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Biomass and mineral capital of epiphytes in an *Acer macrophyllum* community of a temperate moist coniferous forest, Olympic Peninsula, Washington State

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The epiphyte community of a Pacific northwest temperate rain forest makes up a conspicuous portion of the canopy, especially on the *Acer macrophyllum* trees that grow along river terraces of wet western slopes of the Olympic Mountains. Destructive sampling methods were used to assess the composition, biomass, and nutrient concentrations of live and dead epiphytes on representative host trees to determine the mineral capital contained in the epiphytic components of the standing vegetation. Average epiphyte standing crop on mature *Acer macrophyllum* trees is 35.5 kg. The nutrient capital (grams) is N, 370; P, 44; K, 145; Ca, 270; Mg, 50; and Na, 9. Although epiphyte biomass constitutes less than 2% of total aboveground ecosystem dry weight, it is equivalent to nearly four times the foliar biomass of host trees on a single-tree basis. Epiphytes are efficient at garnering nutrients from atmospheric sources and retaining them within the biotic portion of the ecosystem. They supplement the nutrient-gathering apparatus of host trees and buffer nutrient pulses on a short-term and on a seasonal basis.

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Dans une forêt ombrophile tempérée du nord-ouest des États-Unis, la communauté épiphyte constitue une fraction importante du couvert forestier, surtout sur les individus arborescents d'*Acer macrophyllum* qui croissent le long des terrasses fluviales des pentes occidentales humides des monts Olympic. Des méthodes d'échantillonnage destructrices ont été utilisées pour évaluer la composition, la biomasse et la concentration d'éléments nutritifs des plantes épiphytes vivantes et mortes sur des arbres-hôtes représentatifs, dans le but de déterminer le capital minéral contenu dans la fraction épiphyte de la végétation. La biomasse moyenne des plantes épiphytes sur les arbres matures d'*Acer macrophyllum* est de 35,5 kg. Leur capital en éléments nutritifs (en grammes) est le suivant: N, 370; P, 44; K, 145; Ca, 270; Mg, 50; Na, 9. Bien que la biomasse des plantes épiphytes constitue moins de 2% du poids sec total des parties aériennes de l'écosystème, elle équivaut, sur la base d'arbres individuels, à presque quatre fois la biomasse foliaire des arbres-hôtes. Les plantes épiphytes sont capables de recueillir efficacement les éléments nutritifs à partir de sources atmosphériques et de les conserver dans la fraction biotique de l'écosystème. Elles ajoutent un supplément au mécanisme de capture des éléments nutritifs des arbres-hôtes et elles tamponnent les variations d'éléments nutritifs à court terme et à l'échelle saisonnière.

[Traduit par le journal]

Introduction

Forests that grow along the west coast of the Olympic Peninsula are unique in their structure and composition and have been singled out for scientific and public attention. The relatively warm winters and dry summers, coupled with orographically induced rains of up to 5000 mm/year, have given rise to what is popularly known as the "Olympic rain forest." As generally recognized, it is an old-growth forest, dominated by *Picea sitchensis* (Bong.) Carr and *Tsuga heterophylla* (Raf.) Sarg., and is found in four major river valleys (Hoh, Queets, Quinalt, and Bogachiel) on the western slopes of the Olympic Mountains (Hult 1954; Kirk 1966; Franklin and Dyrness 1973). These forests are unusual within the *Picea sitchensis* zone because of the massive size but low densities of trees with relatively open canopies and understories. Scattered through the forests along river terraces are groves of large, even-aged stands of bigleaf maple (*Acer macrophyllum* Pursh.).

A distinctive feature of these forests, and one that closely parallels tropical rain forests, is the conspicuous presence of epiphytic plants and their accompanying mats of organic matter. As with the canopy flora of other temperate moist forests (Baur 1964), the epiphytic community is dominated by cryptogams which drape nearly all surfaces of trunks, branches, and fallen logs. These epiphytes have been the object of several studies, most of which have focused on aspects of their taxonomy (Howard 1950; Lawton 1971) and phytosociology (Coleman *et al.* 1956; Sharpe 1956; Hoffman and Kazmierski 1969; Vitt and Ostafichuk 1973; Pike *et al.* 1975).

