

THE IMPORTANCE OF EPIPHYTIC LICHENS
IN MINERAL CYCLING

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The Importance of Epiphytic Lichens in Mineral Cycling^{1,2}

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Abstract. Mineral capital in epiphytic lichens varies considerably from forest to forest depending primarily on the biomass of lichens present and can be at least as high as 27 kg ha⁻¹ for N, 3.6 kg ha⁻¹ for P, 9 kg ha⁻¹ for K, 9.4 kg ha⁻¹ for Ca and 1.7 kg ha⁻¹ for Mg. For three ecosystems, comparing Douglas fir, balsam fir and oak woodland, lichens seldom accounted for more than 10% of the annual, above-ground turnover of a mineral. Lichens were relatively more important in the cycling of N than of P and K and of least importance in the cycling of Ca and Mg. Quantities of minerals leached from lichens appear to be small compared to quantities released through biomass turnover. Lichens may influence entry of minerals into ecosystems through nitrogen fixation and interception of aerosols. Although atmospheric inputs may be sufficient to meet N, Ca and Mg requirements of epiphytic lichens, P and K appear to be obtained primarily as leachates from other canopy components. Minerals that have been taken up by lichens may subsequently reach the surrounding plant or animal communities via litterfall, leaching, bacterial incorporation or non-cellular particle formation.

Lichens contain a pool of stored minerals. Minerals are added as they grow and are removed as they die and decompose. Through this uptake, storage and release of minerals, lichens affect the overall pattern of mineral cycling for any ecosystem in which they occur. Although the relative importance of lichens compared to other components of ecosystems is poorly known, it must range from major, in ecosystems where lichens contribute the bulk of plant biomass, to trivial, in ecosystems where they are present in trace amounts.

The significance of epiphytic lichens in the nutrient cycling of forest ecosystems where lichens are often conspicuous but where their contribution to total biomass is relatively small has been intensively investigated in only a few of these ecosystems. The following questions are addressed in the present paper: 1. What is the magnitude of the standing crop of the mineral capital in lichens? 2. How does the quantity of minerals turned over by lichens as a result of growth and death compare with

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mineral turnover for other components of the ecosystem? 3. What additional mineral fluxes are not accounted for by biomass turnover? 4. What are the sources of minerals utilized by lichens?

METHODS AND SITE DESCRIPTIONS

Lichen biomass, production and nutrient capital have been estimated for five forest ecosystems: Douglas fir, oak woodland, balsam fir, spruce-fir and northern hardwoods. The specific sites studied within each ecosystem are briefly described below together with references to the methods used for establishing the various estimates. The lichen component of each ecosystem was assumed to be at steady state (production equals loss), and the turnover rate was calculated by dividing annual production by biomass. The estimates of lichen turnover are conservative since consumption and decomposition of lichens in the canopy lead to underestimates of annual production.

Douglas Fir Forest.—Data are for a 450-year-old forest of Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, on watershed 10 of the H. J. Andrews Experimental Forest, Blue River, Oregon (Fredriksen, 1972). Lichen biomass estimates are based on an average of 17.6 kg per old-growth tree (dbh > 90 cm) for watershed 10 and the adjacent watershed 2 (Pike et al., 1977; Denison, Pike & Rydell, unpublished) and about 40 old-growth trees per hectare (Grier & Logan, 1977). One-fourth of the epiphytic biomass is assumed to be on understory trees and shrubs. A production estimate of $0.34 \text{ g g}^{-1} \text{ yr}^{-1}$ for *Lobaria oregana* (Tuck.) Müll. Arg. was made by Rhoades (1977 & unpublished) using sequential photography, and production of $0.15 \text{ g g}^{-1} \text{ yr}^{-1}$ was assumed for all other lichens. Mineral concentrations in lichens are based on Pike et al. (1972) and unpublished data of Pike and Cromack. Vascular plant biomass and nutrient capital are based on Grier and Logan (1977) and Sollins et al. (1978). Annual input of minerals to the forest floor by way of incident precipitation, throughfall and litterfall are from Sollins (1978) and Abee (1973).

