

## THE NUTRITIONAL EFFECTS OF EPIPHYTES ON HOST TREES WITH SPECIAL REFERENCE TO ALTERATION OF PRECIPITATION CHEMISTRY

NALINI M. NADKARNI

Department of Biological Sciences, University of California,  
Santa Barbara, California 93106

**ABSTRACT.** Epiphytes have epitomized a neutral, or commensalistic symbiosis with their hosts, and have historically been considered to only minimally affect the nutrient relations of supporting trees and the ecosystem as a whole. Research in the last decade, however, has revealed that epiphytes may significantly contribute to overall nutrient cycling despite their biomass being small, relative to the ecosystem as a whole. This has been confirmed in various forests, ranging from dry temperate oak woodland to very wet neotropical cloud forests. A general model to enumerate the inputs, pools, and outflows of mineral nutrients of the epiphyte component is presented. Studies on the effects of epiphytes on nutrient transfers from epiphytes to other ecosystem members from a temperate and a tropical rainforest show that epiphytes tend to absorb atmospheric-borne nutrients during the dry season. During the wet season, there is a greater net release of nutrients from branches with epiphytes than from those whose epiphytes had been experimentally stripped. Mechanisms by which epiphytes may enhance the nutrient status of individual host trees and the forest as a whole are summarized.

A rainforest canopy is an ecosystem in miniature, complete with inputs, outputs, internal transformations, and transfers of nutrient elements. Nutrients entering the ecosystem in precipitation and in dust can be absorbed by tree foliage and bark, and by epiphytes. Nutrients can also be transferred from all canopy components to other parts of the ecosystem. Epiphyte effects on ecosystem-level nutritional interactions have been investigated in only a few temperate and tropical forests (e.g., Pike, 1971; Denison et al., 1972; Nadkarni, 1984, 1985). In many nutrient cycling studies, epiphytes have been ignored or discounted, as their biomass was considered insignificant in proportion to other ecosystem components.

However, epiphytes have proved to be appropriate subjects of nutritional studies for several reasons: (1) epiphytes contribute a significant portion of many rainforest canopies in terms of overall diversity and biomass (Pike et al., 1975; Pike, 1978; Pócs, 1980); (2) their crown location exposes them to the same micro-environmental conditions that their host trees experience, but their lack of organic connection to the forest floor makes them almost entirely dependent upon aerial nutrient supplies (Benzing, 1970, 1981; LeBlanc, 1972; Johansson, 1975; Benzing & Seeman, 1978). This characteristic allows the researcher to isolate and measure nutrient inputs and losses for epiphytes more easily than for plants drawing upon nutrient resources in the forest floor and soil; (3) epiphytes form a discrete portion of the canopy; they can be physically

separated from the hosts, and lend themselves to within-canopy manipulations.

In this paper, I first review the body of research that exists on the role of epiphytes in nutrient cycling. In the second section, I present new data on how epiphytes may affect one pathway of nutrient flux, the alteration of precipitation chemistry, in a temperate and a tropical wet forest.

### SECTION I. EPIPHYTES AND NUTRIENT CYCLING

#### Summary of Research Approaches to Date

Until recently, most information on epiphytes and nutrient input came indirectly, from subjective and visual sampling (e.g., Sanford, 1968; Johansson, 1975) or from destructive sampling of epiphytes taken from trees that had fallen to the forest floor (e.g., Forman, 1975). The development of reliable canopy access techniques and remote measurement techniques have increased our understanding of canopy nutrient storage, flux, and the mechanisms that regulate them. Four research projects that focused on canopy processes and epiphytes in particular which were carried out in the last ten years exemplify the approaches canopy research has encompassed.

Innovative canopy work by research in Pacific Northwest forests focused on structure, pools, and some of the nitrogen fluxes in old-growth coniferous forest canopies (Pike, 1978; Carroll, 1980; Massman, 1983). This work emphasized the biotic inputs and influences of canopy com-

ponents (including epiphytic lichens, microbial endophytes, and grazing arthropods), and elucidated the complexity of within-canopy interactions. Measurements of litterfall and rainfall chemistry documented that canopy components add significant amounts of nutrients in these old-growth forests (e.g., a net addition of 1.5 to 7.0 kg/ha/yr of nitrogen due to epiphytic lichen *Loberia oregana*) (Pike, 1978).