Many aspects of epiphyte morphology, physiology, and life history contribute to their efficiency at garnering and retaining nutrients from atmospheric sources (Benzing 1981; Richardson 1981). By virtue of their powers of mineral accretion and their location along primary nutrient flux routes, epiphytes can be major participants in the impoundment and movement of mineral elements in forest ecosystems (Pike 1978). The effects of epiphytes on ecosystem-level interactions have been investigated in only a few studies (Pike 1972, 1978; Denison 1973; Benzing and Seeman 1978; Forman 1975; Lang *et al.* 1976; Lang *et al.* 1980; Schlesinger and Marks 1977; Rhoades 1981). Several of these studies provided detailed information on host tree surface area, epiphyte biomass, nutrient capital, and nutrient turnover in forests of the Pacific northwest (Denison *et al.* 1972; Pike 1978; Rhoades 1981).

Assessing the size of the mineral capital contained in epiphytes is an important first step in determining their role in rain-forest nutrient dynamics and in obtaining a more complete and accurate inventory of all ecosystem components. Minerals contained in their living and dead tissues constitute a nutrient pool, distinct from host tree minerals, which are immobilized for some span of time within the canopy. These can be transferred to other parts of the ecosystem via litter fall, crown leaching, herbivory, and in some cases, by host tree canopy root systems (Nadkarni 1981).

In this paper, as part of a comparative study of within-canopy nutrient dynamics in temperate and tropical rain forests, I (*i*) report on the composition, biomass, and nutrient

capital contained in the epiphyte community on bigleaf maple trees in the Olympic rain forest, (ii) compare the Olympic rain forest epiphyte biomass and nutrient pool with those in other temperate and tropical rain forests, and (iii) discuss some of the processes by which epiphytes are able to garner and retain the atmospheric nutrients they encounter in the canopy.

In this paper, *epiphyte mat* is defined as the combined unit of living arboreal plants and their associated detrital matter found within host tree crowns; *biomass* is the dry weight of the living matter and *standing crop* is that of the living and dead components. Nomenclature of plants follows that of Franklin and Dyrness (1973).

Study area

Research was conducted in the Hoh River Valley on the west coast of the Olympic Peninsula, in the northwest corner of Washington State (47°50' N, 124°05' W). The climate is characteristic of cool maritime areas; winter minimum temperatures rarely fall below 0°C. The most outstanding climatic characteristic is the heavy annual rainfall, 4400 to 5000 mm/year (Anonymous 1965). Seasonal rainfall patterns are striking, with nearly 80% of the precipitation falling from November to April, causing the pronounced dry summers when rainfall can be as low as 100 mm/month (Larson 1979).

The Hoh River drainage carries meltwater from five alpine glaciers. Fonda (1974) described the soils along the river terraces from river flats to mountain slopes and found high correspondence between soil profile development and plant community composition. Soils under bigleaf maple stands are classified as udifluvents (Franklin and Dyrness 1973). They are loamy sands, very dark grey, with an A-horizon of about 8 cm and a weakly developed B-horizon of 8 to 22 cm. Mean depth to river cobbles of 40 cm indicates a shallow valley fill. Soils are very wet for most of the year, with nearly 100% saturation during the winter months, drying significantly only during summer droughts (Fonda 1974).

Franklin and Dyrness (1973) classified the vegetation of the Hoh Valley as a variant of *Picea sitchensis* zone forests. It is an old-growth forest supporting *Picea sitchensis* and *Tsuga heterophylla* trees of massive sizes, with relatively open canopies. The shrub layer is also open, except for large clumps of *Acer circinatum* Pursh., *Vaccinium ovalifolium* Smith, *Rubus spectabilis* Pursh., and other shrubs. Members of the forest floor flora include such herbs and ferns as *Oxalis oregana* Nutt. and *Polystichum munitum* (Kaulf.) Presl., accompanied by a thick moss layer, including *Eurhynchium oregonum* (Sull.) J. & S., *Rhytidiadelphus loreus* (Hedw.) Warnst., and *Hylocomium splendens* (Hedw.) B. S. G.

The abundant and diverse epiphyte community is supported by almost all of the tree species with greatest accumulations on *Acer macrophyllum*. Epiphytes include over 130 species of lichens, liverworts, mosses, and ferns (Coleman *et al.* 1956; Sharpe 1956). Some of the common epiphytes are the cryptogams *Isoetes stoloniferum* (Mitt.) Ren. & Card., *Porella navicularis* (Lehm. & Lindenb.) Lindb., *Rhytidiadelphus loreus*, *Radula bolanderi* Gottsche, the club moss *Selaginella oregana* D. C. Eaton, and the fern *Polypodium vulgare* L.

Fonda (1974) classified the vegetation along the Hoh River into five distinct types; study areas for this investigation were located within the *Acer macrophyllum* zone. These even-aged, nearly monospecific stands are restricted to a narrow band along the river, located between the *Alnus rubra* stands adjacent to the river and the *Picea-Acer-Populus* zone on the first river terrace that occurs closer to the valley slopes.