Mineral fluxes for Douglas fir canopy lichens during laboratory simulations of gentle rain episodes have been investigated by Dr. George Carroll and co-workers at the University of Oregon. At monthly (or in some cases, biweekly) intervals throughout the September to May rainy season (1976–77) samples of canopy lichens (*Lobaria oregana* (Tuck.) Müll. Arg., *Alectoria sarmentosa* (Ach.) Ach., *Platismatia glauca* (L.) W. Culb. & C. Culb. and other species) were collected and stored overnight at 4°C in plastic bags to maintain original hydration status. Approximately 10 g of lichen material was then placed in funnels and misted for approximately one h; rainwater which had flowed over the samples was collected in bottles below the funnels. Incident rainwater used for misting lichens was collected in the Laurel Hill Valley south of Eugene. Composition of the approximately 100 ml of leachate collected in bottles under the lichens was compared with that of water collected in control bottles. Water was prefiltered through a 30 µm nylon mesh filter and then filtered through a tared 0.2 µm Nuclepore filter. Total dissolved N and P were determined by the indophenol blue and the molybdenum blue methods (Jaenicke, 1974). Cations were determined using a Varian AA-5 atomic absorption spectrophotometer. Total N content of the microparticulates retained by the 0.2 µm filter was determined by a micro-Kjeldahl digestion of a sample of 10 or more pooled filters followed by analysis of the digestate using an Orion Model 95-10-00 ammonia electrode.

In addition to the 2 h mistings, longer term mistings (ca. 6 h) in which leachates were removed for analysis at approximately 1 h intervals were carried out. Canopy lichens subjected to these time-course studies were *Lobaria oregana* and *Alectoria sarmentosa*, the latter with an admixture of *Bryoria* species.

Oak Woodland.—Estimates of lichen biomass and production for the Cogswell-Foster Preserve in the Willamette Valley near Halsey, Oregon, are taken from Pike (1971). The dominant tree species in this preserve is *Quercus garryana* Dougl.; the trees are of similar age to one another and the forest appears to have originated about 1850. Estimates of lichen production are based on biomass accumulation on young twigs (up to 20 yr old) converted to a per hectare basis by multiplying by both the density of leaves on current year twigs and the number of leaves in litterfall per hectare of forest. Concentration of N, Ca and Mg for lichens and leaf litter are taken from Pike (1971). Concentrations of P and K were not determined but are assumed to be 0.2% and 0.5% respectively, based on values reported for other ecosystems in Table 1.

Balsam Fir Forest.—Estimates of lichen biomass, production and nutrient capital are from Lang et al. (1978) and represent average values for 10 *Abies balsamea* (L.) Mill. stands in various stages of succession (representing stand ages from roughly 20 to 80 years) on Mt. Moosilauke in

TABLE 1. Estimates of biomass, production, mineral concentration, mineral capital and mineral turnover for epiphytic lichens of five forest ecosystems.

	Douglas fir forest	Oak woodland	Ecosystem Balsam fir forest	Spruce-fir forest	Northern hardwood forest
Location	Oregon, USA (44°N, 122°W)	Oregon, USA (44°N, 123°W)	New Hampshire, USA (44°N, 72°W)	British Columbia, CANADA (52°N, 120°W)	New Hampshire, USA (44°N, 72°W)
Predominant lichen	<i>Lobaria oregana</i>	<i>Usnea subfloridana</i>	<i>Hypogymnia</i> spp.	<i>Alectoria sarmentosa</i>	<i>Parmelia sulcata</i>
Lichen biomass (kg ha ⁻¹)	900	1800	630	760	100
Lichen production (kg ha ⁻¹ yr ⁻¹)	260	500	80	50	No estimate made
Mineral concentration (% dry weight)					
N	1.73	1.48	1.69	0.55	1.72
P	0.24	0.20 ^a	0.19	0.14	0.16
K	0.57	0.50 ^a	0.53	0.35	0.60
Ca	0.17	0.52	0.20	0.21	0.54
Mg	0.03	0.09	0.04	0.06	
Mineral capital (kg ha ⁻¹)					
N	15.4	26.7	10.7	4.18	1.72
P	2.1	3.6	1.20	1.04	0.16
K	5.1	9.0	3.34	2.65	0.60
Ca	1.55	9.4	1.26	1.62	0.54
Mg	0.28	1.69	0.25	0.44	
Mineral turnover (kg ha ⁻¹ yr ⁻¹)					
N	4.50	7.48	1.35	0.28	
P	0.61	1.01	0.15	0.07	
K	1.49	2.52	0.42	0.18	
Ca	0.45	2.63	0.16	0.10	
Mg	0.08	0.48	0.03	0.03	

^a P and K concentrations have not been determined for lichens of the oak woodland and are assumed values.

