

MICROBIAL BIOMASS AND ACTIVITY IN CANOPY ORGANIC MATTER AND THE FOREST FLOOR OF A TROPICAL CLOUD FOREST

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(Accepted 15 January 1990)

Summary—In some tropical forests, organic matter derived from epiphytic plants accumulates as mats on tree branches. Microbial characteristics relating to the cycling of C and N were studied in this canopy organic matter (COM) and in the forest floor of a tropical montane forest in Costa Rica. COM was found to have high microbial activity which was, in general, similar to the forest floor H (FF-H) horizon. The concentration of microbial biomass C was 2650, 2670 and 1950 $\mu\text{g g}^{-1}$ soil in COM, FF-H and FF-AI, respectively. Biomass N, laboratory CO_2 evolution and laboratory N mineralization were also higher or similar for COM relative to the forest floor.

In contrast to the H and AI horizons of the forest floor, nitrification was not detectable or only very low in COM during laboratory and field incubations. The potential for denitrification, as evidenced by the decline in added NO_3^- relative to NH_4^+ during laboratory incubation, was higher in the forest floor than in the canopy.

Microbial respiration and biomass in COM and the forest floor responded more to C (as glucose) than N (as NH_4NO_3) amendments. Microbial immobilization of added N appeared to be higher in the forest floor than in COM, although the microbial population in all materials readily immobilized inorganic N in the presence of glucose.

The total pool of COM in this forest is estimated to be between 1000 and 2000 kg ha^{-1} . From this, a preliminary estimate of 0.7 kg ha^{-1} of N immobilized in microbial tissue can be calculated. Because of their high biomass and activity, microorganisms in the canopy could be important in regulating N availability in this forest.

INTRODUCTION

Tropical montane forests typically occur at high elevations where cool, moist conditions predominate (Hartshorn, 1983). This environment results in large accumulations of organic matter and associated plant nutrients in the forest floor relative to most lowland tropical forests due to slowed microbial decomposition (Grubb, 1977). Consequently, although soils under montane forests may have a high nutrient capital, the availability of nutrients, particularly N, is often low and limiting to the productivity of these forests (Edwards, 1982; Edwards and Grubb, 1982; Grubb, 1977; Marrs *et al.*, 1988; Vitousek and Matson, 1988).

Another characteristic of many mid to high elevation tropical forests is their high diversity and biomass of epiphytic plants which survive because of moist conditions in tree canopies (Nadkarni, 1984; Gentry and Dodson, 1987). As these epiphytes die and decompose they form mats of organic material on tree branches (Jenik, 1973). These organic matter mats in the canopy have been found to provide an environment for roots of host trees as well as epiphytic plants (Nadkarni, 1981). Although it has

rarely been studied, organic matter held within the canopy may be an important component of the nutrient cycling characteristics of such forests by trapping and transforming nutrients that are deposited in mist, rain and plant litter.

Since nutrient availability has been found to be low in montane forests, a central question relating to the significance of canopy organic matter (COM) is how it acts as a source of nutrients for plants, either directly to epiphytic plants and host trees with roots in the canopy, or by contributing nutrients to the forest floor via throughfall or stemflow. An early step in this assessment is to determine whether COM is microbially active, and what role microorganisms might play in conserving and transforming C and N inputs in the canopy relative to the forest floor below. Our purpose was to describe some general characteristics of microbial biomass and activity in COM and the forest floor of a tropical montane forest in Costa Rica.

MATERIALS AND METHODS

Study site

The study area was a tropical lower montane wet forest located at the Monteverde Cloud Forest Reserve in west-central Costa Rica (10 18'N, 84 48'W). The site was a leeward cove forest (Lawton and Dyer, 1980) (1550 m elevation) on the continental divide with wind and moisture derived from both the Caribbean and Pacific Oceans. Because of high

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moisture (ca 2000 mm annually) and nutrient input from mist and rain, the trees in this forest have high numbers of epiphytes with large accumulations of organic matter within the canopy.

The soil was a *Typic Dystrandept* with a H horizon, containing a root mat, ranging from 10 to 15 cm thick.

Sample collection

Trees on 2 ha of the 10 ha study area were subjectively stratified into four categories based on their degree of COM accumulation. Previous work on chemical characteristics of COM using 25 sample trees has shown no significant ($P = 0.05$) tree effect on chemical characteristics of COM due to high variability within individuals. COM was sampled using modified mountain climbing techniques (Perry, 1978; Nadkarni, 1988). For laboratory experiments, four large (ca 1–2 kg) composite samples of material were collected from the inner branches (0.4 mm from the trunk, 16–23 m above the forest floor) of a single fig (*Ficus tuerckheimii*) tree. This species is common on the site and normally has high amounts of COM. For biomass C:ATP comparisons, samples from three different fig trees were used. For field buried bag studies, six different trees having high accumulations of COM were randomly selected at each of three sampling dates representing the wet (January), dry (May) and transition (September) seasons. Samples were processed as described below.