Two study areas were established in the bigleaf maple stands along the main fork of the Hoh River (Fig. 1). One was located within the boundaries of the Olympic National Park, 1.5 km west of the Hoh Ranger Station, and was used to determine forest composition and tree density. The second site was used for destructive sampling in determining epiphyte composition and host tree dimensions. It was located

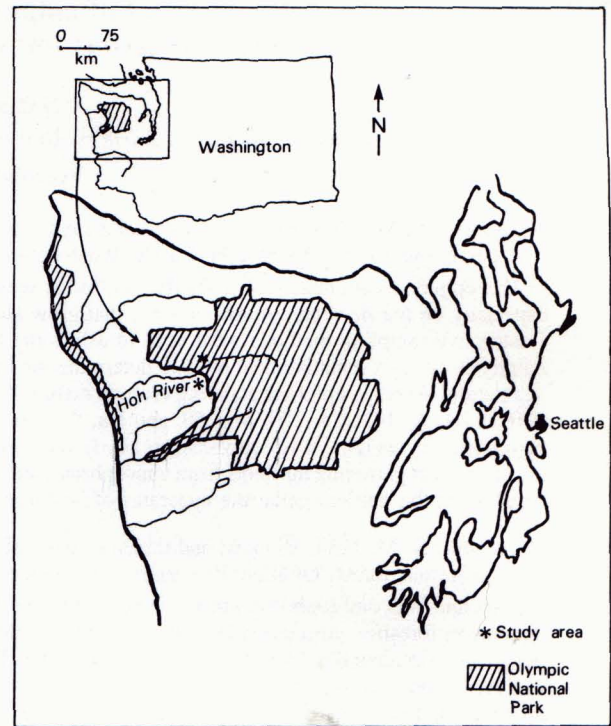


FIG. 1. Location of study area.

on private land on the south side of the Hoh River and was accessible by state logging and private roads 21.5 km east of Highway 101.

Methods

Canopy access

Safe and nondestructive access to the upper tree canopy was accomplished by using modified mountain-climbing techniques developed by Perry (1978) and others (Mitchell 1982). This involves rigging a canopy tree with climbing ropes and ascending to the canopy with seat harness, leg loops, and climbing ascenders. By shooting lines from one part of the tree crown to another with a slingshot and monofilament line, nearly all parts of the crown were within measuring distance.

Epiphyte dry weight and composition

Assessment of epiphyte dry weight was restricted to individuals of *Acer macrophyllum* in the study plots located outside park boundaries. Because the study site was relatively uniform with respect to tree density, size, form, age, and epiphyte loads, one individual from each of three 10 × 10 m plots was chosen as a sample tree. Trees whose branches provided greatest accessibility to all portions of the canopy were selected. The general approach followed Pike *et al.* (1977) and involved estimating the epiphyte substrate surface area and then calculating ratios of epiphyte mat dry weight to substrate surface area on representative host trees. These figures were then expanded to estimates of whole-tree epiphyte standing crop.

To determine the total tree surface area, three sample trees were rigged with ropes, climbed, and then mapped with compass, tape, and clinometer. Sample tree surface area was stratified into three components: trunk, branches, and twigs. The latter category was defined as any branch with a diameter less than 1 cm. Branches were numbered and data on height above the forest floor, length, and angle from vertical were recorded.

The trunk was divided into 1-m segments, with measured diameters. Segments were treated as "cylindrants" for calculation of surface area and for determination of epiphyte dry weight ratios. Five sample branches from each tree (selected randomly with respect to crown location) were cut at the junction with the bole and carefully lowered to the forest floor with pulleys positioned above the sample branches.

TABLE 1. Dimensions of sample *Acer macrophyllum* host trees used in assessing tree surface (SA) and epiphyte standing crop

	Tree height (m)	DBH* (cm)	No. of branches	Trunk SA (m ²)	Branch SA (m ²)	Twig SA (m ²)	Total SA (m ²)
Tree I	23	102	14	19.65	6.04	1.32	27.01
Tree II	28	100	20	22.50	10.96	1.88	35.34
Tree III	21	90	19	21.90	5.92	1.51	29.33
Mean (SE)	24 (2.1)	98 (5.1)	18 (1.8)	21.35 (0.86)	7.64 (1.65)	1.57 (0.16)	30.56 (2.48)

*DBH, diameter at breast height.

