal et al., 1997). We hypothesized that SOC increases with plant lignin content, by virtue of its effect of retarding decomposition (e.g., Paustian et al., 1992).

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MATERIALS AND METHODS

Site Description

Our study was conducted in the Peje Annex of La Selva, which is situated in the Atlantic lowlands of Costa Rica (10°26′ N, 83°59′ W). With an annual rainfall of 3960 mm and mean temperature of 25.8°C (Sanford et al., 1994), the region is classified as Tropical Wet Forest in the Holdridge System (Hartshorn and Hammel, 1994). The 12-ha experimental site is situated on a residual soil that is derived from andesitic lava flows (Alvarado, 1990). The study site soil was mapped as the Matabuey consociation, Typic Tropohumult (Sollins et al., 1994), but reclassified later as Mixed Haplic Haploperox (Kleber et al., 2007). This soil is acidic, highly leached, low in base saturation, and relatively high in organic matter. Topography of the study plots is hilly, with elevations ranging from 44 to 89 m. The plots do not receive alluvial material from the nearby Peje River.

Mature forest at the experimental site was cleared in 1955, the slash was burned, and pasture of *Panicum maximum* Jacq. and *Melinis minutiflora* P. Beauv. was established in 1956, with grazing continuous until abandonment in 1987. This experiment was established in 1988. The randomized complete block design consisted of four blocks of 12 0.25-ha (50- by 50-m) plots, containing 11 tree species plus an abandoned-pasture control (Fisher, 1995). For the purpose of subsampling within plots, all plots were divided into four quadrants. Baseline soil data were collected in 1987, before planting (Fisher, 1995). Trees were planted at a spacing of 3 by 3 m. Understory vegetation in all plots was manually cleared during the first 4 yr. The fastest growing trees, *H. alchorneoides*, *V. ferruginea*, and *V. guatemalensis*, were thinned at age 4 yr to a density of about 50% of the original (Haggar et al., 1997). The plantations were virtually abandoned in 1994 until sampling for the current study commenced, in 2003. To provide a reference for the plantations, boundaries for a fifth block were established in mature primary forest on the same landform, soil consociation, and elevation in July 2003. The closest corner of this block is situated <150 m from the plantations. The abandoned-pasture control plots of the original experimental design were overtopped and shaded out by surrounding plots within the first 3 yr, and hence could not function as an experimental control. To provide an abandoned-pasture reference, we established four 14- by 8-m plots within the 3-ha abandoned pasture situated between Blocks 1 and 4 in January 2004. These plots had the same climate, soil type, and pre-experiment management as the plantations; the plots were dense swards of *Panicum maximum*, but had not been grazed since 1987.

The four exotic species in the original experiment were: *Acacia mangium* Willd., *Gmelina arborea* L., *Inga edulis* Mart., and *Pinus patula* ssp. *tecunumanii* (hereafter referred to as *Pinus patula*). The native species were: *Abarema adenophora* (Ducke) Barneby & J.W. Grimes, *P. macroloba*, *Stryphnodendron microstachyum* Poepp. et Endl., *H. alchorneoides*, *V. koschnyi*, *V. ferruginea*, and *V. guatemalensis*. During the first 6 yr of the experiment, the species differed in their growth rates (González and Fisher, 1994) and effects on woody regeneration (Haggar et al., 1997, Powers et al., 1997) and soil properties (Fisher, 1995). The six species that had survived when surface soil was sampled in 2003 were *H. alchorneoides*, *P. macroloba* (the only N_2-fixing species and the dominant species at La Selva), *P. patula* (the only conifer), *V. koschnyi*, *V. ferruginea*, and *V. guatemalensis*. *Gmelina* had been removed, and the other four species had died by 2003. By 2004 to 2005, *V. ferruginea* was dying of a fungal disease in some blocks; hence, we did not include this species in our correlation analyses in those years.

For the six species remaining in 2004 (age 16 yr), tree densities ranged from 250 (*V. ferruginea*) to 500 stems ha^{-1} (*V. guatemalensis*). Mean diameter at breast height ranged from 22 cm in *Pentaclethra* to 35 cm in *V. ferruginea*, and the mean height from 19 m in *Pentaclethra* to 33 m in *V. guatemalensis* (unpublished data, 2004). Mean basal area was lowest in *Virola*, 19 m^2 ha^{-1} and highest in *V. guatemalensis*, 38 m^2 ha^{-1}. Understories were diverse in all plots, but colonizing trees ≥10 cm diameter at breast height comprised <5% of the basal area. We refer to the effect of "species" as the entire treatment effect of the planted trees, including the contribution from the understory, which comprised <3% of the total aboveground biomass across all species (unpublished data, 2004).

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Sampling Protocols

In June to July 2003, soil properties were measured at two depth intervals, 0 to 15 (surface soil) and 15 to 30 cm, following the protocols of the baseline sampling of surface soil in 1987, before trees were planted (Fisher, 1995). A single, 14-m-long transect was established within each of the four quadrants in each plot, at 5 m from the center of the plot to avoid bias due to edge effects. Soil was sampled at 20 randomly selected points, 4 m to either side of the transect, using a 3.2-cm-diameter soil core in the 0- to 15-cm layer, and a 1.9-cm-diameter core for the 15- to 30-cm depth. The 20 samples within a depth interval and quadrant were combined to yield one composite sample per depth and quadrant, or four subsamples per block for each species at each depth. In all sampling, soil was air dried, roots were removed with the aid of forceps, and the soil was sieved (2 mm) and mixed well. Subsamples were oven dried to determine conversion factors to a dry-weight (105°C) basis.

In February to April 2005, a soil pit study was undertaken to measure bulk density at five depth intervals, 0 to 15, 15 to 30, 30 to 50, 50 to 75, and 75 to 100 cm, and SOC and nutrients at the lower three intervals. For bulk density, the soil mass excavated from a single soil pit per plot was determined by layer. With four pits (one per block) for each of six species, the sample size in the plantations was 24 soil pits, plus three pits in each of the two reference sites. Each pit, 1.00 by 0.75 m in area, was centered among live trees, at randomized locations. Rocks and gravel >2 mm were separated and weighed to correct measurements to exclude rocks. Leaf-cutter ants (*Atta cephalotes* L.) have active nests on this site; obvious nests were excluded in all soil sampling.

Fine-litter production and forest-floor mass were sampled as described by Raich et al. (2007). Briefly, to measure litter production in 2004, fine litter was collected from each of four litter traps (1.3 by 0.4 m) per plot in each of 24 plots ($n = 96$) every 15 d, and sorted into categories of overstory leaves, other leaves, branches ≤1-cm diameter, and other materials such as fruits, flowers, and frass. The mass of all surface litter present in the plots was measured by collecting all material within a randomly selected 0.11-m^2 square in each quadrant per plot (total $n = 96$ per date) at 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 each quadrant in each plot and was hand sorted into woody (≤1-cm diameter, including bark) and nonwoody fractions.

