

The influence of tree species on canopy soil nutrient status in a tropical lowland wet forest in Costa Rica

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Abstract The canopy is host to a large percentage of the flora and fauna in tropical wet forests and is distinct from the forest floor in plant richness, soil type and microclimate. In this study, we examined the influence of tree species and season on soil nutrient cycling processes in canopy soils of four tree species common to Costa Rican wet forests. We also compared the canopy soils to the associated forest floor mineral soils. Both tree species and season had strong effects on canopy soil nutrients and processes.

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Canopy soils from trees with high litter lignin concentrations had higher net N-mineralization rates and higher dissolved inorganic N concentrations than those with low lignin concentrations. During the dry season, net N-immobilization occurred and dissolved organic and inorganic N and available P concentrations were significantly higher than during the wet season. Overall, canopy soils had higher N levels and higher fungi + bacteria richness than forest floor mineral soils. The differences in canopy soil properties observed among tree species indicates that these species have distinct N cycles that reflect differences in both soil origin and biological controls.

Keywords Canopy soil · Organic soil · Tropical rain forest · Discriminant function analysis

Introduction

The rainforest canopy habitat supports a large percentage of the vascular flora, 25–35% (Gentry and Dodson 1987; Nieder et al. 2001) as well as animal biota (i.e. Erwin 1997). The high diversity of epiphytes is supported via nutrients coming principally from canopy soil (Nadkarni 1984), precipitation, throughfall and nitrogen-fixing lichen (Clark et al. 1998b, c; Forman 1975; Liu et al. 2002; Veneklaas 1990) whereas nutrient sources on the forest floor come principally from forest floor soils. The differences in nutrient sources between canopy and

terrestrially rooted plants is reflected in their differences in nutrient concentrations and stable isotopes (Putz and Holbrook 1989; Wania et al. 2002; Watkins et al. 2007). We have only begun to quantify and understand the flow of nutrients into and out of the canopy, yet existing data indicate that the principle source of nutrients, for epiphytes in particular, is canopy soil (Hietz et al. 2002; Stewart et al. 1995).

Canopy soil is an arboreal histosol (Nadkarni et al. 2002) and is composed of decomposed epiphyte and host tree litter. The proportional contributions of each litter source to canopy soil is unknown, however in a premontane rainforest in Costa Rica, host tree leaf attrition in the canopy was high, with 70% of intercepted litterfall lost within 2 weeks (Nadkarni and Matelson 1991). The authors hypothesized that the high attrition rate was, in part, due to the high wind speeds documented for the site ($>100 \text{ km h}^{-1}$ during storms) which lies on the continental divide. The much lower wind speeds in lowland forests (4.5–11.5 km h^{-1} , our study site La Selva Biological Station, Costa Rica and Brazil, respectively (Kruijt et al. 2000; McCay 2003) suggest that residence time is likely higher in the canopy and thus host tree leaf litter may contribute to canopy soil composition.

The host tree defines the canopy habitat; it is the substrate and influences the microclimate through tree architecture and phenology (Cardelús and Chazdon 2005; Cardelús and Watkins 2008; Hietz and Briones 1998; Pittendrigh 1948) and can affect vascular epiphyte abundance and composition (Cardelús 2007). Host tree species-driven effects may extend to canopy nutrient cycling and status via host tree foliar leaching and litter contributions to canopy soil. Such contributions are likely reflected in soil nutrient status and properties. The former leaching effect was highlighted in recent work in an Hawaiian Montane forest where researchers found that increasing forest floor phosphorus (P) inputs increased nonvascular epiphyte flora abundance and diversity (Benner et al. 2007; Benner and Vitousek 2007). The degree to which the host tree species may influence canopy nutrient status and drive nutrient cycling is one of the foci of this study.

Numerous studies in temperate forests have demonstrated tree species effects on soil characteristics, biogeochemistry and microbial composition (Angers and Caron 1998; Binkley and Giardina 1998; Finzi et al. 1998; Hobbie et al. 2006, 2007; Lovett et al. 2002, 2004). These effects are attributed to variation in tree

species litter quality, litter decay rates, root exudation and nutrient uptake and are also likely affected by the soil community (microbes and animals). Our knowledge of such processes in tropical forests is more limited. Recent work in a tropical moist forest examining litter depth effects on tree root biomass indicates that roots can respond quickly to fresh litterfall (Sayer et al. 2005). Differential litterfall among species (i.e. evergreen vs. deciduous) could result in differences in soil nutrients. However, in lowland tropical wet forests, the results of studies on species effects on forest floor soil parameters are ambiguous (Powers et al. 2004; Rhoades et al. 1994) likely because of the high species richness and thus less dominant effects of individual trees on soil processes.

Multiple plant traits can influence soil processes (Eviner and Chapin 2003). Yet, because of the epiphytic canopy community's separation from forest floor soil we can constrain tree species effects on canopy soil properties to litter additions and foliar leaching. Labile litter, such as that with high nitrogen (N) and low lignin, decomposes more quickly making more N available for plant use compared to recalcitrant litter, such as that with low N and high lignin (Chapin 1980). Thus, we predicted that host trees with high litter quality (low C/N ratios and low lignin concentrations) would maintain canopy soil with high bulk density, low C/N ratios, high available N and P concentrations and high N mineralization rates compared to host trees with lower litter quality. In this study we also examined the effect of season on canopy soil nutrients and processes because rates of soil processes may vary with seasons, as microbes respond to changing environmental conditions. Wet seasons often show higher rates of net N-mineralization than dry seasons (Corre et al. 2002). As a result, we also predicted that season would have a significant effect on soil processes with the wet season exhibiting greater N-mineralization rates and available nutrients than the dry season.

We also compared canopy soil to the forest floor mineral soil horizon (A) with the expectation that they would differ in multiple variables given their fundamental differences in composition: canopy soils are organic (Nadkarni et al. 2002) while forest floor A horizon is mineral soil (Clark et al. 1998a). In the few published studies that compare canopy soil and forest floor mineral soil in premontane tropical wet forests,

canopy soils had higher concentrations of bulk soil nitrogen (N) and greater net N-mineralization rates, but similar concentrations of bulk phosphorus (P) and microbial biomass N to forest floor mineral soils (Nadkarni et al. 2002; Vance and Nadkarni 1990). In line with previous studies, we predicted that canopy soils would have lower bulk density and higher %N content and greater N mineralization rates per gram of soil than forest floor mineral soils. To address these hypotheses, we examined the canopy organic soils and forest floor mineral soils associated with four tree species in a lowland tropical rainforest, La Selva Biological Station, in Costa Rica.

Material and methods

Study site

This study was conducted at La Selva Biological Station ($84^{\circ}00'12''$ W, $10^{\circ}25'52''$ N, 40 m a.s.l.) in northeastern Costa Rica. The La Selva forest is 1,600 ha of principally old-growth forest. It is categorized under the Holdridge system as a tropical wet forest (Holdridge 1967), and receives 4,000 mm of precipitation per year. The dominant season is the wet season, May–January, with average monthly precipitation of 382 mm. The dry season, February–April, is mild with an average, monthly precipitation of 172 mm. Average monthly temperature is $25.8^{\circ}\text{C} \pm 0.2$ and varies little throughout the year (McDade et al. 1994).

Tree species

Our study focused on the canopy and forest floor mineral soils of four canopy tree species: *Ceiba pentandra* (Bombacaceae), *Lecythis ampla* (Lecythidaceae), *Hyeronima alchorneoides* (Euphorbiaceae), and *Dipteryx panamensis* (Fabaceae) due to their varying leaf characteristics and phenologies. *Ceiba pentandra* is deciduous in the dry season, while *L. ampla* is deciduous in the wet season and drops all of its leaves in a 48 h period (C. A. Cardelús, personal observations) and stays leafless for approximately 1 month. *Dipteryx panamensis* is deciduous in the dry season and stays leafless for approximately 2 months and also has continuously shedding bark. *Hyeronima alchorneoides*, by contrast, is evergreen.