A large body of research on the biogeochemical processes of ecosystems in high-elevation fir forests of New England has been conducted with emphasis on the atmospheric/biotic interactions of forest canopies (Cronan & Reiners, 1983; Reiners & Olson, 1984). Experimental and modeling approaches have been used to understand the mechanisms that regulate canopy capture and transfer of atmospheric inputs (e.g., Reiners & Olson, 1984; Schaefer & Olson, 1984). Lovett (1981) presented a mechanistic model which was consistent with time-course studies of stemflow and throughfall in the field. These studies demonstrated that forest canopies capture and transfer nutrients in complex but predictable ways, depending on the timing, intensities, and forms of meteorological input.

Building on the concept that the canopy "black box" can be illuminated for a better understanding of regulation of nutrient storage and flux in forest ecosystems as a whole, Nadkarni (1983, 1985) focused on the within-canopy nutrient cycles of a temperate moist coniferous forest in western Washington. This research documented the large amounts of nutrient capital held within non-tree canopy components. During this study, it was found that nutrient transfer between epiphytes and their supporting host trees can be highly efficient, via adventitious canopy roots of many of the common host trees (Nadkarni, 1981). This research emphasized the importance of carrying out in situ observations and the potential importance of within-canopy processes in nutrient conservation.

This line of research was extended to a tropical forest in a neotropical montane elfin woodland, where amounts and types of canopy-held organic matter were quantified (Nadkarni, 1984). Some physical, chemical, and biotic aspects of this live and dead epiphytic material have also been described (Nadkarni & Longino, unpubl.). In general, this "crown humus" (*sensu* Jenik, 1973) of the canopy had less water content, greater percent fiber, significantly higher carbon to nitrogen ratios, and lower macrofaunal detritivore diversity and density than humus on the forest floor. Preliminary litterbag measurements suggest that decomposition is significantly slower within the canopy than on the forest floor. These results

indicate that organic matter engendered by epiphytes held within the canopy should be considered when describing mechanisms of nutrient conservation and nutrient cycling in forest bearing live and dead organic matter within their canopies.

### Models of Nutrient Cycling

The traditional model of nutrient cycling considers the bulk of nutrients to reside in the forest floor and soil, with inputs from precipitation and parent rock weathering; internal cycling occurring via crownwash, litterfall, decomposition, and plant uptake; and losses via run-off, streamflow, and drainage. To consider the role of epiphytes in overall nutrient cycling, a model that includes within-canopy storage and circulation is depicted in FIGURE 1.

Epiphyte nutrient sources come from: (a) atmospheric deposition (including rainfall, mist, and dry deposition), (b) decomposition from outer layers of host tree bark, (c) litterfall and leachates intercepted from host tree foliage and epiphylls, (d) excreta from canopy-dwelling animals, (e) debris carried by ants and termites from the forest floor, and (f) free-living and symbiotic nitrogen-fixers. Few data exist on the relative importance of each of these sources to epiphytes; precipitation has been considered the most important (Johansson, 1975; Dressler, 1981). This input can be irregular, especially in tropical forests, with much of the annual elemental influx taking place on only a few rain days (Kellman et al., 1982).

Fog has been recognized as an important ecological factor, for epiphytes. Coastal and tropical montane areas that are often enveloped in fog develop the most abundant and diverse epiphyte communities of any in the world (Madison, 1977). These communities are almost always dominated by bryophytes, which, with their poikilohydric foliage, are able to take up nutrients directly from water flowing over them (Skye & Oechel, 1979). Some bryophytes have a remarkable ability to accumulate large quantities of certain elements such as iron, copper, rare earths, and heavy metals (Gorham, 1959).

The nutrient capital stored within epiphyte components of tree canopies has been quantified in relatively few forest ecosystems. Difficulty of access, the three-dimensional, irregular surfaces of the tree substrate, and high levels of variation (within- and between-tree) of epiphyte distribution make these measurements difficult. Pike (1978) and Nadkarni (1983) have compiled the existing literature on epiphyte standing crop and nutrient capital for temperate and tropical eco-