Fine-root ingrowth (Cuevas et al., 1991) was measured to provide an assay of fine-root detrital inputs, as described by Valverde-Barrantes et al. (2007). To summarize, five 15-cm-deep, 5.35-cm-diameter ingrowth cores constructed of polyethylene tubing were installed per plot ($n = 20$ cores per species). Each core contained sieved, root-free surface soil from the plot, packed at the average bulk density. Four months was the optimal time for measurement, as sufficient growth had occurred during this interval, yet root mortality was very low (Russell et al., 2004), so the measurements were repeated every 4 mo for 1 yr. After the cores were removed, the roots were cut flush with the cylinder walls to provide a measure of the mass produced per core volume, and roots were separated from the soil using a hydropneumatic elutriation system (mesh size = 530 μm; Smucker et al., 1982). The detritus was then separated by hand. Plant-matter samples (litterfall, forest floor, and fine roots) were oven dried at 65°C and weighed.

Laboratory Evaluations and Calculations

Soil organic C and total N were analyzed by dry combustion (DC) using a Thermo-Finnigan EA Flash (Series 1112, EA Elantech, Lakewood, NJ). Duplicates were run on all samples. Baseline SOC for the site had been determined by the Walkley–Black method (WB). To compare our measurements with initial values, we analyzed 36 samples randomly selected from the 2003 sampling (both depths) by both WB and DC methods. The conversion between organic matter by Walkley-Black and organic C was 1.724 (Nelson and Sommers, 1996). The relationship between SOC (%) by the two methods was DC = 0.12 + 0.90WB ($r^2 = 0.96$, $P < 0.0001$). The intent was to analyze rates of plot-level changes in soil C (and nutrients) during the time course of the whole experiment; however, lack of quality control in laboratory procedures in the previous analyses, and loss of archived samples, precluded these time-series analyses. Nevertheless, the randomized complete block design of the experiment allows direct comparisons among

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species in the present experiment, and the baseline soil data provide an unbiased estimate of initial site-level soil C.

To compare soil C storage among species, all data were expressed on an equivalent-mass basis by layer, as recommended for this type of study (Gregorich et al., 1995; Yang and Wander, 1999; Ellert et al., 2000, 2002; Paul et al., 2001). Without baseline soil mass data, the most unbiased estimate of the equivalent soil mass was the mean across species (n = 24 plots). For the A horizon, the mean soil mass was calculated as the product of the mean A-horizon thickness (15 cm) and the mean soil bulk density at 0 to 15 cm (corrected for gravel volume, 0.65 Mg m^{-3}, Table 1). The mean soil mass was multiplied by the plot-level soil C, measured on a per-unit soil basis, to estimate plot-level soil C storage. Similar calculations were made for each subsequent layer. Expression of all C storage data on an equivalent-soil-mass basis effectively incorporated differences among treatments in soil porosity and C concentrations, under the assumptions that total soil mass did not differ under the species, and that the layer sampled for soil mass corresponded to the layer sampled for C concentration. In these highly weathered and consistently well-structured soils, these assumptions were met, as care was taken to sample adequately, using differences in texture and color to distinguish layers.

Potential C mineralization was measured during laboratory incubations at 23°C (Paul et al., 2001). We incubated representative subsamples from each quadrant within each plot for a total of 16 field replicates for each species. The sieved (2-mm), 3-g air-dried subsample was mixed with acid-washed sand (1:1 w/w) and placed in an incubation tube (Russell et al., 2004). The mixture was brought to 60% water-filled pore space using deionized water that contained 2 mL of an inoculant that had been prepared by homogenizing 5 g of field-moist soil (combined from all treatments) with 50 mL of distilled water. The rate of CO_2–C released was measured periodically for 30 d (before CO_2 concentrations reached 4%) by flushing the flask headspace through an infrared gas analyzer (LI-820, LI-COR Biosciences, Lincoln, NE). The incubation-tube atmosphere was kept hydrated by piping the air supply through water.

Exchangeable Ca, Mg, Na, and K were determined by displacement with 1 M NH_4OAc at field pH and subsequent measurement by atomic absorption spectrometry for Ca and Mg and emission spectroscopy for K and Na. Effective cation exchange capacity was determined by summation of exchangeable base cations (Ca^{2+}, Mg^{2+}, and K^+) and exchangeable acidity (Sumner and Miller, 1996; Warncke and Brown, 1998, Sims, 1996). Soil pH was measured using a stirred slurry of 10 g of air-dried soil in 10 mL of deionized water (Thomas, 1996). Olsen-extractable P was determined by extraction with $NaHCO_3$ and ethylenediaminetetraacetic acid (modified Olsen; Kuo, 1996). Total P was measured by the aqua regia method (McGrath and Cunliffe, 1985). Fine-root C and N were measured by the same dry combustion method as for soil. Other elements for roots were measured by microwave-assisted acid digestion and analyzed using inductively coupled plasma spectrometry (Kingston et al., 1997). Ash-free lignin, soluble C, and cellulose fractions of C in fine roots were determined using van Soest's detergent fiber method (van Soest, 1994; Vogel et al., 1999).

Statistical Analyses

Effects of the six tree species were evaluated using the appropriate randomized complete block model. The SAS System's MIXED procedure (Littell et al., 1996) was used for all analyses of soil variables in the 2003 sampling (0–30 cm), to incorporate the four quadrants or subsamples from each plot. For the 2005 soil and fine root sampling, in which one pit per plot was sampled, the SAS System's GLM procedure was used (Freund and Littell, 1981). Block, depth, species, and depth–species interaction (0–30 cm) effects were considered fixed; block–species interaction and quadrant interaction effects were considered random. Treatment means were compared using Tukey–Kramer multiple comparisons tests with an experiment-wise error rate of $\alpha = 0.05$. We tested for homogeneity of variances and normality of distributions. Exchangeable cations and available and total P deviated from the assumptions, so analyses were performed on the appropriate transformed data that did meet the assumptions. The SAS System MIXED procedure was used to evaluate whether adjustments for spatial correlations were warranted (Littell et al., 1996). This program calculates spatial covariance parameter estimates (partial sill, range, and nugget effect), solutions for and tests of fixed effects, and model-fitting information. Location data for these analyses consisted of the center of the sampling transect within each quadrant, identified by x, y

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coordinates on the geographic information system for La Selva. The conclusions did not differ when spatial correlations were included in the model, so we report only the results from the nonspatial models.

