



Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica

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Abstract

Canopy-dwelling epiphytes and their associated dead organic matter exist as complex subsystems of many forests, but they have only rarely been quantified in the context of the whole ecosystem. We assessed the biomass and nutrient capital of canopy-dwelling and terrestrially rooted components of a primary and an adjacent secondary montane forest in Monteverde, Costa Rica. Total aboveground terrestrially rooted biomass (dry weight) was 490.1 and 151 t ha⁻¹ in the primary and secondary forest, respectively. The primary forest supported a total canopy biomass of 33.1 t ha⁻¹; the secondary forest supported only 0.5% of that, 0.2 t ha⁻¹. Trunk and branch epiphyte biomass in the primary forest was over 40 times and 100 times greater than trunk and branch epiphyte biomass in the secondary forest. The bulk (ca. 95%) of the ecosystem biomass is trunk and branch wood, which is slower to decompose than the non-woody, labile components of foliage and non-woody epiphytes. In contrast to the primary forest, where dead organic matter (crown humus, intercepted litterfall) comprised over 60% of the total epiphytic material, there were only trace amounts in the secondary forest. The important ecosystem roles performed by this material in the primary forest (e.g., retention of atmospheric nutrients, habitat for canopy invertebrates, and substrate for wildlife and bird foraging) are virtually absent in the secondary forest canopy.

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1. Introduction

Inventories of biomass and nutrient capital of tropical forests provide a background for understanding processes such as carbon and nutrient cycling. Estimates of biomass and nutrient pools contained within the vegetation and soils of primary and secondary tropical forests have been reported for an increasing number of primary lowland and montane sites (e.g., Vitousek

and Sanford, 1986). Canopy components, however, have only rarely been studied due to their inaccessibility to humans and because their complex structure makes statistically rigorous sampling difficult. However, canopy-dwelling epiphytes and their associated dead organic matter exist as complex subsystems of many tropical, temperate, and boreal forests (Coxson and Nadkarni, 1995). Canopy organic matter (COM) is composed of roots and shoots of vascular and non-vascular plants, abscised leaves of host trees and epiphytes that have been intercepted by branches, “crown humus” (sensu Jeník, 1973), and associated invertebrates, fungi, and microorganisms. This material

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reaches its greatest abundance and diversity in primary tropical montane cloud forests (Madison, 1977; Ingram and Nadkarni, 1993; Coxson and Nadkarni, 1995).

Live and dead components of COM form communities that are distinct from terrestrially rooted plant and forest floor soil communities, but that interact with whole-forest processes. Canopy-held organic matter influences nutrient cycling by altering ecosystem nutrient pools, pathways, and rates of nutrient fluxes (Pike, 1978; Nadkarni, 1981; Benzing and Seeman, 1978; Coxson and Nadkarni, 1995). The live components of COM contribute to nutrient exchange by exudation from and uptake by epiphyte roots and mycorrhizae (Maffia et al., 1993). Litterfall derived from epiphytes can constitute a significant portion of the nutrients and carbon transferred via the litterfall pathway (Nadkarni and Matelson, 1992a,b). Canopy organic matter can also 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., 1998). Direct transfer of nutrients from COM to terrestrially rooted vegetation can occur via host tree canopy root systems (Nadkarni, 1981; Sanford, 1987; Nadkarni and Primack, 1989). This material also provides resources for vertebrates, such as nectar for birds and pollen for rodents. Epiphytic bromeliad tanks are another aquatic subsystem, providing water for bathing and drinking for birds (Nadkarni and Matelson, 1989; Remsen and Parker, 1984).

Although COM has received some attention from botanists (Klinge, 1963; Lyford, 1969; Jeník, 1973; Nadkarni, 1981; Sanford, 1987; Moore, 1989; Putz and Holbrook, 1989), few studies have placed COM in the context of ecosystem- and landscape-level nutrient cycling (e.g., Golley et al., 1971; Pike, 1978; Pócs, 1980; Edwards, 1977; Nadkarni, 1984, 1985; Hofstede et al., 1993). Methods of quantifying this material have included subjective visual estimates (e.g., Sanford, 1987; Sugden and Robins, 1979); non-random subsampling from trees (e.g., Nadkarni, 1984, 1985) or total harvesting of a small number of large trees (e.g., Edwards, 1977).

Some previous work supports anecdotal and qualitative observations that different substrates within a tree support different amounts of COM, different functional groups, and different species of epiphytes and parasites (Frei and Dodson, 1972; Johansson,

1974; Benzing, 1995). Outer and upper crown branches tend to support smaller amounts of COM than inner branches and branch junctions, which contain the bulk of dead canopy organic matter. Humus and other dead COM components that appear to dominate on inner branches of older trees are important in nutrient cycling because they represent a large pool of carbon and nutrients which are microbially active (Vance and Nadkarni, 1990). Understanding the within-tree distribution of COM is critical to understand canopy plant communities and explain the distribution of COM-dependent organisms such as epiphytes, invertebrates, microbes, and vertebrates.

Relative to primary forests, canopy communities in secondary forests have received far less attention from ecosystem ecologists; only a very few such studies exist (e.g., Catling and Lefkovitch, 1989). None of these has placed the canopy community in the context of the terrestrially rooted material (hereafter, TM; trees, shrubs, understory plants, parasitic) with respect to ecosystem-level processes such as nutrient cycling. Rates of deforestation and conversion of tropical primary forests are increasing, and are proportionally highest in montane regions (LaBastille and Pool, 1978; Wheelwright, 2000); increasing amounts of montane forest cover are secondary, rather than primary, in nature.

In this study, we assessed the aboveground biomass and macronutrient capital of a primary and a secondary tropical lower montane forest with a focus on epiphytes and canopy-held organic matter. This study is part of an ecosystem-level study on the ecology of canopy communities and their roles in nutrient cycling and forest dynamics (Nadkarni et al., 2000). Specifically, we: (1) report the biomass, composition, and nutrient pools of seven functional groups of COM components associated with seven substrate types in a tropical lower montane forest of Costa Rica; (2) extrapolate estimates of this material to a forest stand level; and (3) discuss the implications of the presence and characteristics of COM in this forest to ecosystem-level nutrient cycling.

