Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, Monteverde, Costa Rica

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Summary

In many tropical and temperate forests, live and dead components of canopy-held organic matter (COM) form communities that are distinct from terrestrially rooted plant and forest floor soil communities, but that interact with whole-forest processes. We quantified some of the soil characteristics of dead organic matter held within the canopy of mature trees in a tropical lower montane forest of Monteverde, Costa Rica, and compared them to soils from the upper horizons on the ground. The concentration of canopy organic matter was significantly higher than terrestrial soil, but similar for P and Ca. Canopy humus had very low pH compared to terrestrial soils. The terrestrial soil had a tenfold greater amount of extractable cations, but the C/N ratios and cation exchange capacity of COM and the upper soil horizon did not differ significantly. Canopy organic matter has rarely been considered in forest ecosystem studies due to its inaccessibility, the lack of rigorous sampling and extrapolation methods, and because its mass is small relative to total forest soil mass. However, in habitats where COM is large, a canopy root-humus mat occurs on branch and trunk surfaces, similar to that which occurs on the forest floor. Organic matter in the forest canopy may thus have more ecological importance than its mass implies, as the nutrient-retaining ca-

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pacity of the root-humus mat layer could play an important role in nutrient conservation for the individual trees and epiphytes whose roots are imbedded within the mats, and for the forest ecosystem as a whole.

Introduction

In tropical montane forests, live and dead components of canopy-held organic matter form communities that are distinct from terrestrially rooted plant and terrestrial soil communities, but that interact with whole-forest processes. This canopy organic matter (COM) is composed of shoots and roots of vascular and non-vascular plants, abscised leaves of host trees and epiphytes that have been intercepted by branches, arboreal soil, and associated invertebrates, fungi, and microorganisms. This material reaches its greatest abundance and diversity in tropical montane cloud forests (Madison 1977; Gentry & Dodson 1987; Ingram & Nadkarni 1993; Coxson & Nadkarni 1995).

Canopy organic matter influences nutrient cycling by altering ecosystem nutrient pools, pathways, and rates of nutrient fluxes (Pike 1978; Benzing & Seeman 1978; Nadkarni 1984, 1986; Coxson & Nadkarni 1995). In tropical montane forest, live plant components of COM appear to determine the overall structure of canopy communities, and contribute to nutrient exchange by exudation from and uptake by epiphyte roots, mycorrhizae (Maffia et al.1993), and host tree canopy roots (Nadkarni 1981; Sanford 1987). Litterfall derived from live COM can contribute a significant portion of the nutrients and carbon transferred to the forest floor via the litterfall pathway (Nadkarni and Matelson 1992).

In tropical montane forests, the dead components of COM consist of „crown humus" (*sensu* Jeník 1973), intercepted epiphyte and tree litter, animal feces and frass, decaying bark, and airborne particulates (Torn et al. 1997). Crown humus constitutes a true but hitherto undescribed arboreal histosol. This material is derived principally from epiphytic bryophytes that die and decompose *in situ* (Clark et al. 1998). It represents a pool of carbon and nutrients that are microbially active, with amounts of microbial biomass and rates of mineralization that are comparable to upper horizons of terrestrial soil (Vance & Nadkarni 1990). However, COM supports significantly lower rates of net nitrification than its terrestrial counterpart, which suggests that nitrogen is more tightly conserved in the canopy than on the forest floor (Vance & Nadkarni 1990). This arboreal soil contributes to whole-ecosystem nutrient cycles; it can be leached of nutrients (Nadkarni 1986) or can absorb and retain nutrients from atmospheric sources through physical, chemical, and biotic processes (Clark 1994, Clark et al. 1997; Clark et al. 2000). This material also provides habitat for a diverse and abundant invertebrate fauna, which includes many of the major groups of decomposers found in terrestrial soil (Nadkarni & Longino 1990). Birds have been recorded as foraging in the crown humus for invertebrates for as much as 20 % of their foraging visits (Remsen & Parker 1984; Nadkarni & Matelson 1989).