RESULTS AND DISCUSSION

Bulk Density and Soil Carbon, Nitrogen, and Phosphorus

In 2003, 15 yr after the initiation of this experiment, many soil properties continued to differ significantly among species, but unless noted otherwise, all differences were confined to the surface soil (Table 1). Bulk density differed significantly, but the trends among species differed from those observed in 1992, by which time changes in bulk density had occurred without concomitant changes in SOC in some species (Fisher, 1995). This suggested that biological activity could have as much or more of an effect on bulk density than the addition of detritus. By 2003, SOC concentrations (Table 1) were correlated with bulk density ($r = 0.62$, $P = 0.06$). We did not sample the soil fauna, so their relationships to SOC and bulk density are unknown. The finding that species differences did not persist below 15 cm is consistent, however, with the patterns of fine-root distribution: 68% of the fine roots were situated in the top 15 cm compared with 14% in the 15- to 30-cm layer (Valverde-Barrantes et al., 2007).

Soil organic C concentrations also differed significantly, with species trends the same as in Year 3 of the experiment (Fisher, 1995). The net change in SOC from Year 0 to Year 15 ranged from a mean (±SE) loss of 0.03 (±0.08) Mg C ha^{-1} yr^{-1} under *P. patula* to a gain of 0.66 (±0.05) Mg C ha^{-1} yr^{-1} under *V. ferruginea*, i.e., equivalent to a 15-yr gain of 9.98 Mg C ha^{-1} (Fig. 1). The variance in net change in SOC was high, such that differences among species were not significant ($P = 0.26$). Rhoades et al. (2000) observed that SOC increased at 1.9 Mg C ha^{-1} yr^{-1} in secondary forest on abandoned sugarcane (*Saccharum officinarum* L.) fields on young, ash-derived soils in Ecuador. Rates were probably lower in our site owing to factors associated with a relatively older soil. Soil organic C stocks under three of the species in our study, *H. alchorneoides*, *V. ferruginea* and *V. guatemalensis*, were similar to or exceeded SOC levels in the mature-forest reference site (Fig. 1). The organic C trends observed in mineral soil were not offset by different trends in accumulation in the O horizon, as SOC was positively correlated with surface litter mass ($P = 0.02$, Fig. 2).

Potential C mineralization also differed significantly among the species (Fig. 3). Thus, SOC differed in quality as well as quantity beneath the species; SOC was not only lower in quantity, but also less labile under *Pentaclethra* and *Virola*. Rates of potential C mineralization were similar in plantation and pasture soils, but half the rate measured in mature forest. In this controlled laboratory study, differences among species in potential mineralization are probably the result of differences in available nutrients or decomposability of organic matter.

Differences among species in total soil N mirrored those of SOC, but with lower variability, so differences among species in soil N were often more significant than were those of SOC (Table 1). Soil C/N did not differ significantly among species ($P = 0.16$), ranging from 12.6 to 13.5 in the plantations compared with 12.5 in the abandoned pasture and 11.6 in the mature forest. Under all of the experimental species, total soil N was low

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compared with the mature forest level of 4.31 g kg^{-1}, and only two of the species had higher values than that of the abandoned pasture, 3.74 g kg^{-1}. Nitrogen loss from the system would have been a probable consequence of the burn that followed forest felling and subsequent establishment and maintenance of the pasture. Vitousek and Denslow (1987) found high availability of soil N in the mature forest under all soil types at La Selva. In our study site, N flux rates in litter are quite high, up to 210 kg N ha^{-1} yr^{-1} (Raich et al., 2007). Decomposers are unlikely to be limited by N at these sites.

In Year 3 of the experiment, Fisher (1995) found that soil N declined significantly under the N_2-fixing species at this site. By Year 15, *Pentaclethra*, the only N_2-fixing species remaining, had the second lowest level of soil N. Of all the species, *Pentaclethra* had the highest N concentration in senesced leaves (Raich et al., 2007) and fine roots (Table 2), indicating that N_2 fixation was indeed occurring within the observed nodules. These results of consistently low SOC and N concentrations under this N_2-fixing species contradict one of the proposed generalizations regarding tree–soil interactions, i.e., that N_2-fixing trees increase soil C and the rate of nutrient cycling (Binkley and Giardina, 1998). This generalization may well apply to N-limited sites. At our study site, where cycling of N is high under all species (Raich et al., 2007), and soil N accumulation closely tracks that of C (Table 1), some factor other than N availability must limit SOC increase.

Olsen-extractable soil P did not differ significantly among species (Table 1). By Year 15 of the experiment, extractable P in the surface soil was similar to the mature forest (3.4 mg kg^{-1}), lower than that in the abandoned pasture (6.0 mg kg^{-1}), and lower than that in Year 3 of the experiment (Fisher, 1995). Total soil P followed similar trends, with means (±SE) in surface soil under the respective species and reference plots as follows: *H. alchorneoides*, 549 (±52) mg kg^{-1}; *P. macroloba*, 645 (±143) mg kg^{-1}; *P. patula*, 624 (±128) mg kg^{-1}; *V. koschnyi*, 751 (±117) mg kg^{-1}; *V. ferruginea*, 705 (±141) mg kg^{-1}; and *V. guatemalensis*, 476 (±15) mg kg^{-1}; abandoned pasture, 620 mg kg^{-1}; and mature forest, 434 mg kg^{-1}. For the 15- to 30-cm depth, the range was 320 (±22) to 680 (±88) mg kg^{-1}, with the same trends among species. Variability was high, such that no differences among species were significant ($P = 0.54$ and 0.53, respectively, for the two depths). These data suggest, however, that P becomes less available as reforestation proceeds. This is consistent with the finding that P is potentially limiting in mature forest at La Selva (Denslow et al., 1987).

Soil pH and Exchangeable Cations

Soil pH differed significantly among species in both the 0- to 15-cm and 15- to 30-cm layers, with pH under *Pentaclethra* significantly lower than under *V. ferruginea* and *V. guatemalensis* (Table 1). In the abandoned-pasture reference site, the pH of 4.46 was relatively high compared with the tree species, with the exception of the two *Vochysia* species. The mature forest pH was 4.06. This general trend of soil acidification by trees has been observed in a variety of circumstances (Binkley and Valentine, 1991; Augusto et al., 2002; Jobbágy and Jackson, 2003), and especially on advanced weathering-stage soils with limited weatherable minerals (Krishnaswamy and Richter, 2002).

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Exchangeable cations did not differ among species at any depth, with the exception of K in the 15- to 30-cm depth (Table 1). We have no clear explanation for these trends in K, as the tree species did not differ significantly in the depth distributions of fine roots (Valverde-Barrantes et al., 2007). Exchangeable Ca and Mg concentrations in the mature forest reference plots, 0.50 and 0.38 $cmol_c\ kg^{-1}$, respectively, were similar to the plantations (Table 1). In contrast, Ca and Mg concentrations were higher, 1.02 and 0.70 $cmol_c\ kg^{-1}$, respectively, in the abandoned pasture surface soil. Below 15 cm, however, cation concentrations were similar across vegetation types. Concentrations of K of 0.31 mg kg^{-1} in abandoned pasture and 0.14 mg kg^{-1} in mature forest followed similar trends relative to the plantations. These trends are consistent with the hypothesis that lower cation concentrations in plantation and mature forest soils may be explained by storage in tree biomass.