Grafton Co., New Hampshire. Production estimates are based on biomass accumulation and litterfall during succession. These stands were not at steady state and the turnover rate represents an average value for the chronosequence. Water input to the ecosystem is approximately 150 cm yr^{-1} as precipitation and 300 cm yr^{-1} as horizontal interception (Lang et al., 1978); this water is assumed to have the same chemistry as precipitation at the Hubbard Brook Experimental Forest in an adjacent watershed (Likens et al., 1970).

Lang et al. (1976) have conducted a series of studies to determine the possible effects that lichens may have on precipitation chemistry as water moves through the Balsam fir canopy. They submerged lichens in mineral salt solutions which were formulated to simulate incident rain-water and monitored changes in water chemistry.

Spruce-Fir Forest.—Data are from Edwards et al. (1960) for their study area #3 in Wells Gray Park, British Columbia, a site dominated by *Picea engelmannii* Parry (Engelmann spruce) and *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir). In computing mineral turnover, a production value for lichens of $50 \text{ kg ha}^{-1} \text{ yr}^{-1}$ is used. This figure appears to be of the correct order of magnitude based on the following considerations. A production value of $33 \text{ kg ha}^{-1} \text{ yr}^{-1}$ is computed from biomass accumulation given the age-specific distributions of tree density and epiphytic biomass in Table III of Edwards et al. (1960) and assuming a stable age distribution for trees in the stand. This estimate is likely to be too low, not only because of in-canopy consumption and decomposition, but also because of lichens falling into the litter, independent of the death of whole trees. A production value of $44 \text{ kg ha}^{-1} \text{ yr}^{-1}$ can be deduced from the 23 kg ha^{-1} of lichens on trees falling annually, added to the 21 kg ha^{-1} of lichen material added to the litterfall in the general area during a single winter. This estimate (of $44 \text{ kg ha}^{-1} \text{ yr}^{-1}$) is also likely to be too low, not only because of in-canopy consumption and decomposition, but also because the litterfall estimates themselves may have been too low, since collections were not made year-round and since some decomposition may have occurred in the snow before collections were made. Due to a decimal error in their Table III, Edwards et al. (1960) computed a higher value of 37 kg ha^{-1} of lichens on trees falling annually instead of 21 kg ha^{-1} , the value used above.

Estimates of mineral concentrations are based on values for *Alectoria sarmentosa* and *Bryoria "jubata"* from Rodin and Bazilevich (1967), Scotter (1965) and Pike (unpublished), weighted for the relative proportions of *Alectoria* and *Bryoria* in the stand.

Northern Hardwoods Forest.—Data are for Tunnel Brook and Hubbard Brook Watersheds in Grafton County, New Hampshire (Reiners, Lang and Pike, unpublished). Several species of deciduous trees were common at the sites sampled—the most abundant were *Acer saccharum* Marsh (sugar maple) and *Betula lutea* Michx. (yellow birch). The lichen biomass value given represents an approximation of the amount to be found in a 100-year-old hardwood forest dominated by *Acer saccharum*. Estimates of the quantity and chemical composition of leaf litterfall are from Gosz et al. (1972) for the control watershed in the Hubbard Brook Experimental Forest.

DISCUSSION

Mineral Capital of Lichens.—With the exception of lichens of the spruce-fir forest, concentration of N is 1.5 to 1.7% (Table 1). Of course individual species within each ecosystem may have N concentrations which vary considerably from the weighted mean of all lichens for the ecosystem. For example, the nitrogen-fixing lichens which contribute about 2% of the lichen biomass in the Douglas fir forest and 5% of the lichen biomass in the oak woodland have N concentrations considerably higher than other lichens which do not fix N. Nitrogen-fixing lichens are rare or absent in the remaining ecosystems. Standing crop of N in lichens ranges from 1.7 to 27 kg ha^{-1} depending primarily on biomass present and to a lesser extent on N concentration. The amount of N in new biomass produced annually is estimated to range from 0.3 to 7.5 kg ha^{-1} with highest values in the two Oregon localities where turnover rates are high. Phosphorus and potassium have patterns of distribution among the five ecosystems similar to that of N, with maximal standing crops of 4 kg ha^{-1} for P and 9 kg ha^{-1} for K, and maximal turnovers of $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for P and $2.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for K.