In tropical montane forests, crown humus dominates arboreal communities, but

has been little studied or compared to organic matter on the forest floor due to diffi-culties of field sampling and lack of established methods to sample the complex three-dimensional crowns of trees with statistical validity. Although crown humus has re-ceived some attention as a substrate for roots of epiphytes, vines, or trees, (Klinge 1963; Lyford 1969; Jeník 1973; Pócs 1980; Nadkarni 1981; Sanford 1987; Moore 1989), it has only rarely been quantitatively compared to organic matter on the forest floor or placed in the context of terrestrially rooted material (trees, shrubs, understory plants, and parasites) (e.g., Putz & Holbrook 1989; Vance & Nadkarni 1990).

In this paper, we: 1) quantify chemical characteristics of arboreal soil associated with large branches of mature trees in a primary tropical lower montane forest of Costa Rica; 2) compare characteristics of this material to the upper horizons of terres-trial soil; and 3) discuss the implications of the presence and characteristics of arbo-real soil in this forest to ecosystem-level nutrient cycling. This study is part of an ecosystem-level assessment of the ecology of canopy communities and their roles in nutrient cycling and forest dynamics (Nadkarni et al. 2000).

Materials and Methods

Study area

Arboreal and terrestrial soil samples were collected between April and June 1988 in the Mon-teverde Cloud Forest Preserve (MCFP), Monteverde, Puntarenas Province, Costa Rica (10´ 18° N, 84´ 48° W). The study area was in primary tropical lower montane moist forest (1480 m.a.s.l.), which is described as Leeward Cloud Forest (Lawton & Dryer 1980). The area is composed of trees 15–30 m in stature, and possessing a well-developed subcanopy (Nadkarni et al. 1995). The epiphyte community is one of the most abundant and diverse recorded (In-gram & Nadkarni 1993; Nadkarni & Wheelwright 2000). The continually moist soils below are derived from volcanic rhyolites, and classified as *Typic Dystrandept* (Vance & Nadkarni 1990). The canopy is exposed to frequent and intense wind and mist events throughout much of the year, especially during the windy-misty season (November – March) and the dry season (April – May) (Clark et al. 2000). The upper tree canopy experiences greater extremes in temperature, and more frequent and extreme wetting and drying cycles than on the forest floor (Bohlman et al. 1995).

In April 1987, a 4 ha area was established in the Research Area of the MCFP. Tree compo-sition, density, basal area, and structural characteristics are reported in Nadkarni et al. (1995). Stem density and stem diameters of trees > 2 cm diameter at breast height (DBH) were mea-sured and identified to species. A quartile "climbability index" was assigned to all trees > 30 cm DBH, based on our 17 years of experience with tree-climbing and our assessment of the rela-tive ease, safety, and degree of damage to the tree. Of those with an index of 3 or 4 (33 % of the total), a random subset (15 individuals, Table 1) were climbed using single-rope techniques (Perry 1978) to collect samples of crown humus.

Characterization and comparison of canopy humus and forest floor soil

The majority of arboreal soil is associated with the surfaces of inner branches and branch junc-tions of large trees (Nadkarni et al. 2000). We climbed to the mid-canopy (14 – 30 m) of the sample trees and took 3 – 7 subsamples from all accessible branches greater than 8 cm in di-ameter within 5 m of the trunk (89 canopy soil samples total). COM was removed from each branch by cutting through live and dead material around the circumference of the branch and peeling the mat away from the branch surface. Branch circumference was recorded at the mid-

dle of each segment. We separated the crown humus from other COM components and passed it through a 2 mm sieve to remove roots. Each sample of crown humus was analyzed separately.

A sample of terrestrial soil (FF-H = 0-10 cm, and FF-A = 10-20 cm) was taken from each of 15 randomly located points with a corer (10 cm diameter) on the ground in areas directly adjacent to the trees we climbed. Accumulated standing fine litter and stems were removed before sampling. These samples were bulked to yield a total of six composite samples. Each composite sample was sieved twice (6.5 mm, then 2.0 mm) to provide adequate mixing and to remove as many roots as possible.