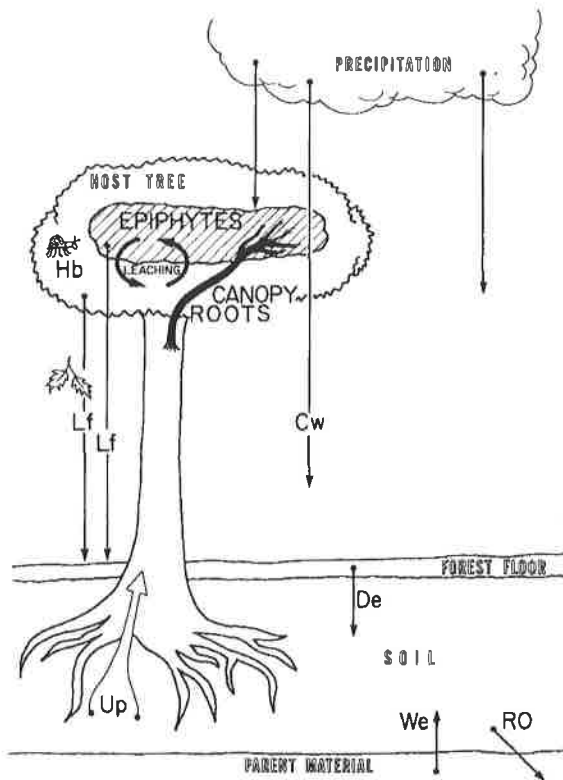


FIGURE 1. Rainforest nutrient cycling model with details of within-canopy components depicted. Nutrients enter the canopy ecosystem via weathering (We) of parent material and precipitation which can be intercepted and retained by live and dead parts of epiphyte mats. Nutrients are subsequently transferred to other ecosystem parts within the canopy and to the forest floor via litterfall (Lf), herbivory (Hb), crown-wash (Cw), and, in some rainforest tree species, via canopy roots. They can then circulate within the ecosystem via soil-rooted vegetation uptake (Up) and decomposition (De), be stored in the soil, or move from the system via run-off (RO).

systems (TABLE 1). Although these values range widely, in forests where they reach their greatest abundance they can exceed the biomass contained in the foliage of their supporting host trees. For example, in *Acer macrophyllum* stands of temperate coniferous moist forests in the Olympic National Park, the mineral capital contained in live and dead epiphytes is equivalent to 60 percent of the host tree foliar nutrient capital (Nadkarni, 1985) (TABLE 2).

Nutrients that are intercepted and stored by epiphytes can be transferred to other members of the ecosystems by herbivory of epiphytes, epiphyte litterfall via abscission and branchfalls, host tree uptake by within-crown canopy roots and stem surfaces, and by alteration of precipitation chemistry by epiphytes (Nadkarni, 1981) (FIGURE

1). The latter pathway may be particularly important where a large proportion of nutrient input occurs from atmospheric sources, and/or where heavy rains potentially leach soil and leaves. This pathway will be considered in detail in Section II.

Another important but as yet unquantified pathway of nutrient flux from epiphyte to forest floor is by litterfall. The rate at which this occurs depends upon branch longevity, and rates of epiphyte growth, mortality, and decomposition. Values specific to epiphytes in tropical forests have, to my knowledge, never been measured directly; this is an important step for future studies.

A pathway of nutrient transfer that takes place within the canopy itself exists in some species of host trees. Twenty-two species of host trees in temperate and tropical forests of the New and Old Worlds were found to produce networks of canopy roots that originated above ground, beneath mats of epiphytes on branches and boles (Nadkarni, 1981). Their anatomy, morphology, and symbiotic relationships with nitrogen-fixing and mycorrhizal organisms indicate a function in nutrient uptake and transfer. Recent work with gamma-emitting radioisotopes under laboratory conditions confirms that mineral uptake by canopy roots occurs at rates comparable to their below ground counterparts (Nadkarni & Primack, unpubl.). However, the net amounts of nutrients removed from canopy nutrient pools via host tree canopy roots remains as yet unknown.

## SECTION II. PRECIPITATION AND NUTRIENT CYCLING

The existing literature portrays precipitation to be one of the most important pathways of nutrient input for canopy-dwelling plants and to wet forest ecosystems as a whole. Potentially, epiphytes could add, delete, or have no effects on precipitation nutrient chemistry. The most direct means to test for effects of epiphyte mats on precipitation chemistry is to experimentally manipulate epiphyte loads on individual branches. In order to address the question of epiphyte effects on precipitation chemistry, I chose to examine two forests where epiphytes are very abundant and diverse. In the following section, I report original data on the nutritional effects of epiphytes from a temperate and a tropical rainforest.