Soil effective cation exchange capacity did not differ significantly among the species (Table 1), and values of 3.11 and 3.57 $cmol_c\ kg^{-1}$ in the abandoned pasture and mature forest did not differ markedly from the plantations. Mean (±SE) exchangeable acidity in surface soil ranged from 1.34 (±0.29) under the *Vochysia* species to 1.71 (±0.18) $cmol_c\ kg^{-1}$ under *Pentaclethra* (the N_2-fixing species), but variability was high, such that the differences were not significant. In comparison, exchangeable acidity was 1.09 (±0.11) $cmol_c\ kg^{-1}$ in the abandoned pasture and 2.56 (±0.21) $cmol_c\ kg^{-1}$ in the mature forest, which is dominated by *Pentaclethra*. These trends are consistent with the finding that a relatively larger decline in pH under an N_2-fixing species [*Albizia falcataria* (L.) Fosberg], compared with a non-N_2-fixer, was the result of greater acidification of the exchange complex (Rhoades and Binkley, 1996).

Quantity and Chemistry of Inputs

Across all species, SOC was significantly correlated with fine-root ingrowth, an assay of fine-root detrital inputs (Fig. 4A), but not with non-woody litterfall inputs (Fig. 4B), or with other measures of aboveground litterfall (Raich et al., 2007). This is consistent with results from other studies in which the quantity of root inputs drove SOC accrual (Norby et al., 2004; Russell et al., 2004). Potential C mineralization, on a g-C basis, also differed among species (Fig. 3), indicating that the quality of the SOC differed among species. The species in our study differed significantly in the tissue chemistry of leaves (Raich et al., 2007) and fine roots (Table 2), including lignin, soluble C, N, P, Mg, K, Mn, and Al. We focus on fine-root chemistry, given that the quantity of fine-root inputs influenced SOC stocks more than the quantity of aboveground inputs (Fig. 4).

We hypothesized that SOC would increase with the lignin content of the detritus, as found in other field studies (Paustian et al., 1992). Lignin is expected to retard decomposition rates by virtue of its low bioavailability to microbes (reviewed by Heal et al., 1997), and therefore accumulate to build SOC stocks. We found the opposite: SOC declined with increasing fine-root lignin content (Fig. 5A). Potential C mineralization also declined with increasing fine-root lignin content (Fig. 5B). This suggests that lignin does impede microbial activity, but does not explain why lignin content does not drive trends in total SOC. One explanation is that compounds of microbial origin contribute relatively more to the refractory SOC pool than do lignin-derived compounds (Kiem and

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Kögel-Knabner, 2003). If this is the case, then we would expect that a plant trait that promotes C sequestration would: (i) enhance soil microbial activity and turnover; and (ii) promote the production of stable microbial products.

Of all the fine-root chemical variables that we measured (Table 2), the only ones that were positively correlated with SOC were Mn ($P = 0.05$, $r^2 = 0.20$) and Al ($P = 0.03$, $r^2 = 0.23$). Fine-root Mn was not, however, significantly correlated with potential C mineralization ($P = 0.12$), whereas Al was ($P = 0.03$, $r^2 = 0.25$). Both *Vochysia* species had senesced-leaf Al concentrations approaching 2% in this study, and *Vochysia elliptica* (Spr.) Mart. and *Vochysia thyrsoidea* Pohl have also been found to accumulate Al (Haridasan, 1981). Aluminum is abundant in acid soils, but its effects on the mineralization and stabilization of SOC are undoubtedly complex and only poorly understood. For example, Schwesig et al. (2003) found that the effects of Al on mineralization of dissolved organic C in litter depended on the initial molar Al/C ratio, and that effects differed between "rapid" and "slow" mineralizable pools. Aluminum-tolerant plants can detoxify Al through a variety of mechanisms, including root secretion of organic acid anions (malate, oxalate, and citrate) that complex with Al^{3+} to protect plant roots (Ma et al., 2001). Microbes can be a considerable sink for this secreted organic acid; a study of microbial kinetics in four acid soils showed that malate was decomposed very rapidly (Jones et al., 1996). A better understanding of the effects of Al on SOC dynamics might explain why some factor apparently trumps the effect of lignin in this system.

The tree species in this experiment differed in a number of traits that could influence SOC dynamics, in traits that we measured and quite likely in ones that we did not. The effect of "species" constitutes an observational study in which multiple factors co-vary; hence we cannot equate the observed correlations with causation. Nevertheless, this experiment, in which six species were assigned at random to plots that had similar climate, soil type, previous vegetation, and management, enabled us to address four broad hypotheses regarding the effects of tree species on soil. First, in this site with a warm, humid climate and rapid tree growth, differences among species in effects on soil persisted into Year 15 of the experiment. Second, most of the significant effects of species were confined to the surface soil, where 68% of the fine roots were situated. These findings highlight the need to incorporate the factor of species composition into our analyses of land-use-change effects, and also the relevance of surface-soil data for assessing these effects. Third, the differences in SOC were correlated with the quantity of detrital inputs, but from roots rather than from aboveground inputs. Fourth, the species differed in their effects on SOC quality, but not in the way that we expected. We hypothesized that SOC quantity would be positively correlated with the lignin content of detrital inputs, but found the opposite. Our results indicated that species with root traits that promoted microbial dynamics drove the biggest changes in soil C. This concept, that the increase in SOC is driven by microbial turnover, differs fundamentally from our original hypothesis that SOC accrual is driven by inputs of recalcitrant plant detritus.

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Fig. 1. Soil organic carbon (SOC) stocks in Year 15 in experimental plantations on abandoned pasture at La Selva Biological Station, Costa Rica. Data are for the 0- to 15-cm depth. Hyal = *Hyeronima alchorneoides*; Pema = *Pentaclethra macroloba*; Pipa = *Pinus patula* ssp. *tecunumanii*; Viko = *Virola koschnyi*; Vofe = *Vochysia ferruginea*; and Vogu = *Vochysia guatemalensis*. Dashed line indicates baseline SOC. Abandoned pasture and mature forest reference sites were not included in the ANOVA. Error bars are standard errors.

Fig. 2. Soil organic C and total forest floor litter mass under six tropical tree species at La Selva Biological Station, Costa Rica. Soils data are for the 0- to 15-cm depth.

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Symbols: ● = *Hyeronima alchorneoides*, ○ = *Pentaclethra macroloba*, ▲ = *Pinus patula*, ▽ = *Virola koschnyi*, and ■ = *Vochysia guatemalensis*.

