Forest Canopies: Complex and Independent Subsystems

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The growth of trees, indeed that of all vascular plants , involves the transfer of matter and energy through two critical interfaces between the organism and its environment: one between roots and the soil and a second between the canopy and the atmosphere. Studies on the root–soil interface have largely dealt with the movement of plant nutrients other than carbon, while investigations in the canopy have centered on carbon fixation and energy budgets (Monteith, 1975). Where the movement of nutrients across the canopy interface has been investigated, the canopy has been regarded as a homogeneous black box for which only total inputs from the atmosphere and forest floor and total outputs to the forest floor can be known. Thus, multiple exchanges of substances within the canopy itself and the processes which mediate such exchanges have largely been ignored.

Even the measurement of net inputs are outputs for the canopy subsystem has often proved fraught with difficulties. The collection, sorting, and chemical analysis of litterfall is a time-consuming and expensive task which has burdened ecosystems investigations since their inception. In moist climates substantial amounts of material may move from the canopy to the forest floor in solution or in suspension. While an exhaustive review of the literature on elemental cycling in stemflow and throughfall is beyond the purview of the present discussion, some mention of the problems involved is in order, if only to justify the microcosm experiments discussed in this paper. Many of the difficulties associated with throughfall/stemflow collection and analysis relate to the necessity for a cumulative sample if seasonal or annual totals are to be generated for elemental budgets. Collectors containing water are left in the field for periods varying from one day to four weeks; the integrity of such samples begins to deteriorate the moment the water is collected, with the degree of alteration in water chemistry varying with the climate, the length of the interval before the sample is processed, and the load of microbial cells and other suspended particulates in the water. Beyond this, the size of the collecting area for field samples is seldom adequate to provide a sample large enough for multiple analyses (Lewis and Grant, 1978). Use of small sampling areas generates high variability in the data and requires that large numbers of collectors be installed to provide estimates of satisfactory precision at a stand level (Kimmins, 1973; Best, 1976). Most of the throughfall studies in the literature provide insufficient information about sampling design, collector construction, and/or sample processing to allow consistent interpretation of the results.

Lewis and Grant (1978) have discussed this entire array of difficulties with admirable succinctness and have proposed an improved design for throughfall collectors. While use of such collectors will resolve certain of the problems discussed (adequate sample size, collection of snow), they do not help with the fundamental quandary of sample integrity versus cumulative collections. The only truly satisfactory method for handling throughfall involves immediate filtration of the water through microbiological filters and freezing the filtrate prior to analysis; if tared filters are used, estimates for the microparticulate fraction in throughfall can also be generated. Such an approach is labor–intensive and can only be used on an episodic basis. Because concentrations of substances in canopy wash change over short intervals during the course of single rainstorms and seasonally, from one rainstorm to the next, data from single–storm episodes or portions thereof cannot be simply extrapolated to provide annual totals.

Even if such extrapolations were legitimate and if the data reported in the literature could be regarded as an accurate reflection of real nutrient exchanges, most investigations of elemental cycling in stemflow and throughfall suffer from a fundamental debility: they are essentially descriptive and empirical, and as such they lack predictive power. The information from such studies is peculiar to the forest stands, seasons, and climatic conditions for which it was garnered. Consequently, few inferences are possible from existing studies about probable nutrient exchanges in canopy wash from different forest stands under a different climatic regime. Thus, the basic measurement of nutrient concentrations in precipitation, stemflow, and throughfall must be repeated each time a new ecosystem is studied. This will continue to be the situation as long as we regard the canopy as a black box, as long as we lack basic knowledge of the processes involved in nutrient exchanges as incident precipitation flows and trickles over canopy surfaces.

NUTRIENT EXCHANGES IN AN OLD-GROWTH CONIFEROUS CANOPY

During the last ten years, as a result of pioneering work of W. C. Denison and his colleagues, access techniques for the canopies of old-growth Douglas fir trees have been developed, and a large amount of information is available on the biomass and distribution of various canopy components (Denison et al., 1972; Denison, 1973; Pike et al., 1975; Pike et al., 1977). The availability of accessible, described canopies has permitted me and my colleagues to make a more analytical approach towards estimating annual nutrient fluxes in the canopy wash. In brief, we hope to construct simulation models of nutrient fluxes in the canopy solution, based on experiments with laboratory microcosms in, which isolated canopy components are misted with rainfall and nutrient concentrations in the water are monitored before and after contact with the canopy sample. After describing our progress and comparing results with those from the pertinent literature, I will discuss the role of insects in the system briefly.

Nutrient Exchanges in the Canopy Solution

Materials and Methods. All studies described were carried out with samples from old-growth Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) trees located at' *two* sites within the H. J. Andrews Experimental Forest. Both sites were located in stands corresponding to the Tshe/Rhma/Bene community type (Franklin and Dyrness, 1970) and were composed predominantly of 400- to 500-year-old Douglas-fir trees. Samples were taken from the canopies of permanently rigged trees (Denison et al., 1972) and stored overnight at the laboratory at 4°C. The following day they were picked clean, placed in funnel assemblies, and misted for one hour at 16ºC with previously collected incident rainwater that had been stored frozen until just prior to use. After misting, the leachates were filtered sequentially through 30 um nylon mesh and Nuclepore filters with 0.2 um pore size; aliquots were removed for cation, total dissolved solids, and total nitrogen determinations; the remainder of the filtrate was lyophilized, reconstituted to 10 ml, and stored at -20ºC for subsequent analysis. In some cases where nitrogen concentrations were extremely low, determinations of total nitrogen were carried out on the lyophilized samples.

A flow chart is presented in Figure 1 and a synopsis of analytical methods with references is shown in Table 1. In all cases net fluxes of materials were computed by subtracting concentrations of substances in the control rainwater from those in the corresponding leachates and by correcting for the amount of water with dissolved substance retained by the components in the funnel assemblies. In order to assess the possible magnitude of nutrient transfers mediated by the canopy solution, we initiated a biweekly, and later a monthly, sampling and laboratory misting program.

We have misted Lobaria oregana, moss bolsters, 2- to 3-year-old foliage and twigs, dead twigs, and living twigs 0.5 to 2.0 cm in diameter from three heights in the canopy during each regular sampling episode. The sample has been expanded to include 1-year-old foliage, 5- to 7-year-old foliage, trunk bark, Alectoria spp., Sphaerophorus globosus, Platismatia glauca, Hypogymnia spp., and Lobaria pulmonaria on a quarterly basis. Occasionally we have misted rotting Lobaria thalli, both from the canopy and from the forest floor. This program has provided information in fluxes of cations (Na^+, K^+, Ca^{++}, Mg^{++}), total organic nitrogen, and total phosphorus both in dissolved, and particulate form. Subsequently, we have carried out prolonged misting experiments with some of the dominant canopy components. Since the data for the cation fluxes have been treated differently from those for other nutrients, they are dealt with first.

Results: cations. Information on cation fluxes was analyzed and summarized by my colleague, Dr. L. H. Pike, for the bi-weekly misting episodes from September 1976 through August 1977. A multivariate approach was taken in attempting to assess the importance of several factors which may influence cation fluxes from canopy components. Specifically, multiple regressions were carried out with cations concentration in incident rainwater, day in the water year when samples were collected, presence or absence of at least 2.0 cm rain in the three days preceding sample collection, and height of sample in the canopy as independent variables and mean net cation flux as the dependent variable. This information is summarized in Table 2. We do not ascribe great significance to the absolute numbers in the upper portion of the table, but many of the trends are highly significant, with the r^2 in the multiple regressions often greater than 0.7. Actual plots of Ca^{++} and K^+ fluxes for Lobaria oregana are provided in Pike (1978).

Reference to Table 2 reveals several general trends:

1. Uptake of Ca^{++} and Mg^{++} from the incident rainwater occurs quite commonly for the four components regularly tested. Uptake of Na^+ occurs less commonly and seems to be restricted to Lobaria and moss; uptake of K^+ occurred only once in all the samples monitored.

2. Generally, the concentration of cations in the incident rain is the most important independent variable in the multiple regressions. In virtually every case an increase in the concentration of a cation in the incident rainwater has resulted either in increased uptake or decreased leaching of that cation by the canopy component.

3. The leaching of Na^+ and K^+ from foliage and of Na^+ from twigs is strongly influenced by the day in the water year when the samples were collected, with leaching losses decreasing with increasing exposure to rain in the field during the fall and winter.

