

The role of mosses in the phosphorus cycling of an Alaskan black spruce forest

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Summary. Mosses account for 75% of the annual phosphorus accumulation in aboveground parts of an Alaskan black spruce forest, although they comprise only 17% of the phosphorus pool in aboveground vegetation. *Sphagnum subsecundum* and feathermosses (*Hylocomium splendens* and *Pleurozium schreberi*) have a higher capacity to absorb phosphate than do the fine roots of black spruce (*Picea mariana*) that are situated beneath the moss layer. In three of the four moss species studied, phosphate absorption capacity increases with increasing age of green tissue and decreases with increasing age of brown tissue. In the two feathermosses, which acquire moisture primarily from the air, and in *Sphagnum*, phosphate absorption is more rapid in green than in brown tissue. In contrast, the endohydric moss *Polytrichum commune*, which transports water through stem tissue from soil, absorbs phosphate most rapidly from stems in mineral soil. Two treatments designed to reduce activity of mycorrhizae (cutting of roots extending beneath the moss carpet or application to the moss surface of a fungicide that kills mycorrhizal hyphae) tended to increase phosphate retention by mosses and reduce phosphate transfer out of the experimental plots. This suggests that mycorrhizae are an important avenue of phosphorus movement out of the moss carpet and a means by which the black spruce competes with the overlying mosses for nutrients.

Key words: Mosses – Mycorrhizae – Phosphorus cycling – *Picea mariana*

In the boreal forest tree growth is strongly limited by nutrient availability (Weetman 1971; Van Cleve and Zasada 1976; Chapin et al. 1986). Black spruce forests appear extreme in this respect (Weetman 1971). For example, in interior Alaska, tree productivity and phosphorus availability are lower in black spruce than in any other forest type, because low soil temperature restricts rates of decomposition and nutrient cycling (Van Cleve et al. 1983). However, these black spruce forests are characterized by a dense carpet of mosses 10–20 cm thick (Weetman and Timmer 1967; Busby et al. 1978; Viereck et al. 1983) that has an annual production equal to that of the black spruce overstory (Skre and Oechel 1979). In contrast to the trees (Weetman 1971),

growth of the dominant moss species is not nutrient-limited (Skre and Oechel 1979). This raises questions about how mosses are so effective in acquiring nutrients and what impact they may have upon nutrient supply to the forest overstory.

Mosses readily accumulate cations by cation exchange (Clymo 1963; Ruhling and Tyler 1970), but we are aware of only one study (Wells and Richardson 1985) on absorption of phosphate or other anions by mosses in controlled experiments (see Proctor 1981; Brown 1982). The study by Wells and Richardson (1985) demonstrated that *Hylocomium* actively absorbs phosphate by the same carriers that accumulate the pollutants, arsenate and selenite.

Mosses play an important role in nutrient cycling in many forest ecosystems, because they intercept nutrients from litter and throughfall before nutrients return to the rooting zone (Tamm 1953, 1964; Weetman and Timmer 1967; Rieley et al. 1979; Binkley and Graham 1981). However, their importance in nutrient uptake, accumulation, and cycling relative to the vascular vegetation has not been documented. In Alaskan black spruce forests, trees are particularly dependent upon recycling of nutrients within the ecosystem, because most mineral soil is permanently frozen, and there are no spruce roots in the shallow layer of mineral soil that thaws briefly during summer (Tryon and Chapin 1983). Because all spruce roots are situated in the organic mat between the mosses and mineral soil (Tryon and Chapin 1983), it is important to know the extent to which nutrients move through the moss carpet to the spruce rooting zone. Here we report on the phosphate uptake potential of mosses in an Alaskan black spruce forest in comparison with the fine roots of black spruce, evaluate the capacity of mosses to retain the phosphate they have absorbed, and document their role in the cycling of phosphorus in a black spruce forest.