### Materials and Methods

The temperate study site was located in a moist coniferous forest in Washington State (Hoh Riv-

TABLE 1. Nutrient concentrations (ppm) averaged from rain and mist sampled at biweekly intervals, Olympics (November 1980–November 1981) and at three-day intervals, Monteverde (October–November 1981 and January–March 1982). (Standard errors are in parentheses.)

	Element						
	N	P	Ca	Mg	K	Na	Cl
Olympics, rain	0.131 (0.02)	0.003 (0.001)	0.175 (0.10)	0.080 (0.02)	0.028 (0.005)	0.028 (0.005)	0.765 (0.13)
Monteverde, rain							
Wet season	0.276 (0.14)	0.049 (0.03)	0.097 (0.02)	0.021 (0.004)	0.073 (0.02)	0.212 (0.05)	0.663 (0.06)
Dry season	0.951 (0.37)	0.106 (0.04)	0.125 (0.08)	0.071 (0.04)	0.149 (0.08)	0.505 (0.05)	0.992 (0.07)
Monteverde, mist							
Wet season	0.111 (0.02)	0.011 (0.04)	0.109 (0.03)	0.033 (0.001)	0.124 (0.07)	0.566 (0.04)	0.880 (0.08)
Dry season	0.347 (0.09)	0.029 (0.005)	0.246 (0.05)	0.037 (0.06)	0.161 (0.05)	0.341 (0.05)	0.718 (0.08)

er Valley, Olympic National Park, 47°50'N, 124°05'W). The tropical site was a neotropical elfin woodland (Monteverde Cloud Forest Reserve, Costa Rica, 10°20'N, 84°50'W). In both forests, the epiphyte community is dominated (with respect to biomass) by cryptogams, with large amounts of dead organic matter accumulated on branches and trunks of host trees (Nadkarni, 1984, 1985).

Nutrients from rainfall were measured with standard rain gauges located in open areas during the study period (November 1980 to November 1981, temperate site, and from 10 October to 4 November 1981 and 25 January to 4 March 1982, tropical site). Samples were preserved with phenyl mercuric acetate, refrigerated (frozen at the Monteverde site), filtered and analyzed using standard methods (Likens & Bormann, 1970).

TABLE 2. Average dry weight of live and dead epiphytes on a representative individual tree and in representative stands in temperate and tropical rainforests. n.d. = not determined.

Forest type	Location	Epiphyte standing crop		Reference
		Single tree (kg)	Stand level (kg/ha)	
<b>Temperate ecosystems</b>				
<i>Acer macrophyllum</i> (big-leaf maple) stands, temperate rainforest	Hoh River Valley, Washington, USA	35.5	6,870	Nadkarni, 1985
<i>Abies lasiocarpa</i> (subalpine fir) forest	Mt. Baker, Washington, USA	9.3	4,220	Rhoades, 1981
<i>Pseudotsuga menziesii</i> (Douglas-fir) forest	Blue River, Oregon, USA	17.9	900	Pike et al., 1977
Oak woodland	Willamette Valley, Oregon, USA	n.d.	1,800	Pike, 1971
<b>Tropical ecosystems</b>				
Cloud forest	Monteverde Cloud Forest, Costa Rica	141.9	4,820	Nadkarni, 1984
Mossy elfin forest	Uluguru Mountains, Tanzania	n.d.	14,000	Pócs, 1980
Submontane forest	Uluguru Mountains, Tanzania	n.d.	2,130	Pócs, 1980
Premontane forest	Darién, Panama	n.d.	1,400	Golley et al., 1971

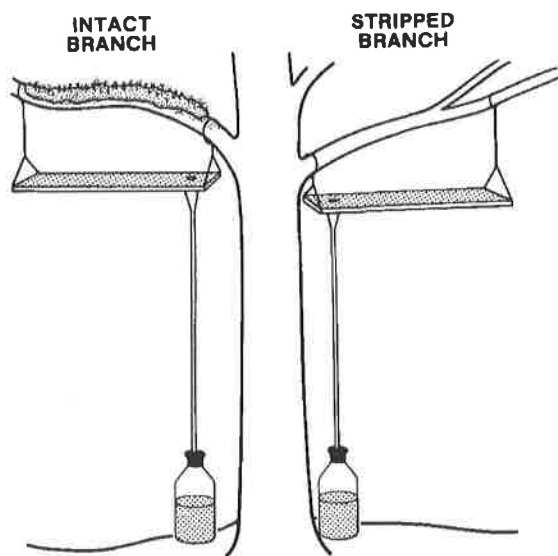


FIGURE 2. Schematic representation of branch frame used to collect throughfall directly beneath individual branches.