2. Study area

Field research was conducted from 1 December 1990 to March 1991, in the Monteverde Cloud Forest

Preserve (MCFP), Monteverde, Puntarenas Province, Costa Rica (10°18'N, 84°48'W). The study area was in tropical lower montane moist forest (1480 m) which is described as Leeward Cloud Forest (Lawton and Dryer, 1980). The continually moist soils are derived from volcanic rhyolites, and classified as *Typic Dys-trandept* (Vance and 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 the forest floor (Bohlman et al., 1995).

In April 1987, a 4-ha study area was established within the primary forest of the research area of the MCFP. This forest is composed of trees that are 15–30 m in stature, with a well-developed subcanopy. Epiphytes are extremely diverse and abundant (Ingram and Nadkarni, 1993; Nadkarni et al., 2000). Stem

density and stem diameters (>10 cm diameter at breast height, DBH) were measured and identified to species. Tree density was 555 trees/ha, with a size distribution of a reverse J-shape (Fig. 1). Tree species composition, density, basal area, and structural characteristics are reported in Nadkarni et al. (1995).

In 1989, a 1-ha research plot was established in the adjacent secondary forest, which is also within the research area of the MCFP. In the early 1960s, the area had been cleared for cattle pasture, but was left to regrow because the area was too cold and wet to be productive for agriculture. All trees were measured, identified to species, and tagged. This forest is strongly dominated (91%) by a single tree species (*Conostegia oerstediana*, Melastomataceae) (Table 1), with a density of 1124 trees/ha and a size class distribution typical of early successional montane forests (Fig. 1). The forest supports a well-developed understory, with saplings of some of the primary forest trees from the adjacent primary forest in evidence (Table 1).

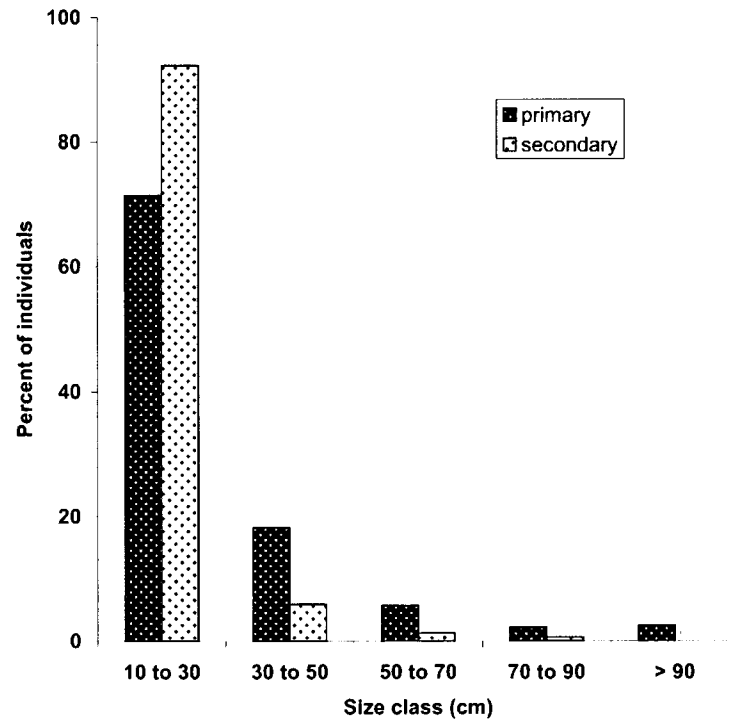


Fig. 1. Size class distribution of tree stems in the primary and secondary forest study areas of the Monteverde Cloud Forest Preserve. Total stem density in the primary forest is 555 stems/ha and in the secondary forest is 1124 stems/ha.

Table 1
Composition (percent of basal area) of trees and understory (shrubs and saplings) in the secondary forest study area (1 ha) of the Monteverde, Costa Rica

Genus and species	Family	Percent basal area	
		Trees	Understory
<i>Conostegia oerstediana</i>	Melastomataceae	90.7	52.6
<i>Heliocarpus appendiculatus</i>	Tiliaceae	4.5	n.p.
<i>Cordia cymosa</i>	Boraginaceae	0.8	n.p.
<i>Cecropia polyphlebia</i>	Cecropiaceae	0.7	n.p.
<i>Sapium oligonerum</i>	Euphorbiaceae	0.5	1.2
<i>Myrsine coriacea</i>	Myrsinaceae	0.5	n.p.
<i>Perronetia longistylis</i>	Celastraceae	0.3	0.6
<i>Hampea appendiculata</i>	Malvaceae	0.2	3.1
<i>Trema micrantha</i>	Ulmaceae	0.2	n.p.
<i>Quararibea costaricensis</i>	Bombacaceae	0.2	n.p.
<i>Ilex costaricensis</i>	Aquifoliaceae	0.2	0.3
<i>Cedrela tonduzii</i>	Meliaceae	0.2	n.p.
<i>Citharexylum viride</i>	Verbenaceae	0.2	3.7
<i>B. pendula</i>	Lauraceae	0.2	n.p.
<i>Casearia tacanensis</i>	Flacourtiaceae	0.1	0.6
<i>Chione sylvicola</i>	Rubiaceae	0.1	n.p.
<i>Daphnopsis americana</i>	Thymelaeaceae	0.1	2.4
<i>Hasseltia floribunda</i>	Flacourtiaceae	0.1	3.4
<i>Ocotea meziana</i>	Lauraceae	0.1	11.3
<i>Saurauia veraguasensis</i>	Actinidiaceae	0.1	0.3
<i>Weinmannia pinnata</i>	Cunoniaceae	0.1	3.7
<i>Zanthoxylum procerum</i>	Rutaceae	0.1	0.9
<i>Oreopanax xalapensis</i>	Araliaceae	n.p.	3.7
<i>Ardisia palmana</i>	Myrsinaceae	n.p.	2.4
<i>Nectandra salicina</i>	Lauraceae	n.p.	2.1
<i>Elaeagia auriculata</i>	Rubiaceae	n.p.	1.2
<i>Miconia brenesia</i>	Melastomataceae	n.p.	1.2
<i>Viburnum costaricanum</i>	Caprifoliaceae	n.p.	0.9
<i>Cassipourea elliptica</i>	Rhizophoraceae	n.p.	0.6
<i>Ficus velutina</i>	Moraceae	n.p.	0.6
<i>Prunus cornifolia</i>	Rosaceae	n.p.	0.6
<i>Cinnamomum cinnamomifolium</i>	Lauraceae	n.p.	0.3
<i>Clethra</i> sp.	Clethraceae	n.p.	0.3
<i>Clusia palmana</i>	Clusiaceae	n.p.	0.3
<i>Inga mertoniana</i>	Fabaceae	n.p.	0.3
<i>Tovomotopsis psychotriifolia</i>	Clusiaceae	n.p.	0.3