Study site and methods

All field work and sample collections for this study were conducted in a 135-year-old black spruce (*Picea mariana* (Mill.) B.S.P.) forest at Washington Creek (65° 10' N, 147° 50' W, 300 m elevation), 45 km north of Fairbanks in interior Alaska. Black spruce is the only major overstory species, and beneath a scattered shrub understory is a thick carpet of the feathermosses *Hylocomium splendens* (Hedw.) Brid. and *Pleurozium schreberi* (Brid.) Mitt (Dyrness and Grigal 1979; Viereck et al. 1983). The soil is a poorly developed silt loam overlain by a 20–30-cm thick organic mat. Permafrost is present, and the maximum summer thaw is 50 cm.

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Phosphorus pools

We measured phosphorus concentrations in current and non-current green moss tissue. Mosses were dried at 70° C, ground in a Wiley mill, digested with selenous-sulfuric acid, and analyzed colorimetrically with a Technicon autoanalyzer, using the ammonium molybdate method. Using published data on weight per shoot (Skre and Oechel 1979) and shoot density (Oechel and Van Cleve 1986), we calculated phosphorus pool size in current and non-current green tissue for each moss species. All data for these calculations were collected along the same transects at Washington Creek in 1976. Annual phosphorus allocation to new growth represents a maximum estimate of phosphorus uptake that includes an unknown amount of phosphorus translocation from older tissue to new growth.

Phosphate absorption potential

The absorption of phosphate by roots and mosses when immersed in solutions was measured as an index of physiological absorption capacity under conditions where supply to the tissue was controlled. In the first experiment we determined the effect of solution concentration and temperature upon two moss species and the fine roots of black spruce. We then examined in detail the effect of tissue type and age class upon absorption in four moss species. In late May 1978 fine ectomycorrhizal roots of black spruce were carefully removed from the forest floor at Washington Creek, placed in 0.5 mM CaCl₂ and immediately returned to the laboratory for measurement of phosphate absorption (Chapin and Tryon 1983). Phosphate absorption was measured from dilute solutions (0.5–20 μM) of ³²P-labeled phosphate, containing 0.5 mM CaCl₂, pH 5.0 (Epstein et al. 1963; Chapin and Bloom 1976). These solutions span the natural range of phosphate concentrations (3–6 μM) and have the average pH (5.0) of both soil solution and throughfall in 1976–1977 (Van Cleve and Dryness 1983). Following a 10-min period of phosphate absorption at 1, 10, 20 or 30° C, roots were transferred to an unlabeled solution of 500 μM phosphate to exchange off any phosphate that was adsorbed but not actively absorbed by root cells. Solution depletion was less than 1% during the experiment. Roots were then counted for ³²P by liquid scintillation (Chapin and Bloom 1976).

The following week we collected moist patches of the mosses *Hylocomium splendens* and *Polytrichum commune*, returned them to the laboratory in plastic bags, and separated them into green and brown tissue. Phosphate absorption was measured for the two tissue classes from dilute solutions of ³²P-labeled phosphate using the same technique as for roots but with mosses illuminated at 100 μmol m⁻² s⁻¹ PhAR and with solution temperatures of 5° and 15° C.

In mid June 1979, we collected moist mosses of all major species at Washington Creek (i.e. *Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum commune*, and *Sphagnum subsecundum* Nees.) and separated them into yearly age classes (Skre and Oechel 1979), with G₁ representing the current year's green, G₂ the 1-year-old green, etc. and B₁ the youngest brown tissue, B₂ the next youngest brown tissue, etc. In *Polytrichum* we also collected "stem" (caulidia) from mineral soil with associated rhizoids (B_M). This was the only species that extended through the forest floor

into mineral soil. Age classes were readily recognized in each species as a result of seasonal change in leaf length or annual branching of new shoots (Tamm 1964; Callaghan et al. 1978; Pakarinen 1978; Skre and Oechel 1979). Phosphate absorption by selected age classes of each species was measured at 10° C from solutions of low (0.5 μM) and moderate (10 μM) phosphate concentration, using the techniques described above. Each sample (except in the youngest age class) was immediately separated into "leaves" (phyllidia) and "stems" (caulidia) after the absorption experiment and prior to drying, weighing, and counting.