Field collection

We randomly selected three individuals of each tree species (*C. pentandra*, *D. panamensis*, *H. alchorneoides* and *L. ampla*) from five to six individuals of each tree species that we had identified as healthy and thus, safe to climb. The elevation of the selected trees varied little, 80.2 ± 8.6 m, however forest floor soil type varied with species and individuals. All *C. pentandra* individuals, two of the three *D. panamensis* and *H. alchorneoides* individuals, and one of the three *L. ampla* individuals were found on alluvial soils and the remaining individuals were found on residual soils. In 2004, litter was collected from all *D. panamensis*, *H. alchorneoides* and *L. ampla* individuals and one *C. pentandra* individual that was not a part of the current study as we missed the deciduous leaf fall of our study individuals.

In the beginning of the 2004 dry season (before *D. panamensis* and *C. pentandra* had dropped their leaves), we removed all leaf litter from the soil surface and volumetrically sampled 80–125 g of field moist canopy soil from two areas on each of two lower branches: the area directly next to the trunk and 2.5 m from the trunk. We then volumetrically sampled forest floor soil, two 10 cm deep cores, below each sampled branch next to the trunk and 2.5 m from the trunk. La Selva conventionally has two forest floor soil types, alluvial and residual, both are deeply-weathered, clay, volcanically derived forest floor soils that are oxisols, specifically Typic Haploperox, the difference being that the alluvial soil is considerably younger than the residual soil (Veldkamp et al. 2003). As with canopy soils, leaf litter was removed from the surface before collection. Unlike canopy soils, forest floor mineral soils had an undetectable organic layer furthering our expectation of different nutrient dynamics between the two soil types.

Our second season of sampling was in the wet season when all trees were fully leaved; we did not collect soils during *L. ampla*'s leafless phase. For our second season of sampling, we reduced the number of canopy samples to one per branch, next to the trunk, as we found no statistically significant differences associated with location along the branch for nutrient and soil characteristics during the dry season. All soils were sampled on rainless days because of safety issues related to tree climbing.

Nutrient analyses

Five grams of litter from each individual of *D. panamensis*, *H. alchorneoides* and *L. ampla*, and the single individual of *C. pentandra*, were ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ), passed through a #40 screen and analyzed for percent carbon (C), %N and % lignin concentrations. Total % C and %N were determined on a Costech Analytical Elemental Analyzer (Valencia, California). Total %P concentration was determined using an ash-digestion (Jones and Case 1996) followed by colorimetric analysis (Astoria Pacific, Clackamas, Oregon). Lignin concentrations were determined using a fiber analysis procedure which uses multiple extraction solutions to determine different C fractions, and ultimately total lignin content (Ankom 1996a, b).

All soil samples were homogenized by hand in the laboratory and roots and coarse materials (>2 mm) were removed and weighed. All soils from both sampling periods were analyzed for pH (H_2O ; Thomas 1996), concentrations of total bulk %C, $\delta^{13}\text{C}$ (‰) (Soltanpour et al. 1996), total bulk % N (Dumas Method, Bremner 1996), $\delta^{15}\text{N}$ (‰), dissolved inorganic N (DIN; $\mu\text{g N-NH}_4^+$ or $\text{N-NO}_3^- \text{ g}^{-1}$ oven dry equivalent (ode) soil (Mulvaney 1996)), dissolved organic N (DON; mg-N g^{-1} ode soil, (Sollins et al. 1999)), net N-mineralization, ammonification and nitrification ($\mu\text{g-N g}^{-1}$ ode soil day $^{-1}$) and available P ($\mu\text{g-P g}^{-1}$ ode soil, (Murphy and Riley 1962)). Soil samples from the dry season were also analyzed for bulk density (g cm^{-3} , oven dried mass/sample volume (Blake and Hartge 1986)), total bulk % P, dissolved organic C (DOC; mg-C g^{-1} ode soil), and microbial biomass C and N (mg-C or -N g^{-1} ode soil). Soil samples from the wet season were also analyzed for microbial and fungal functional richness.

Total C, N and P, and natural abundance $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were determined from soil samples which were ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ), and passed through a #40 screen. Carbon, N and isotopes were measured on a Costech Analytical Elemental Analyzer (Valencia, California) coupled to a Delta Plus Isotope Ratio mass spectrometer (Bremen, Germany). Bulk P was determined via inductively coupled plasma mass spectrometry (ICP-MS (Soltanpour et al. 1996)) method (ALS Chemex, Reno, Nevada).

Mineralization rates were determined ex situ using a 7-day laboratory incubation. One, 10 g fresh soil subsample was extracted with 50 ml of 0.5 N K_2SO_4 at time zero, while another 10 g fresh soil subsample was incubated in a 250 ml urinalysis cup for 7 days at ambient temperature (25°C) and then extracted with 0.5 N K_2SO_4 . Dissolved inorganic N was then analyzed for nitrate and ammonium concentrations with colorimetry. Initial samples were also analyzed for DON and DOC (dry season only). In the dry season, total dissolved C and N (TDC or N) were measured on a Shimadzu TIC/TOC analyzer coupled to a chemi-luminescent total N analyzer (Columbia, MD) at the University of Colorado. In the wet season, TDN was measured through persulfate oxidation of DON (Sparling et al. 1996) followed by colorimetric analysis. Dissolved organic N concentrations were determined by the difference between TDN and DIN.

Microbial biomass C and N were extracted using the fumigation-extraction method (Brookes et al. 1985) and later analyzed for total C and N on the TOC/TN analyzer at the University of Colorado. To calculate microbial biomass C and N, we subtracted unfumigated and extracted soil TDC or TDN from fumigated and extracted soil TDC or TDN. We applied conversion factors of K_{EC} of 0.45 and K_{EN} of 0.54 for C and N, respectively (Brookes et al. 1985; Joergensen 1996). We used a resin extraction for available P (5 g Biorad, AG 1-X8, Cl^- form; in concentrate bag, ANKOM Technology part #R510) (Lajtha et al. 1999) followed by colorimetry.

Microbial functional richness

The functional richness of fungi + bacteria was determined with the use of Biolog™ Filamentous Fungi (FF) MicroPlates (catalog #1006, Biolog™, Hayward CA) and FF inoculating fluid (catalog #72106, Biolog™). During the wet season, one branch and one forest floor sample was analyzed from each replicate tree of each species ($n=12$). In addition, Biolog™ EcoPlates (catalog #1506, Biolog, Hayward, CA) were applied as a course index of bacterial functional richness (Garland 1997; Garland and Mills 1991). Well absorbance for each method was measured at 490 nm using a microplate reader (EL800 Bio-tek instruments, Winooski, VT). The number of positive wells per sample was an indication

of the functional richness of the community of fungi + bacteria (for FF plates) and bacteria (for Biolog plates) that can be effectively cultured in EcoPlates (Dobranic and Zak 1999).

Statistical analyses

This study was designed to examine differences in canopy soil properties and nutrients both among tree species and within tree species between seasons. To determine differences among the four species we used analysis of variance on normally distributed data or Kruskal–Wallis rank sums tests on non-normally distributed data. Our continuous variable was the nutrient in question and our categorical variable was tree species. This was followed by a post-hoc student's *t*-test to determine the least significant difference among species pairs. To determine differences between seasons within a species or between canopy and forest floor mineral soils, we used *t*-tests on normally distributed data and Wilcoxon Rank Sums tests on non-normally distributed data. We used a non-parametric discriminant function analysis (DFA) to determine if tree species groupings accurately predicted canopy soil groupings for both seasons. For the latter, we only included variables that were measured in both seasons (available P, %N, %C, net N-mineralization rate, DON, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values). Finally, to examine the relationship between host tree litter variables and net mineralization rates we used linear regression.

