BIOTROPICA 27(1): 13–19 1995

Moisture and Temperature Patterns of Canopy Humus and Forest Floor Soil of a Montane Cloud Forest, Costa Rica[1]

Stephanie A. Bohlman,[2] Teri J. Matelson,[3] and Nalini M. Nadkarni[4,5]
The Marie Selby Botanical Gardens, 811 South Palm Avenue, Sarasota, Florida 34236, U.S.A.

ABSTRACT

Accumulations of organic material can be found in the crowns of trees in tropical wet forests. We investigated moisture and temperature patterns of dead organic matter in the canopy and of soil in the upper horizons of the forest floor over a 42-month period. Temperatures of the canopy material and forest floor soil fluctuated throughout the year (range = 11.5°C to 21.0°C), but remained within an average of 1°C of each other. Both canopy material and forest floor soils were moist throughout the wet and misty seasons (over 70% water content). Although canopy organic substrate experienced periods of rapid and severe dehydration during the dry season (20%–40% water content), forest floor soils remained at a consistently high water content (60%–70%). The more extreme and fluctuating moisture conditions of canopy organic material may be important in determining the distribution and activity of epiphytic plants and associated canopy organisms.

RESUMEN

En las copas de los árboles de los bosques tropicales se pueden encontrar acumulaciones de material orgánico. Durante un período de 42 meses, investigamos modelos de la humedad y la temperatura del material orgánico muerto en las copas de los árboles y tambien en los estratos superiores del suelo. Las temperaturas del material en la copa y del suelo fluctuaron durante el año (variación = 11.5°C–21.0°C), pero la diferencia entre ambas fue 1°C como promedio. Durante la estación humeda y la estación brumosa tanto la copa de los árboles como los suelos forestales estuvieron humedos (continiendo 70% de agua). Aunque el material de la copa tuvo períodos de deshidratación rápida y severa durante la estación seca (continiendo 20%–40% de agua), los suelos mantuvieron un alto porcentaje de agua (60%–70%). La fluctuación de la humedad del material orgánico en la copa puede afectar posiblemente la distribución y la actividad de plantas epifíticas y otros organismos en la copa.

Key words: arboreal substrate; canopy; Costa Rica; Monteverde; organic matter; soil moisture; soil temperature; tropical cloud forest.

MOST STUDIES OF SOILS IN TROPICAL forests have taken place on the forest floor. In many tropical wet forests, however, considerable amounts of organic matter (up to 14,000 kg ha^{-1}) exist within the crowns of trees (Golley *et al.* 1971, Pócs 1980, Nadkarni 1984). A principal component of canopy organic matter has been called "crown humus" (Jenik 1974), "Epiphytenhumus" (Klinge 1963), "humic soil" and "canopy soil" (Lesica & Antibus 1991), "aerial humus" (Pócs 1980), and "dead organic matter" (Veneklaas *et al.* 1990). This material consists of decomposing organic materials such as abscised epiphytic plant parts, bark of host trees, invertebrate frass, and intercepted detritus.

In mature montane tropical forests, canopy-held humus, which is interwoven with the roots of living epiphytes and canopy roots (Nadkarni 1981), occurs as carpetlike mats along branch surfaces and in crotches of bifurcating tree trunks and branches. This canopy substrate, as yet unclassified in any soil taxonomic system, can be considered an arboreal histosol. It supports a great diversity and biomass of vascular and nonvascular epiphytic plants and associated invertebrates and vertebrates (Dunn 1937, Gentry & Dodson 1987, Longino & Nadkarni 1990). In this study, we refer to this material as the O horizon within the canopy (herein C-O, referred to as C-H in previous papers by the authors), because we consider it analogous to the O horizon on the forest floor (FF-O). We also measured attributes of the contiguous A horizon on the forest

[1] Received 14 July 1993; revision accepted 10 January 1994.

[2] Present address: University of Washington, College of Forest Resources, Seattle, Washington 98115, U.S.A.
[3] Present address: 38 Rockview St. #3, Cambridge, Massachusetts 02130, U.S.A.
[4] Present address: The Evergreen State College, Olympia, Washington 98505, U.S.A.
[5] Author for reprints.