4. Loss of K from the lichen Lobaria oregana is strongly affected by the occurrence of rain in the three days prior to sample collection (leaching losses decreased after rain) and by the height in

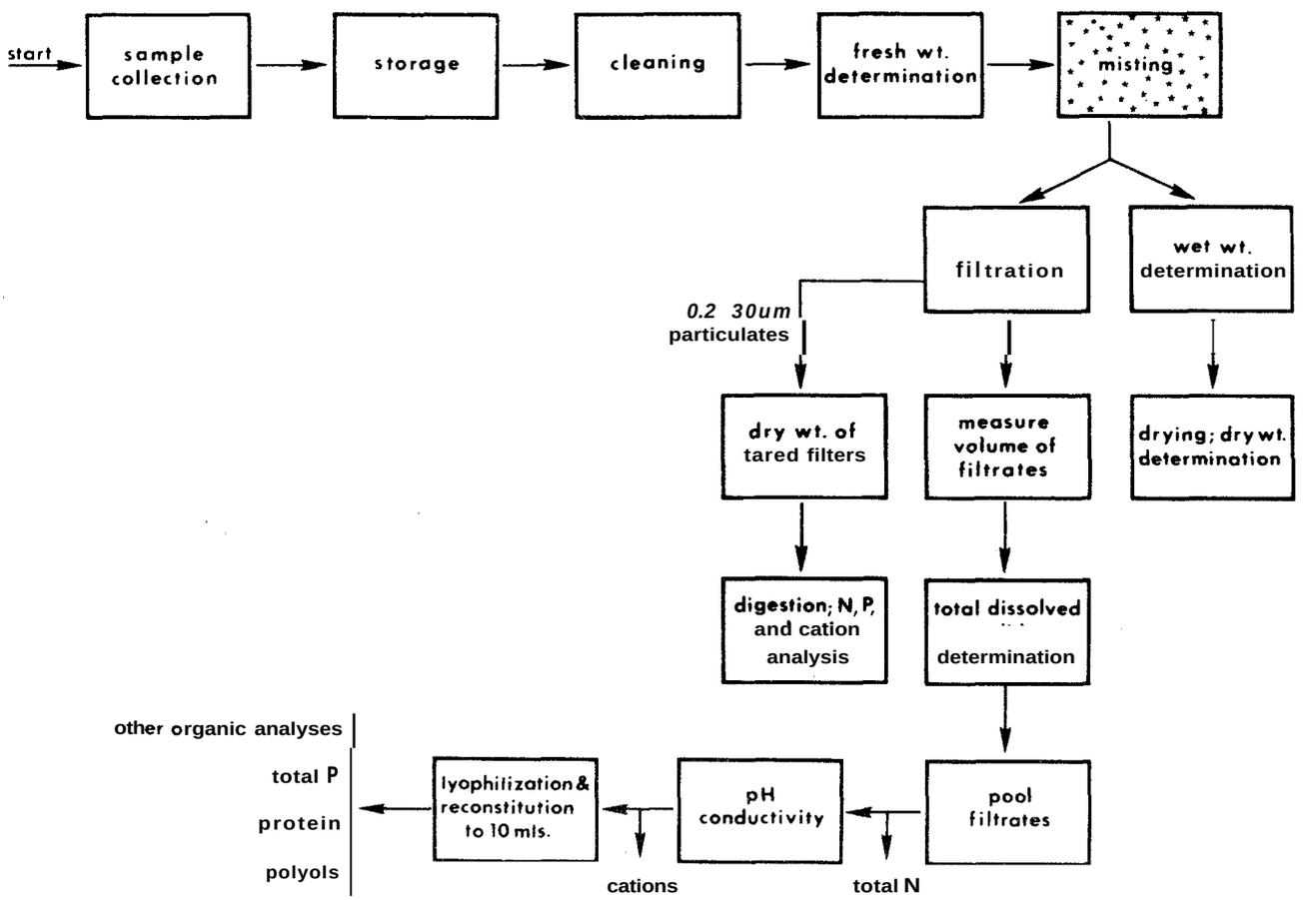

Figure 1. Flow chart for processing and analyzing canopy samples and leachates

Table 1. Synopsis of chemical analyses for leachates.

Analysis	Method	Nature of sample	No. of samples per sampling period
Suspended particulates, 0.2–30 um	Serial filtration through 30u mesh + 0.2 um Nucleopore filters; dry weights of material on tared filters	No prior treatment	36 + 2 controls
Leachate volume	Measured in graduated cylinder	Filtered leachate	36 + 2 controls
Pigment (post-filtration optical density)	O.D. reading (λ=410 nm)	Filtered leachate	36 + 2 controls
Total dissolved solids	Evaporation of 5 ml aliquots in tin-foil boats (tared); subsequent weights of tared boats	Filtered leachate	36 + 2 controls
pH	Beckman pH meter	Filtered, samples pooled	9 + 1 control
Conductivity	Markson conductivity meter	Filtered, samples pooled	9 + 1 control
Total organic nitrogen	Perchloric acid digest of 200 ul aliquots; N determined as NH_4^+ by indophenol blue method (Jaenicke, 1974)	Filtered, samples pooled	9 + 1 control
Cations (Na^+,K^+,Ca^{++},Mg^{++})	Atomic absorption spectrophotometry	Filtered, samples pooled	9 + 1 control
Total phosphorus	Perchloric acid digest of 200 ul aliquots; P determined by molybdenum blue method (Jaenicke, 1974)	Filtered, pooled, concentrated to 10 ml	9 + 1 control
Total protein	Measurement of absorption increase at 595 nm by Coomassie Blue G-250 on binding to protein (Bradford, 1976; Sedman and Grossberg, 1977)	Filtered, pooled, concentrated to 10 ml	9 + 1 control
Total polyols	Periodate oxidation followed by spectrophotometric determination of formaldehyde formed using chromotrophic acid (λ=570 nm) (Tibbling, 1968)	Filtered, pooled, concentrated to 10 ml	9 + 1 control

the canopy where the sample was collected (leaching losses less for samples collected high in the canopy). Pike (1978) has provided a chart of these trends.

Similar trends have already been reported or can be inferred from other reports in the literature. For instance, studies by Lang, Reiners, and Heier (1976) have documented uptake of NH_4^+ and losses of K^+ from thalli of Platismatia glauca, a chlorophycophilous lichen. Throughfall studies of Abee and Lavender (1972) have shown that concentrations of K+ in the throughfall decrease greatly during the course of a rainy season in the Pacific Northwest.

Particulate matter >0.2um <30um collected from these misting episodes has not been analyzed for cations. Where concentrations in solution are low (e.g. Mg++), fluxes in particulate form may completely overshadow the effects reported here. If such material is derived from microepiphytes, it may be extraordinarily efficient in cation uptake; this has been well demonstrated by Odum et al. (1970) and Witkamp (1970) for microepiphylls in a tropical rain forest in Puerto Rico. In any case, as Table 2 makes clear, the multiple exchanges of cations in a canopy can be affected by a number of factors, and any predictive models for cation fluxes in real canopies will be necessarily complex.

Results: nitrogen. The canopies of the stands studied here contain large populations of cyanophycophilous lichens which are capable of fixing nitrogen (Pike et al., 1977; Caldwell et al., 1979). Because such stands are frequently nitrogen-limited, the flow of fixed nitrogen through the canopy has been a focus for our laboratory and field studies and related modeling efforts. Total organic nitrogen in solution has been analyzed by an extremely sensitive micromethod which involves block digestion of 0.2 ml samples with 25 u1of perchloric acid and which can reliably detect as little as 0.03 ug of nitrogen (Jaenicke, 1974). The colorimetric reagents are added to the same tube in which the digestion is carried out. The analysis is simpler, faster, and far more sensitive than the conventional micro-Kjeldahl digestion followed by ammonia distillation; it deserves to be widely adopted by laboratories where organic nitrogen and ammonia are of interest. Nitrate concentrations in throughfall have been found to be very low in the Pacific Northwest, so nitrate was not analyzed in this study. Organic nitrogen in particulate matter was determined by digesting with a conventional Kjeldahl procedure tared Nuclepore filters on which microparticulates had been collected and by measuring the nitrogen in the digest spectrophotometrically as described above.

In our initial consideration of data from our biweekly and monthly misting Program we discovered that the meteorological history of the samples prior to collection greatly affected fluxes of particulate and dissolved nitrogen from canopy components. To assess the susceptibility of various components in canopy leaching, misting episodes were designated "Wet" (>0.5 cm rain in three days preceding sample collection) or "Dry" (<0.5 cm rain in same period), and the data for biweekly (9/20/76 - 12/27/76) and monthly (1/10/77 - 2/12/78) episodes were lumped accordingly. Figures 2 through 5 show these data in summary form. Although the standard errors are high for some components, several striking trends are evident:

1. Net fluxes of both dissolved and particulate nitrogen are high for cyanophycophilous lichens and relatively low for tree components. Nitrogen content for filterable solids = microparticulates varies from 3 to 4 percent.

2. Chlorophycophilous lichens and moss bolsters take up dissolved nitrogen from the incident rain.

3. Fluxes of dissolved nitrogen are higher for "dry" episodes than for "wet" episodes; for particulate nitrogen this pattern is reversed. These trends are particularly striking for cyanophycophilous lichens.