Results

Host tree litter chemistry

Litter chemistry was variable among tree species (Table 1). The only leguminous species, *D. panamensis*, had the highest N and P concentrations and lowest C/N ratios of all species. Both *C. pentandra* and *H. alchorneoides* had the highest C/N ratios, lignin concentrations and lignin/N (Table 1). *Lecythis ampla* had the lowest P concentrations, but also the lowest lignin and mean lignin/N ratios of all species.

Canopy soil: physical properties, nutrients and processes

Canopy soil bulk density varied two-fold among tree species with *D. panamensis* having significantly higher bulk density than all other species (Table 2). Soil pH was not significantly different within tree species between seasons however it varied significantly among species with *C. pentandra* consistently having the highest pH in each season (Table 2).

Dry season Within the dry season, differences in canopy soil among canopy tree species were detected in %N, C/N ratios and $\delta^{13}\text{C}$ values (Table 2). *Ceiba pentandra* and *D. panamensis*, both dry season deciduous species, were consistently similar to each other and *H. alchorneoides* and *L. ampla*, both dry season evergreen species, were consistently similar to

Table 1 Mean ($\pm 1\text{ SE}$) initial tree litter chemistry of four tree species ($n=3$) studied at La Selva Biological Station and the statistical results of a one-way ANOVA and post-hoc Tukey tests for differences in initial litter chemistry among species that is indicated by lowercase letters

	<i>Ceiba</i>	<i>Dipteryx</i>	<i>Hyeronima</i>	<i>Lecythis</i>	<i>df</i>	<i>F</i>	<i>p</i>
%C	45.3	51.3 (0.2)	49.7 (0.9)	49.5 (0.6)	2, 8	2.48	0.164
%N	1.16	2.39 ^a (0.03)	1.48 ^b (0.17)	1.83 ^c (0.050)	2, 8	20.64	0.002
%P	0.057	0.133 ^a (0.009)	0.08 ^b (0.016)	0.037 ^c (0.003)	2, 8	21.48	0.002
C/N	39	21 ^a (0)	34 ^b (3)	27 ^c (1)	2, 8	10.37	0.011
%lignin	30.7	22.9 ^a (0.6)	30.3 ^b (0.8)	14.9 ^c (1.7)	2, 8	33.60	<0.001
Lignin/N	27	10 ^a (0.2)	21 ^b (1.5)	8 ^a (0.9)	2, 8	47.49	<0.001

Ceiba was excluded from statistical analyses because $n=1$

Table 2 Mean (± 1 SE) of soil properties, nutrients and processes from canopy soils collected from four different tree species at La Selva Biological Station, Costa Rica, in both the wet and dry seasons

Tree Species	Dry Season				Wet Season			
	Ceiba	Dipteryx	Hieronima	Lecythis	Ceiba	Dipteryx	Hieronima	Lecythis
Bulk density (g cm ⁻³)	0.064 ^a (0.003)	0.097 ^b (0.009)	0.055 ^a (0.005)	0.063 ^a (0.009)	NA	NA	NA	NA
pH DI	3.86 ^a (0.15)	3.79 ^{ab} (0.15)	3.42 ^c (0.05)	3.50 ^{bc} (0.07)	3.92 ^a (0.10)	3.70 ^{ab} (0.11)	3.48 ^b (0.54)	3.49 ^b (0.12)
%N	2.480 ^a (0.154)	2.520 ^a (0.175)	2.07 ^b (0.035)	2.122 ^b (0.039)	2.582 (0.110)	2.504 (0.115)	2.194 (0.146)	2.345 (0.102)
C/N	19.91 ^a (1.19)	19.87 ^a (1.37)	23.44 ^b (0.44)	23.36 ^{ab} (0.42)	18.62 (0.75)	19.81 (1.04)	22.34 (1.71)	20.90 (1.06)
$\delta^{13}\text{C}$ (‰)	-28.31 ^a (0.30)	-27.96 ^a (0.34)	-29.46 ^b (0.12)	-30.16 ^b (0.96)	-29.02 ^a (0.24)	-27.47 ^b (0.46)	-29.34 ^a (0.20)	-28.64 ^a (0.19)
Available P (µg-P g ⁻¹ soil)	18.16*	19.60*	12.29*	17.44*	0.667	0.110	0.309	0.347
Dissolved organic N (mg-N g ⁻¹ soil)	1.291*	1.049*	1.268*	2.422*	0.092	0.062	0.091	0.126

Different lower case letters indicate significant differences among species within a season using one-way ANOVA for normal data or Kruskal Wallace (χ^2 statistic) for non-normal data ($p < 0.05$).

* $p < 0.05$, significant differences between seasons within a species using a student's *t*-test

each other. *Ceiba pentandra* and *D. panamensis* had significantly greater %N, lower mean C/N ratios and significantly more enriched $\delta^{13}\text{C}$ signatures than *H. alchorneoides* and *L. ampla*. Net N-immobilization occurred in canopy soils of all species during the dry season and no differences were found in DOC ($F_{16}=0.65$, $p=0.596$), or microbial biomass C ($F_{16}=1.31$, $p=0.312$) or N ($F_{16}=0.58$, $p=0.639$) during this season.

Wet season Differences in canopy soils among species were not consistent between seasons. The wet season saw significant differences in: ammonium concentrations (Fig. 1), ammonification, nitrification and net N-mineralization rates (Fig. 2) and natural abundance $\delta^{13}\text{C}$ values (Table 2). Interestingly, *H. alchorneoides*, the species with one of the highest C/N ratios and lignin concentrations, had the highest mean

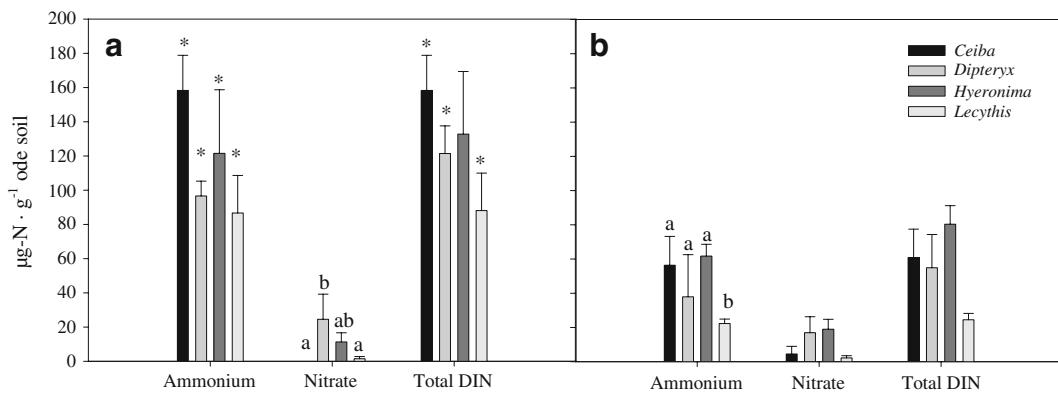


Fig. 1 Mean (± 1 SE) dry season (a) and wet season (b) ammonium, nitrate and total dissolved inorganic nitrogen (DIN) concentrations in canopy soils collected from four tree species at La Selva Biological Station, Costa Rica, during the dry and

wet seasons. Means with different lower case letters indicate significant differences among species within a season ($p < 0.05$) and asterisks indicate significant differences between seasons within a species ($p < 0.05$)