These branches were then divided into segments 1 m long; midsection diameters, length, and number of twigs along the main branch axis were measured. Total surface area of branches was calculated by multiplying mean branch surface area by the total number of branches per tree. Twig surface area was calculated by multiplying total twig length for each of the five sample branches by an estimated mean circumference of 0.5 cm. This was extrapolated to whole-tree twig surface area by multiplying that figure by the total number of branches per tree. Total tree substrate surface area was calculated by summing total trunk, total branch, and total twig surface area for each tree.

Trunks were systematically stripped of their epiphyte mats in 1-m sections, separated into live and dead components (which included accumulated organic matter and humus), and weighed in the field. Epiphyte mat subsamples (bands that were 20 cm in width) from each 1-m trunk segment were transported to the laboratory in plastic bags to prevent water loss for further separation and determination of epiphyte mat nutrient composition. Subsamples were oven-dried to constant weight at 75°C for 48 h. Epiphyte standing crop on branches was assessed similarly, by weighing epiphytes from the five branches used for surface area determinations. Epiphyte mats were stripped from 1-m long segments, separated into live and dead components, and weighed in the field. Subsamples were taken for determining composition and equivalent dry weights. All epiphytes on twigs were also collected. As there were only negligible amounts of dead epiphytes or organic matter, all twig epiphytes were classified as live biomass.

Epiphyte mat dry weight on trees was estimated by determining the standing crop of epiphytes on sampled areas of the trees used for determination of surface area and obtaining ratios of standing crop to tree substrate surface area. These were averaged for each of the tree components and multiplied by that component surface area to yield total component epiphyte standing crop; these were summed to estimate total tree epiphyte standing crop.

Epiphyte nutrient content

Assessment of epiphyte nutrient content was carried out at the University of Washington Soils Laboratory with the oven-dried subsamples which were used in determining dry-weight equivalences. Three replicates of each epiphyte mat component were ground in a Wiley mill (20-mesh screen), and 0.5-g samples were digested in lithium sulfate in a micro-Kjeldahl apparatus (Parkinson and Allen 1975). These were filtered and quantitatively transferred to flasks. Total nitrogen and phosphorus were analyzed by a Technicon auto-analyzer. Calcium, magnesium, and potassium were determined with an atomic absorption spectrophotometer (model IL 951), and sodium was determined by atomic emission, using standard methods. Replicate sample concentrations were within 2% of the mean, and their averages were used to calculate epiphyte mat nutrient capital.

Results

The substrate surface for representative whole trees was estimated to be 30.6 m² (SE = 2.5 m², n = 3). Dimensions of sample host trees and the distribution of their surface areas within their crowns are presented in Table 1.

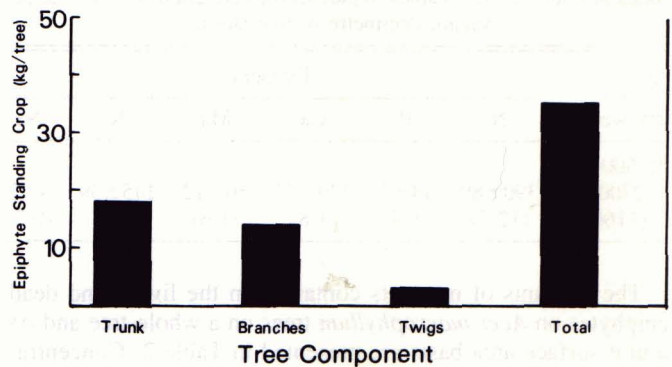


FIG. 2. Distribution of epiphyte standing crop (live and dead components) on single representative *Acer macrophyllum* host trees.

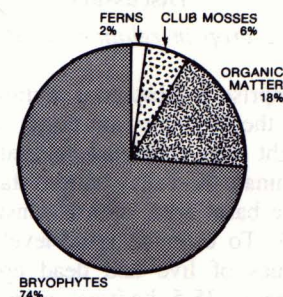


FIG. 3. Composition of epiphyte mats on host trees, expressed as percentages of total epiphyte mat dry weight. Data given are for a representative *Acer macrophyllum* tree (diameter at breast height = 98 cm; height = 24 m).

The average fresh weight of epiphyte mats on individual representative host trees was 42.5 kg. Dry weight per fresh weight ratios of epiphytes from subsamples taken from each tree component ranged between 0.3 and 0.7 but varied little (within 5%) for each epiphyte type. Dry weight per unit area was calculated separately for each component, with a whole-tree average of 11.6 g/cm². The average epiphyte standing crop (dry weight) for these trees was 35.5 kg (SE = 2.7 kg, n = 3). The distribution of epiphyte mat dry weight is presented in Fig. 2.