Table 1. Tree taxon and size (diameter at breast height, DBH, cm) from which materials for canopy organic matter were sampled at the Monteverde Cloud Forest Preserve

DBH		
Fabaceae	*Dussia macroprophyllata*	113.0
Lauraceae	*Beilschmiedia costaricensis*	89.1
Lauraceae	*Beilschmiedia costaricensis*	87.3
Lauraceae	*Beilschmiedia costaricensis*	114.2
Lauraceae	*Ocotea tonduzii*	60.1
Lauraceae	*Ocotea tonduzii*	119.0
Lauraceae	*Ocotea tonduzii*	126.2
Lauraceae	*Ocotea tonduzii*	100.1
Fabaceae	*Dussia macroprophyllata*	153.7
Moraceae	*Ficus tuerckheimii*	238.8
Moraceae	*Ficus tuerckheimii*	183.3
Moraceae	*Ficus velutina*	192.5
Myrtaceae	*Myrcia splendens*	101.3
Sabiaceae	*Meliosma vernicosa*	92.5
Sapotaceae	*Pouteria reticulata*	70.0

Analytical methods for plant and soil sample

We carried out analysis of pH on fresh material in the Monteverde laboratory. Analyses of elemental content, total exchangeable cations, base saturation, cation exchange capacity, loss-on-ignition, and total carbon (C) were carried out on air-dried samples in the soils laboratory at the University of California, Santa Barbara.

Subsamples of soils for analysis of nutrients were oven-dried at 105 °C for 24−48 h and were ground in a Wiley Mill to pass a 40 mesh screen. Total elemental composition of samples was analyzed by a modified Kjeldahl wet-oxidation procedure, using H_2O_2 and Li/Se as a catalyst (Parkinson & Allen 1975). A commercial block digester (Technicon BD-40) was used and samples were maintained at 340 °C for two hours after clearing (Nelson & Sommers 1980). Typical sample size was 300 mg and different types of samples were digested in replicates of three each to establish a precision for the procedure. Solutions of organic nitrogen (urea, niacimamide) and organic phosphorus (phytic acid) compounds were analyzed throughout the study to establish accuracy of the digestion procedure for N and P. Pre-treatment for recovery of nitrate was not incorporated in the protocol; separate analysis of NO_3 (extracted with 1 N KCL)

was performed on soils and was typically less than 3 % of total N. A modified indophenol blue colorimetric method (Keeney & Nelson 1982) and a molybdenum blue procedure (Watanabe & Olsen 1982) were used to determine ammonium and phosphate digests. Cations were analyzed on a Varian 006 atomic absorption spectrophotometer.

Soil solution pH of humus samples was determined with an Orion 904 combination electrode in a 5:1 water:soil ratio. Organic carbon was determined by Walkley-Black dichromate digestion using a correction factor of 1.3 (Nelson & Sommers 1980). Loss-on-ignition (an index of organic matter and mineral content) was by ashing in a muffle furnace at 450 °C for 3 h. Cation exchange capacity (CEC) was determined by a modified 10 % NaCl pH 2 leaching procedure on ammonium-saturated material. Exchangeable cations were determined by atomic absorption spectrophotometry in 1 N NH_4 OAc in 1 N KCL extracts (Robertson et al. 1999).

To compare nutrient content and other characteristics (elemental composition, CEC, base saturation (BS), total exchangeable cations (TEC), loss-on-ignition, and pH) between canopy and terrestrial soil samples, a one-way ANOVA was performed with the SYSTAT programming package (Systat, Inc.) with location of soil (canopy, FF-H, FF-A) as the treatment. A post-hoc Tukey test was used to differentiate differences between the treatments. Simple regression analysis was used to explore relationships between branch size and the abundance of crown humus on branches.

Results

The concentration between terrestrial and canopy soils differed significantly of N, K, and Mg, with COM having a higher elemental content (Table 2). Soil from the FF-A horizon was also significantly lower in N than the FF-H horizon. Phosphorus and Ca concentrations were comparable for upper and lower soil horizons and did not differ significantly from COM.