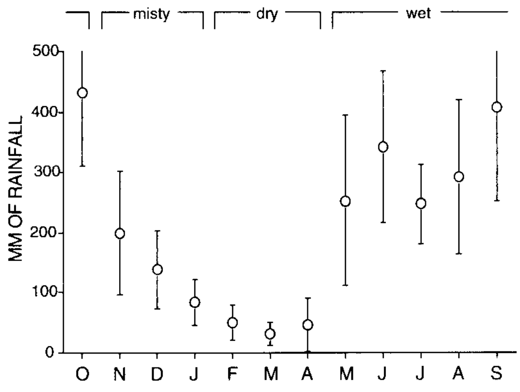

FIGURE 1. Mean monthly rainfall for Monteverde, averaged from measurements between 1953 and 1989. Rain gauge was located 2 km from the study site. Error bars are one standard error of the mean. Seasons are indicated at the top of the graph: M = misty-windy season; D = dry season; W = wet season.

floor (FF-A), since it may affect properties of the FF-O soil.

Comparisons between C-O and FF-O as substrates for biological activity have been explored in several tropical forests (Putz & Holbrook 1989, Vance & Nadkarni 1989, Lesica & Antibus 1991). C-O functions as a storage pool of organically bound nutrients and as a "capacitor" for inorganic nutrients originating from allochthonous atmospheric sources and materials mineralized *in situ* (Pike 1978, Nadkarni 1986, Nadkarni & Matelson 1991). In general, C-O has macronutrient concentrations similar to FF-O (Lesica & Antibus 1991; N. Nadkarni, pers. obs.). As with FF-O, C-O supports an active microbial community, although rates of nitrification are lower in the canopy than on the forest floor (Vance & Nadkarni 1989). The invertebrate community in the canopy is taxonomically similar at the level of order to the forest floor community, but the overall density of invertebrates is lower in the canopy (Nadkarni & Longino 1990).

Soil moisture and temperature are particularly important to the distribution of soil-based organisms (Kuhnelt 1976, Levings & Windsor 1984). Differences in organismal activities between C-O and FF-O may result from differences in soil moisture and temperature and/or the microclimatic conditions that govern these soil characteristics. Although various studies have reported soil moisture and temperature patterns for tropical forest floor soils (Cachan 1963, Baynton 1969, Dietrich *et al.* 1982), moisture and temperature patterns of canopy-held humic material in tropical forests have not been reported. In this paper, we report the moisture and temperature patterns of C-O and compare them to moisture and temperature patterns of FF-O and FF-A over a 42-month period in a lower montane wet forest in Costa Rica. This is a necessary step in characterizing arboreal histosols and understanding their roles at an ecosystem level.

STUDY SITE

This study was conducted in the Research Area of the Monteverde Cloud Forest Reserve (MVCFR) (10°18′N, 84°48′W) at 1480 m elevation. This area of tropical lower montane wet forest (Holdridge 1967) is described by Lawton and Dryer (1980) as Leeward Cloud Forest, with a broken canopy 15–30 m in height. Stem density of trees >30 cm diameter at breast height (DBH) is *ca* 150 trees ha^{-1} (Nadkarni *et al.*, pers. obs.). Annual rainfall averages *ca* 2500 mm and is distributed over three seasons (Fig. 1): wet-misty season (November–January, low rainfall and substantial wind-driven mist); dry season (February–April, little precipitation with high winds); and wet season (May–October, low wind speeds and high rainfall resulting from frequent convective storms in the Pacific lowlands). The forest floor soil is classified as a Typic Dystrandept (Vance & Nadkarni 1989). Mature trees of all taxa support diverse and abundant epiphytic flora and dead organic material, estimated at a minimum of 5000 kg ha^{-1} (Nadkarni 1984, 1986; Vance & Nadkarni, 1992).

METHODS

In April 1987 we established a 4-ha research plot in which we tagged and numbered all trees >30 cm DBH, recorded DBH, and subjectively assessed epiphyte cover. We assigned each tree an epiphyte-cover class using a quartile index (1 = 0–25%, 2 = 25–50%, 3 = 50–75%, 4 = 75–100% cover). Of these trees, we selected 14 climbable trees from the two highest epiphyte classes, regardless of taxa, for sampling. During the course of our research we climbed and collected epiphytic material from at least 30 other trees of the same size class in the study area and have observed similar amounts and distributions of C-O.