Live epiphytes make up approximately 82% of the total standing crop on a whole-tree basis. Mosses, liverworts, and the club moss *Selaginella oregana* contribute approximately 95% of the living component, with the balance consisting of the epiphytic fern *Polypodium vulgare* and "accidental" terrestrial herbs such as *Oxalis oregana* and *Tiarella trifoliata* L. (Fig. 3).

TABLE 2. Mean nutrient concentrations of epiphyte mat components on *Acer macrophyllum* host trees. Concentrations are expressed in percent of nutrient on a dry weight basis. Standard errors are in parentheses

Epiphyte mat component	Element					
	N	P	Ca	Mg	K	Na
Live epiphytes	1.10 (0.08)	0.125 (0.01)	0.76 (0.07)	0.14 (0.001)	0.41 (0.025)	0.026 (0.002)
Dead epiphytes	1.47 (0.02)	0.14 (0.003)	2.43 (0.09)	0.18 (0.005)	0.294 (0.014)	0.017 (0.001)

TABLE 3. Epiphyte mat dry weight and nutrient capital for representative *Acer macrophyllum* host trees ($n = 3$). Results are whole-tree totals in grams \pm SE. Values in parentheses are grams of material per square decimetre of tree surface

Total dry weight	Element					
	N	P	Ca	Mg	K	Na
35 500 \pm 2700 (1160)	390 \pm 89 (12.7)	44 \pm 7 (1.4)	270 \pm 72 (8.8)	50 \pm 12 (1.6)	145 \pm 39 (4.7)	9 \pm 2 (0.3)

The amounts of nutrients contained in the living and dead epiphytes on *Acer macrophyllum* trees on a whole-tree and on a unit surface area basis are presented in Table 2. Concentrations of epiphyte nutrients that were used in these calculations are shown in Table 3.

Discussion

Epiphyte standing crop in relation to other ecosystem components

Epiphytes comprise a substantial portion of within-canopy standing crop in the Olympic rain forest. Assessment of epiphyte mat weight was restricted to mature bigleaf maple trees, which dominate the valley bottom stands. They make up 90% of total tree basal area, with a density of 185 trees/ha (Nadkarni 1983). To estimate stand-level epiphyte standing crop, mean values of live and dead epiphyte dry weight for individual trees (35.5 kg/tree) were extrapolated to a theoretical pure stand of *Acer macrophyllum* (191 trees/ha), equivalent to a stand-level standing crop of 6870 kg/ha.

This value is larger, though of the same order of magnitude, than estimates of epiphyte standing crop of other forests of the Pacific northwest. Those range from 900 kg/ha in an old-growth Douglas-fir forest (Pike *et al.* 1977) to 4220 kg/ha in an *Abies lasiocarpa* forest (Rhoades 1981) (Table 4). Because *Acer macrophyllum* trees carry the largest epiphyte loads of all tree species in the Olympic rain forest, this higher value is reasonable.

The nutrient capital which would be contained in the epiphyte standing crop of a pure bigleaf maple stand (calculated by multiplying the total dry weight of epiphyte mats by their elemental concentrations) are (in kilograms per hectare) N, 72; P, 8; K, 32; Ca, 51; Mg, 9; and Na, 2. The relative proportions contained in live and dead components are presented in Fig. 4.

Epiphyte abundance is generally considered to reach a peak in tropical rain forests, specifically in neotropical montane cloud forests and elfin woodlands (Madison 1977). Estimates from the few tropical nutrient cycling studies which have included assessments of epiphyte dry weights range widely, from 1400 kg/ha in a Panamanian montane forest (Golley *et al.*

1971) to 14 000 kg/ha in a Tanzanian elfin forest (Pócs 1980) (Table 4). The estimate of 6870 kg/ha for the temperate Olympic rain-forest epiphyte standing crop is within the range for values of tropical rain forests. This confirms the general impression that epiphyte standing crop in temperate-latitude rain forests can reach comparable levels with their tropical counterparts.

Epiphytes have often been discounted or ignored in mineral cycling studies. In many forests, they compose but a small fraction of total ecosystem dry weight. The total ecosystem standing crop of a temperate moist coniferous forest similar to the Olympic site (*Pseudotsuga-Acer-Polystichum* stands in the H. J. Andrews Experimental Forest, western Oregon) was estimated at 1513 t/ha (Grier and Logan 1977). The estimated 5.9 t/ha of epiphyte biomass is 82% of total epiphyte standing crop in the Hoh Valley. This is equivalent to less than 0.1% of total ecosystem biomass and 1% of the 554.5 t/ha aboveground biomass of the Oregon forest.