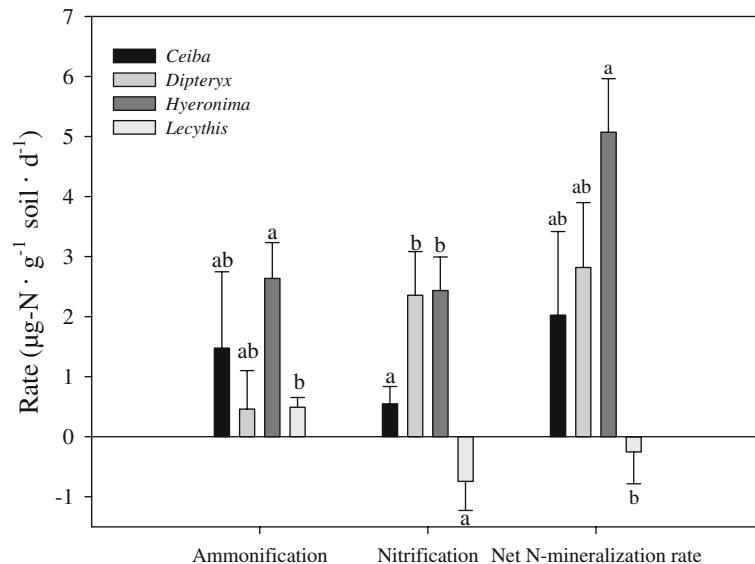


Fig. 2 Wet season mean (± 1 SE) ammonification, nitrification and net N-mineralization rates in canopy soil from our four study tree species (*Ceiba pentandra*, *Dipteryx panamensis*, *Hyeronima alchorneoides* and *Lecythis ampla*) at La Selva Biological Station, Costa Rica. Lowercase letters indicate significant differences among species ($p < 0.05$). Dry season mineralization rates exhibited net N-immobilization for all species and were excluded from graph

Biological Station, Costa Rica. Lowercase letters indicate significant differences among species ($p < 0.05$). Dry season mineralization rates exhibited net N-immobilization for all species and were excluded from graph

net N-mineralization rates of all species and *L. ampla*, the species with the lowest lignin/N ratio and lignin concentrations, exhibited only net N-immobilization (Fig. 2). Delta ^{13}C values were significantly more enriched in *D. panamensis* canopy soils compared to all other species (Table 2).

Of note are the soil parameters that did not vary among species within either season, namely: %C (dry: $F_{22}=2.90$, $p=0.062$; wet: $\chi^2_{21}=5.53$, $p=0.137$),

available P (Table 2), total DIN (Fig. 1), DON (Table 2) and $\delta^{15}\text{N}$ values (Fig. 3).

Seasonal effects within tree species Seasonal differences within species were found in multiple variables. Net N-mineralization and ammonification rates were significantly higher in the wet season than the dry season in all species, while DON showed the reverse pattern (Table 2). Dissolved inorganic nitrogen con-

Fig. 3 Mean (± 1 SE) natural abundance $\delta^{15}\text{N}$ values of canopy and forest floor soils of four tree species at La Selva Biological Station during both the wet and dry seasons. Asterisks (*) indicate significant difference between seasons within a tree species

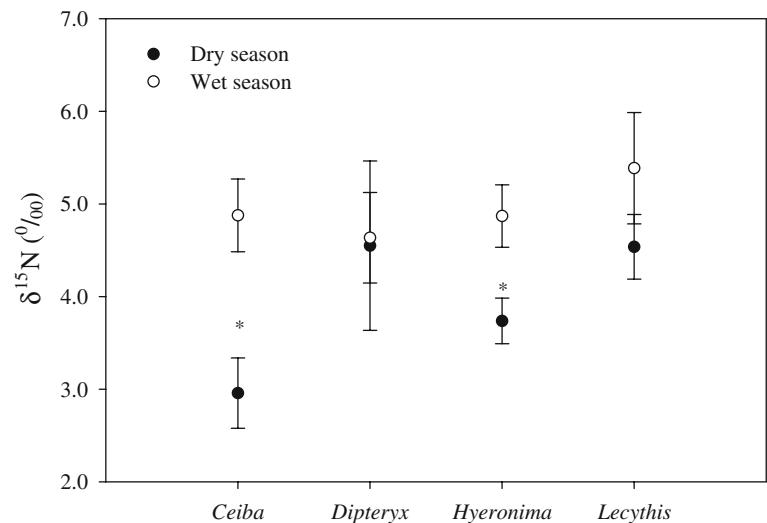
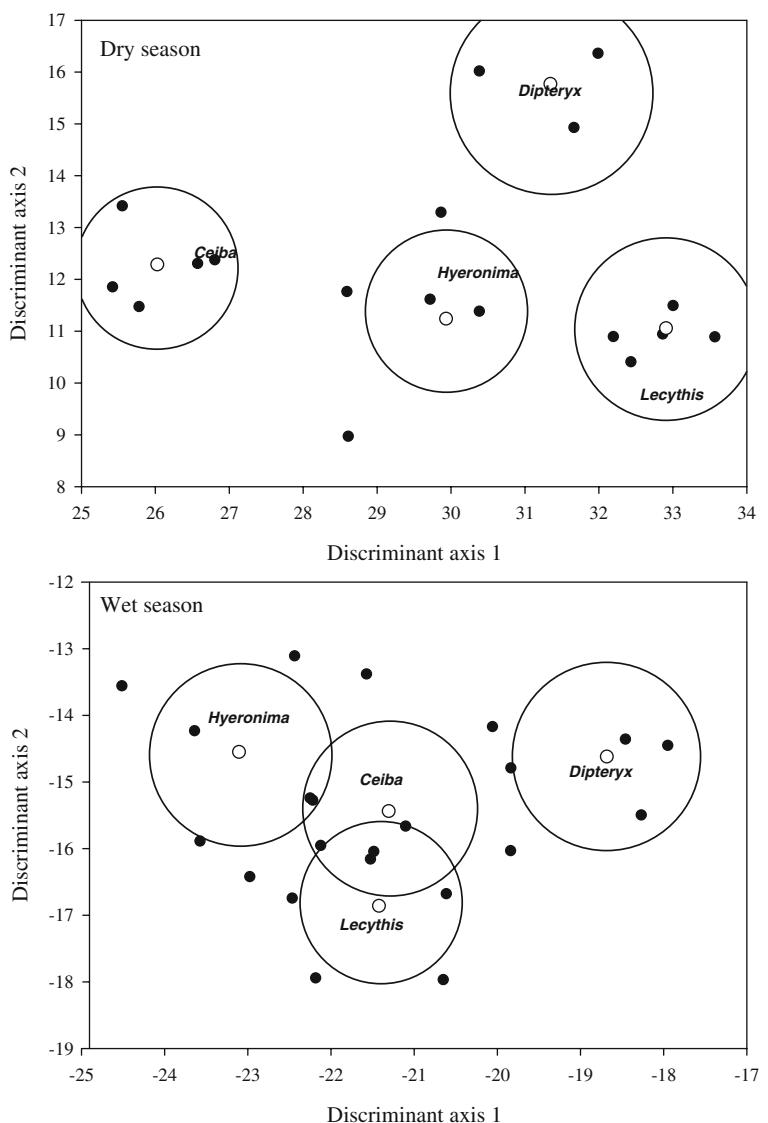


Fig. 4 Canonical plots of discriminant function analyses of canopy soil nutrient properties among host trees during the dry (upper graph) and wet seasons (lower graph). Open dots indicate means for labeled species and large circles denote 95% confidence intervals for the means. When large circles overlap, there is no significant difference between species