Phosphorus cycling

To evaluate the potential of the dominant feathermosses to absorb and retain phosphate in situ, and to test the potential of mycorrhizal fungi to transport phosphate from the living moss layer to the underlying root zone, we carried out a field experiment in August 1984. Twenty circular plots 50 cm in diameter were selected from uniform swards of pure *Hylocomium* (with no shoots of vascular plants) and assigned to 4 treatments, using a randomized block design: control, fungicide, roots cut, and fungicide + roots cut.

In the fungicide treatment we sprayed each plot with a water solution equivalent to 14 g m⁻² of Captan fungicide containing 0.7 g m⁻² N[trichloromethyl thio]-4-cyclohexene-1,2-dicarboximide. Captan is a non-resistant fungicide that reduces levels of ectomycorrhizae and saprophytic fungi but does not affect phycomycetes, earthworms, mites, bacteria, and actinomycetes (Ingham 1985). This is the application rate recommended to reduce damping-off fungi in seed beds. In the roots-cut treatment, we cut vertically to a depth of 40 cm with a shovel and ax at the perimeter of the plot to sever all roots entering the plot.

Ten days after these treatments were initiated, we re-cut any new roots entering the roots-cut plot, collected a few mosses from the perimeter of the control and fungicide plots for uptake measurements (see below), and then sprayed each plot with a fine mist of a ³²P-labeled solution of phosphate with a specific activity of 100 MBq mol⁻¹ at a rate of 6 mg P m⁻², 10% of the annual uptake by black spruce at Washington Creek (Chapin 1983). The actual rate of P application in each plot was measured by placing 3 2-cm diameter discs of No. 1 filter paper in each plot just outside the area of final sampling (see below), then digesting and counting the discs by liquid scintillation. Rate of phosphate absorption from a 10 μM ³²P-labeled phosphate solution did not differ between fungicide-treated and control mosses (P > 0.05), indicating that the fungicide did not impair the phosphate uptake capacity of mosses at the time of ³²P application in the field.

One week after ³²P application, a 15-cm diameter core was taken from the center of each plot to mineral soil (approximately 20 cm) and separated into moss (green + brown), the upper 2 cm of forest floor, and the remaining forest floor. In order to minimize contamination of the forest floor by the corer, the moss layer of each core was collected first (and the remaining mosses in the 50-cm diameter plot disposed of), then the soil corer was washed, and the cores of the forest floor were collected. Sections from each core were dried, weighed, ground in a Wiley mill, digested in selenous-sulfuric acid, and counted by liquid scintillation. Results for each core are expressed on a unit ground area basis as percent of applied ³²P.

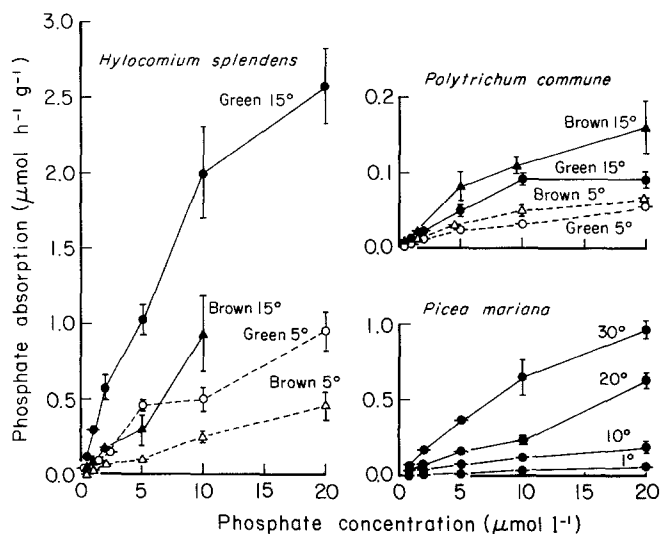


Fig. 1. Rate of phosphate absorption from solutions by green and brown parts of the two mosses *Hylocomium splendens* and *Polytrichum commune* at 5° and 15° C and by mycorrhizal fine roots of black spruce *Picea mariana* at 4 temperatures. Note difference in scale for *Polytrichum*. Data are means \pm S.E., $n=4$