C-O was sampled for moisture content by hand, taking three samples (each 10–20 g fresh weight) per tree from each of the three trees for a total of nine canopy measurements each sampling day. The sampling locations were on branches 16–23 m above the forest floor, in or near branch crotches within 1 m of the central trunk where C-O accumulations were at least 10 cm thick. Temperature was measured with a standard soil thermometer probe 2–5 cm below the C-O surface.

FF-O and FF-A samples were taken on the same sampling days from nine randomly chosen forest floor locations within the plot. Approximately 10–20 g (fresh weight), which equaled ≈50–100 cc of material, were taken at 0–10 cm and at 10–20 cm depth at each location using a soil probe. Temperature was measured with the same thermometers used in the canopy by placing the probe *ca* 5 cm and 15 cm beneath the soil surface.

Moisture and temperature measurements were taken from the canopy and forest floor on the same day between 1000 and 1500 hr. To facilitate comparison between the two soil types, samples were collected within two hours of each other so that climate conditions were similar in the two microsites. The paired canopy and forest floor samples were taken approximately once every two weeks between October 1987 and July 1991 (mean sampling interval = 16.5 ± 11.8 days). The average sampling interval was nine days during the first four months and 18 days thereafter for a total of 84 sampling dates. Each sample was placed in an airtight bag and processed within 6 hours of collection. Samples were weighed fresh in the lab, dried in an oven at *ca* 65°C for 24–48 hr and weighed dry. Percent water content was calculated as:

((fresh weight − dry weight)/fresh weight)).

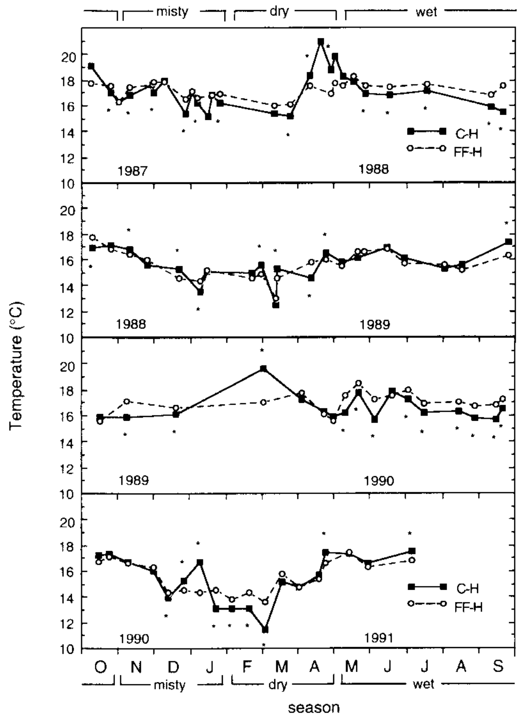

FIGURE 2. Soil temperature of canopy organic matter (C-H) at 5 cm depth and the forest floor H horizon (FF-H) at 0–10 cm depth at the study area in Monteverde, Costa Rica. Seasons are indicated at the top of the graph. Asterisks (*) represent a significant difference ($P < 0.05$) between C-H and FF-H.

RESULTS

Analysis of variance (Mendenhall *et al.* 1990) performed on the canopy data revealed no effect of tree ($P < 0.05$) on temperature or moisture content of C-O, allowing each canopy measurement to be treated as an independent sample. The temperature of C-O ranged between 11.5°C and 21.0°C; the range for FF-O was narrower (13.0°C to 18.5°C). Fluctuations for both C-O and FF-O during any one year were within 6°C. The temperatures of C-O closely paralleled those of FFO, with differences between the two averaging only 1.0°C. The only seasonal trend was that the extremes of temperature in the canopy (both high and low) occurred during the dry seasons (Fig. 2). The temperatures of FF-A differed little from those of FF-O, averaging only 0.3°C (Table 1). Although 31 of the 76 sampling days showed statistically significant differences in temperatures between FF-O and FF-A (Fig. 3), nearly all differences were within 1°C, which is probably not biologically meaningful.