For trees, all stems >10 cm in the whole hectare were included. For the understory, all woody stems (2–10 cm DBH) in seven quadrats (9 m²) were measured. n.p.: not present in that category.

3. Materials and methods

3.1. Biomass sampling for canopy organic matter

Because COM occurs on many different substrates in differing amounts, we developed multiple sampling strategies to capture the amount, composition, and variability of materials on different surface types, on different tree sizes, and in the two different forest

types. We developed our sampling protocol to reduce destructive effects, while still characterizing COM distribution. For certain substrates, our sampling methods differed between the primary and secondary forests because of the lack of canopy access into the secondary forest trees and the much larger and more variable amounts of COM in the primary forest.

Choice of sample trees was critical, as the amount of COM appears to vary with tree size, tree species,

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and location within forest. In the primary forest, we gained access to COM both by climbing and sampling within trees, and by climbing trees and cutting and lowering branches to the forest floor. In the secondary forest, trees are small, with weak limbs, and so we sampled COM by cutting whole trees and gently lowering them to the forest floor. We stratified our sampling of trees into two size classes: large trees (>30 cm DBH in the primary forest and >20 cm DBH in the secondary forest) and small trees (10–30 cm DBH in the primary forest and 10–20 cm DBH in the secondary forest).

In the primary forest, before climbing, we assigned a quartile “climbability index” (1 = not climbable, 4 = easily climbable) to all trees in our plot, based on their size, architecture, and branch strength. We also assigned a qualitative “epiphyte index” to each tree (1 = no epiphytes; 4 = heavily covered) to all large trees in the primary forest site. Two observers rated a 10% subset of the 1440 trees in our plots and had over 90% calibration of the ratings. Climbable trees constituted about one-third of the trees (climbability index of 3 and 4 were 16 and 17%, respectively). Epiphyte load class was distributed on trees fairly evenly (epiphyte ratings of 1 (39%), 2 (31%), 3 (34%) and 4 (20%)).

Of those with a climbability index of 3 or 4, we selected an initial random subset (16 individuals for sampling of trunk, branch junction, inner branch, main branch, and tip substrates). This selection process may have biased our results toward an overestimate of epiphyte biomass, as we necessarily focused on large trees with strong branches since those are ones with high climbability. However, our sample trees included all four epiphyte indices in equal proportions. Also, other trees were chosen for destructive sampling of branch substrates (see below) were chosen regardless of climbing index. All trees that were climbed were ascended with single-rope techniques (Perry, 1978). These trees included representatives of the most common genera in the forest (Nadkarni et al., 1995) (Table 2).

A random subsample of nine of these trees with the full range of epiphyte loads were chosen for destructive sampling of branch systems. Below each of these trees, a small area was cleared with machetes. A professional arborist climbed into the crown and made a sketch of all major branch systems, depicting

Table 2

Tree taxon and diameter at breast height (DBH, cm) from which materials for canopy organic matter was sampled in the primary and secondary forest study areas, Monteverde Cloud Forest Preserve

Family	Genus and species	DBH
Primary forest		
Fabaceae	<i>Dussia macrophyllata</i>	93.2
Fabaceae	<i>Dussia macrophyllata</i>	89.3
Flacourtiaceae	<i>Hasseltia floribunda</i>	13.4
Flacourtiaceae	<i>Hasseltia floribunda</i>	22.2
Icacinaceae	<i>Calatola costaricensis</i>	22.1
Lauraceae	<i>B. pendula</i>	89.8
Lauraceae	<i>B. pendula</i>	114.0
Lauraceae	<i>Ocotea tonduzii</i>	60.9
Lauraceae	<i>Ocotea tonduzii</i>	119.1
Lauraceae	<i>Ocotea tonduzii</i>	126.1
Lauraceae	<i>Ocotea tonduzii</i>	100.6
Lauraceae	<i>Persea americana</i>	23.5
Moraceae	<i>Ficus tuerckheimii</i>	83.4
Moraceae	<i>Ficus crassiuscula</i>	192.5
Myrsinaceae	<i>Ardisia costaricensis</i>	29.2
Myrtaceae	<i>Myrcia splendens</i>	76.9
Rubiaceae	<i>Coussarea austin-smithii</i>	22.4
Rubiaceae	<i>Guettarda poasana</i>	17.9
Sabiaceae	<i>Meliosma vernicosa</i>	72.2
Sabiaceae	<i>Meliosma vernicosa</i>	92.3
Sapindaceae	<i>Matayba oppositifolia</i>	101.0
Moraceae	<i>Ficus tuerckheimii</i>	238.5
Sapotaceae	<i>Pouteria fossicola</i>	70.7
Tiliaceae	<i>Mortiodendron costaricense</i>	19.9
Verbenaceae	<i>Citharexylum donnell-smithii</i>	26.6
Secondary forest		
Melastomataceae	<i>Conostegia oerstediana</i>	16.6
Melastomataceae	<i>Conostegia oerstediana</i>	20.5
Melastomataceae	<i>Conostegia oerstediana</i>	21.5
Melastomataceae	<i>Conostegia oerstediana</i>	11.8
Melastomataceae	<i>Conostegia oerstediana</i>	11.1
Melastomataceae	<i>Conostegia oerstediana</i>	10.1
Melastomataceae	<i>Conostegia oerstediana</i>	24.2
Melastomataceae	<i>Conostegia oerstediana</i>	22.6
Melastomataceae	<i>Conostegia oerstediana</i>	29.6