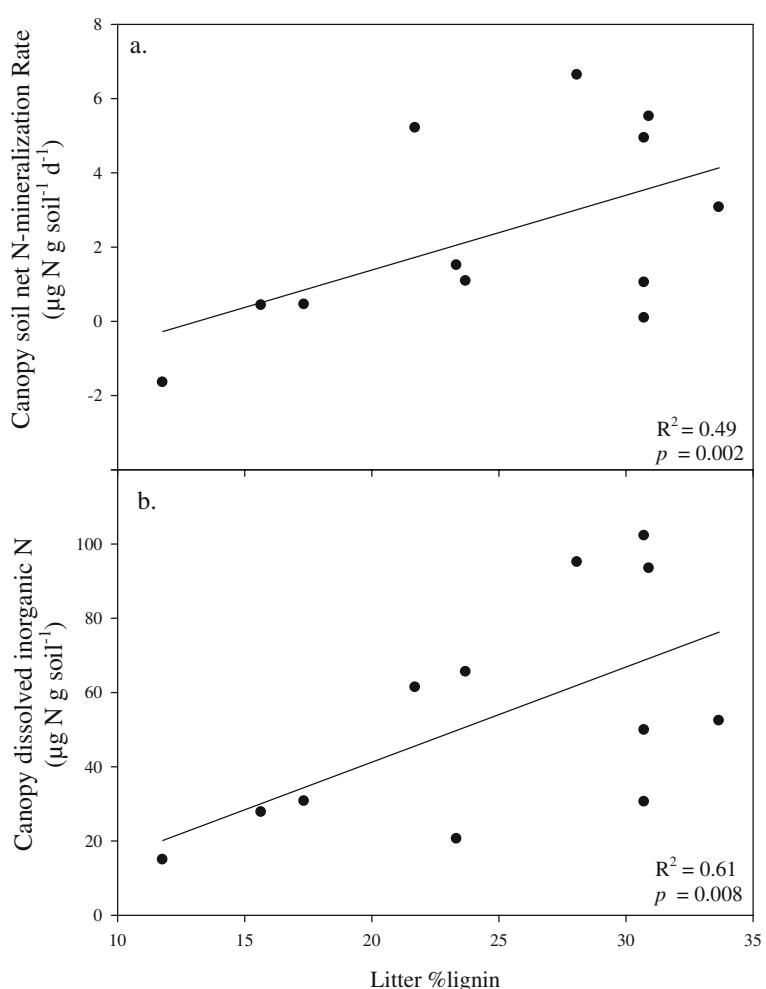


centrations were significantly higher in the dry season in *C. pentandra*, *D. panamensis* and *L. ampla* canopy soils (Fig. 5). *Ceiba pentandra* and *H. alchorneoides* $\delta^{15}\text{N}$ values varied between seasons with values more depleted during the dry season (Fig. 3). Available soil P was significantly higher during the dry season than wet season in all species (Table 2).

To determine overall soil nutrient differences among species within seasons, we conducted a DFA using most of the nutrient variables measured in both seasons. We found that patterns among species differed with seasons. During the dry season each host tree species was statistically distinct (Fig. 4a; MANOVA: Pillai's trace=2.13, $F=3.47$, $p=0.001$).

Axis 1 explained 65.9% of the variance and axis 2 explained 27.6% (Eigenvalues 8.36 and 3.50, respectively). Percent N loaded most heavily on axes 1 and 2, followed by $\delta^{15}\text{N}$ and %C. During the wet season, the relationship among tree species was different from the dry season: *D. panamensis* canopy soils were statistically distinct from *C. pentandra*, *H. alchorneoides* and *L. ampla*, and *H. alchorneoides* and *L. ampla* canopy soils were distinct from each other (Fig. 4b; MANOVA: Pillai's trace=1.52, $F=2.04$, $p=0.024$). The first discriminant function explained 64.1% of the data with an Eigenvalue of 2.61, and the second discriminant function explained 26.7% with an Eigenvalue of 1.08 (total variance explained

Fig. 5 Linear regressions of initial litter %lignin concentrations against canopy soil wet season net N-mineralization rates (**a**) and canopy soil wet season dissolved inorganic nitrogen (**b**)



was 90.8%). Dissolved organic N loaded most heavily on both axes, followed by %N and $\delta^{13}\text{C}$.

Host tree litter % lignin was strongly and positively correlated with two canopy soil nutrient variables: wet season net N-mineralization rates (Fig. 5a) and wet season DIN (Fig. 5b).

Forest floor soils

Forest floor mineral soil characteristics varied little among tree species and within seasons. During the dry season DON, DOC and pH were significantly higher in *Ceiba* than the other tree species (DOC: $F_{20}=7.61, p=0.02$; DON: $F_{23}=4.85, p=0.01$; $F_{23}=11.00, p<0.01$). During the wet season, DON was significantly higher in *D. panamensis* and *H. alchorneoides* forest floor mineral soils than both *C. pentandra* and *L. ampla*

soils (DON: $F_{23}=7.82, p<0.01$); while *H. alchorneoides* had significantly more depleted $\delta^{13}\text{C}$ values than all trees ($F_{23}=5.02, p<0.01$).

Canopy and forest floor mineral soils: physical properties, nutrients and processes

Canopy soil bulk density was 7.5-times lower than that of forest floor soil (Table 3). Overall, canopy soils were significantly more acidic than forest floor mineral soils in both the dry and wet seasons (Table 3). Canopy and forest floor mineral soils differed significantly in most nutrients and processes in both seasons.

Dry season In the dry season, %C, C/N ratios (Table 3), %N, N/P ratios (Fig. 6) nitrification rates

Table 3 Mean (± 1 SE) of soil properties, nutrients and processes from canopy and forest floor soils collected from four different tree species at La Selva Biological Station, Costa Rica, in both the wet and dry seasons

	Dry Season					Wet Season				
	Canopy	Forest Floor	df	t	p	Canopy	Forest Floor	df	t	p
Bulk density (g cm ⁻³)	0.07 (0.00)	0.04 (0.01)	46	25.75	<0.001	NA	NA	NA	NA	NA
pH DI	3.63 (0.07)	4.29 (0.09)	43	6.09	<0.001	3.64 (0.06)	4.46 (0.08)	44	8.16	<0.001
%C	48.6 (0.1)	6.7 (0.4)	44	-39.92	<0.001	48.2 (0.3)	7.4 (0.7)	45	-23.58	<0.001
C/N ratio	21.72 (0.57)	13.12 (0.52)	44	-11.14	<0.001	20.44 (0.63)	11.9 (0.3)	45	-12.35	<0.001
$\delta^{13}\text{C}$ (‰)	-29.3 (0.4)	-27.88 (0.31)	45	2.81	0.007	-28.67 (0.19)	-27.90 (0.09)	45	3.6	0.001
$\delta^{15}\text{N}$ (‰)	3.92 (0.27)	5.56 (0.24)	45	4.59	<0.001	4.95 (0.22)	5.46 (0.22)	45	1.62	0.111
Available P	16.81 (1.80)	18.74 (1.25)	45	0.92	0.364	0.38 (0.09)	0.62 (0.12)	43	1.55	0.128
Net N-mineralization (µg-N g ⁻¹ soil day ⁻¹)	-71.6 (6.4)	-24.65 (1.74)	43	7.45	<0.001	2.40 (0.60)	1.14 (0.27)	43	-1.91	0.065
Ammonification (µg-N g ⁻¹ soil day ⁻¹)	-72.1 (6.5)	-19.39 (1.08)	45	-8.09	<0.001	0.98 (0.48)	0.039 (0.229)	43	-1.77	0.086
Nitrification (µg-N g ⁻¹ soil day ⁻¹)	0.54 (0.17)	-5.25 (1.32)	43	-4.32	<0.001	1.42 (0.29)	1.10 (0.13)	43	-1	0.325

Statistics report differences between habitats using a student's *t*-test.

(Table 3), DON and microbial biomass C and N (Fig. 7) were significantly higher in canopy than in forest floor mineral soils. Percent N was 4.3 times greater in canopy compared to forest floor mineral

soils. Forest floor mineral soils had significantly greater %P as well as 2‰ more enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than canopy soils (Table 3).