4. Older foliage tends to leach more dissolved nitrogen than younger foliage.

The differences in leaching patterns between wet and dry episodes suggest that important changes in the leaching potential of canopy components occur during the transition from a dry to a wet canopy. We investigated this transition by monitoring nutrient fluxes during prolonged (6-48 hr) laboratory misting experiments. Our results for one such experiment with &-toria (a chlorophycophilous lichen) and Lobaria (a cyanophycophilous lichen) have been discussed by Pike (1978). For &-toria, dissolved nitrogen is taken up from the incident rainwater almost from the start of the experiment, while particulate nitrogen is released. For Lobaria, an initial pulse of leaching releases nitrogen to the incident rain; after 2 to 3 hours (1-1.5 cm rain), uptake from the incident rain commences, and when cumulative net flux for a prolonged experiment is plotted, the Lobaria is also found to be a net sink for dissolved nitrogen (Figs. 9-10). While cumulative nitrogen output in particulates only partially compensates for uptake of dissolved nitrogen in Alectoria, the two quantities are roughly equivalent in Lobaria. More recent misting experiments have shown similar patterns for other canopy surfaces, notably 2- to 4-year-old

Table 2. Trends in net cation fluxes from four canopy components as influenced by several independent factors[1]

	Lobaria				Moss				Foliage (2–3 yrs)				Dead twigs (0.5–2.0 cm diam.)			
	Ca	Mg	Na	K	Ca	Mg	Na	K	Ca	Mg	Na	K	Ca	Mg	Na	K
Data from misting episodes																
Mean net flux±SX ($ng\ g^{-1}ml^{-1}$)	−10.1 +/-1.7	−1.5 k0.39	10.0 ±3.9	131.5 k13.6	11.5 ±4.1	1.7 ±0.65	16.8 ±5.1	95.7 k18.1	−5.1 k2.1	0.60 ±0.23	10.2 ±1.5	52.7 k3.4	2.8 k1.9	1.23 ±0.21	9.75 ±1.4	52.2 k5.5
Mean control rainwater concentration (PPm)	.90	.19	1.56	.66	.88	.19	1.60	.58	.93	.18	1.53	.57	.92	.19	1.69	.55
No. of samples showing:																
output	4	11	31	42	28	25	33	35	16	28	36	36	27	29	32	36
Uptake	38	31	11	0	8	11	9	1	20	8	0	0	9	7	4	0
Factors affecting net fluxes																
Cation concentration in incident rainwater	− (1)	− (1)	− (1)		− (1)	− (1)	− (1)		− (1)	− (1)						
Day in water year (Sept. 1 = Day 1)			− (2)			− (4)	− (2)				− (1)	− (1)	− (2)	− (2)	− (1)	
Wet or dry period (Dry = 0, Wet = 1)		+ (2)	+ (3)	− (1)	+ (3)	+ (3)	+ (3)		− (2)	− (2)			+ (3)			
Height in canopy			− (4)	− (2)	− (2)	− (2)						− (2)				
Maximum r^2 in multiple regression with above variables	.79	.78	.81	.26	.61	.76	.76		.89	.40	.39	.60	.85	.34	.50	

[1] + and - indicate the direction of change in flux with increasing values of the variable listed. Numbers in parentheses indicate order of entry into multiple stepwise regression and, by extension, relative importance in influencing cation fluxes. Blank spaces indicate no significant effect. Samples from "wet" periods were exposed to 2.0 cm or more precipitation in the field during three days prior to collection; samples from dry periods were exposed to 0.3 cm or less precipitation.

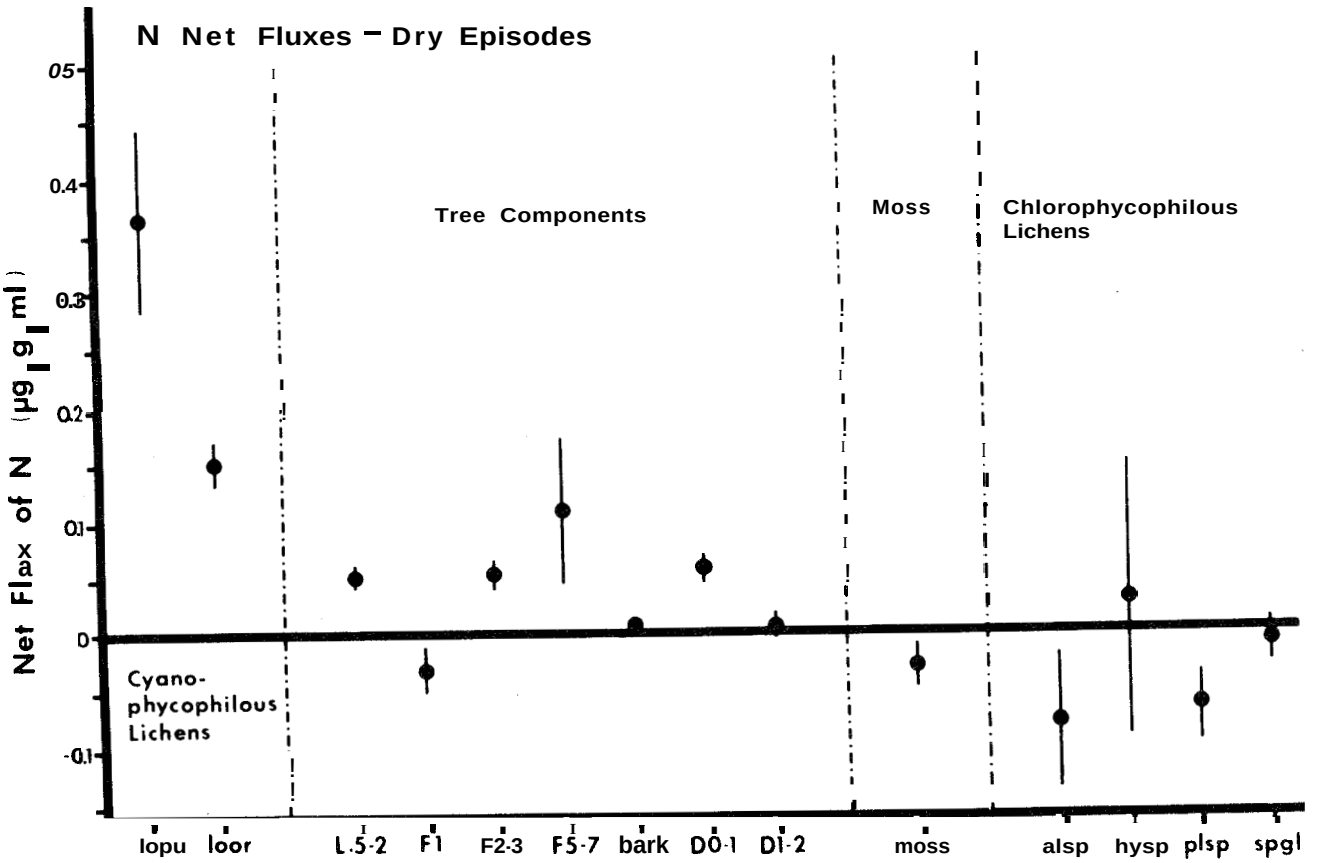

Figure 2. Mean net fluxes of dissolved nitrogen from canopy components collected during dry periods. Less than 0.3 cm of rain fell in the three days preceding collections. Bars indicate one standard error above and below the mean. lopu = Lobaria pulmonaria; loor = Lobaria oreyana; room = rotten Lobaria oregana; L.5-2.0 = living twigs 0.5-2.0 cm in diameter; F1 = aye class 1 foliage, 0-1 yr old; F2-3 = aye classes 2-3 foliage; F5-7 = age classes 5-7 foliage; DO-1 = dead twigs 0-1 cm in diameter; D1-2 = dead twigs 1-2 cm in diameter; alsp = Alectoria spp.; hysp = Hypogymnia spp.; plsp = Platismatia Spp.; spgl = Sphaerophoros globosus .

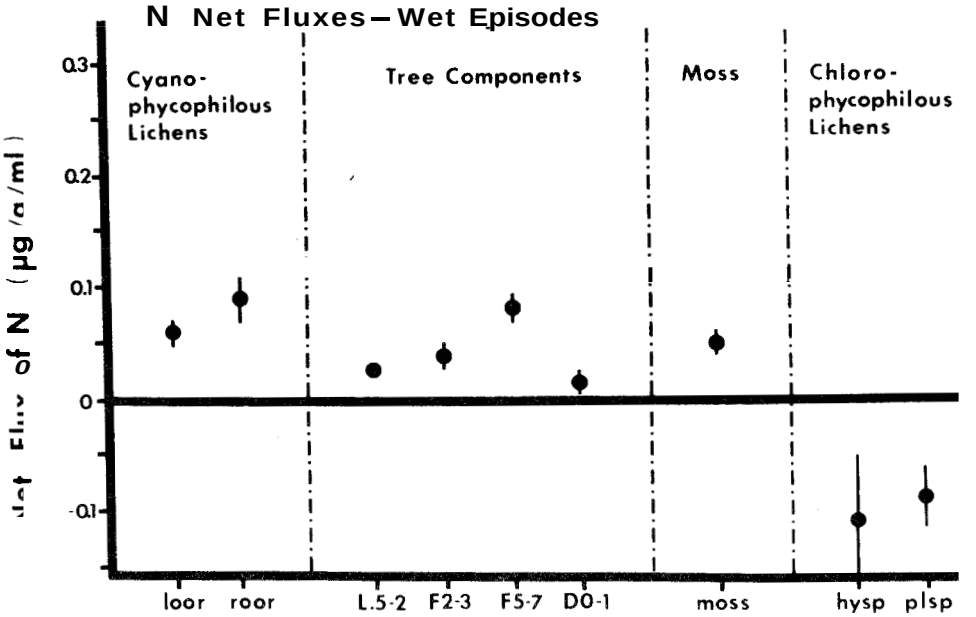

Figure 3. Mean net fluxes of dissolved nitrogen from canopy components collected during wet periods. More than 2.0 cm of rain fell in the three days preceding collections. Bars indicate one standard error above and below the mean. Code names for canopy components are the same as in Figure 2.