approximate branch angle, estimating length of branch, and numbering the major branch systems. Of all branches that could be cut and lowered safely, with a minimal amount of damage upon lowering, three were selected for removal. A lowering cord was placed within the same tree or a neighboring tree, and a tag line was attached to guide the branch to the ground. Using a hand and/or small chain saw, the branch was cut close to the junction with the trunk and carefully lowered to the forest floor with the help of a

ground crew. The loss of epiphytes during the descent was minimal; very little fell off the branch. The branch was maneuvered to an upright position on the forest floor for sampling.

In the secondary forest, we chose a random sample of nine trees, all of which were the dominant species (five large, four small) (Table 2). Ropes were attached to the uppermost portion of the trunk by the arborist, which were then attached to pulleys on adjacent trees. The whole trees were then cut at the base, and lowered gently to the ground.

We stratified the types of surfaces upon which COM occurs as seven substrate types: (1) trunks, (2) junctions of major branches and trunks, (3) inner branches, (4) main branch systems, (5) branch tips, (6) subcanopy plants (trees, saplings, and shrubs 2–10 cm DBH), and (7) understory (plants <3 m in height). Different substrates required different protocols for sampling. Two of the substrates (inner branches and branch junctions) were relevant only to the primary forest, as the secondary forest branch junctions and inner branches supported sparse COM communities and ones which were not distinct from the trunk or outer branches.

(a) *Trunk*. For the primary forest, we placed a rope close to the top of the tree and a climber descended along the bole using a rope anchored at the top of the trunk. Starting at the top of the bole, the climber took a 20 cm wide cylindrat encircling the trunk at 3 m intervals until reaching the forest floor. All epiphytic material within 20 cm of the trunk, including DOM and vines were taken. We measured the diameter at the midpoint of the cylindrat after we removed the COM. For small trees in the primary forest and all trees in the secondary forest, tree trunks were sampled in the same way as the large trees, except that trunks were horizontal on the ground, rather than vertical.

(b) *Branch junctions*. In the primary forest, we randomly selected two to four major accessible branch–branch or branch–trunk bifurcations (branches that had a diameter at the trunk junction of >20 cm) in the upper crowns of the sample trees. We cut cores (ca. 10 cm × 15 cm × 25 cm) into the humus pocket of humus and roots with a soil knife. We also estimated the total

volume (length × width × depth) for all of the accessible branch junctions (2–10 per tree). A total of 19 branch junctions from 8 trees were sampled.

(c) *Inner branches*. In the primary forest only, on the same branches that were adjacent to the branch junctions, we cut cylindrats of COM from branch segments (12–15 cm in length) around the entire branch. All material was bagged and separated in the lab. A total of 53 branch segments from 8 trees were sampled.

(d) *Main branch systems*. In both forests, the branches that were cut and lowered were measured and divided into three (inner, middle, and outer). We removed a 20 cm swath of COM from each meter length of 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 middle of each segment. We took these segments to the lab for processing. The COM on the rest of the lowered branches was removed and weighed fresh in the field. We sampled 3 branches from each of 18 trees (9 large, 9 small) in the primary forest and 3 branches from each of 9 trees (5 large, 4 small) in the secondary forest.

(e) *Branch tips*. In both forests, we collected COM from three of the trees from which branches had been cut and lowered to the ground. From each of the three cut branches, nine “branch tips” were randomly selected. Branch tips were defined as the branch segment between the distal end of the branch system and the segment location that had a diameter of 1 cm. We cut the segment at the point, and from the base of the cut tip, we measured a 15 cm segment, which was placed in a clean plastic bag and taken to the lab for removal of all COM. A total of 81 tips were sampled in each of the primary and secondary forest.

(f) *Subcanopy vegetation*. In both forests, we established subplots (9 m², 20 in the primary forest, 8 in the secondary forest) to sample the COM and terrestrially rooted plant material. Treelets and shrubs between 2 and 10 cm in diameter were cut. All epiphytic material was removed and brought to the lab for processing.

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(g) *Understory vegetation.* In both forests, we established subplots (1 m², 16 subplots in the primary and 10 in the secondary forest) from which all the aboveground plant material below 2 m in height was taken. All COM was removed and taken to the lab for processing.

Harvested materials from each substrate type were separately bagged, and transported to the field laboratory. We separated all the entire samples into components to determine the composition of the mats. We used subsets of each sample to derive a fresh/dry weight ratio. Each sample from the first five substrates was separated into seven components: epiphytic higher vascular plant stems, leaves, roots, reproductive parts, ferns, cryptogams (bryophytes and lichens), and dead organic matter (DOM, crown humus and intercepted detritus); samples from subcanopy and understory vegetation were separated into epiphyte leaves, epiphyte stems, and DOM. Each component from each sample was oven-dried and weighed. Subsamples were ground and transported to the USA for nutrient analysis.