Wet season There were fewer differences between canopy soils and forest floor mineral soils during the wet season. Consistent with the dry season were the significantly greater %C, %N, C/N ratios and DON in canopy than forest floor mineral soils as well as the more enriched $\delta^{13}\text{C}$ values of forest floor mineral soils. However, $\delta^{15}\text{N}$ values were not statistically distinct nor were there differences in mineralization rates (Table 3). Although total bulk P concentrations were higher in forest floor mineral soils, available P did not differ between habitats in either season (Table 3).

Functional richness of bacteria and fungi between habitats

In the wet season, canopy soils harbored greater fungal + bacterial functional richness (the number of FF Plate substrates utilized) than forest floor mineral soils ($F_{22}=4.45$, $p=0.047$). However, bacterial func-

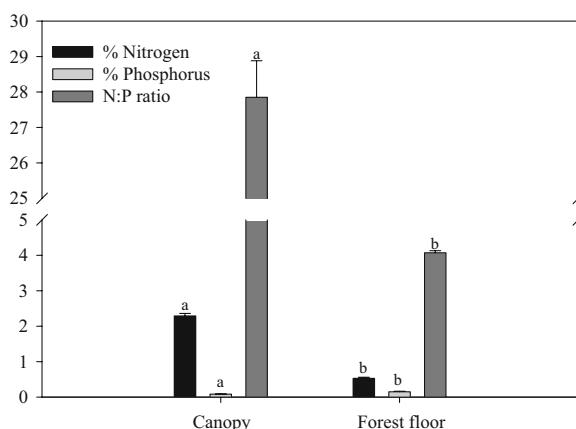


Fig. 6 Mean (± 1 SE) %N (a), %P (b) and N/P ratio (c) of canopy and forest floor soils collected in both the wet and dry seasons at La Selva Biological Station, Costa Rica. Lower case letter indicates significant differences between habitats for nutrients ($p<0.05$)

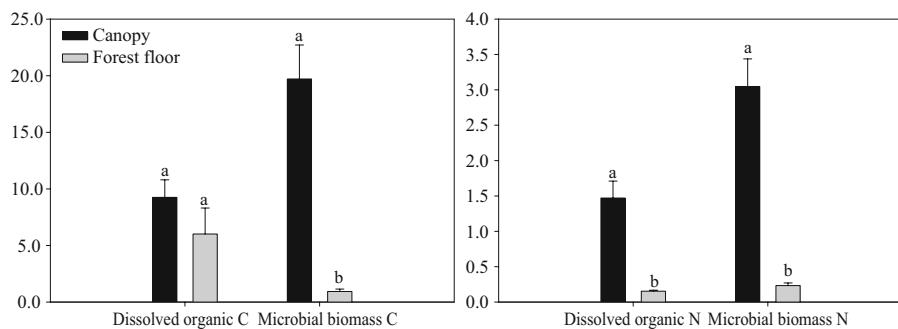


Fig. 7 Dry season mean (± 1 SE) dissolved organic C and microbial biomass C (first panel) and dissolved organic N and microbial biomass N (second panel) concentrations in canopy

tional richness alone (the number of EcoPlate substrates utilized) was lower in canopy than forest floor mineral soils ($F_{21}=16.30$, $p=<0.001$).

Discussion

The rainforest canopy is a hot-spot of species richness (Connell 1978; Ellwood and Foster 2004; Gentry and Dodson 1987; Nieder et al. 2001). While we know there are vast differences between the canopy and forest floor habitats in microclimate (Cardelús and Chazdon 2005), species composition (Gentry and Dodson 1987; Nadkarni and Longino 1990; Watkins et al. 2006) and soil composition (Nadkarni et al. 2002), we know much less about how tree species influence canopy processes. We examined whether canopy soil nutrient dynamics varied among tree species and with season in a lowland wet forest in Costa Rica and found that the canopy soil of different tree species varied in fundamental ways and that season had a strong effect.

Canopy soil: dry season

The dry season in this lowland wet forest site receives >100 mm of rainfall per month (McDade et al. 1994). This drier period has a significant impact on the canopy microclimate in which the variation in % light transmittance and % humidity is higher and more variable than the wet season when trees are evergreen (e.g. dry season % humidity: 75–93% vs. wet season % humidity 81–98%) (Cardelús and Chazdon 2005). In this period of more extreme microclimate, differences in soil parameters among species were pro-

ounced and were exemplified in the DFA which showed that all species were significantly separated from each other during the dry season (Fig. 4a). These dry season differences among species were largely driven by canopy soil %N, %C and $\delta^{15}\text{N}$ values which were more variable during the dry season.

While the overall differences in soil properties and nutrient concentrations among tree species are likely due to a combination of factors, including the effects of canopy architecture on microclimate and soil trapping, there were interesting similarities in the dry season among species with similar phenologies. For example, *H. alchorneoides* and *L. ampla*, both dry season evergreen species, had %N and $\delta^{13}\text{C}$ values similar to each, and significantly different from each other, *C. pentandra* and *D. panamensis*, both dry season deciduous, which were similar to each other (Table 2). These similarities do not appear to be linked to host tree litter quality because *H. alchorneoides* and *L. ampla* varied significantly in all measured litter characteristics except %C, while *D. panamensis* had the highest and *C. pentandra* the lowest %N and C/N ratios of all species (Table 1). It appears that the differences among species in phenology directly affects microclimate, which in turn could affect nutrient processes.

Canopy soil: wet season

Soil parameters were less variable during the wet season than the dry season and the linking of species with similar phenologies was not evident. As demonstrated by the wet season DFA, trees species were more similar to each other during the wet season than the dry season (Fig. 4). *D. panamensis* was the only

species that was statistically distinct and this distinction was largely driven by DON and N concentrations and $\delta^{13}\text{C}$ values. *Dipteryx panamensis* canopy soils were also distinct from other species in bulk density, which was significantly higher than other species (Tables 2), potentially indicating that its soil had undergone greater decomposition.

Studies have shown that a negative correlation exists between host tree litter % lignin and wet season N-mineralization rates and DIN concentrations (i.e. (Chapin 1980). However, we found a strong positive correlation between these variables in the wet season (Fig. 5), which was the opposite of our prediction. This counter-intuitive result may reflect a negative correlation between lignin and more readily available C compounds in litter and soil organic matter. Microbes breaking down low lignin substrates may have access to higher concentrations of available C compounds, resulting in higher rates of N immobilization than in substrates with high lignin and low available C compounds (Hobbie et al. 2007).

Canopy and forest floor mineral soils

Canopy soils were highly organic, with six times more carbon per unit mass than forest floor mineral soils (Table 3). Canopy soils were also more acidic than forest floor mineral soils (Table 3), a pattern also found in a premontane rainforest in Costa Rica (Vance and Nadkarni 1990). Soil %N was greater in soils from the canopy than those from the forest floor, which is consistent with findings in other studies (Nadkarni et al. 2004; Veneklaas et al. 1990; Wania et al. 2002). Net N-mineralization rates, overall, were also higher in canopy soils compared to the forest floor mineral soils during the wet season. Both these lines of evidence suggest that per unit soil mass, N availability is higher in canopy soil, at least during the wet season. Carbon concentrations were also higher in canopy soils and C/N ratios were twice those of forest floor mineral soils (Tables 3). Higher N mineralization rates in the soils with the highest C/N ratios suggests that N mineralization is more closely linked to the chemical composition of the carbon compounds present rather than the stoichiometry of the two elements.