Obviously, the largest part of the total forest biomass is in the tree component. However, this biomass represents many years of growth and is stored in unavailable organic forms. In contrast, the epiphyte biomass represents only 1 to 10 years of growth. Epiphytic bryophytes, lichens, and ferns function much as the foliar and twig components of tree and understory members in terms of decomposition rates. They are composed mainly of photosynthetically active, labile materials, and turnover times are rapid (Pike 1972).

Comparison of living epiphyte biomass to foliar biomass of host trees and understory members reveals a different picture from the comparison to total stand biomass. Data on weights of individual *Acer macrophyllum* trees in the western Oregon stands of Grier and Logan (1977) were used as a basis for comparison with epiphyte biomass on bigleaf maple in the Olympic study site. *Acer macrophyllum* trees at these sites are of comparable heights ($\bar{x} = 20.6$ m) but with somewhat smaller diameters ($\bar{x} = 20.4$) than those of the Olympic forest (Table 1). Estimates of foliar biomass of the former may be an underestimation; no comparable data exist for the Olympic trees. Living epiphyte dry weight exceeds that of the Oregon host-tree foliage fourfold (29.1 kg/tree versus 7.3 kg/tree). By using values computed for pure *Acer macrophyllum* stands, epiphyte biomass would exceed herb and small shrub biomass combined (5.26 t/ha versus 1.8 t/ha, respectively). Thus, epiphytes swell the mineral capital of the aboveground portions of temperate moist forests.

Processes of epiphyte nutrient accretion

Epiphytes may increase the nutrient capital contained in the aboveground portions of the ecosystem in two general ways: (i) epiphytes can increase the nutrient-gathering apparatus of a host tree (and, by expansion, a forest), and (ii) epiphytes can

TABLE 4. Average dry weight of epiphyte mats on representative host trees (kilograms per tree) and in representative stands (kilograms per hectare) in temperate and tropical rain forests. ND, not determined

Forest type	Location	Single-tree epiphyte standing crop	Stand-level epiphyte standing crop	Source
Temperate ecosystems				
Old-growth Douglas-fir	Blue River, OR	17.9	900	Pike <i>et al.</i> 1977
Oak woodland	Willamette River, OR	ND	1 800	Pike 1972
<i>Abies lasiocarpa</i>	Mt. Baker, WA	9.3	4 220	Rhoades 1981
Bigleaf maple stands, Olympic rain forest	Hoh River, WA	35.5	6 870	This study
Tropical ecosystems				
Premontane	Darien, Panama	ND	1 400	Golley <i>et al.</i> 1971
Submontane	Uluguru Mountains, Tanzania	ND	2 130	Pócs 1980
Cloud forest	Monteverde, Costa Rica	ND	4 730	Nadkarni 1983
Mossy elfin woodland	Uluguru Mountains	ND	14 000	Pócs 1980

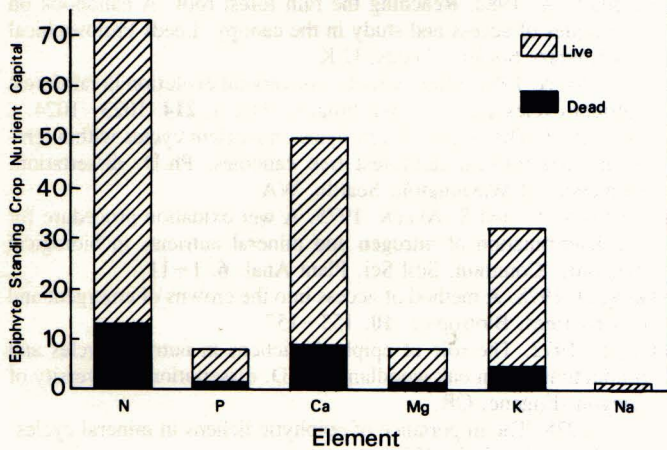


FIG. 4. Nutrient capital contained in epiphyte mats (live and dead epiphytes and accumulated organic matter) in *Acer macrophyllum* stands (kilograms per hectare).

act as "nutrient capacitors," buffering nutrients that arrive in pulses by holding within the biotic components incoming nutrients that might otherwise be lost to the ecosystem.

Epiphytes enhance the nutrient-gathering capacity because of their physical, chemical, and physiological attributes. First, epiphyte mats increase the surface area of their substrate; surface area of branches plus epiphytes is greater than the surface area of branches alone. The filigree of mosses and other bryophytes exposes a larger physical surface which dust encounters and upon which rainfall and drifting mist condense as they pass through the forest canopy. Second, the chemical nature of an epiphyte mat lends itself to trapping nutrients; negatively charged sites in the mats of organic matter no doubt contribute to garnering and holding cations in throughfall. Third, many cryptogamic epiphytes have physiological and morphological features, such as poikilohydric foliage, which make them efficient at intercepting aerial-borne nutrients (Gorham 1959; Hoffman 1966; Rieley *et al.* 1979; Proctor 1981).