3.2. Terrestrially rooted material (TM) biomass sampling

We measured the mass of components of TM on the same trees for which we sampled COM components. TM was partitioned into four components: (1) tree trunk wood, (2) branch wood, (3) foliage, and (4) reproductive parts. A total of 30 subsamples of trunk and branch wood (in the form of disks or “cookies” of wood, 5–10 cm in length) were taken from 15 trees to assess wood density. These were measured for volume, and then the whole pieces were oven-dried and weighed to encompass both sapwood and heartwood (Harmon et al., 1986). Parasites (mistletoes), which derive their nutrients and water from terrestrially rooted plants, were also included in the TM category. Subcanopy and understory biomass of materials rooted in the ground were measured in the same plots used for determination of subcanopy and understory COM components. Materials were weighed fresh in the field, dried in the lab, and analyzed as for COM. The forest floor was considered to be part of the soil and was not assessed in this study. The biomass and nutrient capital of soil and roots are reported elsewhere (Vance and Nadkarni, 1992).

3.3. Analytical methods for plant and soil samples

Subsamples of plants and organic matter for biomass and nutrient analysis were oven-dried at 80 °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 H₂O₂ and Li/Se as a catalyst (Parkinson and Allen, 1975). A block digester (Technicon BD-40) was used and samples were maintained at 340 °C for 2 h after clearing (Nelson and Sommers, 1980). Typical sample size was 300 mg and different types of samples were digested in triplicates to establish the precision for the procedure. Solutions of organic nitrogen (urea, niacinamide) and organic phosphorus (phytic acid) compounds were analyzed throughout the study to establish accuracy of the digestion procedure for N and P. A modified indophenol blue colorimetric method (Keeney and Nelson, 1982) and a molybdenum blue procedure (Watanabe and Olsen, 1982) were used to determine ammonium and phosphate digests. Cations were analyzed on a Varian 600 atomic absorption spectrophotometer.

3.4. Ecosystem-level estimates of COM and TM

To extrapolate biomass from a branch- and tree-level to a stand-level basis, we counted or estimated the number of branches of our sample trees and trees in their immediate vicinity. From either the canopy of the climbed sample trees, or the forest floor below sample trees, we counted the number of major branch systems (i.e., congruent with the branch systems that we sampled). A total of 96 branches in 46 trees in the primary forest and 85 branches in 22 trees in the secondary forest were counted.

We then visually estimated the total branch length (to the nearest 2 m), the length of inner branch (to the nearest 2 m), and the circumference (to the nearest 0.5 m) on all visible branches on the sample trees, and all the visible surrounding trees within 25 m. Two observers practiced assessing branch length using 23 branches that we had previously measured, so we were confident we could assess branch lengths and diameters at this scale. From these counts, we calculated the total surface area of branches, the surface area of inner branches, and the number of branch junctions per tree. These estimates were multiplied by the

biomass estimates of COM on the different substrates (inner branch, main branch, and branch junction) for each epiphyte class load to extrapolate to whole-tree estimates of COM biomass. This estimate was multiplied by the mean density of trees in the same size class (small or large) and epiphyte load class to calculate a whole-forest estimate of biomass. Because the number of trees that represented each epiphyte load class was small, we report biomass values that were averaged over all epiphyte load classes. We used the analogous process to extrapolate TM components to an area basis. Subcanopy and understory biomass were calculated by multiplying values from our sample plots to an area basis.

4. Results

4.1. Composition, distribution, and biomass of canopy organic matter

In the primary forest, the majority of mass of COM was DOM (63%). Bryophytes and roots comprised

similar amounts (12 and 15%, respectively). Epiphyte reproductive parts, stems, leaves, and ferns made up a very small proportion (<10% total) of the total (Table 3). In contrast, the secondary forest biomass of COM was heavily dominated by bryophytes (95%), with only small amounts of DOM (3%), and trace amounts of the other components (Table 3).

In the primary forest, the greatest proportion of COM was located in the branch junctions, followed by branches and trunks, with only very small amounts on branch tips, the subcanopy, or the understory. In contrast, branches supported the greatest amount of COM in the secondary forest, with a substantial amount of COM (ca. 30%) on the subcanopy and understory components (Table 3).

Different substrates supported different proportions of COM components. In the primary forest, branch junction COM was comprised exclusively of DOM and roots. In contrast, branch tips, subcanopy, and the understory substrates supported only bryophytes. Trunk cover was diverse in terms of COM components, and was dominated by vascular plants and bryophytes, with relatively little associated dead

Table 3
Biomass (kg ha⁻¹) of canopy organic matter components on substrates in the primary and secondary forest study area of the Monteverde Cloud Forest Preserve, based on destructive sampling

Substrate	COM component						
	BRY	DOM	EPS	EPL	EPRO	EPREP	FERN
Primary forest							
On trunks	482	498	1590	155	222	3	43
On branch junctions	0	18600	0	0	3800	0	0
On inner and outer branches	3235	1646	465	506	1222	0	198
On branch tips	200	0	0	0	0	0	0
On subcanopy	120	0	0	0	0	0	0
On understory	21	1	0	1	0	0	0
Total primary	4058	20745	2055	662	5244	3	241
Secondary forest							
On trunks	12	0.6	0.6	0.2	0.1	0	0.1
On branch junctions	0	0	0	0	0	0	0
On branches	103	3.1	0	0.4	0.4	0	0
On branch tips	0	0	0	0	0	0	0
On subcanopy	43	1	0	0	0	0	0
On understory	6	0	0	0	0	0	0
Total secondary	115	3.7	0.6	0.6	0.5	0	T

BRY: bryophytes and lichens; DOM: dead organic matter (crown humus, dead leaves); EPS: epiphyte stems; EPL: epiphyte foliage; EPRO: epiphyte roots; EPREP: epiphyte reproductive parts (flowers and fruits); FER: ferns. T: trace (<0.01%). See text for sample size for each component.

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organic matter. In the secondary forest, there was little differentiation between trunks and branches with respect to COM composition, since the community was so strongly dominated by bryophytes (Table 3). Substrate dimensions within substrate groups (as indicated by diameter measurements) did not appear to be an important determinant of the total amount of COM present on any of the surfaces (primary and secondary forest tree trunks and branches), as regressions between stem diameter and the amount (dry weight) of COM biomass were not significant ($P > 0.05$).