Calcium has its highest concentration (0.5%) in lichens of the two deciduous forests (oak woodland and northern hardwoods) where foliage is relatively rich in this cation. The Mg concentration is also relatively high in lichens of the oak woodland where

TABLE 2. Ratios of nutrient capital or turnover for lichens to nutrient capital or turnover for other ecosystem components.

Ecosystem	Ratio	Element					
		Bio- mass	N	P	K	Ca	Mg
Douglas fir forest	$\frac{\text{Lichen capital}}{\text{Foliage capital}}$	0.06	0.11	0.06	0.06	0.02	0.02
Douglas fir forest	$\frac{\text{Lichen turnover}}{\text{Total litterfall and throughfall}}$	0.06	0.19	0.09	0.06	0.01	0.01
Oak woodland	$\frac{\text{Lichen turnover}}{\text{Leaf litter}}$	0.15	0.15			0.09	0.07
Northern hardwoods	$\frac{\text{Lichen capital} \div 5}{\text{Leaf litter}}$	0.007	0.011	0.017	0.010	0.005	

foliage is also high in Mg. Data on Mg are not available for the northern hardwoods ecosystem. Calcium and magnesium have their highest standing crops (9 and 2 kg ha⁻¹) and turnovers (2.6 and 0.5 kg ha⁻¹ yr⁻¹) in the oak woodland.

Relative Contribution of Lichens to Mineral Turnover.—In the Douglas fir forest the lichen biomass of 900 kg ha⁻¹ is 0.1% of the approximately 900,000 kg ha⁻¹ of above- and below-ground plant biomass (Grier & Logan, 1977). The bulk of plant biomass is woody material which has an extremely slow turnover rate. Since foliage and lichens have similar, relatively rapid turnover rates, it is reasonable to compare nutrient capitals for these components (Table 2): The relative importance of the mineral capital in lichens is seen to be highest for N, intermediate for K and P and lowest for Ca and Mg. For the Douglas fir forest the same pattern is shown by comparing the quantity of a specific mineral in lichen production to the quantity of the same mineral turned over annually within the ecosystem. Annual turnover for the ecosystem is approximated as the mineral content of litterfall plus that of net throughfall. The ratios in Table 2 for the Douglas fir forest are probably reasonable approximations of the proportion of the total annual turnover (exclusive of root turnover) for these minerals which cycles through the epiphytic lichens.

Since data on throughfall and chemistry of non-leaf litterfall are not available or incomplete for the oak woodland, lichen turnover is compared to leaf litterfall in Table 2. The ratio of lichen turnover to leaf litterfall is higher for N than it is for Ca and Mg. Data of Carlisle et al. (1966) suggested that if throughfall data were included in the denominator, the ratio for N would be unchanged and the ratios for Ca and Mg would be one-half as great.

Although the turnover rate for lichens in the northern hardwoods ecosystems is unknown, data in Table 1 suggest that it is likely to fall in the range of $\frac{1}{4}$ to $\frac{1}{7}$ of total biomass per annum. Calculations in Table 2 assume lichen biomass turns over in five years. The quantity of minerals contained in lichen turnover is on the order of 1% of the quantity of minerals cycled through leaf litter.

Similar comparisons cannot be made for the balsam fir and spruce-fir forests for lack of data on the standing crop or litterfall of the forest trees.

Nitrogen in the Douglas fir forest is one case (in Table 2) for which the quantity cycled through lichens is higher than that expected from biomass relations. This result

could be anticipated since the predominant lichen in the Douglas fir forest is a nitrogen fixer. Another situation in which lichens may be responsible for cycling a larger quantity of an element than would be predicted on the basis of biomass relations is that of P in the northern hardwoods forest. In general, lichens appear to be less important in the cycling of Ca and Mg than would be expected on the basis of biomass.