The H (022) and Al horizons of the forest floor (designated FF-H and FF-Al, respectively) were randomly sampled from four gridded 10 × 40 m plots (three plots were used for initial field measures) using a 15 cm dia corer. Canopy organic matter resembled the H horizon more than the L (01) in appearance. Twelve core samples were taken per plot and composited, yielding a total of four composite samples.

Sample processing

Canopy and soil samples were sieved twice (6.5, then 2.0 mm) to provide adequate mixing and to remove as many remaining roots as possible. Freshly excised roots can obscure measurements of microbial ATP, and microbial C, N and P using fumigation extraction methods (Sparling *et al.*, 1985). For laboratory incubations, COM and forest floor samples were shipped cold to California and stored at 5°C until lab experiments commenced. Coarsely sieved (<6.4 mm) COM and soil was used for field buried bag incubations. The general characteristics of COM and forest floor samples are shown in Table 1.

Microbial measures

Microbial biomass was measured by the fumigation-extraction method for biomass C (Vance *et al.*, 1987b) and biomass N (Brookes *et al.*, 1985). This method involves chloroform fumigation of soils with subsequent extraction and analysis of total organic C and N released. Microbial biomass C is calculated from: $B_C = F_C/k_C$, where F_C = (total C extracted from 24 h fumigated soil) - (total C extracted from non-fumigated soil), and k_C , the fraction of microbial C rendered extractable, is 0.38 (Vance *et al.*, 1987b). Biomass N is calculated using a similar relationship

Table 1. General characteristics of COM and the FF-H and FF-Al horizons

Sample	pH(H ₂ O)	%C	%N	C/N
COM	3.7	37.4	2.16	17.3
FF-H	4.4	27.0	1.44	18.8
FF-Al	4.7	15.3	0.98	15.6

and a k'_N factor of 0.45 for a 24 h fumigation (Jenkinson, 1988). Soils were extracted using ca 6:1 extractant (0.5 M K₂SO₄):moist soil ratio. Soil ATP was measured using the trichloroacetic acid-phosphate-paraquat method (Tate and Jenkinson, 1982).

Incubation experiments

Incubation experiments were carried out at 25°C on soils adjusted to ca 60% of their water holding capacity with deionized water. Soil samples which had higher moisture content than this were air-dried slightly. Moist soil samples (10 g dry wt) were incubated in 250 ml polyethylene bottles covered with 0.013 mm polyethylene film to allow gaseous diffusion. Soil samples were prior incubated for 2 days under these conditions before time zero measurements in order to allow microbial mineralization and respiration activities to stabilize following storage at 5°C and water addition. Four replicate samples were used to determine N mineralization and nitrification (1, 3, 5, 10 and 20 days), and microbial biomass C and N (5 and 20 days) at each time interval. Samples used in incubation experiments were extracted with 0.5 M K₂SO₄ using an extractant:soil ratio of 8:1. For field incubations, ca 200 g (fresh wt) of COM and soil samples were weighed into thin plastic bags (ca 0.013 mm thickness) and placed in their respective locations in the canopy and the forest floor H and Al horizons one day following collection. Samples were extracted as described above at the time of collection and after 10 days incubation. Extracts from field incubations were shipped cold to California for analysis.

Soil respiration was also measured during the laboratory incubation. Samples were incubated in 1 l. sealed glass jars containing 10 ml 1 M NaOH and 5 ml water in separate bottles to prevent drying. The unreacted NaOH was titrated at 1, 3, 5, 10 and 20 days using 1 M HCl following addition of excess 3 N BaCl₂ to precipitate carbonate as insoluble BaCO₃ (Anderson, 1982). The NaOH was replaced after each incubation interval. The jars were opened at these times to allow adequate aeration. To test the C vs N limitation of microbial activity and biomass, glucose (5000 µg C g⁻¹ soil) or NH₄NO₃ (400 µg N g⁻¹ soil) amendments were added in solution (0.3 ml) to individual samples. A corresponding amount of deionized water was added to control samples at the same time.

Analytical methods

Soil C was measured by Walkley-Black dichromate digestion using a correction factor of 1.3 (Nelson and Sommers, 1982) and soil N was measured by Kjeldahl digestion using H₂O₂ and Li/Se as a catalyst. Ammonium was measured using a modified indophenol blue colorimetric method and nitrate by a