The biomass of COM on all tree substrates was much greater in the primary than the secondary forest. On a substrate-area basis, trunk and branch epiphyte biomass in the primary forest was over 40 times and 100 times greater than trunk and branch epiphyte biomass in the secondary forest, respectively

Table 4

Biomass (S.D.) of COM on tree substrates in the primary and secondary forest study areas in Monteverde, Costa Rica

Substrate	Forest type	
	Primary	Secondary
Trunks (g dm^{-2})	223.3 (114.2)	5.0 (1.3)
Branch junctions (g dm^{-3})	67.9 (9.5)	NR
Inner branches (g m^{-2})	2421.1 (2311.0)	NR
Main branches (g m^{-2})	2450.0 (670.3)	21.7 (9.9)
Branch tips (g per tip)	0.3 (0.5)	T

Values were averaged over all epiphyte load classes. T: trace; NR: not relevant.

(Table 4). On a whole-forest basis, the primary forest supported a total COM biomass of 33.1 t ha^{-1} (Table 5). The secondary forest supported only 0.5% of that, at 0.2 t ha^{-1} (Table 6).

Table 5

Aboveground biomass (t ha^{-1}) and nutrient capital (kg ha^{-1}) contained in canopy organic matter and terrestrially rooted material in the primary forest study area of the Monteverde Cloud Forest Preserve

	Biomass	N	P	Ca	K	Mg
Canopy organic matter						
On trunks	3.0	41.9	2.2	35.9	23.0	3.9
On branch junctions	22.4	305.0	13.5	112.0	76.9	25.8
On branches	7.3	85.9	5.1	42.9	49.5	12.8
On branch tips	0.2	2.6	0.2	0.9	1.4	0.3
On subcanopy	0.1	2.7	0.1	1.6	0.7	0.2
On understory	T	0.5	0.1	0.4	0.5	0.1
Total COM	33.1	438.7	21.1	193.7	152.0	43.1
Terrestrially rooted material						
Tree trunk wood	418.8	2847.8	167.5	2931.6	3476.0	879.5
Tree branch wood	60.0	624.0	42.0	702.0	372.0	84.0
Tree foliage*	6.5	149.5	7.1	63.1	69.6	19.5
Tree reproductive parts*	0.2	4.1	0.5	1.2	2.9	0.4
Parasites*	0.2	2.3	0.2	1.4	1.1	0.3
Subcanopy stems	1.7	37.8	2.2	17.0	21.0	4.2
Subcanopy foliage*	0.2	5.4	0.4	2.6	3.0	0.6
Understory stems	1.9	49.4	1.9	20.9	41.8	5.7
Understory foliage*	0.5	19.5	1.0	10.0	13.5	3.0
Total TM	490.0	3739.8	222.8	3055.0	4000.9	997.2
Total ecosystem	523.1	4178.3	243.9	3248.7	4152.9	1040.3
Non-woody TM	7.6	180.8	9.2	78.3	90.1	23.8
%COM/total ecosystem	6.3	10.5	8.6	5.9	3.7	4.1
%COM/non-woody	435.5	242.6	229.3	247.4	168.7	181.1

Non-woody terrestrial material is foliage, reproductive parts, herbaceous vegetation, and parasitic plants. Percentages of epiphytic material as part of the forest are calculated as (1) the proportion of epiphytic material to the total aboveground ecosystem (TM + COM totals) and (2) the proportion of COM to non-woody TM components (indicated with an asterisk). T: trace ($<0.1 \text{ kg ha}^{-1}$).

Table 6

Aboveground biomass (kg ha^{-1}) and nutrient capital (kg ha^{-1}) contained in canopy organic matter and terrestrially rooted material TM [trees, parasites, subcanopy (saplings and shrubs, DBH = 2–10 cm), and understory (vegetation <3 m tall)] in the secondary forest study area of the Monteverde Cloud Forest Preserve

Material	Biomass	N	P	Ca	K	Mg
Canopy organic matter						
On trunks	13	0.2	T	0.1	0.1	T
On branch junctions	0	0	0	0	0	0
On branches	108	1.7	0.1	0.8	1.1	0.2
On branch tips	0	0	0	0	0	0
On subcanopy	44	0.6	0.1	0.7	0.2	0.1
On understory	6	0.1	T	T	T	T
Total COM	171	2.6	0.3	1.6	1.4	0.3
Terrestrially rooted material						
Tree trunk wood	126500	366.8	25.3	948.7	417.4	75.9
Tree branch wood	17230	99.9	5.2	492.8	53.4	18.9
Tree foliage*	2657	42.0	2.7	55.3	28.9	7.4
Tree reproductive parts*	54	0.8	0.1	0.7	0.4	0.1
Parasites*		T	T	T	T	T
Subcanopy stems	2815	14.4	0.3	25.3	5.6	2.8
Subcanopy foliage*	79	1.2	0.1	1.4	0.5	0.5
Understory stems	1923	25.0	1.9	19.2	30.8	3.8
Understory foliage*	597	16.7	1.2	13.1	11.9	2.4
Total TM	151855	566.8	36.8	1556.5	548.9	111.8
Total ecosystem	152026	569.4	37.1	1558.1	550.3	112.1
Total non-woody TM	3387	60.7	6.9	70.5	41.7	10.4
% COM/total ecosystem	0.1	0.1	0.1	0.1	0.2	0.3
%COM/non-woody TM	5.1	4.3	4.3	2.3	3.4	2.9

Percentages of epiphytic material as part of the forest are calculated as (1) the proportion of epiphytic material to the total aboveground ecosystem (terrestrially rooted + epiphytic totals) and (2) the proportion of epiphytic material to non-woody terrestrially rooted components. T: trace ($<0.1 \text{ kg ha}^{-1}$).