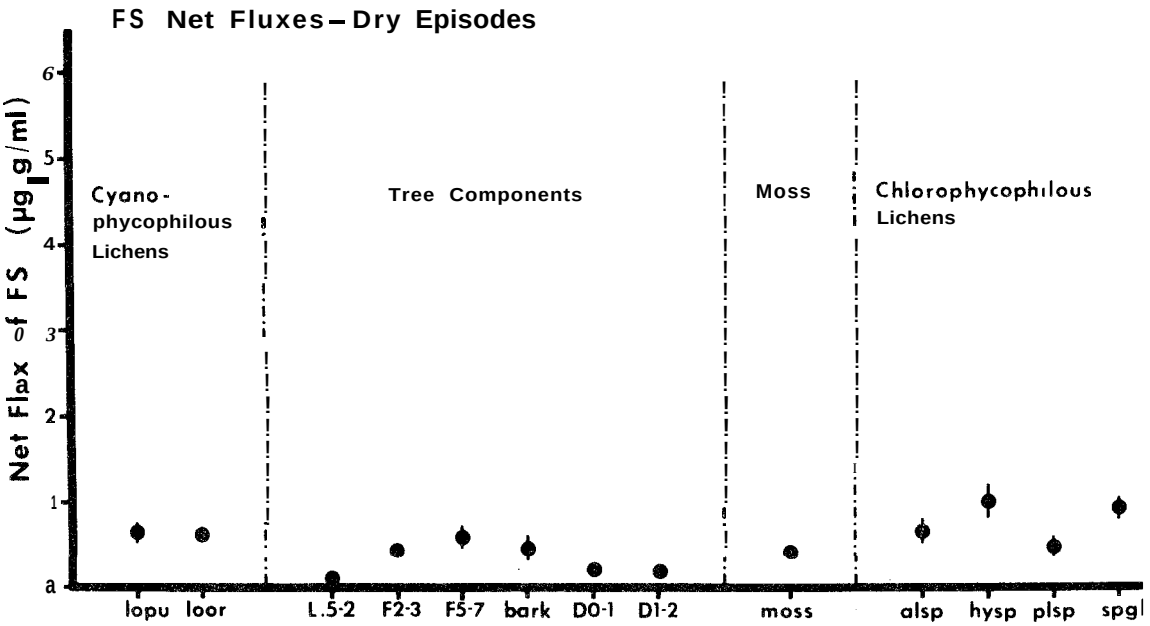

Figure 4. Mean net fluxes of filterable solids <30 um >0.2 um from canopy components collected during dry periods. Less than 0.3 cm of rain fell in the three days preceding collections. Bars indicate one standard error above and below the mean. FS = filterable solids. Code names for canopy components are the same as in Figure 2.

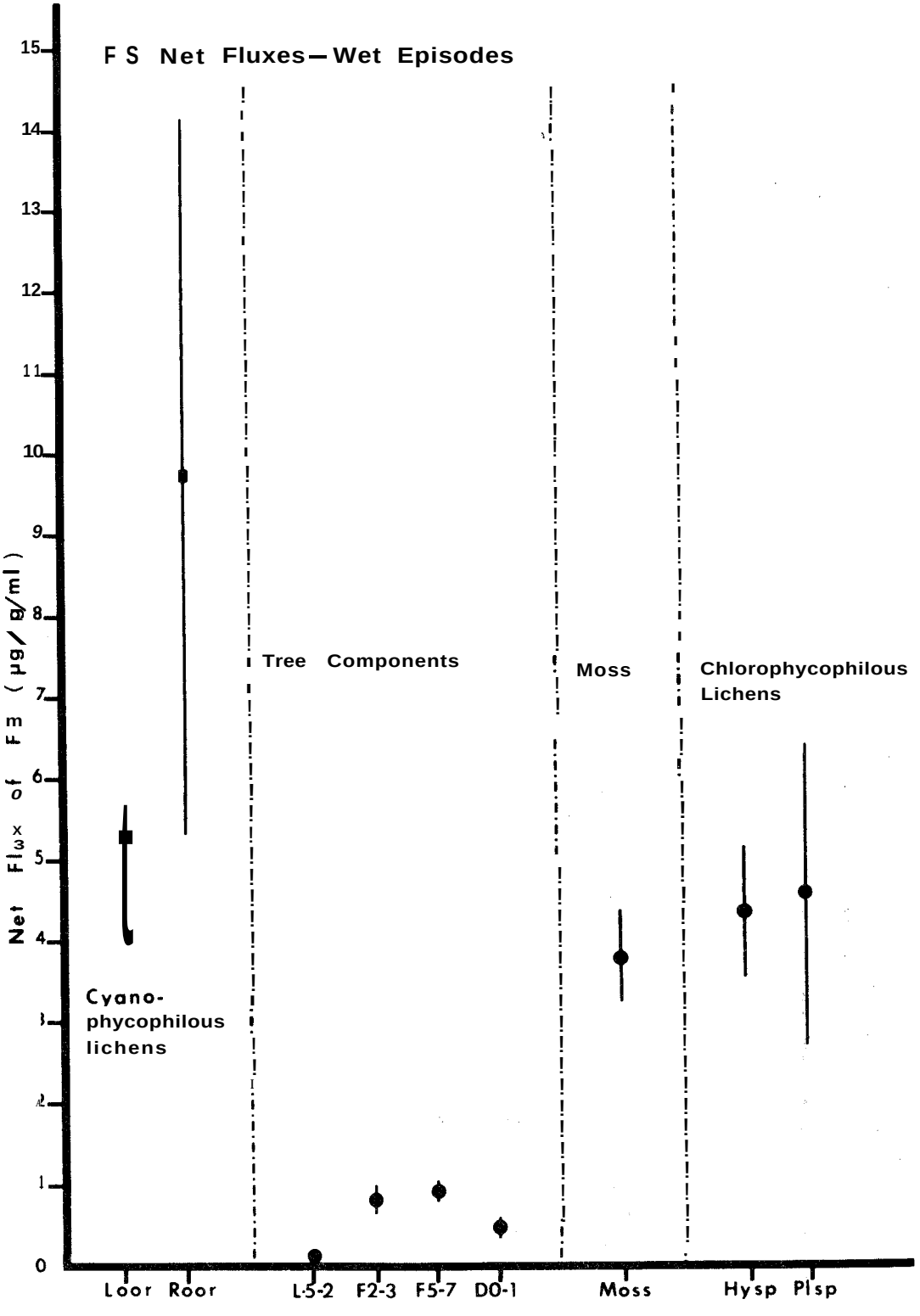

Figure 5. Mean net fluxes of filterable solids <30 um >0.2 um from canopy components collected during wet periods. More than 2.0 cm of rain fell in the three days preceding collections. Bars indicate one standard error above and below the mean. FS = filterable solids. Code names for canopy components are the same as in Figure 2.

foliage (Fig. 6), living twigs, and moss bolsters. For the tree components the net fluxes per unit weight are lower than for the epiphytes, and longer periods of misting are required before uptake of dissolved nitrogen begins.

The behavior of canopy surfaces in regard to their interactions with dissolved nitrogen becomes more explicable when the nature of the released particulates is examined. Particulates washed from the surface of Lobaria and other cyanophycophilous lichens consist almost exclusively of rod-shaped bacteria (Fin. 7); inspection of the surface of a Lobaria oregana thallus with the scanning electron microscope after a misting episode reveals dense populations of similar bacteria (Fig. 8). Caldwell et al. (1979) have isolated and identified bacteria from this substrate. They report 5-10 x 10^5 colony-forming units (CFU)/g from Lobaria collected during dry periods and 100-200 x 10^5 CFU/g during wet periods, observations consistent with data on outputs of microparticulates during dry and wet misting episodes in the laboratory. Pseudomonas fluorescens, Arthrobacter-like rods, and Gram-negative aerobic rods were found to be dominant bacterial taxa on Lobaria thalli.

Examination of the microparticulate fraction from misting episodes with foliage reveals a large number of fungal and algal cells, microorganisms which are also predominant on needle and twig surfaces (Bernstein et al., 1973; Bernstein and Carroll, 1977; Carroll, 1979; Carroll et al., 1980). In fact the observed differences between cyanophycophilous lichens and other canopy components in efficiency of dissolved nitrogen uptake can be largely ascribed to the prevalence of bacteria on lichen surfaces and of eukaryotic microorganisms on other canopy surfaces: the response time and doubling times for bacterial cells are much faster than those for eukaryotic microorganisms. In summary, all canopy surfaces examined during leaching time-course experiments have proved ultimately to be net sinks for dissolved nitrogen. For some components (chlorophycophilous lichens) this involves nitrogen uptake by the sample itself; for most other leaching substrates nitrogen uptake is mediated by epiphytic microorganisms whose cells are released into the rainwater as the populations grow.