Net N-mineralization essentially halted during the dry season in both habitats (Table 3). The high immobilization rates in the dry season could be caused, in part, by low water availability which

causes limited diffusion of substrates, simple inactivity, or microbial die-off (Maier et al. 1999). The slowing of N-mineralization rates during the dry season was reflected in the accumulation of DON in both canopy and forest floor mineral soils (Table 3). There was a significant decrease in wet season DON concentrations in both the canopy and forest floor habitats which was likely due to a combination of increased net N-mineralization and plant uptake. In the canopy, plant uptake of DON may be more important than on the forest floor as some amino acids have been demonstrated to be a preferred source of N in some tropical epiphytic ferns (Watkins 2006) and tank bromeliads (Benzing 1970; Endres and Mercier 2003) and have been shown to be an important source of N for arctic tundra plants where soils are also highly organic (Kielland 1994, 1997; Persson et al. 2003; Schimel and Chapin III 1996).

There were surprising similarities in the availability of nutrients in canopy and forest floor mineral soils. Higher P-availability during the dry season was followed by low concentrations during the wet season in both habitats. The high P concentrations in the dry season may reflect the accumulation of available P due to decreased plant activity and leaching (Campo et al. 1991). A similar pattern was found in a Mexican dry forest where dry season soils released P through mineralization when wetted, whereas wet season soils immobilized P when wetted (Campo et al. 1991). The similar patterns and concentrations of available P in both habitats across seasons indicate possible conservation and tight cycling of P. This finding is supported by recent work in Hawaiian Montane forests which showed increases in nonvascular epiphyte biomass and diversity with increases of P to both the forest floor and the canopy directly (Benner et al. 2007; Benner and Vitousek 2007) as well as studies on individual plant species demonstrating that P limits reproduction in one species of bromeliad (Zotz and Richter 2006) and is retranslocated more readily than N in multiple epiphyte species (Zotz 2004).

These data exemplify the differences between the canopy soils and forest floor mineral soils in fundamental soil properties which are direct effects of litter inputs and the rate of nutrient cycling. Our data also demonstrate that tree species has significant effects on canopy soil nutrients and processes and these effects change with season. This is the first study to quantify species differences in canopy soil

nutrient status. While these findings are intriguing they are not, however, surprising given the direct inputs of foliar leachate and litter that they contribute to the canopy. While host trees can have direct effects on the fertility of their associated forest floor soil (Prescott 2002; Zinke 1962), our data as well as data from three of the tree species studied here (in the same site) were found to have no effect on their local soil chemistry (Powers et al. 2004) which indicates that the influences of the host tree extends to the canopy but not below it.

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References

- Angers DA, Caron H (1998) Plant-induced changes in soil structure: Processes and feedbacks. *Biogeochemistry* 42:55–72
- Ankom (1996a) Acid detergent fiber in feeds filter bag technique (ANKOM200). Ankom Technology
- Ankom (1996b) Neutral detergent fiber in feeds filter bag technique (Ankom200). Ankom Technology
- Benner JW, Vitousek PM (2007) Development of a diverse epiphyte community in response to phosphorus fertilization. *Ecol Lett* 10:628–636
- Benner JW, Conroy S, Lunch CK, Toyoda N, Vitousek PM (2007) Phosphorus fertilization increases the abundance and nitrogenase activity of the cyanolichen *Pseudocyphellaria crocata* in Hawaiian Montane Forests. *Biotropica* 39:400–405
- Benzing DH (1970) Foliar permeability and the absorption of minerals and organic nitrogen by certain tank bromeliads. *Bot Gaz* 131:23–31
- Binkley DAN, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree–soil interactions. *Biogeochemistry* 42:89–106
- Blake GR, Hartge KH (1986) Bulk density. In: Klute A (ed) Methods of soil analysis, Part 1. Physical and mineralogical methods. American Society of Agronomy, Inc. & Soil Science Society of America, Inc., Madison, WI, pp 363–382
- Bremner JM (1996) Nitrogen-total. In: Bartels JM (ed) Methods of soil analysis. Part 3. Chemical methods. Soil Science Society of America and American Society of Agronomy, Madison, WI
- Brookes PC, Kragt JF, Powlson DS, Jenkinson DS (1985) Chloroform fumigation and the release of soil-nitrogen—the effects of fumigation time and temperature. *Soil Biol Biochem* 17:831–835
- Campo J, Jaramillo VJ, Maass JM (1991) Pulses of soil phosphorus availability in a Mexican tropical dry forest: effects of seasonality and level of wetting. *Oecologia* 115:167–172
- Cardelús CL (2007) Vascular epiphyte communities in the inner-crown of *Hieronima alchorneoides* and *Lecythis ampla* at La Selva Biological Station, Costa Rica. *Biotropica* 39:171–176
- Cardelús CL, Chazdon RL (2005) Inner-crown microenvironments of two emergent tree species in a lowland wet forest. *Biotropica* 37:238–244
- Cardelús CL, Watkins Jr, JE (2008) Habitat differentiation of ferns in a lowland tropical rainforest. *Am Fern J* (in press)
- Chapin FS (1980) The mineral nutrition of wild plants. *Ann Rev Ecol Syst* 11:233–260
- Clark DB, Clark DA, Read JM (1998a) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *J Ecol* 86:101–112
- Clark KL, Nadkarni Nalini M, Gholz HL, Schaefer DS (1998b) Atmospheric deposition and net canopy retention in a tropical montane forest. *J Trop Ecol* 14:27–45
- Clark KL, Nadkarni NM, Schaefer D, Gholz HL (1998c) Cloud water and precipitation chemistry in a tropical montane forest, Monteverde, Costa Rica. *Atmos Environ* 32:1595–1603
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Corre MD, Schnabel RR, Stout WL (2002) Spatial and seasonal variation of gross N transformations and microbial biomass in a Northeastern US grassland. *Soil Biol Biochem* 34:445–457
- Dobranic JK, Zak JC (1999) A microtiter plate procedure for evaluating fungal functional diversity. *Mycologia* 91:756–765
- Ellwood MDF, Foster WA (2004) Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature* 429:549–551
- Endres L, Mercier H (2003) Amino acid uptake and profile in bromeliads with different habits cultivated in vitro. *Plant Physiol Biochem* 41:181–187
- Erwin T (1997) Biodiversity at its utmost: tropical rainforest beetles. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II: Understanding and protecting our biological resources. Joseph Henry, Washington, DC, pp 27–40
- Eviner VT, Chapin FS (2003) Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Ann Rev Ecol Evol Syst* 34:455–485
- Finzi AC, Canham CD, van Breemen N (1998) Canopy tree–soil interactions within temperate forests: species effects on pH and cations. *Ecol Appl* 8:447–454
- Forman RT (1975) Canopy lichens with blue-green algae: a nitrogen source in a Colombian rainforest. *Ecology* 56:1176–1184
- Garland JL (1997) Analysis and interpretation of community-level physiological profiles in microbial ecology. *FEMS Microbiol Ecol* 24:289–399
- Garland JL, Mills AL (1991) Classification and characterization of heterotrophic microbial communities on the basis of patterns of community level sole carbon source utilization. *Appl Environm Microbiol* 57(8):2351–2359
- Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19:149–156