In contrast to the temperature patterns, soil moisture fluctuated seasonally and showed striking differences between the canopy and the forest floor (Table 1). Both C-O and FF-O have the capacity to hold large amounts of water. The FF-O moisture pattern was quite constant throughout the year (at or above 55% moisture content). C-O showed great extremes in wetting and drying (Fig. 3). C-O consistently maintained a significantly higher moisture content during the wet and misty seasons (above 70%), but had periods of very low soil moisture (20–40% moisture content) during the dry season (Fig. 3). C-O could dehydrate substantially, losing 30 percent of its water content within a week. Although the annual mean difference in water content was only 6 percent, C-O averaged 20 percent lower water content than FF-O during the dry season. The actual duration of these periods of desiccation

TABLE 1. *Mean annual and seasonal soil temperature and moisture of canopy dead organic matter (C-O) and of the forest floor at 0–10 cm (FF-O) and 10–20 cm (FF-A) at the study area in Monteverde, Costa Rica. Means averaged from samples taken approximately once every two weeks between 10 October 1987 and 20 September 1990. Forty measurements were taken in the wet season (May to October), 23 in the misty season (November to January), and 21 in the dry season (February to April). Data are means ± one standard deviation with ranges in parentheses.*

	Annual mean	Seasonal mean		
		Wet	Misty	Dry
Soil temperature, °C				
C-O	16.5 ± 1.5 (11.5–21.0)	16.6 ± 1.0 (15.3–19.8)	15.9 ± 1.2 (13.1–18.0)	15.8 ± 2.4 (11.5–21.0)
FF-O	16.6 ± 1.2 (13.0–18.5)	17.0 ± 0.8 (15.2–18.5)	16.2 ± 1.3 (14.3–17.9)	15.5 ± 1.3 (13.0–17.8)
FF-A	16.7 ± 1.1 (13.3–18.2)	17.1 ± 0.6 (15.8–18.2)	16.4 ± 1.0 (14.6–17.7)	15.4 ± 1.2 (13.3–17.3)
Soil moisture, (% H_2O by weight)				
C-O	0.66 ± 0.14 (0.27–0.79)	0.72 ± 0.09 (0.39–0.79)	0.67 ± 0.11 (0.37–0.79)	0.53 ± 0.15 (0.27–0.73)
FF-O	0.66 ± 0.04 (0.54–0.76)	0.67 ± 0.05 (0.54–0.76)	0.67 ± 0.03 (0.61–0.73)	0.62 ± 0.03 (0.56–0.67)
FF-A	0.54 ± 0.03 (0.47–0.59)	0.54 ± 0.03 (0.47–0.59)	0.54 ± 0.03 (0.49–0.59)	0.51 ± 0.03 (0.47–0.56)

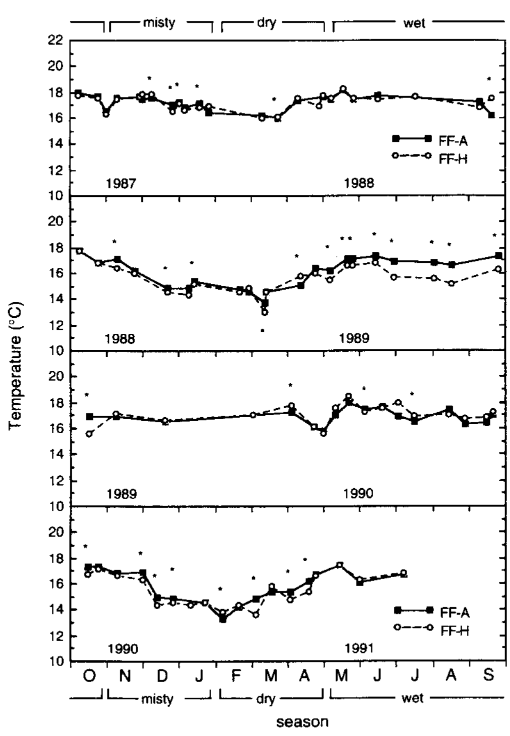

FIGURE 3. Soil temperature of forest floor H horizon (FF-H) at 0–10 cm depth and forest floor A horizon (FF-A) at 10–20 cm depth at the study area in Monteverde, Costa Rica. Asterisks (*) represent a significant difference ($P < 0.05$) between FF-H and FF-A.

are uncertain because of occasional long intervals between sampling days during the dry season which coincided with high winds and dangerous climbing conditions. However, periods of frequent sampling during the 1988 and 1991 dry season indicate that the C-O may rehydrate within two weeks of moisture loss.