A second means by which epiphytes can enhance the nutrient status of the forest is by serving as "nutrient capacitors." They intercept and hold within their biomass a nutrient "charge" from aerial sources that might otherwise be lost to the system. This would be most apt to occur when nutrients arrive in pulses and have a greater potential to temporarily "overload" the

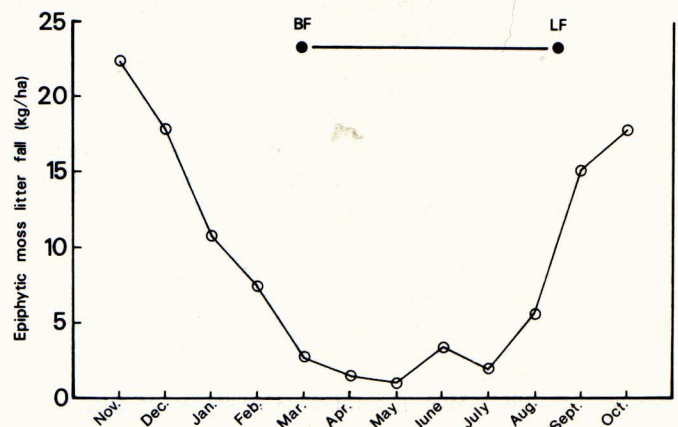


FIG. 5. Epiphytic moss production in an Oregon oak woodland, estimated from 18 months of litter-fall data (Pike 1972). Lowest production occurs from May to August and coincides with the presence of deciduous host-tree foliage, indicated by line between tree bud flush (BF) and leaf fall (LF).

system on either a daily or on a seasonal time scale.

One situation where "buffering" of nutrient pulses can occur is exemplified by the water-retaining capacity of the organic matter which accumulates beneath living epiphytic bryophytes. Even after week-long dry periods, when other canopy and forest components have thoroughly dried, mats of canopy organic matter remain moist. This increases the time available for nutrient transfer and incorporation into living tissue to take place, which must enhance nutrient impoundment.

Seasonal growth patterns may allow epiphytes to intercept and retain nutrients which host trees cannot. In temperate rain forests, epiphytic bryophytes grow most vigorously during the late autumn, winter, and early spring, when precipitation is greatest, utilizing nutrient-charged fluids that frequently and regularly pass through the canopy. Pike's (1972) litter fall and harvest data on epiphytic bryophyte productivity in an environment similar to that of the Olympics confirm that maximal growth occurs from October through March (Fig. 5). This is when deciduous host trees are leafless and incapable of extracting mineral ions from precipitation within the canopy. Host tree root uptake is presumably lowest at this time, as a result of reduced winter insolation, saturated soils, and low temperatures. Conversely, epiphytic bryophyte growth is

lowest during the dry summer months, when deciduous host trees are most active. Personal observations in the *Acer macrophyllum* canopy showed drying and extensive browning of *Selaginella* and bryophyte tissues during June, July, and August. Upon rehydration with the arrival of steady rains in October, green shoots soon appear. Thus, seasonal partitioning occurs between epiphytes and host trees in terms of timing of canopy nutrient uptake, which is imposed by their respective phenologies. Some of the nutrients in precipitation which otherwise might be lost to overstory trees during times of maximal flush can be intercepted and retained in epiphyte tissues, thus enlarging the mineral capital of the entire ecosystem.