Results

Phosphorus pools

Although mosses comprised only 17% of the aboveground phosphorus pool of the black spruce forest, they accounted for 75% of the annual accumulation in aboveground new growth (Table 1). The feathermosses (*Hylocomium splendens* and *Pleurozium schreberi*) accounted for most of the moss phosphorus accumulation, because they had higher shoot densities than did *Polytrichum commune* and *Sphagnum subsecundum* and because phosphorus concentrations in new growth were higher in *Hylocomium* and *Pleurozium* than in *Polytrichum* or *Sphagnum*. Thus, although mosses represent only a small proportion of the biomass and total phosphorus pool, mosses dominate the phosphorus flux to new growth in the black spruce forest.

Phosphate absorption potential

In controlled experiments, green shoots of *Hylocomium*, a major moss species, had a maximum rate of phosphate absorption about 5-fold higher than that of the absorbing roots of black spruce (Fig. 1), reflecting the advantage of mosses over spruce in phosphate absorption from solutions. Green shoots of *Polytrichum*, however, had rates of absorption even lower than spruce roots. In *Hylocomium*, a feathermoss that depends primarily on atmospheric moisture for hydration (Skre and Oechel 1981), green tissue absorbed phosphate more rapidly than brown tissue, whereas in *Polytrichum*, which transports moisture upward from the soil (Proctor 1981; Skre et al. 1983a), brown tissue absorbed phosphate from solution more rapidly than green tissue. In both species and tissues, absorption was more rapid at 15° than at 5° C. Green shoots of *Hylocomium* at 5° C absorbed phosphate more rapidly than did spruce roots at any temperature, indicating the potential of this moss to absorb actively at low temperature.

We then examined the variation in phosphate absorption potential in greater detail with respect to four moss species and a variety of tissue types and ages. There was a 20- to 40-fold range in absorption rate among the four

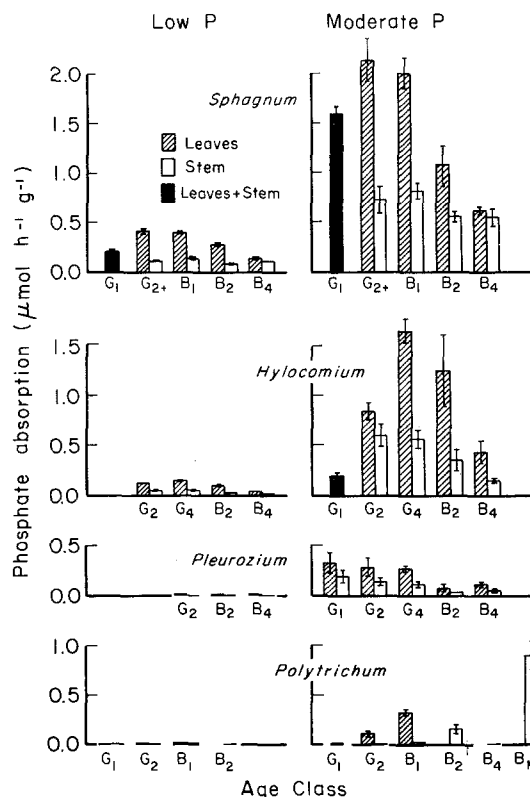


Fig. 2. Rate of phosphate absorption by 4 moss species at 10° C from solutions of low (0.5 μM) or moderate (10.0 μM) phosphate concentration. Each species was divided into age classes: Current year's green (G_1), the previous year's growth (G_2), etc. Green material of *Sphagnum* below the capitulum could not be aged and was lumped (G_{2+}). Brown moss tissue was also grouped into age classes in each species (e.g., B_2 and B_4) and, in *Polytrichum*, into stems in the mineral soil (B_M). Each age class was subdivided into "leaves" (phyllidia) and "stems" (caulidia) except for the youngest age class of green where the two components were analyzed together. Data are means \pm S.E., $n=4$