On every sampling day except one (January 1988), FF-A contained significantly less water than FF-O by an average of 13 percent water content (Fig. 5). Changes in FF-A soil moisture paralleled those in FF-O, but with less fluctuation. There was no significant statistical relationship between soil moisture and soil temperature in any soil layer ($r^2 = 0.032$ for C-O temperature and moisture, $r^2 = 0.021$ and $r^2 = 0.037$ for F-H and F-A, respectively).

DISCUSSION

Differences between canopy and forest floor soil moisture patterns could reflect differences in the physical characteristics of the soils and/or variations in microclimate. Both C-O and FF-O have high water holding capacities due in part to their high organic matter content. However, the fibrous nature of C-O may allow it to dry out more easily than the more colloidal FF-O. C-O is derived in large part from the accumulation of dead bryophytes,

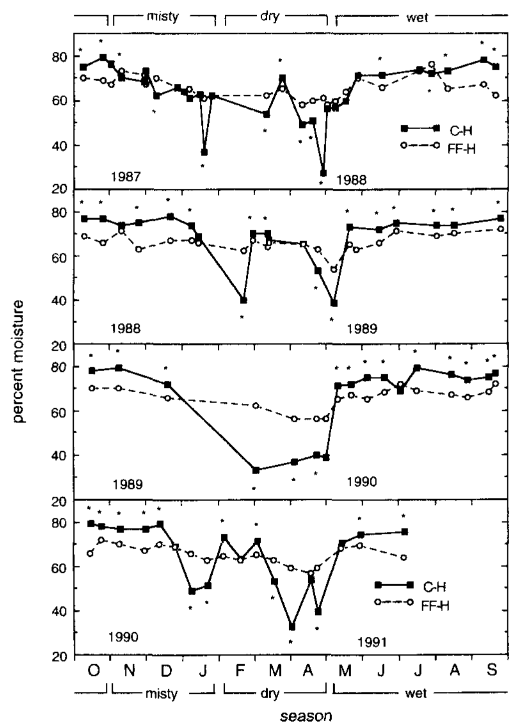

FIGURE 4. Moisture content of canopy organic matter (C-H) and the forest floor H horizon (FF-H) at the study area in Monteverde, Costa Rica. Moisture content, determined from 10 g samples taken from the top 10 cm of soil, is expressed as (water content/total wet weight). Asterisks (*) represent a significant difference ($P < 0.05$) between C-H and FF-H.

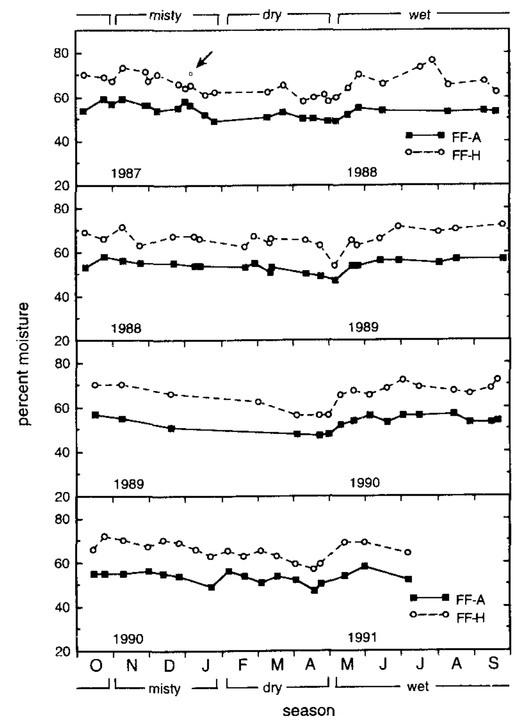

FIGURE 5. Moisture content of the forest floor H horizon (*FF-H*) at 0–10 cm depth and the *A* horizon (*FF-A*) at 10–20 cm depth at the study area in Monteverde, Costa Rica. FF-H and FF-A moisture contents are significantly different ($P < 0.05$) on all sampling days except for the day with the ° in January 1988.

which are susceptible to extreme and rapid wetting/ drying cycles when alive (Coxson *et al.* 1992). The lack of contact with a lower mineral horizon may contribute to the tendency of C-O to lose water rapidly during the dry season. The physical connection of the FF-O horizon with nearly saturated lower soil horizon (FF-A) may help maintain the moisture content of the upper horizon of the forest floor. C-O is also exposed to different microclimatic conditions than FF-O, which could explain the greater extremes of C-O moisture. During the day, greater wind speeds, higher air temperatures and solar radiation, and lower humidity in the canopy (Cachan 1963, Odum *et al.* 1970, Allen *et al.* 1972, Lawton 1982, Longman & Jenik 1987, Kira & Yoda 1989) promotes greater evaporation of water from C-O.