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- ANONYMOUS. 1965. Climatological data, Washington annual summary. U.S. Weather Bureau. No. 69. pp. 228–239.
- BAUR, G. 1964. The ecological basis of rain forest management. United Nations Educational, Scientific and Cultural Organization, New York. pp. 4–34.
- BENZING, D. 1981. Mineral nutrition of epiphytes: an appraisal of adaptive features. *Selbyana*, **5**: 219–223.
- BENZING, D., and J. SEEMAN. 1978. Nutritional piracy and host tree decline. *Selbyana*, **2**: 133–148.
- COLEMAN, B., W. MUENSCHER, and D. CHARLES. 1956. A distributional study of epiphytes of the Olympic Peninsula. *Am. Midl. Nat.* **56**: 54–87.
- DENISON, W. 1973. Life in tall trees. *Sci. Am.* **207**: 75–80.
- DENISON, W., D. TRACY, F. RHOADES, and M. SHERWOOD. 1972. Direct, non-destructive measurement of biomass and structure in living, old-growth Douglas-fir. Proceedings of the Symposium on Research on Coniferous Forest Ecosystems. Edited by J. Franklin, L. Dempster, and R. Waring. Pacific Northwest Forest and Range Experiment Station, Portland, OR. pp. 147–158.
- FONDA, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology*, **55**: 924–942.
- FORMAN, R. 1975. Canopy lichens with blue-green algae: a nitrogen source in a Colombian rainforest. *Ecology*, **56**: 1176–1184.
- FRANKLIN, J., and C. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
- 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. *Can. J. Bot.* **37**: 327–329.
- GRIER, C., and R. LOGAN. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* **47**: 373–400.
- HOFFMAN, G. 1966. Observations on the mineral nutrition of *Funaria hygrometrica* Hedw. *Bryologist*, **69**: 182–192.
- HOFFMAN, G., and R. KAZMIERSKI. 1969. An ecologic study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula. *Bryologist*, **72**: 1–19.
- HOWARD, G. 1950. Lichens of the State of Washington. University of Washington Press, Seattle, WA.
- HULT, R. 1954. Untamed Olympics. Binford & Mort., Portland, OR.
- KIRK, R. 1966. The Olympic Rainforest. University of Washington Press, Seattle, WA.
- LANG, G., W. REINERS, and R. HEIER. 1976. Potential alteration of precipitation chemistry by epiphytic lichens. *Oecologia*, **25**: 229–241.
- LANG, G., W. REINERS, and L. PIKE. 1980. Structure and biomass dynamics of epiphytic lichen communities of Balsam fir forests in New Hampshire. *Ecology*, **61**: 541–550.
- LARSON, A. 1979. Origin of the chemical composition of undisturbed forested streams, western Olympic Peninsula, Washington State. Ph.D. dissertation, University of Washington, Seattle, WA.
- LAWTON, E. 1971. Moss flora of the Pacific Northwest. The Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan.
- MADISON, M. 1977. Vascular epiphytes: their systematic occurrence and salient features. *Selbyana*, **2**: 1–13.
- MITCHELL, A. 1982. Reaching the rain forest roof. A handbook on techniques of access and study in the canopy. Leeds Philosophical and Literary Society, Leeds, U.K.
- NADKARNI, N. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. *Science (Washington, D.C.)*, **214**: 1023–1024.
- . 1983. The effects of epiphytes on nutrient cycles within temperate and tropical rainforest tree canopies. Ph.D. dissertation, University of Washington, Seattle, WA.
- PARKINSON, J., and S. ALLEN. 1975. A wet oxidation procedure for the determination of nitrogen and mineral nutrients in biological materials. *Commun. Soil Sci. Plant Anal.* **6**: 1–11.
- PERRY, D. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica*, **10**: 155–157.
- PIKE, L. 1972. The role of epiphytic lichens in nutrient cycles and productivity in an oak woodland. Ph.D. dissertation, University of Oregon, Eugene, OR.
- . 1978. The importance of epiphytic lichens in mineral cycles. *Bryologist*, **81**: 247–257.
- PIKE, L., 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.
- PIKE, L., R. RYDELL, and W. DENISON. 1977. A 400-year-old Douglas-fir and its epiphytes: biomass, surface area, and their distributions. *Can. 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.
- PROCTOR, M. 1981. Physiological ecology of bryophytes. *Adv. Bryol.* **1**: 79–166.
- RHOADES, R. 1981. Biomass of epiphytic lichens and bryophytes on *Abies lasiocarpa* on a Mt. Baker lava flow, Washington. *Bryologist*, **84**: 39–47.
- RICHARDSON, D. 1981. The biology of mosses. Blackwell, London, England.
- RIELEY, J., P. RICHARDS, and A. BEBBINGTON. 1979. The ecological role of bryophytes in a north Wales woodland. *J. Ecol.* **67**: 497–528.
- SCHLESINGER, W., and P. MARKS. 1977. Mineral cycling and the niche of Spanish moss, *Tillandsia usneoides* L. *Am. J. Bot.* **64**: 1254–1262.
- SHARPE, G. 1956. A taxonomic-ecological study of the vegetation by habitats in eight forest types of the Olympic rainforest. Ph.D. dissertation, University of Washington, Seattle, WA.
- VITT, D., and M. OSTAFICHUK. 1973. Follicolous bryophytes and lichens of *Thuja plicata* in western British Columbia. *Can. J. Bot.* **51**: 561–580.