Minerals stored in lichen tissues are released when the lichens decompose. Epiphytic lichens may decompose in the canopy, but substantial quantities fall to the forest floor. Lichen litterfall is probably only a few $\text{kg ha}^{-1} \text{yr}^{-1}$ in the northern hardwoods ecosystem, but it exceeds $300 \text{ kg ha}^{-1} \text{yr}^{-1}$ in the oak woodland (Pike, 1971). The standing crop of lichen litter in Douglas fir forests in western Oregon is commonly on the order of $50\text{--}100 \text{ kg ha}^{-1}$ (Pike, Howe & Topik, unpublished). This lichen litter decomposes relatively rapidly: in litterbags lichens have half-lives from as short as three months in the oak woodland (Pike, 1971) to one year in the Douglas fir forest (Rossman, pers. comm.) and balsam fir forest (Lang, pers. comm.).

Additional Mineral Fluxes.—Lang et al. (1976) found that lichens from the balsam fir forest were able to take up NO_3^- and NH_4^+ but lost metallic cations when submerged in artificial rainwater. Thus there may be additional fluxes of minerals between lichens and canopy solutions, which would lead to an underestimation of the quantity of minerals cycled through lichens when computations of minerals turnover are based solely on biomass turnover.

In the submersion studies of Lang et al. (1976), lichens lost Ca, Mg and K to the solution. Although the direction of flux for K reversed (from output to uptake) after the lichens were submerged for one hour, cumulative uptake was never observed for these cations even after five hours. Clearly, lichens cannot continue to lose cations in this manner under field conditions and maintain thallus levels. Submergence may be a sufficiently unnatural condition that lichens respond very differently from the way they would respond to natural rain. Lang et al. (1976) suggest that fog mist and light rain may be insufficient to remove minerals from lichens under field conditions. Epiphytic lichens dry out quickly and frequently in most ecosystems and, since 1–2 ml of water are needed per gram of thallus to rehydrate it, light rains may often not supply the water needed to leach substances from the lichen. Lang et al. (1976) also suggest that lichens may take up minerals from the underlying bark through the rhizines. This possibility seems unlikely to be a factor, since rhizines are rare or absent on most of the species investigated and since rhizines do not, in general, have absorptive functions (Henssen & Jahns, 1974).

In the laboratory misting studies of Douglas fir lichens (Carroll & Pike, unpublished), net output of monovalent metallic cations from the lichens has been detected in all cases examined; however, uptake of divalent cations was observed on numerous occasions. Direction and magnitude of cation fluxes appeared to be related to a number of factors having to do with both prior history of the lichens and chemistry of the rainwater. For example, loss of K from *Lobaria oregana* (Fig. 1) was much greater when collection and misting of the lichens followed a dry period (defined as $<0.5 \text{ cm}$ of rain in prior 3 days) than when collection and misting followed a wet period ($>3 \text{ cm}$ of rain in prior 3 days). The position the lichens occupied in the canopy is also important; in general, lichens from the lower portion of the canopy lose minerals more readily than lichens from the upper canopy (Fig. 1). Leaching losses from the lichens are small when compared to mineral capital: mean leaching loss from *Lobaria oregana* during one hour laboratory mistings is about 0.05% for P, Ca and Mg and 0.3% for K.