Mist input was measured at the Monteverde site with a cylinder of aluminum mesh screen mounted over a collecting funnel. Although it is impossible to quantify absolute amounts of mist arriving upon canopy surfaces, the values I collected agree with the few mist input figures that exist in the literature (Azevedo & Morgan, 1974).

To test for the effects of epiphyte mats on crownwash nutrient flux, throughfall was caught directly beneath branches that had been stripped of all epiphytes and compared to throughfall caught beneath paired intact branches within the canopy. Branches were matched in size, angle from vertical, epiphyte mat composition and abundance, and crown location; throughfall that arrived at each branch pair was assumed to be of the same quantity and quality. Three sets of paired branches were selected at each site. Stripped branches were brushed of all residual material without injuring the bark. Intact branches were disturbed as little as possible.

Because traditional throughfall collectors (funnels and bottles on the forest floor) mask intracanalopy differences, within canopy throughfall collectors were devised to hang directly beneath each of the sample branches. Permanent "branch frames" were installed in the sample trees (*Acer macrophyllum*, temperate site; *Clusia alata*, tropical site). These trough-like frames (2.8 m × 1.0 m), constructed of wood, wire screen, and plastic sheeting, were hung by pulleys and nylon cord within the canopy. Hoses from the frame underside ran down the bole to 8-liter polyethylene jugs, providing continuous collection (FIGURE 2). At two-week (temperate site) or three-

day (tropical site) intervals, the collected throughfall was sampled, preserved and analyzed as for rainfall nutrients.

The effects of epiphytes were assessed by comparing the amounts of nutrients in crownwash caught beneath stripped vs. intact branches. Results reported are the amounts of each element (rainfall volume multiplied by sample concentrations) collected from beneath an intact branch minus the amounts of each element collected beneath a paired stripped branch. A positive value indicates net release of that nutrient by epiphytes, relative to stripped branches for that time interval. For each nutrient and each branch frame pair, Wilcoxon signed-rank tests were used to compare the paired throughfall nutrient values.

### Results

In the Olympics, the total volume of rainfall (3,320 mm/yr) and its seasonal distribution was typical of the area, following trends consistent with the past 24 yr at the temperate site. In the dry summer months (June through September), this forest received only 10 percent of total rainfall. In the Monteverde site, rainfall nutrient input was distributed more evenly throughout the year than it was in the Olympics, with 75 percent of total rainfall arriving during the wet season (June to November). Total volume was 2,200 mm/yr, only slightly drier than the 20-yr average of 2,620 mm/yr (Nadkarni, 1983). Mist and fog added approximately 520 mm to total precipitation. The concentrations of precipitation nutrients are presented in TABLE 2; total amounts of nutrients arriving from wet atmospheric sources are in FIGURE 3.

In the temperate site, variation was found in the direction of flux, timing, and quantities for all nutrients, but the annual cumulative values indicate a net *addition* of all of the nutrients measured beneath epiphytes. At this site, greater amounts of nitrogen, phosphorus, and calcium arrived beneath intact branches relative to stripped branches ( $P < 0.05$ ). Conversely, there was no significant difference in throughfall content of potassium on any of the branch frames (TABLE 3).

### Discussion

Excess nutrients derived from branches with epiphyte loads left intact are either from atmospheric sources gathered by epiphytes in excess of their needs, or lost in spite of efforts to retain them. Epiphytes are garnering enough nutrients to maintain themselves within the canopy (to the extent of the observed standing crop), but nutrients are nonetheless leached from them to oth-