Canopy humus had a very low pH compared to terrestrial soils, and the FF-H horizon was significantly higher than the FF-A horizon (Table 2). The percent ash of COM

Table 2. Mean (and standard deviation) of percent carbon (% C), percent nitrogen (% N), carbon/nitrogen ratio (C/N), nutrient concentration (mg/g dry weight), pH, and percent ash (% ash) of canopy and forest floor soils at 0-10 cm (FF-H) and 10 – 20 cm (FF-A) below the surface at the Monteverde Cloud Forest Preserve, Costa Rica. Different letters for the superscript within a row indicate a significant difference at the 0.01 level. N.M. = not measured

Characteristic	Location		
	Canopy	*FF-H*	*FF-A*
%C	37.4 (1.9)[a]	27.0 (1.8)[b]	25.3 (2.7)[b]
%N	2.4 (0.1)[a]	1.4 (0.2)[a]	0.9 (0.1)[b]
C/N ratio	15.5[a]	19.2[a]	28.1[b]
P	0.7 (0.2)[a]	0.7 (0.1)[a]	0.8 (0.1)[a]
Ca	5.8 (4.0)[a]	9.5 (2.1)[a]	7.2 (1.7)[a]
K	1.4 (0.5)[a]	0.3 (0.1)[b]	0.4 (0.3)[b]
Mg	1.0 (0.5)[a]	0.6 (0.2)[b]	0.4 (0.1)[b]
pH	3.7[a]	4.6[b]	5.4[c]
% ash	4.4 (1.1)[a]	40.0 (7.8)[b]	N.M.

varied between 3 % and 6 %, which is typical for highly organic histosols. The terrestrial soils had a tenfold greater amount of extractable cations than canopy humus. There was a significant difference in % C and % N between canopy COM and the lower terrestrial soil horizon. The C/N ratios of COM and the floor upper horizon did not different significantly (Table 2).

Total exchangeable cations and cation exchange capacity of canopy humus vs. terrestrial soils were not significantly different at the 0.01 level. The canopy was particularly low in exchangeable cations and high in H^+ and Al^+ (Table 3). Therefore, although there is a high potential for nutrient retention in the interior branch mats and branch junctions, many of the cations have been displaced, and the availability of macronutrient cations to canopy biota (plant roots, invertebrates, microbes) may be very low.

There was no significant relationship between the amount (dry weight) of arboreal soil and substrate size (stem diameter) of the branches ($P < 0.05$). This is contrary to trends reported for the relationship between live epiphytes and branch substrate at this site (Ingram & Nadkarni 1993) and other forest types (Lyons et al. 2000). However, in this study, we focused on trees and substrates within trees that had the greatest amounts of DOM (inner branches of large, mature trees). Our sample may also have been biased because we were necessarily restricted to trees that were large enough and had a suitable architecture to climb safely, which meant our range of branch diameters was fairly narrow relative to those used in other studies.

Discussion

In the past, organic matter that his held in the canopy – in particular, crown humus – has rarely been considered in forest ecosystem ecology or soils studies due to its inaccessibility, the lack of rigorous sampling and extrapolation methods, and because its biomass appears small relative to total forest biomass. However, recent studies have documented numerous forest types where COM is abundant: tropical montane forests, temperate rainforests, elfin woodlands, and some lowland forests (review in Coxson & Nadkarni 1995).

This material holds ecological importance for five reasons. First, crown humus represents a repository of nutrients and carbon that is an independent but related subsystem within the forest, swelling the nutrient capital of the ecosystem as a whole. In the Monteverde forest, the mass of crown humus is estimated as 20.7 t/ha in the Monteverde forest (Nadkarni et al. 2000), which is equivalent to 62 % of the total canopy organic matter. This is equal to 4 % of the total aboveground biomass. Compared to the labile portion of the forest, it is equivalent to 220 % of the total aboveground non-woody biomass (Nadkarni et al. 2000).