Fig. 3. Potential C mineralization in experimental plantations at La Selva Biological Station, Costa Rica, determined as CO_2–C released during laboratory incubations of soil from 15-yr-old plantations and abandoned pasture and mature forest reference sites. Data are for the 0–15 cm depth. Hyal = *Hyeronima alchorneoides*; Pema = *Pentaclethra macroloba*; Pipa = *Pinus patula* ssp. *tecunumanii*; Viko = *Virola koschnyi*; Vofe = *Vochysia ferruginea*; and Vogu = *Vochysia guatemalensis*. Reference sites were not included in the ANOVA. Error bars are standard errors.

Fig. 4. Soil organic C as a function of fine-root ingrowth and non-woody litterfall in experimental plantations at La Selva Biological Station, Costa Rica. Symbols: ● = *Hyeronima alchorneoides*, ○ = *Pentaclethra macroloba*, ▲ = *Pinus patula*, ▽ = *Virola koschnyi*, and ■ = *Vochysia guatemalensis*.

Fig. 5. Relationships between soil organic C, potential C mineralization (as CO_2–C released), fine root lignin, and fine-root Al in experimental plantations at La Selva Biological Station, Costa Rica. Symbols: ● = *Hyeronima alchorneoides*, ○ = *Pentaclethra macroloba*, ▲ = *Pinus patula*, ▽ = *Virola koschnyi*, and ■x = *Vochysia guatemalensis*.

Table 1. Bulk density (ρ_b), organic C, total N, Olsen-extractable P, exchangeable cations, effective cation exchange capacity (ECEC), and pH (in water) of mineral soil for five depth intervals, 15 yr following planting of tree species in abandoned pasture at La Selva Biological Station, Costa Rica.

Species	ρ_b	C	N	P	Ca	Mg	K	ECEC	pH
	Mg m^{-3}	g kg^{-1}		mg kg^{-1}	cmol$_c$ kg^{-1}				
					0–15 cm				
Hyeronima alchorneoides	0.69 ab†	49.3 ab	3.66 ab	3.3	0.39	0.53	0.13	2.71	4.31 ab
Pentaclethra macroloba	0.60 ab	44.5 a	3.51 ab	4.2	0.37	0.26	0.15	2.49	4.15 a
Pinus patula	0.78 b	44.5 a	3.36 a	4.2	0.44	0.36	0.15	2.37	4.36 ab
Virola koschnyi	0.71 ab	46.1 a	3.55 ab	4.7	0.31	0.31	0.11	2.14	4.30 ab
Vochysia ferruginea	0.51 a	55.1 b	4.22 b	4.2	0.85	0.46	0.16	2.81	4.47 b
Vochysia guatemalensis	0.61 ab	50.6 ab	4.01 ab	3.2	0.41	0.57	0.13	2.45	4.48 b
MSD‡	0.26	7.7	0.71	2.9	0.72	0.47	0.09	1.00	0.26
P§	0.05	0.01	0.01	0.15	0.24	0.27	0.61	0.37	0.01
					15–30 cm				
Hyeronima alchorneoides	0.90	30.3	2.34	3.3	0.27	0.24	0.05 ab	2.02	4.41 ab
Pentaclethra macroloba	0.82	28.4	2.31	4.6	0.22	0.20	0.05 ab	2.02	4.39 ab
Pinus patula	0.99	28.8	2.18	5.1	0.35	0.20	0.07 b	2.10	4.37 a
Virola koschnyi	1.04	25.7	2.13	3.9	0.25	0.19	0.06 ab	1.86	4.48 ab
Vochysia ferruginea	0.90	30.0	2.46	4.1	0.40	0.26	0.07 b	2.19	4.51 b
Vochysia guatemalensis	0.95	30.1	2.49	4.2	0.19	0.22	0.04 a	2.00	4.53 b
MSD	0.31	5.8	0.40	2.9	0.28	0.21	0.04	0.78	0.15
P	0.30	0.16	0.06	0.15	0.20	0.88	0.01	0.84	0.02
					30–50 cm				
Hyeronima alchorneoides	0.91	18.3	1.52 ab	1.0	0.10	0.08	0.01	3.30	4.60
Pentaclethra macroloba	0.82	15.3	1.22 a	1.3	0.11	0.09	0.02	3.37	4.57
Pinus patula	0.83	14.4	1.27 a	0.9	0.13	0.08	0.01	3.38	4.61
Virola koschnyi	0.98	15.9	1.43 ab	2.1	0.15	0.18	0.02	2.97	4.70
Vochysia ferruginea	0.93	17.1	1.49 ab	1.1	0.10	0.13	0.03	3.34	4.65
Vochysia guatemalensis	0.86	19.5	1.67 b	0.9	0.09	0.08	0.02	3.45	4.73
MSD	0.30	6.1	0.36	2.4	0.09	0.19	0.02	1.55	0.22
P	0.53	0.13	0.009	0.55	0.28	0.46	0.27	0.81	0.20
					50–75 cm				
Hyeronima alchorneoides	0.95	12.9	1.08	0.6	0.09	0.06	0.01 a	3.01	4.61
Pentaclethra macroloba	0.77	10.0	0.91	1.0	0.10	0.09	0.02 ab	3.36	4.61

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Pinus patula	**0.99**	**11.0**	**1.04**	**0.7**	**0.12**	**0.06**	**0.01 a**	**3.20**	**4.66**
Virola koschnyi	**1.09**	**12.3**	**1.13**	**1.4**	**0.18**	**0.18**	**0.01 ab**	**2.77**	**4.74**
Vochysia ferruginea	**1.00**	**12.5**	**1.13**	**0.9**	**0.09**	**0.13**	**0.04 b**	**3.13**	**4.72**
Vochysia guatemalensis	**0.95**	**14.1**	**1.25**	**0.6**	**0.08**	**0.06**	**0.01 a**	**3.24**	**4.67**
MSD	**0.34**	**5.5**	**0.41**	**1.4**	**0.16**	**0.21**	**0.03**	**1.60**	**0.23**
P	**0.13**	**0.28**	**0.24**	**0.52**	**0.38**	**0.39**	**0.02**	**0.70**	**0.35**
					75–100 cm				
Hyeronima alchorneoides	**0.92**	**10.3**	**0.95 ab**	**0.5**	**0.08**	**0.05**	**0.00**	**2.82**	**4.61**
Pentaclethra macroloba	**0.87**	**6.8**	**0.72 ab**	**1.1**	**0.11**	**0.10**	**0.01**	**3.33**	**4.65**
Pinus patula	**1.06**	**7.2**	**0.65 a**	**0.6**	**0.12**	**0.06**	**0.01**	**3.16**	**4.69**
Virola koschnyi	**1.18**	**10.6**	**1.00 b**	**1.5**	**0.15**	**0.12**	**0.01**	**2.76**	**4.72**
Vochysia ferruginea	**1.02**	**9.4**	**0.91 ab**	**0.8**	**0.09**	**0.15**	**0.06**	**2.84**	**4.77**
Vochysia guatemalensis	**1.00**	**10.7**	**1.02 b**	**0.5**	**0.07**	**0.05**	**0.01**	**3.04**	**4.66**
MSD	**0.44**	**4.6**	**0.32**	**1.8**	**0.10**	**0.13**	**0.07**	**1.70**	**0.17**
P	**0.33**	**0.04**	**0.01**	**0.44**	**0.21**	**0.10**	**0.08**	**0.80**	**0.08**

† Means within a column followed by the same lowercase do not differ significantly among species (Tukey's minimum significant difference, *P* = 0.05). Each value is the mean of four blocks.