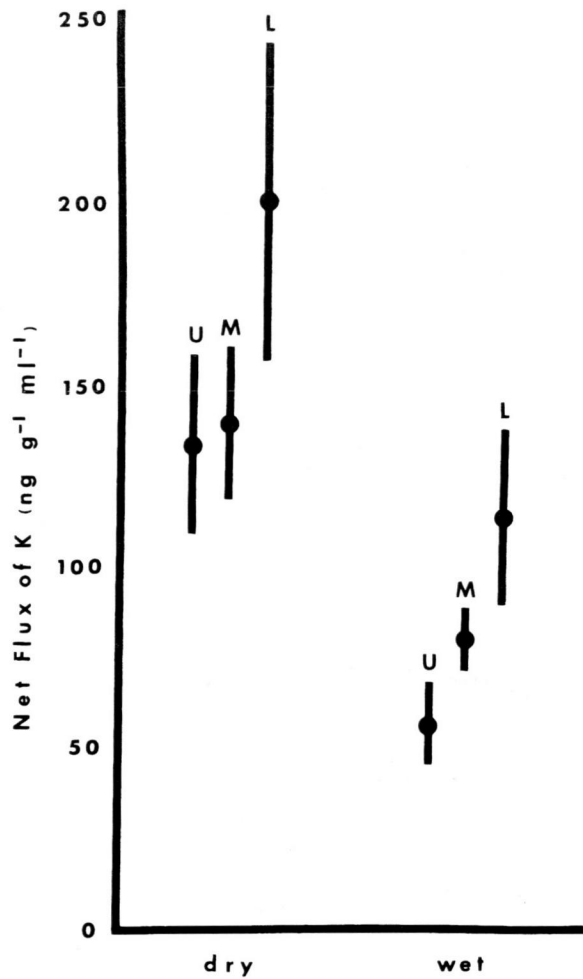


FIGURE 1. Mean net flux of K from *Lobaria oregana* (Tuck.) Müll. Arg. during laboratory leaching. Dry and wet refer to meteorological conditions in field prior to collection of samples. Dots indicate means of 3 replicates from each of 3 canopy heights, upper (U), middle (M) and lower (L), for nine dry and five wet leaching episodes; vertical lines represent 1 standard error on both sides of the mean. Results of 2-way analysis of variance indicate that effects of wet or dry period and height in the canopy are significant with $p < 0.01$ in both cases.

Investigations of nitrogen flux during laboratory mistings have shown that, as expected, organic nitrogen compounds are leached from nitrogen fixing lichens whereas N is taken up by lichens which do not fix N. Results of time-course studies of N fluxes indicate that the interactions between lichens and N compounds in rainwater may be quite complex. *Alectoria sarmentosa* removed N from solution throughout the time-course study (Fig. 2). When N in small, non-cellular particulates ($0.2 \mu\text{m} < \text{particulates} < 30 \mu\text{m}$) is taken into account, the total net uptake of N is not so great as analysis of dissolved N alone would suggest, but the net movement of N is, nonetheless, into the thallus. When *Lobaria oregana* is misted, there is an initial output of dissolved N