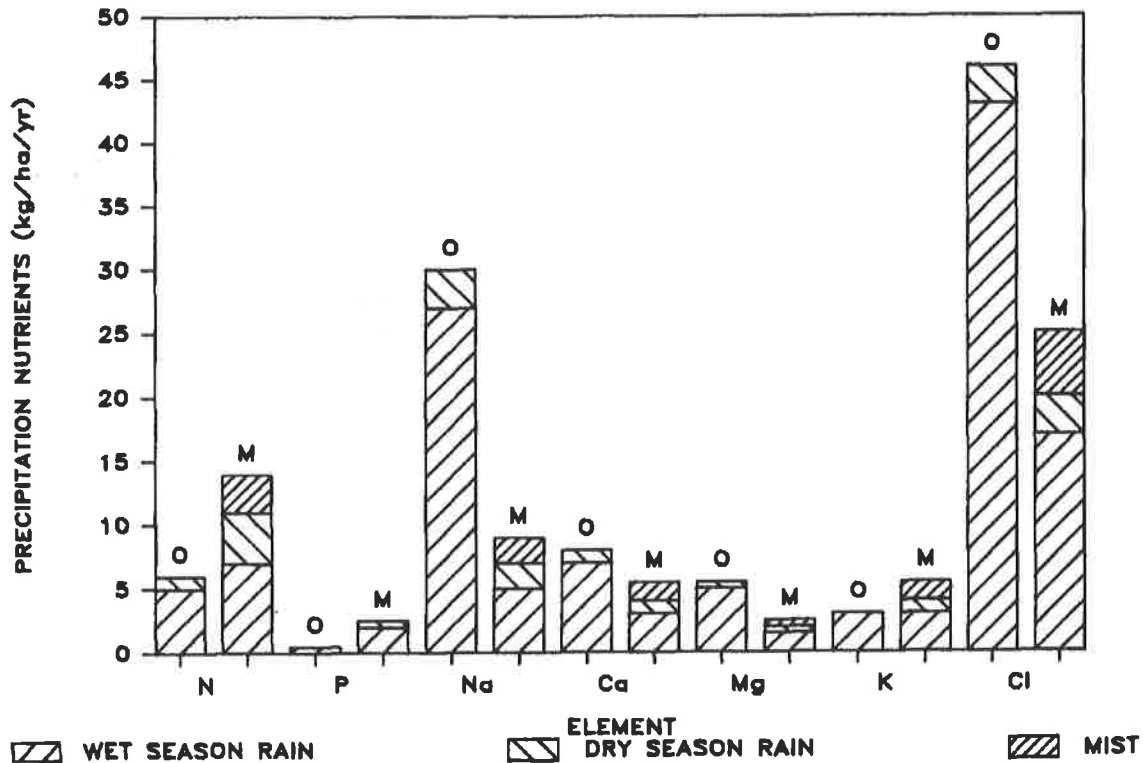


FIGURE 3. Seasonal distribution of precipitation nutrients in the Olympic rainforest (O) and Monteverde (M). Total annual input of nutrients, based on volumes and concentrations of rainfall samples collected at two-week (Olympics) and three-day (Monteverde) intervals throughout the year, was separated into wet season and dry season inputs.

er ecosystem components. It should be noted that this argument rests upon the assumption that a steady-state exists in terms of epiphyte occupation of tree substrate, much as a mature and steady-state forest ecosystem may maintain its biomass and productivity while still exhibiting nutrient losses via run-off.

Some of the physical, morphological, and physiological attributes of many temperate and tropical epiphytes that may lead to the processes of forest nutrient enhancement have been discussed by Benzing (1981). The mechanisms behind these patterns are due to the increased nutrient gathering potential, nutrient retention capacity, and nutrient buffering capacity of branches and trunks of trees supporting epiphytes (Nadkarni, 1984, 1985). It must be kept in mind, however, that epiphytes comprise an extremely diverse group, not only in terms of their taxonomy (Madison, 1977), but also in terms of morphology and physiology, and so-called "epiphyte nutrient conservation mechanisms" are generalities which vary from plant to plant and ecosystem to ecosystem. Such generalities mask differences in the way a poikilohydric epiphytic cryptogam, for example, could conserve atmospheric nutrients vs. a succulent bromeliad.

Unfortunately, research on epiphyte nutrition has not encompassed the wide range of potential morphology, physiology, and anatomy that may be responsible for dynamics in nutrient uptake and release observed in this study.

It should also be kept in mind that the alteration of precipitation is but one pathway of nutrient flux from canopy to forest floor. Measurements of epiphyte-specific rates of litterfall and decomposition, as well as quantification of uptake by host tree canopy roots in a wide range of forest types are crucial to accurately assess how epiphytes function in overall nutrient cycles.