Second, canopy-held soil is comprised of nutrients that are obtained and retained primarily from allochthonous sources – rain, mist, and dry deposition, i.e., sources that originate outside the system. Experimental work with marked leaves showed that the residency times for intercepted leaves (the major potential autochthonous nutrient source) is extremely short (less than 16 weeks), and so input from decomposition of intercepted leaves is negligible relative to epiphytes' nutrient needs (Nadkarni & Matelson 1991). Many epiphytes (particularly non-vascular plants and filmy ferns) are extremely efficient at capturing nutrients from mist and rain and incorporating them

Table 3. Soil characteristics of arboreal soils (CAN) and soils on the forest floor (FF-H, 0-10 cm; FF-A, 10–20 cm). Data are total exchangeable cations and cation exchange capacity (extracted in ammonium acetate, meq 100 g soil⁻¹); base saturation (%) at ambient pH, exchangeable bases (meq 100g soil⁻¹), extractable Al (Ext. Al, meq 100 g soil⁻¹), and extractable H (Ext H⁺, in KCL, meq 100 g soil⁻¹). Means are presented with standard deviations in parentheses. Different letters for the superscript within a column indicate a significant difference at the 0.05 level

Location	Total Exchangeable Cations	Cation Exchange Capacity	Percent Base Saturation	Exchangeable Bases				Ext Al	Ext H⁺
				Ca	Mg	K	Na		
CAN	15.6 [a] (6.1)	55.4 [a] (13.5)	30.1 [a] (15.3)	2.5 [a] (2.4)	1.3 [a] (1.0)	0.5 [a] (0.5)	0.4 [a] (0.05)	3.3 [a] (0.8)	7.7 [a] (4.3)
FF-H	18.9 [a] (12.1)	43.6 [a] (12.8)	98.4 [b] (3.0)	16.1 [b] (6.2)	2.1 [a] (0.9)	0.2 [a] (0.1)	0.2 [a] (0.01)	0.1 [b] (0.1)	0.2 [b] (0.1)
FF-A	11.9 [a] (2.9)	36.9 [a] (1.9)	86.9 [b] (2.1)	6.9 [b] (2.1)	1.1 [a] (0.1)	0.05 [a] (0.01)	0.2 [a] (0.01)	2.8 [a] (2.3)	0.8 [b] (0.9)

into their biomass. These epiphytic plants eventually die and decompose in place to form the bulk of the canopy soil. These mats also efficiently retain nutrients; the negatively charged sites that occur in the mats of these arboreal hisotsols represent loci where cations that arrive from atmospheric sources can be retained and held for subsequent uptake by canopy plants or microbes.

Third, the characteristics of the material, particularly the acidic nature of this substrate, may have a profound effect on within-mat nutrient dynamics. For example, the lack of nitrification in canopy mats documented by Vance and Nadkarni (1990) may be due to the low pH of the crown humus, similar to other peat-dominated soils (Bohn et al. 1985).

Fourth, these mats provide significant habitat for animals of many kinds. Entomologists have documented that the dead organic matter is inhabited by numerous and speciose invertebrates in both tropical and temperate forest canopy mats (Nadkarni & Longino 1990; Behan-Pelletier & Winchester 1998). Many of these are canopy specialists, which are never encountered on the forest floor (Longino & Nadkarni 1990). These invertebrates in turn provide food resources for birds and other arboreal vertebrates (Remsen & Parker 1984; Nadkarni & Matelson 1989).

Finally, canopy root-humus mat occurs on branch and trunk surfaces, similar to that which occurs on the forest floor. Roots that penetrate the arboreal soil may belong to either the canopy-dwelling epiphytes and/or the supporting host trees (Nadkarni 1981, Moore 1989). Experiments with canopy rooting in a tropical montane forest indicated that the presence of crown humus on branches has a significantly positive effect on the initiation and growth rates of canopy roots (Nadkarni 1994). Thus, soils of the forest canopy may thus have more ecological importance than its biomass implies, as the nutrient-retaining capacity of root-humus mat layer could play an important role in nutrient conservation for the individual trees and epiphytes imbedded within the mat, as well as for the forest ecosystem as a whole.

Acknowledgments

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