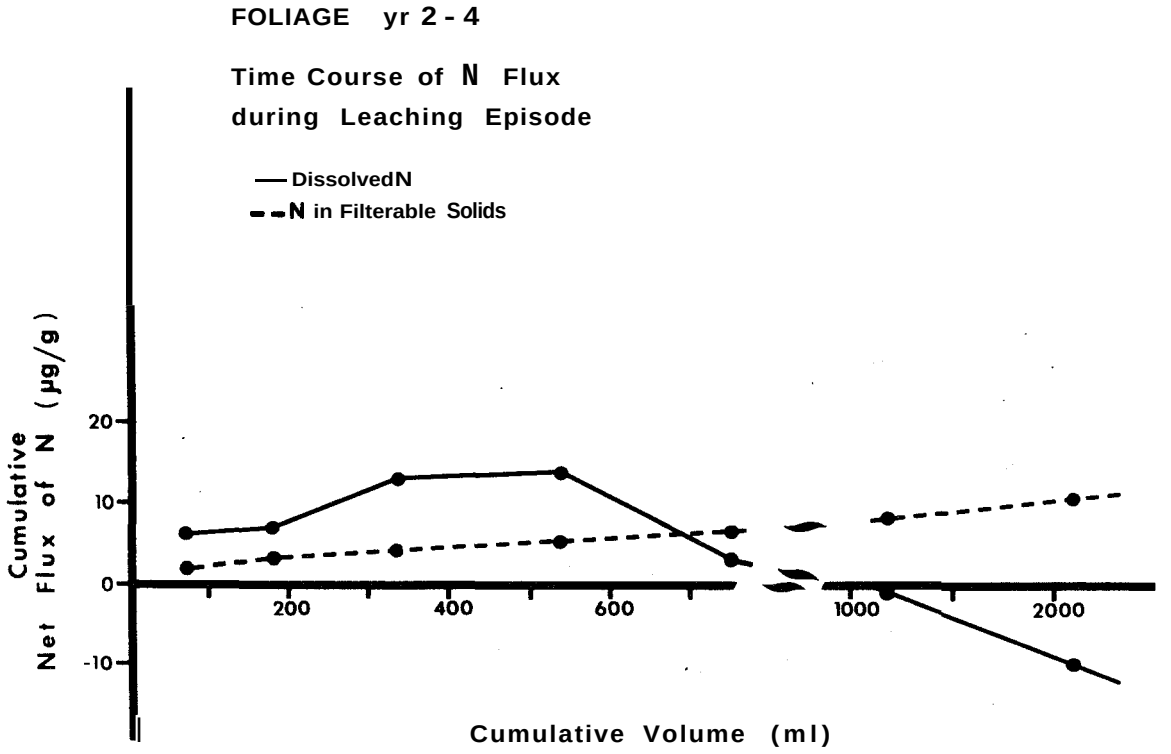

Figure 6. Cumulative net flux of dissolved nitrogen from foliage age classes 2-4 yr during a prolonged misting episode.

These results are consistent with the data of Lang et al. (1976), who showed nitrogen uptake as NH_4^+ for Platismatia glauca, and with numerous throughfall studies showing coniferous canopies to be net sinks for dissolved nitrogen in incident rainfall (Tamm,. 1951; Voigt, 1960; Nihlgaard, 1970; Foster, 1974; Miller et al., 1976; Feller, 1977; Cronan, 1980). This effect is particularly pronounced where glass wool plugs have been inserted in the necks of the collecting funnels to partially block the entrance of microparticulate matter into the collecting funcel.

Given this consistency, one may ask how far the patterns of nitrogen uptake and loss observed for individual components in microcosm rainstorms can be extended to actual canopies in the field, where multiple layers of intermingled components are stacked to a depth of 40 to 50 m. Loading the funnels with multiple layers of a single canopy component prior to misting represents a first approximation to the field situation. Figures 9 and 10 show results from a prolonged misting of Lobaria oregana in which different amounts of lichen were put into the funnels. In Figure 9 amean dry weight of 1.8 g per funnel was used; in Figure 10, 16.8 g per funnel was used. The trend is clear: as multiple layers of lichen are added to the microcosm, less and less nitrogen escapes in dissolved form and more and more is released in particulate form, as bacterial cell mass. Similar experiments with other canopy components revealed the same trend.

In addition to laboratory time-course experiments, we attempted to monitor the fluxes of nitrogen in the field during a single rainstorm in February 1979. Samples were taken from six 0.3 m2 throughfall collection troughs placed at random beneath a single old-growth tree (MINERVA) at one of our collection sites in the H. J. Andrews Experimental Forest. Incident rainfall was collected in a single sampler located in an adjacent clearcut. Water samples beneath the tree were taken at 1, 2, 3, and 4 hours, those in the clearcut at 2 and 4 hours. Samples were filtered in the field and were stored on ice prior to analysis. Although samples for the control rainwater were not replicated in this preliminary experiment, the trends in nitrogen fluxes are readily apparent in Figure 11: nitrogen was taken up from the incident rain throughout the portion of the storm that was monitored, a result that might have been predicted on the basis of our

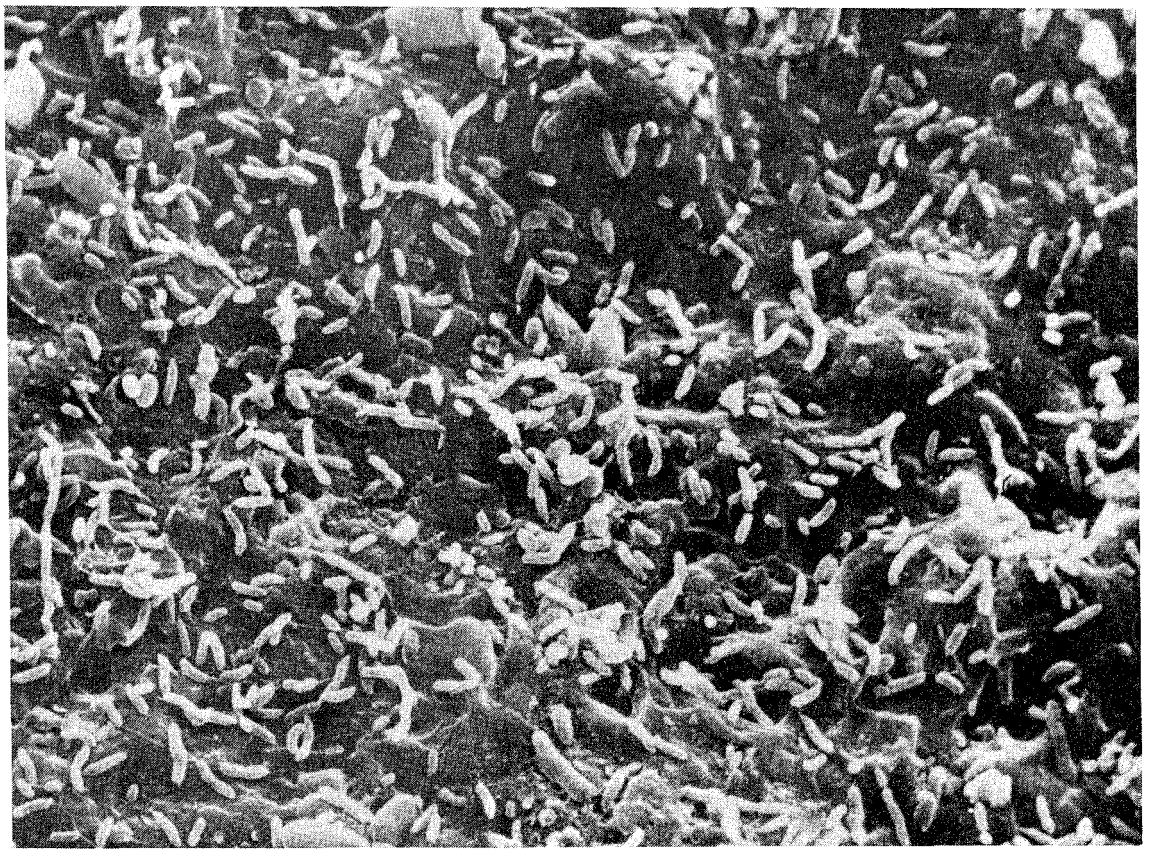

Figure 7. Bacteria from a thallus of Lobaria oregana collected on a Nucleopore filter as seen under the scanning electron microsopce (x 2,500).

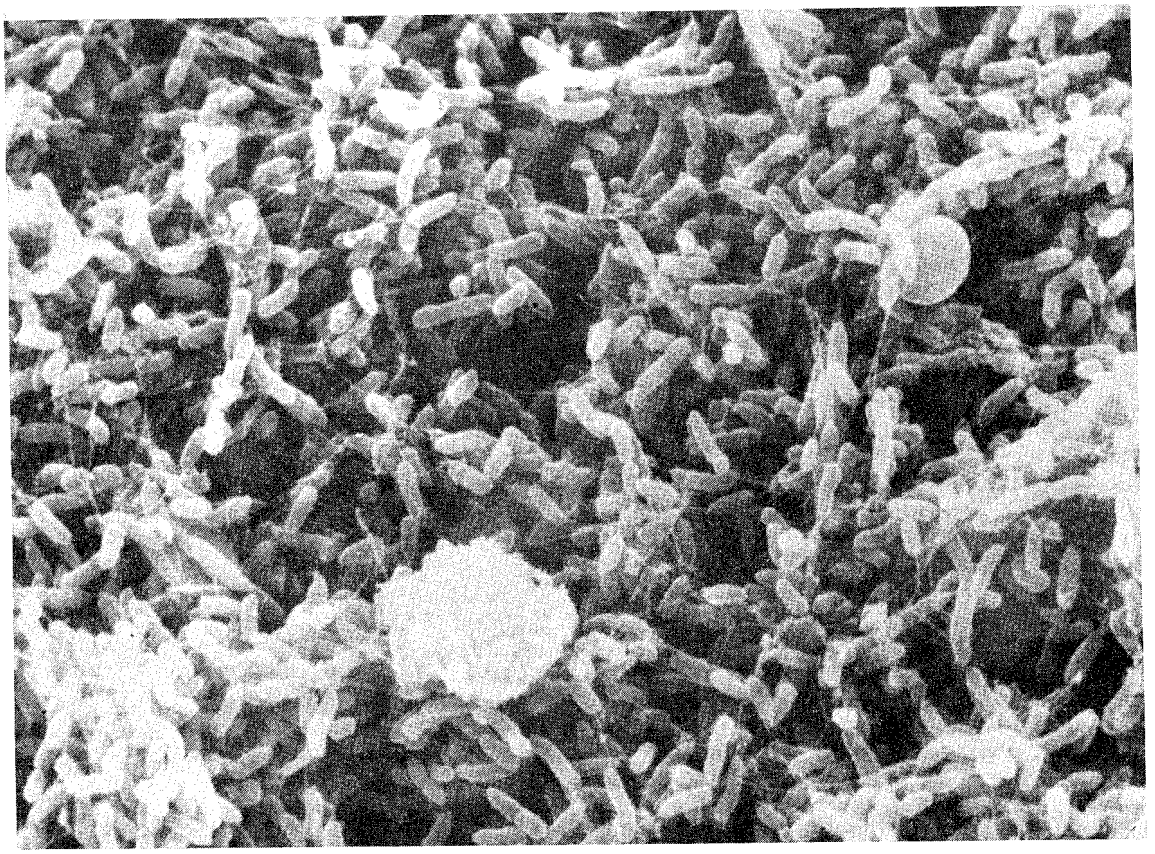

Figure 8. Bacteria on the surface of a Lobaria thallus as seen under the scanning electron microscope (x 1,800).