#### SUMMARY AND CONCLUSIONS

Results from this and other studies support the hypothesis that epiphytes in both temperate and tropical forests form an independent but related sub-unit of many rainforest tree crowns. The literature on epiphyte ecology suggests that their role in nutrient cycling may be greater than their size (relative to other forest components). A review of the growing body of information on epiphytes and nutrient cycling suggests that a nutrient cycling model of finer resolution than is traditionally considered is necessary to accurately-

TABLE 3. Alteration of throughfall nutrient flux by epiphyte mats, Olympics (November 1980–1981, January–November 1981 for branch pair III) and Monteverde (October–November 1981 and January–March 1982). Values are total throughfall nutrients from intact branches minus total throughfall nutrients from stripped branches (mg/m<sup>2</sup>). Wilcoxon signed-rank tests were used on the paired throughfall nutrient values for each time interval to test for differences between intact and stripped branches. E\* = significantly greater amounts beneath branches with epiphytes intact. S\* = significantly greater amounts beneath stripped branches. NS = no significant difference between intact vs. stripped branch pair ( $P < 0.05$ ).

Branch pair	Element					
	N	P	Ca	K	Mg	Na
Olympics, wet season						
I	+595 E*	+247 E*	+1,758 E*	+3,774 NS	+1,114 E*	+1,676 E*
II	+821 E*	+88 NS	+2,709 E*	+3,953 NS	+215 NS	+887 NS
III	+360 E*	+458 E*	+2,256 E*	+247 NS	+296 NS	-492 NS
Monteverde, wet season						
I	+55.8 E*	+0.9 E*	+55.0 E*	+35.7 NS	+17.3 E*	+5.6 NS
II	+0.6 NS	+0.1 NS	+10.9 E*	+2.4 NS	+2.3 NS	+0.3 NS
Monteverde, dry season						
I	-18.8 S*	-1.5 S*	-113.6 S*	-94.9 S*	-8.6 NS	-8.2 S*
II	-16.7 S*	-0.3 NS	-34.5 S*	-35.4 NS	+4.5 NS	-0.4 NS
III	-1.5 NS	-0.3 NS	-52.1 S*	-52.2 NS	+27.2 NS	-2.8 S*

ly describe patterns and processes of nutrient cycling in ecosystems such as those described here, i.e., forest with high precipitation, potentially infertile soils, massive loads of live epiphytes and accumulations of large amounts of dead organic matter within the canopy.

In these systems, epiphytes may enhance the nutrient status of their host trees by virtue of their physical, chemical, and physiological attributes. They may swell the nutrient capital of the canopy because their large substrate surface area and their efficient nutrient absorptive capacity provide greater interception of nutrient sources that may be unavailable or less available to other canopy components. Epiphytes may also act as "nutrient capacitors," by buffering the pulses of nutrients that arrive in the dry season, and releasing them only under heavy rainfall conditions of the wet season. The minerals they accrue are then transferred to the forest floor and within the canopy via the same pathways that circulate minerals acquired by host trees. This could reduce the chances of their loss from the ecosystem. Thus, although epiphytes make up a relatively small portion of the total ecosystem in terms of the amounts of nutrients they contain, they may

contribute to nutrient conservation of the rain-forest as a whole and should be considered as functional elements in future nutrient cycling studies.

#### LITERATURE CITED

- AZEVEDO, J. AND D. MORGAN. 1974. Fog precipitation in coastal California forests. *Ecology* 55: 1135–1141.
- BENZING, D. 1970. Availability of exogenously-supplied nitrogen to seedlings of Bromeliaceae. *Bull. Torrey Bot. Club* 97: 154–159.
- . 1981. Mineral nutrition of epiphytes: an appraisal of adaptive features. *Selbyana* 5: 219–223.
- AND J. SEEMAN. 1978. Nutritional piracy and host tree decline. *Selbyana* 2: 133–148.
- CARROLL, G. 1980. Forest canopies: complex and independent subsystems. Pp. 1–16 in R. WARING, ed., *Forests: fresh perspectives from ecosystem analysis*. Oregon State Univ. Press, Corvallis.
- CRONAN, C. AND W. REINERS. 1983. Canopy processing of acidic precipitation by coniferous and hardwood forests in New England. *Oecologia* 59: 216–223.
- DENISON, W., D. TRACY, F. RHOADES, AND M. SHERWOOD. 1972. Direct, non-destructive measurement of biomass and structure in living, old-growth