‡ Minimum significant difference. Any two means within a column do not differ significantly if values differ by <MSD.

§ Significance (*P* > *F*) of ANOVA.

Table 2. Fine-root chemistry of six tree species in 16-yr-old plantations at La Selva Biological Station, Costa Rica.

Species	Lignin	Soluble C	N	P	Ca	Mg	K	Mn	Al
	g kg^{-1}		g kg^{-1}	mg kg^{-1}					
Hyeronima alchorneoides	**202 bc**	**458 a**	**13.4 abc†**	**1315 ab**	**2381**	**4970 a**	**3871**	**352 ab**	**3964 b**
Pentaclethra macroloba	**249 a**	**348 c**	**16.9 a**	**787 bc**	**3350**	**1035 c**	**3162**	**164 b**	**4705 b**
Pinus patula	**216 ab**	**407 abc**	**9.9 c**	**542 c**	**2105**	**969 c**	**4117**	**170 b**	**5684 b**
Virola koschnyi	**252 a**	**386 bc**	**13.8 ab**	**1752 a**	**2107**	**3393 b**	**3778**	**163 b**	**6827 b**
Vochysia ferruginea	**190 bc**	**412 ab**	**12.9 bc**	**1059 abc**	**2230**	**1729 c**	**5371**	**369 ab**	**16324 a**
Vochysia guatemalensis	**164 c**	**448 ab**	**12.3 bc**	**776 bc**	**2383**	**1909 c**	**4672**	**532 a**	**19501 a**
MSD‡	**38**	**64**	**3.7**	**735**	**2460**	**1215**	**4438**	**317**	**5407**
***P*§**	**<0.0001**	**0.001**	**0.001**	**0.001**	**0.61**	**<0.0001**	**0.70**	**0.007**	**<0.0001**

† Means within a column followed by the same lowercase do not differ significantly among species (Tukey's minimum significant difference, *P* = 0.05). Each value is the mean of four blocks.

‡ Minimum significant difference. Any two means within a column do not differ significantly if values differ by < MSD.

§ Significance (*P* > *F*) of ANOVA.

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Figure Legends

Fig. 1. Soil organic carbon (SOC) stocks in Year 15 in experimental plantations on abandoned pasture at La Selva Biological Station, Costa Rica. Data are for the 0-15 cm depth. Tree species are identified by four letters, the first two letters of the species and genus listed in the text. Dashed line indicates baseline SOC. Abandoned pasture and mature forest reference sites were not included in the ANOVA. Error bars are standard errors.

Fig. 2. Soil organic carbon and total forest floor litter mass under six tropical tree species at La Selva Biological Station, Costa Rica. Soils data are for the 0-15 cm depth. Symbols: ● = *Hyeronima alchorneoides*, ○ = *Pentaclethra macroloba*, ▲ = *Pinus patula*, ▽ = *Virola koschnyi*, and ■ = *Vochysia guatemalensis*.

Fig. 3. Potential carbon mineralization in experimental plantations at La Selva Biological Station, Costa Rica. CO_2-C released during laboratory incubations of soil from 15-yr-old plantations and abandoned pasture and mature forest reference sites. Data are for the 0-15 cm depth. Units are expressed per gram soil C. Reference sites were not included in the ANOVA. Error bars are standard errors.

Fig. 4. Soil organic C as a function of fine-root ingrowth and non-woody litterfall in experimental plantations at La Selva Biological Station, Costa Rica. Symbols: ● = *Hyeronima alchorneoides*, ○ = *Pentaclethra macroloba*, ▲ = *Pinus patula*, ▽ = *Virola koschnyi*, and ■ = *Vochysia guatemalensis*.

Fig. 5. Relationships between SOC, potential C mineralization, fine root lignin, and fine-root Al in experimental plantations at La Selva Biological Station, Costa Rica. Symbols: ● = *Hyeronima alchorneoides*, ○ = *Pentaclethra macroloba*, ▲ = *Pinus patula*, ▽ = *Virola koschnyi*, and ■ = *Vochysia guatemalensis*.

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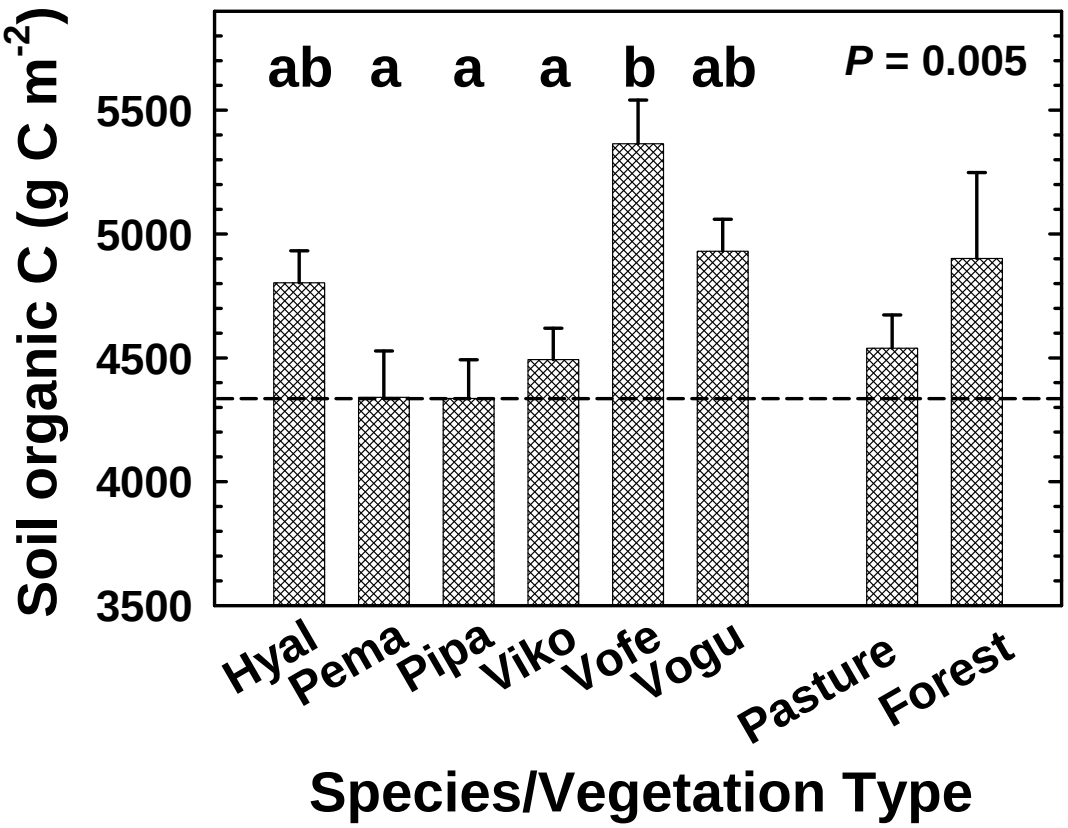