4.2. Composition, distribution, and biomass of TM

In the primary forest, total aboveground terrestrially rooted biomass was 490.1 t ha^{-1} , of which 85% was trunk wood and 12% was branch wood; other constituents made up only 3% (Table 5). The non-woody constituents (foliage, reproductive parts, and parasites) contain the most labile (readily decomposed) portions, and constituted 9.3 t ha^{-1} (2%) of the terrestrially rooted aboveground biomass. In the secondary forest, total aboveground biomass was ca. 151 t ha^{-1} (Table 6). The primary and secondary forests had similar proportions of biomass allocated to different components (Fig. 2).

4.3. Nutrient content of COM and TM

Nutrient concentrations of the different components were generally similar for the primary and secondary

forests, although DOM and epiphyte leaves were higher in N and P than in the secondary forest, and several components had higher Ca in the secondary forest (Table 7). In both forest types, DOM and epiphyte leaves had the highest nutrient concentrations of all the COM components. For all components, the subcanopy and understory COM and TM components were higher in concentration than overstory COM and TM. In the secondary forest, tree leaves were much richer in all elements than leaves of epiphytes; in the primary forest, this was true for N and P, but not Ca, K, or Mg (Table 7).

In both forests, the nutrient capital contained in COM and TM components followed the pattern of biomass. The majority of nutrients were found in branch junctions, followed by branches and on trunks, with only small amounts on branch tips, the subcanopy, and the understory (Tables 5 and 6). The terrestrially rooted component with the greatest pool of

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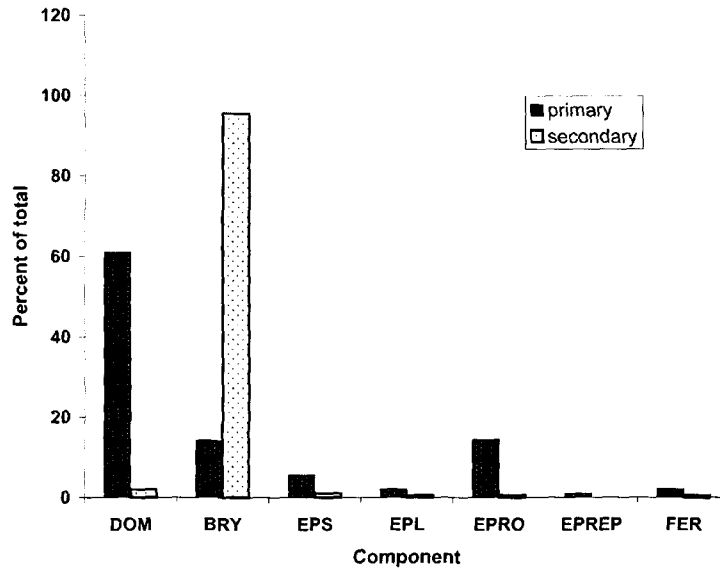


Fig. 2. Percent of total aboveground terrestrially rooted biomass by ecosystem component in the primary and secondary forest study areas of the Monteverde Cloud Forest Preserve. TW: trunkwood; BW: branchwood; TF: tree foliage; TR: tree reproductive parts; PA: parasites; SS: subcanopy stems; SF: subcanopy foliage; US: understory stems; UF: understory foliage.

nutrients was trunk wood, followed by branch wood, tree foliage, ground cover, understory wood, reproductive parts, and parasites.

5. Discussion

This is one of the few studies that has combined within-canopy sampling and ground-level sampling of intact branches with whole-forest extrapolation of COM. Our methods of assessment revealed several surprising patterns of distribution within the canopy. First, the branch junctions of the primary forest support a unique COM community in that they are dominated by dead organic matter and epiphyte roots, but is lacking entirely in live vascular plants. Inner and outer branches, however, support one-tenth the biomass of branch junctions, but four times and five times the amount of epiphyte stems and leaves, respectively. This indicates that epiphytes exploit resources along multiple microhabitats of the canopy, with the photosynthetic apparatus of these plant communities occupying regions that get greater amounts of sunlight, and their roots occupying regions that support pools of nutrients and material of high water retention capacity. We also learned that the branch junctions do not

support bryophytes, which was surprising, because mosses and liverworts in other ecosystems and other ecosystem locations can live in conditions of low light, low acidity, and high organic matter content that we documented in these branch junctions. Further investigations that could involve transplanting bryophytes or measuring the microbial populations of these microsites, will be needed to explain this pattern.

This is one of the very few studies that has placed COM in the context of all aboveground biomass and nutrient capital for the same study area. The proportion of biomass and nutrients contained in COM compared to aboveground biomass in both the primary and secondary forest is small (6 and 0.1%, respectively, Tables 5 and 6). However, the bulk (ca. 95%) of the aboveground biomass is trunk and branch wood, which is slower to decompose than the labile ecosystem components. If the biomass of COM in the primary forest (33.1 t ha^{-1}) is compared to the labile (non-woody) components of TM (sum of tree foliage, reproductive parts, parasites, and subcanopy and understory foliage, 7.6 t ha^{-1} , Table 5), then the ratio of COM to TM is very different (4.4:1). In the secondary forest (Table 6), this ratio of COM biomass (171 kg ha^{-1}) to TM labile biomass (3387 kg ha^{-1}) was only 0.05:1.

Table 7
Mean (S.D.) nutrient concentrations (%) for canopy organic matter and terrestrially rooted materials in the primary and secondary forest sites of the Monteverde Cloud Forest Reserve, Costa Rica