- Douglas-fir. Pp. 147-158 in J. FRANKLIN, L. DEMPSTER, AND R. WARING, eds., Proceedings of the symposium on research on coniferous forest ecosystems. Pacific Northwest Forest and Range Experiment Station, Portland.
- DRESSLER, R. 1981. The orchids: natural history and classification. Harvard Univ. Press, Cambridge.
- FORMAN, R. 1975. Canopy lichens with blue-green algae: a nitrogen source in a Colombian rainforest. *Ecology* 56: 1176-1184.
- GOLLEY, F., J. MCGINNIS, AND R. CLEMENTS. 1971. La biomasa y la estructura de algunos bosques de Darién, Panama. *Turrialba* 21: 189-196.
- GORHAM, E. 1959. Comparison of lower and higher plants as accumulators of radioactive fallout. *Canad. J. Bot.* 37: 327-329.
- JENIK, J. 1973. Root systems of tropical trees. 8. Stilt-roots and allied adaptations. *Preslia* 45: 250-264.
- JOHANSSON, D. 1975. Ecology of epiphytic orchids in West African rain forests. *Amer. Orchid Soc. Bull.* 44: 125-136.
- KELLMAN, M., J. HUDSON, AND K. SANMUGADAS. 1982. Temporal variability in atmospheric nutrient influx to a tropical ecosystem. *Biotropica* 14: 1-9.
- LEBLANC, F. 1972. The epiphytic vegetation of *Populus balsamifer* and its significance as an air pollution indicator in Sudbury, Ontario. *Canad. J. Bot.* 50: 519-528.
- LIKENS, G. AND F. BORMANN. 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. *Bull. Yale Univ. School Forest.* 79. 25 pp.
- LOVETT, G. 1981. Forest structure and atmospheric interactions: predictive models for subalpine Balsam-fir forests. Ph.D. thesis, Dartmouth College, Hanover, New Hampshire.
- MADISON, M. 1977. Vascular epiphytes: their systematic occurrence and salient features. *Selbyana* 2: 1-13.
- MASSMAN, W. 1983. The derivation and validation of a new model for the interception of rainfall by forest. *Agric. Meteorol.* 28: 261-286.
- NADKARNI, N. 1981. Canopy roots: convergent evolution in nutrient cycles. *Science* 214: 1023-1024.
- . 1983. The effects of epiphytes on nutrient cycles within temperate and tropical rainforest tree canopies. Ph.D. dissertation, Univ. Washington, Seattle.
- . 1984. Biomass and mineral capital of epiphytes in an *Acer macrophyllum* community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. *Canad. J. Bot.* 62: 2223-2228.
- . 1985. Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* 16: 249-256.
- PIKE, L. 1971. The role of epiphytic lichens in nutrient cycles and productivity in an oak woodland. Ph.D. dissertation, Univ. Oregon, Eugene.
- . 1978. The importance of epiphytic lichens in mineral cycles. *Bryologist* 81: 247-257.
- , W. DENISON, D. TRACY, M. SHERWOOD, AND F. RHOADES. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *Bryologist* 78: 389-402.
- , R. RYDELL, AND W. DENISON. 1977. A 400-year-old Douglas-fir and its epiphytes: biomass, surface area, and their distributions. *Canad. J. For. Res.* 7: 680-699.
- PÓCS, T. 1980. The epiphytic biomass and its effect on the water balance of two rainforest types in the Uluguru Mountains. *Acta Bot. Acad. Sci. Hung.* 26: 143-167.
- REINERS, W. AND R. OLSON. 1984. Effects of canopy components on throughfall chemistry: an experimental analysis. *Oecologia* 63: 320-330.
- RHOADES, F. 1981. Biomass of epiphytic lichens and bryophytes on *Abies lasiocarpa* on a Mt. Baker lava flow, Washington. *Bryologist* 84: 39-47.
- SANFORD, W. 1968. The distribution of epiphytic orchids in Nigeria in relation to each other and geographic location, climate, type of vegetation, and tree species. *J. Linn. Soc., Biol.* 1: 247-258.
- SCHAEFER, D. AND R. OLSON. 1984. Forest canopy chemical processing of nitrogen and sulfur during a summer storm. *Bull. Ecol. Soc. Amer.* 65: 238.
- SKYE, O. AND W. OECHEL. 1979. Moss production in a black spruce *Picea mariana* forest with permafrost near Fairbanks, Alaska, as compared with two permafrost-free stands. *Holarctic Ecol.* 2: 249-254.