Fig. 1.

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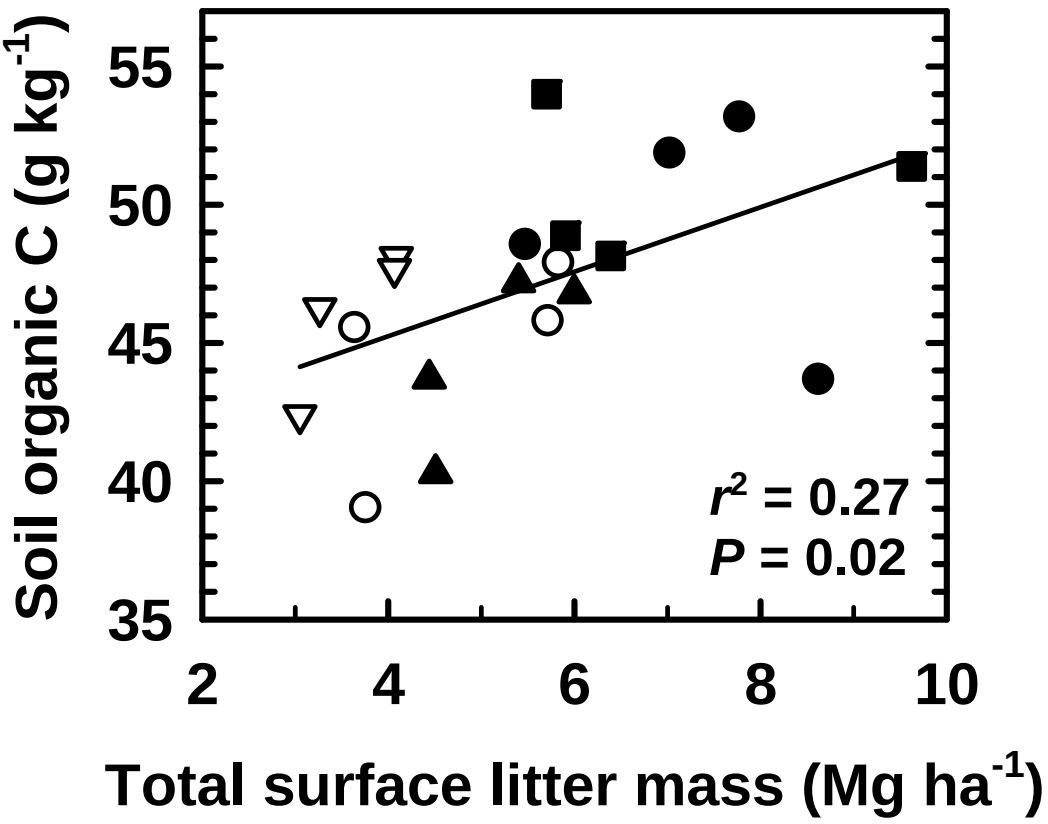

Fig. 2

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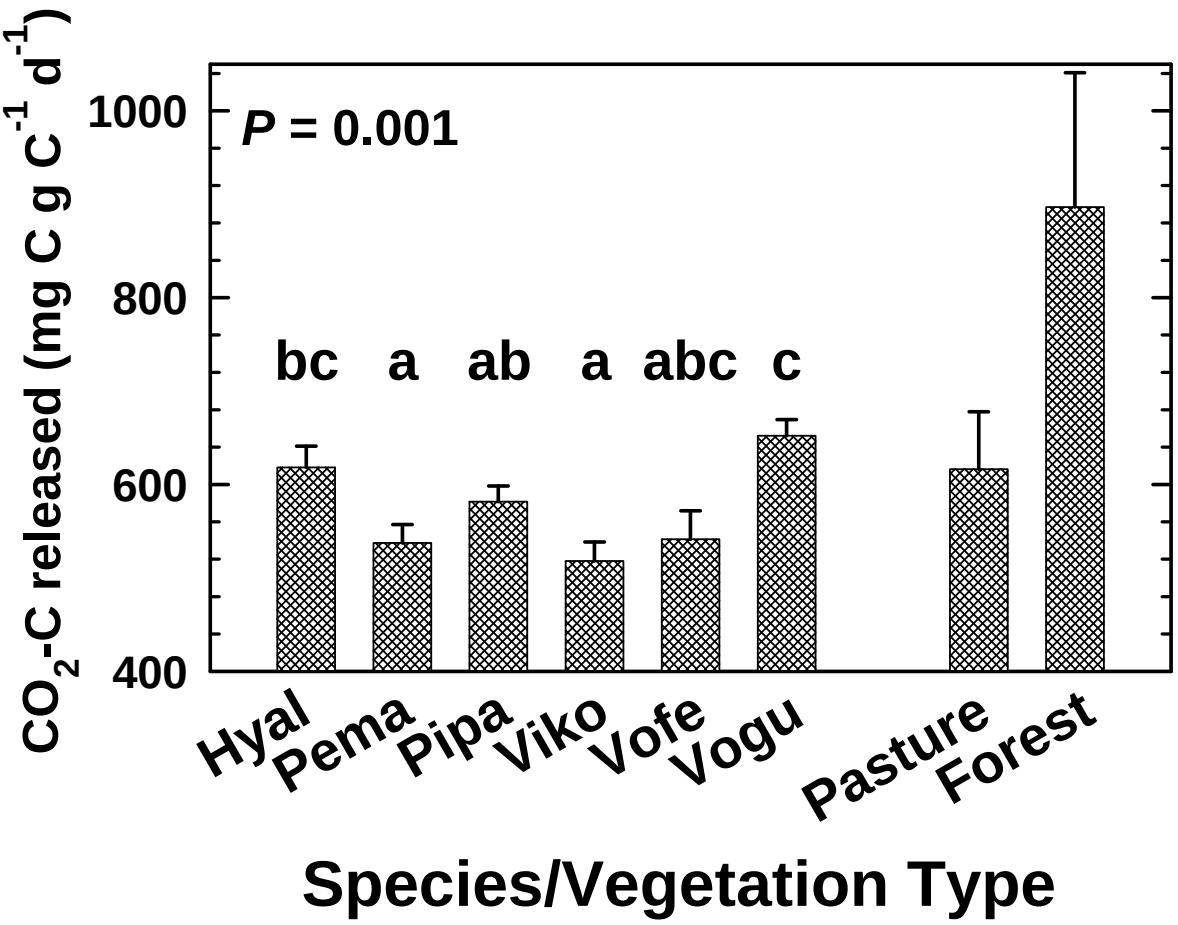

Fig. 3.