moss species from Washington Creek when immersed in solutions containing low and moderate concentrations of phosphate (Fig. 2). *Sphagnum* had the highest rate of phosphate absorption, followed by the feathermosses *Hylocomium* and *Pleurozium*, while *Polytrichum* had the lowest rates. All species except *Pleurozium* showed increased absorption with increased tissue age in green tissue. In brown tissue, absorption decreased with increasing tissue age in *Sphagnum* and *Hylocomium*. *Pleurozium* showed no significant effect of tissue age upon absorption rate by either green or brown tissue. With the exception of *Polytrichum*, absorption rate was higher in green than in brown tissue. In *Polytrichum*, stems from mineral soil had nearly 3-fold higher phosphate absorption potential than any other plant part in that species. In all other species leaves within a given age class had higher absorption potential than did stems.

There were strong species differences in the response of phosphate absorption to solution concentration. In *Sphagnum* G_2 - B_4 age classes, phosphate absorption at the low solution concentration averaged 20% of that at the higher concentration, 4-fold more than expected from the 1:20 ratio in solution concentrations (Fig. 2). In *Hylocomium* the G_2 - B_4 age classes absorbed phosphate from the dilute solution at 11% of the rate from the more concen-

Table 1. Components of annual phosphorus accumulation in new growth and pool size in above-ground parts of green moss and major vascular plant species of black spruce forest, Washington Creek, Alaska. Data sources are: shoot density (Oechel and Van Cleve 1986), shoot weight (Skre and Oechel 1979), vascular plants (Chapin 1983)

	<i>Hylocomium</i>		<i>Pleurozium</i>		<i>Polytrichum</i>		<i>Sphagnum</i>		Total moss
Shoot density (shoots m ⁻²)	1928	±105	6892	±675	444	±34	581	±55	9845
Shoot weight (mg shoot ⁻¹)	58.2	± 5.4	24.4	± 1.3	46.2	± 3.5	26.1	± 4.5	–
Shoot production (mg shoot ⁻¹ yr ⁻¹)	19.1	± 2.2	9.3	± 0.4	13.3	± 1.4	3.6	± 2.1	–
Moss biomass (g m ⁻²)	112		167		21		15		315
Moss production (g m ⁻² yr ⁻¹)	36.8	± 8.9	64.1	± 6.2	5.9	± 1.8	7.9	± 2.5	114.7
Current growth P (%)	0.203±	0.032	0.188±	0.006	0.159±	0.016	0.159±	0.011	–
Green moss P (%)	0.104±	0.003	0.091±	0.001	0.098±	0.006	0.098±	0.004	–
Moss P pool (g m ⁻²)	0.117		0.151		0.020		0.015		0.303
Current growth P accumulation (g m ⁻² yr ⁻¹)	0.075		0.121		0.009		0.013		0.218

	<i>Picea</i>	<i>Ledum</i>	<i>Vaccinium</i>	Total vascular	Total system
Biomass (g m ⁻²)	5216	29.5 ± 5.9	14.5 ± 2.9	5260	5575
Production (g m ⁻² yr ⁻¹)	102	11.2 ± 0.8	7.6 ± 1.0	121	236
P pool (g m ⁻²)	1.410	0.024	0.010	1.444	1.747
Current growth P accumulation (g m ⁻² yr ⁻¹)	0.060	0.010	0.004	0.074	0.292

Table 2. ³²P distribution between mosses (green + brown) and roots + forest floor following ³²P application to mosses after mosses had been treated with fungicide or spruce roots had been severed surrounding the plot. Unrecovered ³²P is indicated as missing. Data are means ± S.E., n = 5