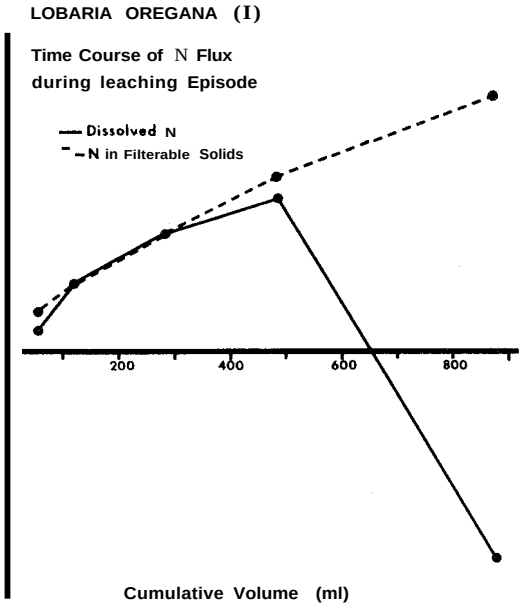

Figure 9. Cumulative net flux of nitrogen from Lobaria oregana during a prolonged misting episode; 1.8 g dry weight of Lobaria were placed in each funnel.

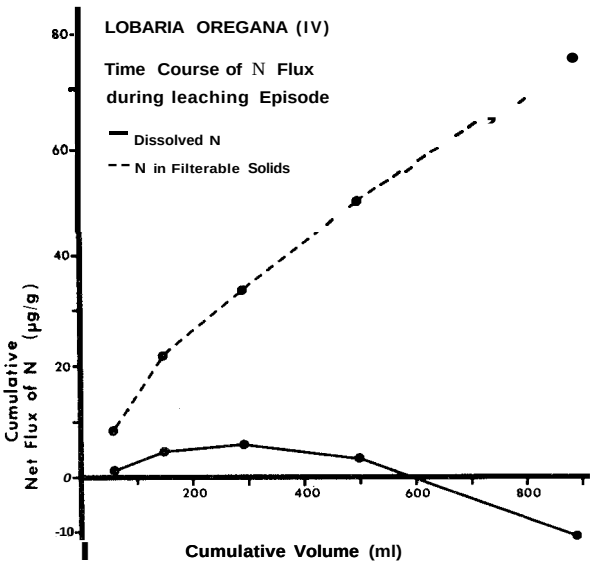

Figure 10. Cumulative net flux of nitrogen from Lobaria oregana during a prolonged misting episode; 16.8 g dry weight of Lobaria were placed in each funnel.

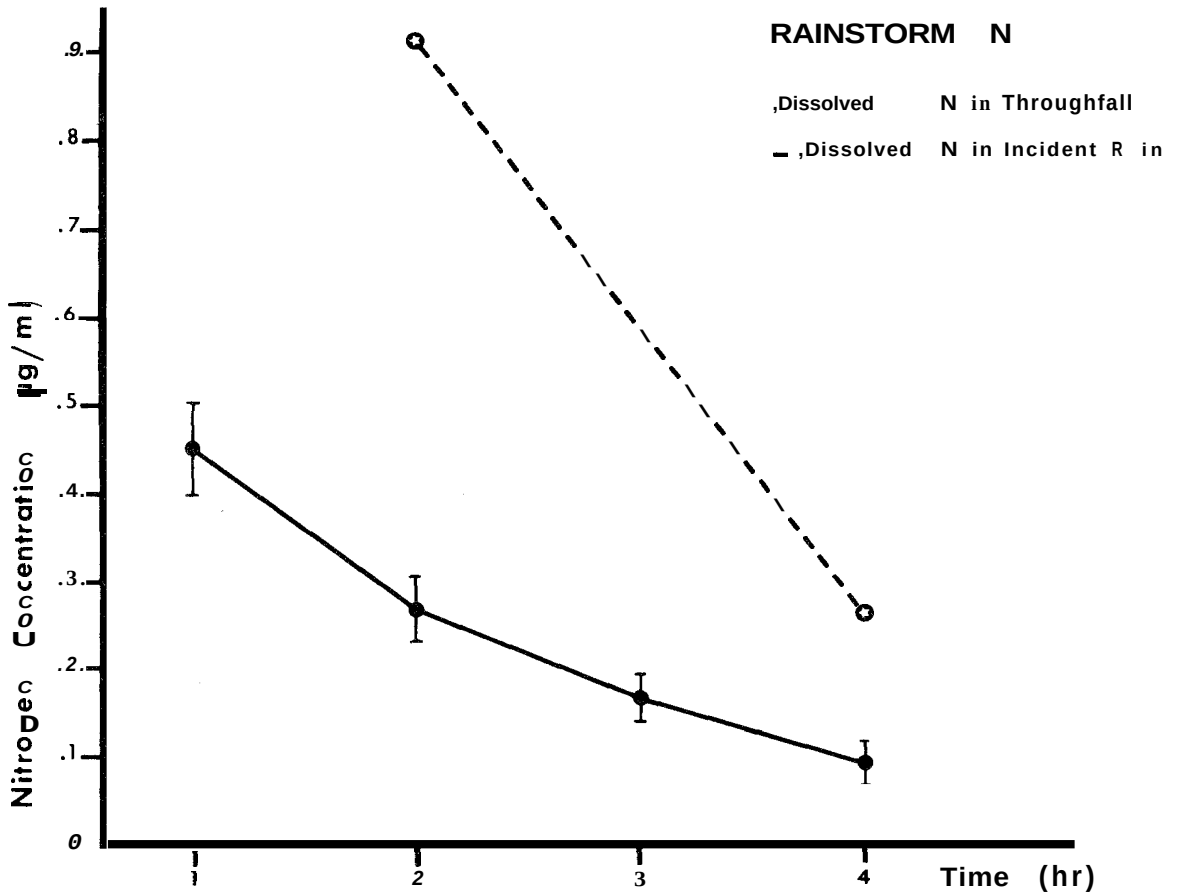

Figure 11. Concentrations of dissolved nitrogen in incident precipitation and throughfall during the course of a single rainstorm in the field.

microcosm experiments. However, when patterns of particulate output from the canopy are considered, the extrapolation fails. Analysis of filter weights from the field experiment reveals an initial flux of particulates out of the canopy during the first hour of the storm and low levels of suspended particulates in the throughfall thereafter. An entire canopy is, of course, more complex than a funnel with several layers of Lobaria.

In an attempt to deal with this complexity and to resolve discrepancies between laboratory and field observations, we have resorted to computer simulation models. My colleague, Dr. W. J. Massman, has developed a preliminary model of canopy nitrogen fluxes in which the paramount role of surface microorganisms in regulating nitrogen uptake and release is explicitly recognized. The model is based on chemostat theory, but has been generalized such that neither a consfant dilution rate nor a constant volume must be assumed. Further, the model allows for luxury nitrogen consumption by microbes. Certain simplifying assumptions have. however, been made. These include: (1) nitrogen is the only limiting nutrient; (2) grazing of microbial cell mass does not occur; (3) microbial growth is non-colonial; (4) the canopy strata are homogeneous; (5) nitrogen is not lost from the system in gaseous form; and (6) the flow of nitrogen into microbial cells is unidirectional; i.e., losses of nitrogen from microbial cells do not occur. Although certain of these assumptions are blatantly incorrect (no. 4 above), most of them are reasonable, at least over the time span of a single storm event. Currently the model deals with the behavior of stacked strata of only one component, Lobaria oregana.

Considering the assumptions and limitations of this model, the degree of qualitative agreement between the predictions of the simulation runs and the observed patterns of nitrogen flux in both laboratory and field is encouraging. Specifically, runs of the model for just a single stratum show a rough agreement with time-course experiments in the laboratory; most notably, dissolved nitrogen is released initially, but is taken up later as bacterial

growth and release of particulate nitrogen commences. When several strata are stacked, such that the output from one becomes the input for the next lower one, the model predicts that efficiency of uptake will increase, but that the output of particulates will be delayed. With five strata in the model, this delay amounts to four or five hours. Thus, for our field experiment (Fig. 11) we might well have seen a pulse of particulates from the bottom of the canopy if the storm had been monitored for several more hours. During storms of short duration the microparticulate fraction may never be flushed from the canopy. Instead it may be left as a particulate residue as water evaporates from the tree, only to be washed from the canopy during the initial phases of the next storm. This process could well account for the observed flush of microparticulates at the beginning of the single storm we monitored.