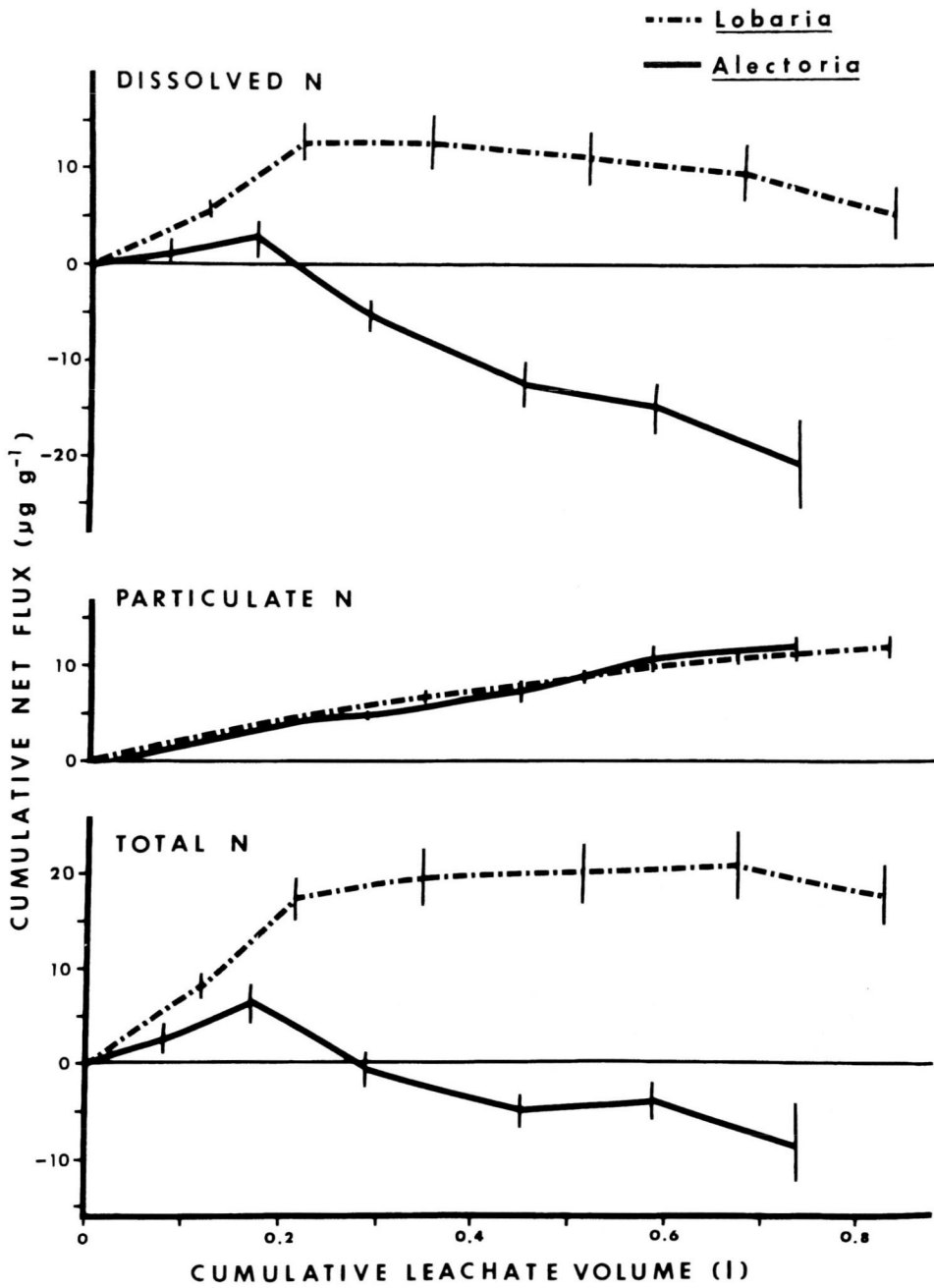


FIGURE 2. Results of a time-course study of N flux during laboratory leaching of *Alectoria sarmentosa* (Ach.) Ach. and *Lobaria oregana* Tuck. Müll. Arg. For *Alectoria*, means are for 2 replicates from upper and lower canopy; for *Lobaria* there are 3 replicates from upper and lower canopy. Vertical lines represent one standard error on both sides of the mean. Negative values indicate cumulative uptake; positive values indicate cumulative output. Filtered particles were 0.2–30 μm .

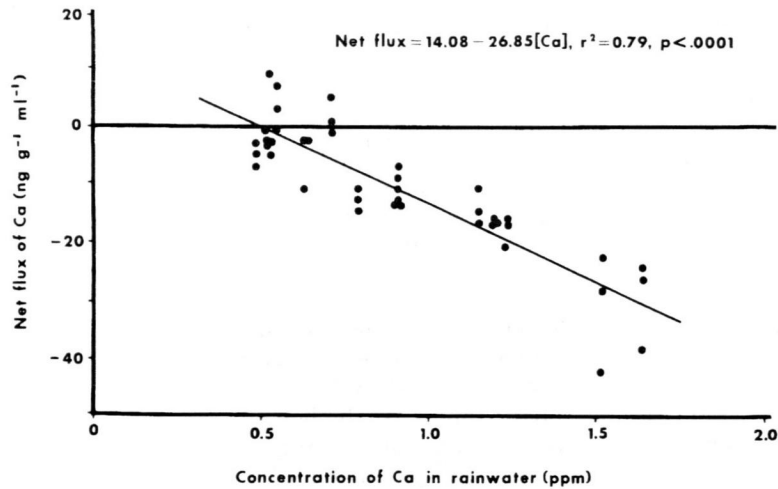


FIGURE 3. Influence of concentration of Ca in rainwater on flux of Ca from *Lobaria oregana* (Tuck.) Müll. Arg. during laboratory leaching. Each point indicates a single sample. Negative values indicate uptake; positive values indicate output.

(Fig. 2). With continued misting, dissolved N is taken up, thus decreasing the net loss of dissolved N. Filterable solids are again exported, and microscopic examination of the solids under the scanning electron microscope indicates that the N here is largely in the form of bacterial cells which were living on the thallus surface (G. Carroll & F. Carroll, pers. comm.). This raises the question of which component (*Lobaria* or bacteria) is taking up dissolved N after the initial period of output. In fact, *Lobaria* could have been releasing soluble N compounds throughout the time-course study, these compounds being simply converted to bacterial cells.