Despite the differences in forest floor and canopy microclimate, differences in the temperatures of C-O and FF-O were minor. This may be a result of high water content, which increases a soil's capacity to buffer temperature changes (Brady 1974, Fitz-Patrick 1980). With respect to temperature, C-O and FF-O offer similar microhabitat conditions for canopy-dwelling organisms.

The moisture pattern we documented for C-O has undoubtedly played a role in determining the composition and activity of the canopy-dwelling organisms, although no data exist on these relationships. The lower densities of invertebrates in the canopy relative to forest floor (particularly the absence of isopods and amphipods in C-O reported by Nadkarni and Longino (1990), may be a response to low moisture (Levings & Windsor 1984). Drought adaptations in epiphytes that are rooted in C-O may be related to periodic low soil moisture. The availability of moisture to epiphytes could be better understood by determining the moisture release curve for C-O. Previous studies have linked wetting/drying cycles with increased rated of litter decomposition (Birch 1958, Sorensen 1974). In this study, we found more fluctuations and greater extremes in the moisture pattern in the canopy, but the turnover time of detritus in the canopy has been documented as nearly twice as long as litterfall on the forest floor (2.7 vs 1.5 yr) (Nadkarni & Matelson 1991). We speculate that the greater frequency and intensity of "dry-downs" in the canopy may be responsible for the slower decomposition rates recorded. Dry conditions could affect the density, composition, and life cycles of organisms responsible for decomposition processes. Further studies examining the relationship between moisture and temperature patterns and biological activity in C-O and FF-O are needed.

ACKNOWLEDGMENTS

We thank the staff of the Monteverde Cloud Forest Reserve and the Tropical Science Center for use of the study area and logistical support. R. Solano and Z. Fuentes provided valuable field and laboratory assistance. S. Gilchrist and E. Vance gave assistance with analyses and ideas discussed in this paper. D. Schaefer, H. Van Miegroet, and P. Hanson gave helpful critical advice on early drafts of the manuscript. This research was funded by research grants from the National Science Foundation (BSR 87-19735 and BSR 90-18006), an NSF Research Experience for Undergraduate Grant Supplement, the Whitehall Foundation and the National Geographic Society Committee on Research and Exploration.

LITERATURE CITED

ALLEN, L. H., E. R. LEMON, AND L. MULLER. 1972. Environment of a Costa Rican forest. Ecology 53: 102–111.

BAYNTON, H. W. 1969. The ecology of an elfin forest in Puerto Rico. 2. The microclimate of "Pico del Oeste." J. Arnold Arbor. Harv. Univ. 49: 419–430.

BIRCH, H. F. 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10: 9–31.

BRADY, N. C. 1974. The nature and properties of soils. 8th edition. MacMillan Publishing Company, New York, New York.

CACHAN, P. 1963. Signification écologique des variations microclimatiques verticales dans la forêt sempervirente de Basse Côte d'Ivoire. Ann. Fac. Sci. Univ. Dakar 8: 89–155.

COXSON, D. S., D. D. MCINTYRE, AND H. J. VOGEL. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). Biotropica 24: 121–133.

DIETRICH, W. E., D. M. WINDSOR, AND T. DUNNE. 1982. Geology, climate, and hydrology of Barro Colorado Island. *In* D. M. Windsor, E. G. Leigh, and A. S. Rand (Eds.). Ecology of a tropical forest: seasonal rhythms and long-term changes, pp. 21–46. Smithsonian Institution, Washington, D.C.

DUNN, E. R. 1937. Amphibians and reptiles from bromeliads in Costa Rica and Panama. Copeia 3: 163–167.

FITZPATRICK, E. A. 1980. Soils: their formation, classification, and distribution. Longman Publishing Group, New York, New York.