Results: phosphorus and organic matter. Concentrations of phosphorus and certain organic substances have also been measured during laboratory misting experiments. In general, much lower levels of phosphorus than nitrogen are present in the canopy solution; patterns of leaching and uptake resemble those for nitrogen. The occurrence of higher levels of phosphorus in throughfall than in incident precipitation in coniferous stands has been widely reported in the literature (Attiwill, 1966; Nihlgaard, 1970; Abee and Lavender, 1972; Foster, 1974; Hart and Parent, 1974; Henderson et al., 1977). Although phosphorus concentrations were so low in both incident rain and throughfall during the storm sequence mentioned earlier that no consistent trends were evident, data from earlier studies at the same site in which throughfall and incident rain were field-filtered indicate net losses of phosphorus from the canopy. Thus, while microbial uptake of phosphorus certainly occurs, phosphorus is probably not a limiting element for microbial growth in most canopies.

Fluxes of organic matter in the canopy have been little investigated here or in conventional throughfall studies. Where total organic matter or concentrations of specific organic molecules have been determined in throughfall and stemflow, they have been found to be high and to account for a significant return of fixed carbon to the forest floor (Tamm, 1951; Carlisle, 1965; Carlisle et al., 1966; Gersper and Holowaychuck, 1971; Eaton et al., 1973). Concentrations of ammonia and nitrate are low in throughfall from coniferous stands in the Pacific Northwest and the bulk of nitrogen in solution is in organic form; this also appears to be the case for phosphorus.

If the specific nitrogenous compounds leached from Lobaria were identified, radioisotopes could be employed to follow their fate in subsequent transformations within the canopy. Cooper and Carroll (1978) attempted to isolate and identify dominant organic nitrogenous compounds in Lobaria leachates. They found that simple preliminary fractionation of the leachates by means of dialysis and extraction in acetone did not result in nitrogen enrichment in any fraction; they concluded that a number of different nitrogen-containing molecules were present. Ribitol, a five-carbon sugar-alcohol, was, however, identified as a major component of these leachates. Subsequent studies have shown that ribitol accumulates in the thalli during dry periods and leaches very rapidly in subsequent rainstorms.

The chemistry of organic molecular transformations in the canopy is undoubtedly extremely complex. A great deal of further investigation is required before these transformations can be understood, even in broad outline.

Insects and Canopy Processes

In the last ten years the role of canopy arthropods in regulating growth of trees in forest ecosystems has been investigated by a number of workers. Such studies have largely focused on the activities of defoliating insects, particularly their effects on primary production (Franklin, 1970; Rafes, 1970; Reichle et al., 1973), and on elemental cycling (Kimmins, 1972; Nilsson, 1978; Schroeder, 1978). Defoliating and sucking insects appear to be of little importance in old-growth canopies. However, in collaboration with an entomologist, Dr. David Voegtlin, we have noted subtle and pervasive effects of the fauna on nutrient exchanges within the canopy.

Materials and methods. Census work on canopy consumers was carried out over a 3-year period. Initially, we implemented a biweekly sampling program in which important and distinctive canopy habitats were sampled on a cumulative or episodic basis. More recently, intensive sampling of arthropod communities on needles and twigs has been carried out. The habitats sampled and techniques used are summarized in Table 3.

Results: canopy arthropods. The data from the arthropod census suggest that the canopy fauna partitions the tree very finely, both with regard to habitat type and phenology. To date, 1,200 to 1,500 taxa have been collected, from 50 to 70 percent of them more than once. Only about 150 of these taxa can be considered common. In many cases they are abundant only in one habitat or during one particular season.

Table 3. Biweekly sampling techniques, Douglas-fir canopy arthropod survey (Sept. 1976 - Sept. 1977)

Sampling technique	Technique description	Number of samples taken and location	Duration of sampling period	Information produced
Sticky screens	20 cm^2 screens of ¼" hardware, cloth coated with stikem special	12 screens, 4 on each of 3 halyards run into the lower, middle, and upper canopy	Cumulative; screens left up 2 weeks	Qualitative information on the movement and phenology of flying insects provides evidence for intercanopy movement by wingless arthropods, such as ballooning by spiders
Tullgren	A series of funnels which use heat and light above to drive arthropods into a collecting vessel	9 samples (3 per branch system); one branch system in lower, middle, and upper canopy	Episodic; taken every 2 weeks	Quantitative information on microarthropods inhabiting epiphyte-lodged litter-perched soil habitat
Vacuum	A backpack blower with the intake adapted for sucking	3 samples, foliage surface area of branch systems used for tullgren and filtration vacuumed	Episodic; taken every 2 weeks	Semi-quantitative information (surface area vacuumed is estimated) on arthropods found on the needles and twigs. Collects rapidly moving arthropods not collected by other techniques.
Filtration	Branchlets washed vigorously and the wash filtered through a series of nested sieves	6 samples, 3 living and 3 dead branchlets chosen from branch systems used for tullgren and vacuum	Episodic; taken every 2 weeks	Quantitative information on slower moving organisms associated with foliage and dead branchlet material

Table 3 continued on next page

Table 3. Biweekly sampling techniques, Douglas-fir canopy arthropod survey (Sept. 1976 - Sept. 1977)

Sampling technique	Technique description	Number of samples taken and location	Duration of sampling period	Information produced
Pitfall	Plastic containers hung in cavities on trunk, contain .water–alcohol–ethylene–glycol mixture to trap arthropods	4 samples, located from lower to upper canopy	Cumulative; fluid in containers changed every 2 weeks	Qualitative information on movement of arthropods on the trunk
Trunk stickies	Screens of same size as hung from halyards, held approximately 1 cm away from trunk	4 samples, located near the four pitfalls	Cumulative; screens left in place 2 weeks	Qualitative information on movement of arthropods on the trunk and also landing on trunk of flying insects
Blacklight	A large funnel trap run into canopy on halyard	1 sample, trap run one night every 2 weeks	Episodic; 8–12 hours	Qualitative information on night–flying insects in the canopy. Funnels fixed so that only insects flying above it, 42 m, can see the light
Emergence traps	Tent–shaped traps set on forest floor	6 samples, traps located in vicinity of tree with halyards and sticky screens	Cumulative; traps left in place 2 weeks	Qualitative information used as a means of determining which insects collected in the canopy come from the soil
Cookie cutter	Equal sized samples 1 dm^2 taken from a uniform habitat	4 samples, taken from large moss bolsters in lower to middle canopy	Episodic; once every month	Quantiative information on microarthropods in a fairly uniform habitat

Distribution throughout the canopy is often highly aggregated. The major groups of arthropods and the techniques used to collect them are listed in Table 4.

In terms of abundance, microarthropods associated with needles and twigs were the dominant group in the canopy. Mites, in particular a new species of Camisia, Camisia carrollii Andre, were very numerous on needles and small twigs. Microscopic observations of both frass and gut contents revealed that these organisms feed almost exclusively on epiphytic microbial cells. Fungivorous psocids and collembolans were also prevalent in the foliage. Numerous small invertebrates, including tardigrades, rotifers, and testate amoebae were present on various canopy surfaces. We did not study this truly microfaunal community, but these organisms presumably graze on populations of epiphytic bacteria.

While we have no data on the intensity with which canopy microorganisms are grazed, indirect evidence suggests that the canopy microfauna may significantly affect standing crops of microepiphytes and thus indirectly affect patterns of nutrient exchange within the canopy. Bernstein and Carroll (1977) and Carroll (1979) made visual estimates of microbial standing crops for various age-classes of needles at several heights in the canopy, where mites are most abundant (Voegtlin, unpub.). When microbial standing crops are considered with regard to needle age, a striking pattern frequently emerges. Percent cover and cell volume per needle rise steadily from year 1 through year 3 and then drop precipitously on year 4 needles. The microbial populations then return to peak abundance at year 8. More recently these patterns have been confirmed (Carroll, unpub.) using the method of Swisher and Carroll (1980), in which the hydrolysis of fluorescein diacetate and release of fluorescein dye is used as an index of microbial standing crop. A plausible explanation for such patterns invokes grazing by foliar microarthropods, which feed selectively on needles 4 to 6 years old. Andre and Voegtlin (in press) have noted that populations of the twig-dwelling mite Camisia carrollii are concentrated on twigs 4 to 10 years old. Thus,

Table 4. Sampling techniques used during biweekly sampling and major categories of arthropods collected by each method

Techniques	Arthropods	
	Commonly collected	Infrequently collected
Sticky screens	Diptera, Neuroptera, Hymenoptera, Homoptera, Hemiptera, Coleoptera	Trichoptera, Plecoptera, Acarina, Collembola, Thysanoptera
Tullgren and cookie cutter	Acarina, Collembola, Coleoptera larvae and adults	Diptera larvae, Araneae, Pseudococcidae, Hymenoptera
Vacuum	Acarina, Collembola, Thysanoptera, Diptera larvae, Lepidoptera larvae Homoptera	Coleoptera, Psocoptera
Filtration	Acarina, Collembola, Thysanoptera, Diptera larvae, Lepidoptera larvae, Homoptera	Araneae, Hymenoptera
Pitfall	Collembola, Araneae, Phalangida, Coleoptera, Diptera, Psocoptera	Acarina, Hymenoptera, Lepidoptera
Trunk stickies	Araneae, Diptera, Phalangida, Coleoptera, Psocoptera	Acarina, Collembola
Black1ight	Lepidoptera (moths), Trichoptera, Plecoptera, Diptera, Coleoptera, Hymenoptera, Hemiptera	Ephemeroptera, Homoptera
Emergence	Diptera, Collembola	Hymenoptera

there is precedent for such precise partitioning of habitats among foliage- and twig-dwelling microarthropods.