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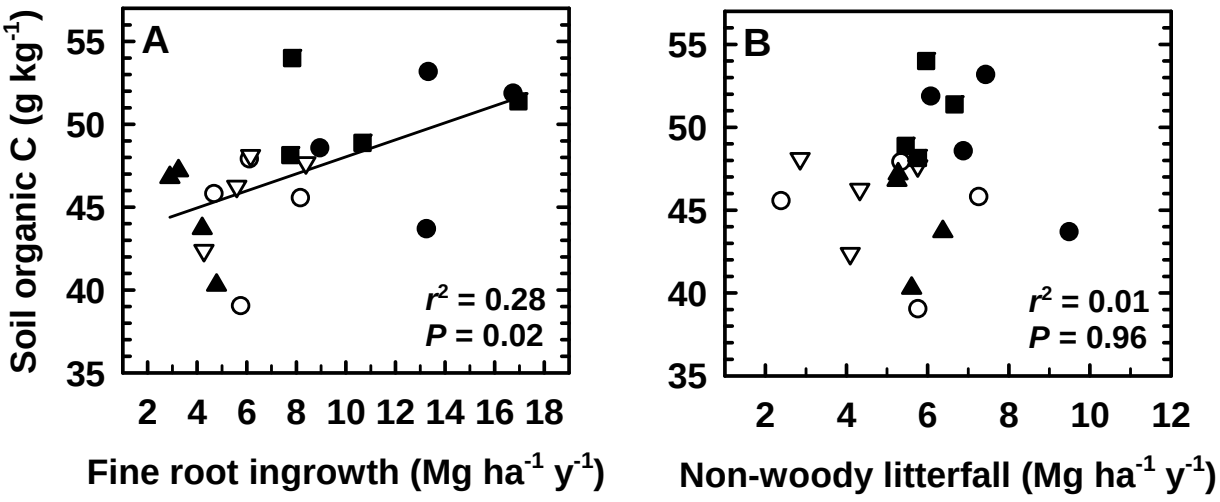

Fig. 4.

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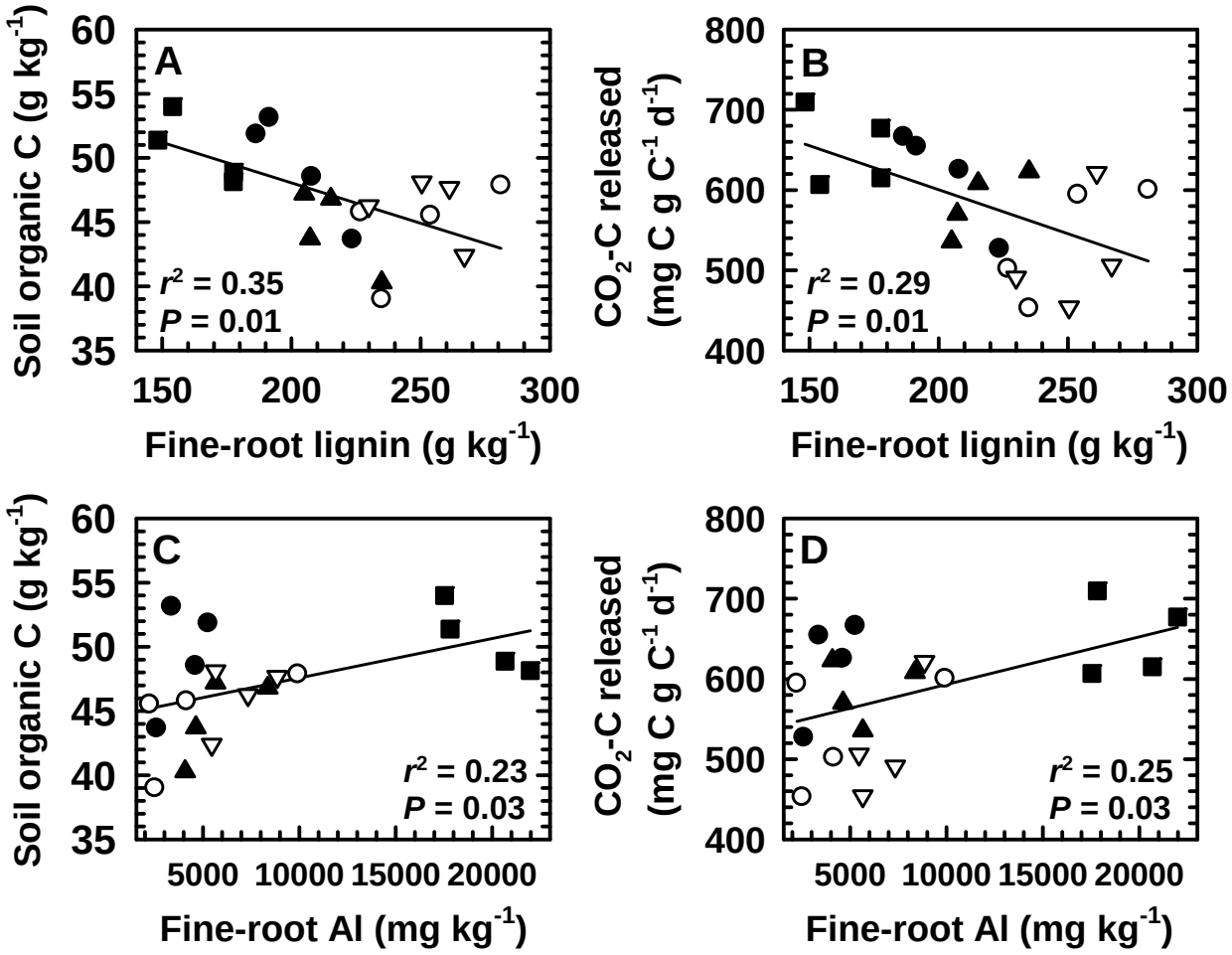

Fig. 5.