- Hietz P, Briones O (1998) Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. *Oecologia* 114:305–316
- Hietz P, Wanek W, Wania R, Nadkarni NM (2002) Nitrogen-15 natural abundance in a montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte nutrition. *Oecologia (Berlin)* 131:350–355
- Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karolewski P (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* 87:2288–2297
- Hobbie SE, Ogdahl M, Chorover J, Chadwick OA, Oleksyn J, Zytkowiak R, Reich PB (2007) Tree species effects on soil organic matter dynamics: the role of soil cation composition. *Ecosystems* 10(6):999–1018
- Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose, Costa Rica
- Joergensen RG (1996) The fumigation-extraction method to estimate soil microbial biomass: Calibration of the k(EC) value. *Soil Biol Biochem* 28:25–31
- Jones JB, Case BW (1996) Soil testing and plant analysis no. 3. In: Sparks DL (ed) Methods of soil analysis Part 3: Chemical methods. Soil Science Society of America, Madison, pp 389–415
- Kielland K (1994) Amino-acid-absorption by arctic plants—implications for plant nutrition and nitrogen cycling. *Ecology* 75:2373–2383
- Kielland K (1997) Role of free amino acids in the nitrogen economy of arctic cryptogams. *Ecoscience* 4:75–79
- Kruyt B, Malhi Y, Lloyd J, Norbre AD, Miranda AC, Pereira MGP, Culf A, Grace J (2000) Turbulence statistics above and within two Amazon rain forest canopies. *Boundary-Layer Meteorology* 94:297–331
- Lajtha K, Driscoll CT, Jarrell WM, Elliott ET (1999) Soil phosphorus: characterization and total element analysis. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) Standard soil methods for long-term ecological research. Oxford University Press, New York, pp 115–142
- Liu WY, Fox JED, Xu ZF (2002) Nutrient fluxes in bulk precipitation, throughfall and stemflow in montane subtropical moist forest on Ailao Mountains in Yunnan, south-west China. *J Trop Ecol* 18:527–548
- Lovett GM, Weathers KC, Arthur MA (2002) Control of nitrogen loss from forested watersheds by soil carbon: Nitrogen ratio and tree species composition. *Ecosystems* 5:712–718
- Lovett GM, Weathers KC, Arthur MA, Schultz JC (2004) Nitrogen cycling in a northern hardwood forest: Do species matter? *Biogeochemistry* 67:289–308
- Maier RM, Pepper IL, Gerba CP (1999) Environmental microbiology. Academic, San Diego
- McCay MG (2003) Winds under the rain forest canopy: The aerodynamic environment of gliding tree frogs. *Biotropica* 35:94–102
- McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) (1994) La Selva: Ecology and natural history of a neotropical rain forest. Chicago University Press, Chicago
- Mulvaney RL (1996) Nitrogen-inorganic forms. In: Bartels JM (ed) Methods of soil analysis. Part 3. Chemical methods. Soil Science Society of America and American Society of Agronomy, Madison, WI
- Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Anal Chim Acta* 27:1–36
- Nadkarni NM (1984) Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* 16:249–256
- Nadkarni NM, Longino JT (1990) Invertebrates in canopy and ground organic-matter in a neotropical montane forest, Costa-Rica. *Biotropica* 22:286–289
- Nadkarni NM, Matelson TJ (1991) Fine litter dynamics within the tree canopy of a tropical cloud forest. *Ecology* 72:2071–2082
- Nadkarni NM, Schaefer D, Matelson TJ, Solano R (2002) Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, Monteverde, Costa Rica. *Pedobiologia* 46:24–33
- Nadkarni NM, Schaefer D, Matelson TJ, Solano R (2004) Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *For Ecol Manag* 198:223–236
- Nieder J, Prosperi J, Michaloud G (2001) Epiphytes and their contribution to canopy diversity. *Plant Ecol* 153:51–63
- Persson J, Hogberg P, Ekblad A, Hogberg MN, Nordgren A, Nasholm T (2003) Nitrogen acquisition from inorganic and organic sources by boreal forest plants in the field. *Oecologia* 137:252–257
- Pittendrigh CS (1948) The bromeliad-Anopheles-malaria complex in Trinidad. I-The bromeliad flora. *Evolution* 2:58–89
- Powers JS, Kalicin MH, Newman ME (2004) Tree species do not influence local soil chemistry in a species-rich Costa Rica rain forest. *J Trop Ecol* 20:587–590
- Prescott CE (2002) The influence of the forest canopy on nutrient cycling. *Tree Physiol* 22:1193–1200
- Putz FE, Holbrook NM (1989) Strangler fig rooting habits and nutrient relations in the llanos of Venezuela. *Am J Bot* 76:781–788
- Rhoades CC, Sanford RL Jr, Clark DB (1994) Gender dependent influences on soil phosphorus by the dioecious lowland tropical tree *Simarouba amara*. *Biotropica* 26:362–368
- Sayer EJ, Tanner EVJ, Cheesman AW (2005) Increased litterfall changes fine root distribution in a moist tropical forest. *Plant Soil* 281:5–13
- Schimel DS, Chapin FS III (1996) Tundra plants compete effectively with soil microbes for amino-acid nitrogen. *Ecology* 77:2142–2147
- Sollins P, Glassman C, Paul EA, Swanston C, Lajtha K, Heil JW, Elliott ET (1999) Soil carbon and nitrogen: pools and fractions. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) Standard soil methods for long-term ecological research. LTER, New York
- Soltanpour PN, Johnson GW, Workman SM, Benton Jones J, Miller RO (1996) Inductively coupled plasma emission spectrometry and inductively coupled plasma-mass spectrometry. In: Bigham JM (ed) Methods of soil analysis. Part 3. Chemical methods. Soil Science Society of America and American Society of Agronomy, Madison, WI, pp 91–139
- Sparling GP, Zhu C, Fillery IRP (1996) Microbial immobilization of ^{15}N from legume residues in soils of differing textures: measurement by persulphate oxidation and ammonia diffusion methods. *Soil Biol Biochem* 28:1707–1715
- Stewart GR, Schmidt S, Handley LL, Turnbull MH, Erskine PD, Joly CA (1995) ^{15}N Natural abundance of vascular

- rainforest epiphytes: implications for nitrogen source and acquisition. *Plant Cell Environ* 18:85–90
- Thomas GW (1996) Soil pH and soil acidity. In: Sparks DL, Page CN, Helmke PA, Loeppert RH, Soltanpour PN, Tabatabai MA, Johnston CT, Sumner ME (eds) Methods of soil analysis. Part 3. Chemical Methods-SSSA Book Series no. 5. Soil Science Society of America and American Society of Agronomy, Madison
- Vance ED, Nadkarni NM (1990) Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. *Soil Biol Biochem* 22:677–684
- Veldkamp E, Becker A, Schwendenmann L, Clark DA, Schulte-Bisping H (2003) Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest. *Glob Chang Biol* 9:1171–1184
- Veneklaas EJ (1990) Nutrient fluxes in bulk precipitation and throughfall in 2 Montane tropical rain-forests, Colombia. *J Ecol* 78:974–992
- Veneklaas EJ, Zagt RJ, Vanleerdam A, Vanek R, Broekhoven AJ, Vangenderen M (1990) Hydrological properties of the epiphyte mass of a montane tropical rain-forest, Colombia. *Vegetatio* 89:183–192
- Wania R, Hietz P, Wanek W (2002) Natural ^{15}N abundance of epiphytes depends on the position within the forest canopy: source signals and isotope fractionation. *Plant Cell Environ* 25:581–589
- Watkins Jr, JE (2006) Functional ecology of the gametophytes and sporophytes of tropical ferns. In Department of Botany, University of Florida, Gainesville
- Watkins Jr, JE, Cardelús CL, Colwell RK (2006) Species richness and distribution of ferns along an elevational gradient in Costa Rica. *Am J Bot* 93:73–83
- Watkins Jr, JE, Rundel PW, Cardelús CL (2007) The influence of life form on carbon and nitrogen relationships in tropical rainforest ferns. *Oecologia* 153:225–232
- Zinke PJ (1962) Pattern of influence of individual forest trees on soil properties. *Ecology* 43:130–133
- Zotz G (2004) The resorption of phosphorus is greater than that of nitrogen in senescing leaves of vascular epiphytes from lowland Panama. *J Trop Ecol* 20:693–696
- Zotz G, Richter A (2006) Changes in carbohydrate and nutrient contents throughout a reproductive cycle indicate that phosphorus is a limiting nutrient in the epiphytic bromeliad, *Werauhia sanguinolenta*. *Ann Bot* 97:745–754