How do the quantities of minerals leached from lichens compare to the quantities released through turnover of lichen biomass? We do not have sufficient data, particularly in light of the complexities involved, to estimate accurately the quantity of minerals leached from lichens under field conditions. However, simple calculations based on laboratory data will yield an order of magnitude estimate that may be compared with turnover values in Table 1. Two estimates which are likely to bracket the leaching losses from lichens of the Douglas fir forest have been calculated from outputs of minerals observed during laboratory leaching. For these calculations mineral fluxes as microparticulates are ignored, and all lichen species are assumed to behave as *Lobaria oregana*. For the lower estimate each laboratory leaching experiment was regarded as representing a single rainstorm. In the Andrews Experimental Forest there are typically about 40 rainstorms (separated from one another by one or more intervening days without measurable rain) per year (U.S. Forest Service Meteorological data). The higher estimates of leaching losses are average quantities of minerals leached from lichens during laboratory misting studies multiplied by the quantity of water intercepted by lichens in the Douglas fir forest. Results of this analysis (Table 3) indicate that elemental flux due to biomass turnover is generally greater than that due to leaching losses for the macronutrients investigated. For N, P, Ca and Mg leaching losses are on the order of 5–30% of the values computed for biomass turnover. Only for K are leaching losses roughly equivalent to fluxes accounted for by biomass

TABLE 3. Elemental turnover due to biomass turnover compared with that due to leaching losses for epiphytic lichens of the Douglas fir forest. Units are $\text{kg ha}^{-1} \text{yr}^{-1}$.

Element	Biomass Turnover	Leaching Turnover
N	4.5	0.2-0.8
P	0.61	0.06-0.2
K	1.5	0.5-2.0
Ca	0.45	0.03-0.1
Mg	0.08	0.004-0.02

turnover. These comparisons must be regarded as quite preliminary; however, they do suggest that biomass turnover is a good index of elemental flux through lichens.

Source of Lichen Minerals.—From where do the minerals stored by lichens in their annual production come? One possibility is atmospheric inputs as rain, horizontal interception and dust. Table 4 shows ratios of quantities of minerals entering the system as atmospheric inputs to quantities of minerals in annual production of the Douglas fir lichens and the balsam fir lichens. Since not all of the water entering the system comes in contact with the lichens, such a ratio must be several times unity in order for growth needs of the lichens to be met by atmospheric inputs. These data indicate that N, Ca and Mg requirements may well be met by atmospheric inputs in the balsam fir forest, whereas those of P and K are probably not. In the Douglas fir forest Ca and Mg requirements are the only ones which may be met by rainfall. Since the major lichen in the Douglas fir forest is a nitrogen-fixer, additional inputs of N are probably not necessary.

The fact that Ca and Mg requirements can be met by atmospheric inputs is consistent with the uptake of these cations from natural rainwater observed regularly during leaching studies. The fact that K and P requirements cannot be met by atmospheric inputs is consistent with the failure to observe uptake of these elements by lichens during leaching studies. Considerable quantities of P and K are leached from the canopy so that throughfall is greatly enriched over incident precipitation in these elements. In the Douglas fir forest ratios of elemental content of throughfall to that of rainfall are as follows: P, 12; K, 200; Ca, 2.1; and Mg, 1.7 (Abee & Lavender, 1972). It seems likely that canopy lichens can absorb P and K from the relatively concentrated canopy solutions even though they do not absorb them from incident rainwater. There appears to be a threshold concentration below which lichens will not remove a cation from solution (Fig. 3). Because of leaching from canopy surfaces, lichens in the lower portion of the canopy are expected to experience higher concentrations of minerals in solution than is true of lichens in the upper canopy. Thus lichens from the upper canopy release minerals less readily than lichens from the lower canopy (Fig. 1).

TABLE 4. A comparison of atmospheric inputs to quantities required for lichen growth (expressed as ratios) for several elements.

Element	Douglas Fir Forest	Balsam Fir Forest
N	0.2	32
P	0.4	1.6
K	0.1	3.5
Ca	5.2	40
Mg	16	37

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