GENTRY, A. H., AND C. DODSON. 1987. Diversity and biogeography of neotropical epiphytes. Ann. Mo. Bot. Gard. 74: 205–233.

GOLLEY, F., J. MCGINNIS, AND R. CLEMENTS. 1971. La biomasa y la estructura de algunos bosques de Darién, Panama. Turrialba 21: 189–196.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

JENIK, J. 1974. Root structure and underground biomass in equatorial forests. *In* Productivity of forest ecosystems, Proceedings of the Brussels Symposium organized by UNESCO and IBP, 27–31 October 1969, pp. 323–337. UNESCO, Paris, France.

KIRA, T., AND K. YODA. 1989. Vertical stratification in microclimate. *In* H. Lieth and M. J. A. Werger (Eds.). Tropical rain forest ecosystems, pp. 55–71. Elsevier, Amsterdam, The Netherlands.

KLINGE, H. 1963. Über epiphytenhumus aus El Salvador, Zentralamerika. Pedobiologia 2: 102–107.

KUHNELT, W. 1976. Soil biology with special reference to the animal kingdom. Faber and Faber, London, England.

LAWTON, R. O. 1982. Wind stress and elfin stature in a montane forest tree: an adaptive explanation. Am. J. Bot. 69: 101–116.

———, AND V. DRYER. 1980. The vegetation on the Monteverde Cloud Forest Reserve. Brenesia 18: 101–116.

LESICA, P., AND R. K. ANTIBUS. 1991. Canopy soils and epiphyte richness. Nat. Geogr. Res. 7: 156–165.

LEVINGS, S. C., AND D. M. WINDSOR. 1984. Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. Biotropica 16: 125–131.

LONGINO, J. T., AND N. M. NADKARNI. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. Psyche 97: 81–94.

LONGMAN, K. A., AND J. JENIK. 1987. Tropical forest and its environment. Longman Scientific and Technical, Essex, England.

MENDENHALL, W., D. D. WACKERLY, AND R. L. SCHEAFFER. 1990. Mathematical statistics with applications. PWS-Kent Publishing Company, Boston, Massachusetts.

NADKARNI, N. M. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. Science 214: 1023–1024.

———. 1984. Epiphyte biomass and nutrient capital of neotropical elfin forest. Biotropica 16: 249–256.
———. 1986. The nutritional effects of epiphytes on host trees with special reference to alteration of precipitation chemistry. Selbyana 9: 44–51.
———, AND J. T. LONGINO. 1990. Invertebrates in canopy and ground organic matter in a neotropical montane forest, Costa Rica. Biotropica 22: 286–289.
———, AND T. MATELSON. 1991. Litter dynamics within the canopy of a neotropical cloud forest, Monteverde, Costa Rica. Ecology 72: 2071–2082.
ODUM, H. T., G. DREWRY, AND J. R. KLINE. 1970. Climate at El Verde, 1963–1966. *In* H. T. Odum and R. F. Pigeon (Eds.). A tropical rainforest: a study of irradiation and ecology at El Verde, Puerto Rico, pp. B347–B418. U.S. A.E.C., Washington, D.C.
PIKE, L. 1978. The importance of lichens in mineral cycling. Bryologist 81: 247–257.
PÓCS, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains. Acta Bot. Acad. Sci. Hung. 26: 143–167.
PUTZ, F. E., AND N. M. HOLBROOK. 1989. Strangler fig rooting habits and nutrient relations in the llanos of Venezuela. Am. J. Bot. 76: 781–788.
SORENSEN, L. H. 1974. Rate of decomposition of organic matter in soil as influenced by repeated air drying-rewetting and repeated additions of organic material. Soil Biol. Biochem. 6: 287–292.
VANCE, E. D., AND N. M. NADKARNI. 1989. Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. Soil Biol. Biochem. 22: 677–684.
———, AND ———. 1992. Root biomass on the forest floor and in the canopy of a neotropical cloud forest, Costa Rica. Plant Soil 142: 31–39.
VENEKLAAS, E. J., R. J. ZAGT, A. VAN LEERDAM, R. VAN EK, A. J. BROEKHOVEN, AND M. VANN GENDEREN. 1990. Hydrological properties of the epiphyte mass of a montane tropical rain forest, Colombia. Vegetatio 89: 183–192.