Components	Nutrient				
	N	P	Ca	K	Mg
Primary forest					
Canopy organic matter					
DOM	1.6 (0.4)	0.07 (0.01)	0.6 (0.2)	0.3 (0.02)	0.1 (0.01)
BRY	1.4 (0.2)	0.08 (0.01)	0.5 (0.1)	0.7 (0.1)	0.1 (0.02)
EPST	0.7 (0.1)	0.06 (0.02)	0.9 (0.3)	0.7 (0.8)	0.2 (0.04)
EPLV	1.4 (1.0)	0.09 (0.1)	1.3 (0.4)	1.6 (0.8)	0.4 (0.01)
EPRO	0.9 (0.2)	0.06 (0.01)	0.7 (0.2)	0.7 (0.1)	0.2 (0.02)
EREP	1.3 (0.1)	0.1 (0.2)	0.5 (0.1)	0.6 (0.001)	0.1 (0.01)
FER	1.2 (0.3)	0.09 (0.04)	1.0 (0.2)	1.7 (0.7)	0.4 (0.01)
Terrestrially rooted material					
TRWD	0.7 (0.1)	0.04 (0.01)	0.7 (0.2)	0.8 (0.3)	0.2 (0.1)
BRWD	1.0 (0.4)	0.07 (0.02)	1.2 (0.3)	0.6 (0.2)	0.1 (0.01)
TLVS	2.3 (0.7)	0.1 (0.03)	1.0 (0.2)	1.1 (0.2)	0.3 (0.03)
TREP	2.1 (0.9)	0.25 (0.2)	0.6 (0.3)	1.5 (1.1)	0.2 (0.2)
PARA	1.1 (0.1)	1.1 (0.7)	0.7 (0.3)	0.6 (0.2)	0.1 (0.01)
Secondary forest					
Canopy organic matter					
DOM	1.5 (0.04)	0.06 (0.001)	0.9 (0.02)	0.6 (0.2)	0.2 (0.01)
BRY	1.4 (0.34)	0.06 (0.02)	0.9 (0.4)	1.0 (0.4)	0.2 (0.05)
EPST	0.8 (0.2)	0.06 (0.01)	1.8 (1.0)	2.0 (0.4)	0.2 (0.1)
EPLV	0.9 (0.3)	0.06 (0.01)	0.7 (0.04)	1.1 (0.8)	0.2 (0.002)
EPRO	1.0 (0.9)	0.09 (0.01)	1.4 (0.3)	1.1 (0.6)	0.3 (0.1)
FER	1.2 (0.2)	0.1 (0.1)	1.0 (0.03)	1.3 (0.7)	0.3 (0.1)
Terrestrially rooted material					
TRWD	0.3 (0.1)	0.02 (0.01)	0.8 (0.2)	0.3 (0.01)	0.1 (0.02)
BRWD	0.6 (0.6)	0.03 (0.1)	2.1 (0.1)	0.3 (0.09)	0.1 (0.1)
TLVS	1.6 (0.7)	0.10 (0.06)	2.1 (0.2)	1.1 (0.7)	0.3 (0.2)
TREP	1.5 (0.4)	0.1 (0.1)	1.2 (0.3)	0.8 (0.2)	0.1 (0.01)
Subcanopy					
Canopy organic matter					
DOM	2.3 (1.2)	0.10 (0.3)	1.3 (0.3)	0.6 (0.1)	0.2 (0.03)
BRY	2.5 (0.4)	0.2 (0.1)	0.8 (0.1)	1.1 (0.3)	0.2 (0.2)
EPST	2.5 (1.3)	0.09 (0.03)	1.1 (0.7)	1.3 (0.6)	0.5 (0.3)
Terrestrially rooted material					
TRWD	1.8 (0.5)	0.1 (0.03)	0.8 (0.3)	1.0 (0.7)	0.2 (0.01)
TLVS	2.7 (1.0)	0.3 (0.2)	1.3 (0.7)	1.5 (0.2)	0.3 (0.1)
Understory					
Canopy organic matter					
DOM	1.9 (0.2)	0.20 (0.03)	1.5 (0.9)	2.1 (0.3)	0.3 (0.01)
Terrestrially rooted material					
TRWD	1.8 (0.2)	0.1 (0.001)	1.1 (0.04)	2.2 (0.8)	0.2 (0.1)
TLVS	3.9 (0.7)	0.3 (0.1)	2.0 (0.3)	2.7 (0.2)	0.6 (0.03)

DOM: dead organic matter, BRY: bryophytes and lichens, EPST: epiphyte stems; EPLV: epiphyte leaves; EPRO: epiphyte roots; EPREP: epiphyte reproductive parts (flowers, fruits); FER: ferns; TRWD: tree trunk wood; BRWD: tree branch wood; TLVS: tree leaves; TREP: tree reproductive parts; PARA: parasites. Subcanopy includes small trees, shrubs, and saplings (2–10 cm DBH); understory includes plants <3 m tall.

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The amount and composition of COM in the secondary forest compared to the primary forest is very striking. The biomass of COM in the secondary forest is only 0.5% of that estimated for the primary forest, and this material is dominated by bryophytes. In contrast to the primary forest, where DOM comprises over 60% of the total COM (Fig. 2), there are only trace amounts of DOM in the secondary forest. The important ecosystem roles performed by DOM in the primary forest, such as retention of atmospheric nutrients, providing habitat for canopy invertebrates, and creating habitats for wildlife and bird foraging, are absent in the secondary forest canopy.

Many studies have shown striking differences between primary and secondary forests in the composition and diversity of arboreal organisms, which may be explained by their responses to differences in structure or resource availability among habitats. For example, some ant taxa such as *Pheidole* may be especially sensitive to disturbance and thus serve as effective indicator taxa; the diversity of their populations is significantly reduced in heavily logged habitat (Alonso and Agosti, 2000). Other taxa (*Procryptocerus bates*, *P. mayr*, *Camponotus* spp. and *Lepthorax* spp.) were found in primary forest and pasture samples, but they were absent from secondary forest, which lacks the large epiphyte mats in which they nest (Schonberg et al., in press). The lack of DOM in secondary forests may also restrict the presence of canopy-foraging birds that use mats of DOM for most or all of their foraging effort (e.g., Ochraceous Wren, Spotted Barbtail) (Nadkarni and Matelson, 1989).

Canopy organic matter has been considered only infrequently in forest ecosystem studies due to its inaccessibility, and because its biomass appears small relative to total forest biomass. The results of this study indicate that the canopy subsystem holds a substantial pool of nutrients, especially when compared to the labile components of the forest ecosystem. COM should be considered in future studies of montane forest ecosystems.

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