Census studies by Voegtlin have shown a relative paucity of defoliators and sucking insects. Measurement of frass-fall during periods of peak needle consumption in the summer suggests that less than 1 percent of the new foliage is consumed by caterpillars each year. Voegtlin (unpub.) considers this striking aspect of old-growth canopy insect communities to be a result of the large numbers of spiders, other predators, and parasitoids found in the canopy. During the winter months large numbers of mycetophilid flies and adults of aquatic insects are trapped on sticky screens. Studies with emergence traps reveal that these insects originate in the forest floor or streams, where they feed as larvae. This input of adult insects from the forest floor may provide a food source for spiders and other canopy predators during the winter and early spring and serve to maintain their populations at high levels throughout the year. Thus, herbivorous insects in these forests never experience a season in which to develop relatively free from predation pressure and, as a consequence, their populations never build to levels which significantly affect the trees.

CONCLUSIONS

Studies in the canopy of an old-growth coniferous forest have revealed biological communities whose diversity and trophic structure resemble those found in the soil and streams. Primary producer, decomposer, and consumer populations are all prominent and appear to function in elemental cycling within the canopy in a fashion parallel to that in the soil and aquatic systems. We now have evidence for the operation of mechanisms for the conservation of nutrients within the canopy. With regard to nitrogen these mechanisms involve the fixation of atmospheric nitrogen by cyanophycophilous lichens, the loss of organic nitrogen from such lichens through leaching, the uptake of leached organics from dilute canopy solution by microorganisms and other epiphytes, and the consumption of a portion of the resulting microbial production by canopy microarthropods. Thus, leached

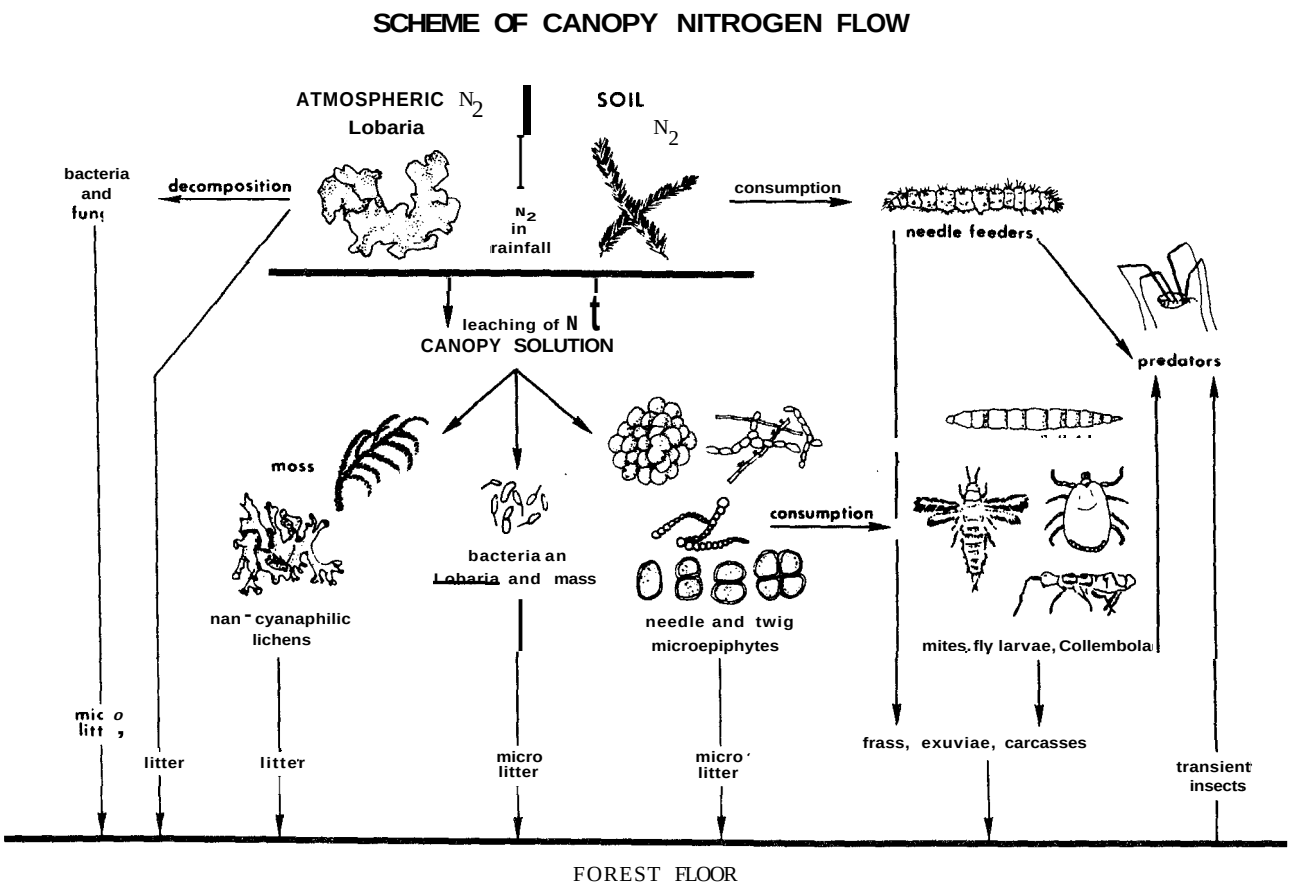

Figure 12. Scheme of nitrogen fluxes incanopy.

organics serve indirectly as a base for many canopy food chains. Conservation of nutrients within the canopy operates continually against the force of gravity; in old-growth stands canopy production must be balanced ultimately by a return of materials to the forest floor (see Fig. 12).

Microorganisms and epiphytes play a key role in regulating fluxes of nutrients from the bottom of the tree. These processes are probably not of universal occurrence in forest stands, and therefore it is of interest to consider the climatic and biological factors which enhance development of these canopy populations. A primary requirement for any system in which leaching plays a role is the input of atmospheric moisture in the form of rain or fog. Leaching is a solution process., In addition, poikilohydric organisms such as lichens, mosses, and microepiphytes require periodic additions of liquid water in order to survive. As a result, the processes described above will not be of much importance in desert environments with low precipitation or in subarctic and subalpine stands where much of the annual precipitation is recieved as snow that falls from the canopy before melting. Beyond this, conditions which lead to the availability of fixed carbon and nitrogen in the canopy solution will foster growth of heterotrophic microepiphytes. These conditions include the prevalence of readily leached surfaces such as those of older evergreen leaves and cyanophycophilous lichens. Evergreen foliage persists for a number of years, providing additional surface area for the buildup of perennial colonies of microepiphytes. Conversely, deciduous canopies in which the leaves are shed annually should show less evidence of nutrient uptake and release by microbial cells. Other situations where concentrations of macroelements in the canopy solution may be high involve: (1) aphid infestations, which are widely reported to encourage the growth of yeasts and sooty molds on canopy surfaces coated with honeydew (Fraser, 1937; Reynolds, 1975); (2) outbreaks of defoliating insects (Kimmins, 1972; Nilsson, 1978; Schroeder, 1978); (3) foliar fertilization; and (4) atmospheric pollution. In this final instance, the extent of nutrient enrichment in precipitation from pollution is attested to by the enhanced growth of pigmented fungi on painted surfaces in cities and by the necessity for adding microbicides to paint to prevent such growth.

In view of the above considerations, canopies of moist evergreen forests in temperate and tropical regions should prove to be microbiologically active, whatever the specific identities of the trees and the canopy inhabitants, wherever they occur within that climatic zone. Indeed, microepiphytes are abundant on the leaves of broadleaved tropical evergreens (Odum et al., 1970; Reynolds, 1975), and several studies suggest that they function in uptake of canopy nutrients just as those studied in the Andrews Forest do (Odum et al., 1970; Witkamp, 1970). If the canopy nitrogen model developed for the old-growth Douglas-fir trees in the Andrews Forest were to be tested in functionally similar forests elsewhere, evergreen broadleaved forests throughout the tropics and the gymnosperm forests of New Zealand and South America should provide appropriate stands. Closer to home, the model could be tested by experimental manipulation of the canopy nutrient regime with fertilization or insect defoliation programs. Such an approach deserves serious consideration.

ACKNOWLEDGMENTS

The original work cited in this review has been a collaborative effort. In particular I should like to acknowledge the contributions of Drs. William Denison, William Massman, Lawrence Pike, and David Voegtlin. Bill Hopper, Terry Montlick, and Robert Rydell have dealt with computer programing and data analysis. Fanny Carroll, Judi Horstmann, and Jan Wroncy have been responsible for the laboratory misting experiments and water analyses. Undergraduate work-study students have put in hundreds of hours in routine laboratory work and analyses; our program would not have been possible without their continuing contributions. This work has been supported with funds from NSF grants BMS 7514003 and DEB 78-03583.

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