Treatment	³² P (% of applied)			
	Moss	Forest floor + roots		Missing
		0–2 cm	2–20 cm	
Mean value				
Control	52.5 ± 4.6	4.8 ± 1.1	2.0 ± 0.8	40.8 ± 4.6
Fungicide	56.2 ± 2.3	7.9 ± 1.7	1.7 ± 0.8	34.2 ± 6.7
Roots cut	64.3 ± 11.4	7.4 ± 2.1	0.4 ± 0.2	27.9 ± 11.4
Fungicide + roots cut	70.8 ± 7.2	13.7 ± 3.8	1.8 ± 0.8	13.7 ± 6.9
Probability of treatment effect				
Fungicide	0.48	0.06	0.48	0.14
Roots cut	0.09	0.10	0.32	0.03
Interaction	0.85	0.52	0.26	0.62

trated solution, still more than twice the rate expected from the ratio of solution concentrations. In contrast, phosphate absorption in *Pleurozium* and *Polytrichum* increased about 20-fold in response to the 20-fold concentration increase. Only in *Sphagnum* did the current year's green tissue absorb appreciable phosphate.

Phosphorus cycling

³²P-labeled phosphate was applied to the moss surface in a dense stand of pure *Hylocomium* (698 ± 29 g m⁻² of green-plus-brown moss). In untreated control plots mosses retained about half of the applied ³²P after a week of rainy weather, and 41% of the applied phosphate had disappeared from the plot entirely (Table 2), presumably due to leaching or to absorption by roots and subsequent translocation out of the plot. The small amount of label (2%) recovered from the lower horizon of forest floor (2–20 cm beneath the moss) makes it unlikely that there was significant amount of label leached down to mineral soil (which we did not sample).

Cutting of roots around the plot (with no disturbance to the mosses) significantly ($P < 0.05$) reduced the loss of applied ³²P from the experimental plots and tended ($0.05 < P < 0.1$) to increase phosphorus retention by the mosses. This is unlikely to be a consequence of a change in direct moss-spruce interaction because all spruce roots are situated *beneath* the moss layer. Similarly, application of fungicide to the moss surface tended ($P = 0.14$) to reduce phosphorus loss from the plot, although it had no effect upon phosphorus retention by mosses. These results suggest that mycorrhizae may be an avenue by which phosphorus moves out of the moss mat to the underlying spruce roots. The large difference in phosphorus loss from mosses in the fungicide treatment and the fungicide + roots-cut treatment suggests that the application rate of fungicide was insuffi-

cient to eliminate completely the function of mycorrhizal hyphae.

Discussion

Phosphate absorption by both green and brown tissues of *Hylocomium* and *Polytrichum* increased asymptotically with increasing solution P concentration and with increasing temperature. Adsorption of anions by plant tissues is minimal under our experimental conditions (Epstein et al. 1963) and is probably particularly low in mosses because of their low iron and aluminum content (Brown 1982) and high cation exchange capacity (Clymo 1963). Thus, the patterns of phosphate accumulation that we observed presumably reflect a process of active absorption similar to that observed in higher plants. The more rapid phosphate absorption by leaves than by stems in all moss species are probably a consequence of the greater surface/volume ratio of leaves. The increase in absorption potential with increasing age of green tissue in all species except *Pleurozium* suggests that (1) the carriers for phosphate absorption continue to be synthesized even after leaf growth ceases, (2) breakdown of the leaf cuticle with age increases phosphate transport into the leaf or (3) moss surfaces are colonized through time by microorganisms that actively absorb phosphate. Similarly, in roots of vascular plants nutrient absorption potential is lower in root tips than in fully differentiated roots. However, in roots, phosphate absorption generally declines in very old suberized roots (Clarkson 1974). Therefore, the high phosphate absorption potential that we measured in 4-year-old moss leaves suggests that these mosses retain their potential to absorb phosphate longer than do roots of vascular plants. The high phosphate concentration of the youngest age class in *Sphagnum* and *Hylocomium* early in the season (Tamm 1953; Weetman and Timmer 1967; Pakarinen 1978; Skre and Oechel 1979) presumably reflects translocation to new shoots and a high ratio of cell contents to structural material, as found in young leaves and shoots of vascular plants (Chapin 1983) rather than a high potential to acquire phosphate from the environment. In our results the new green tissue (G_1) always had a lower phosphate absorption potential than older age classes, perhaps because high tissue P concentrations in young tissues inhibit uptake (Harrison and Helliwell 1979). The relatively high phosphate absorption potential of young brown tissue indicates the importance of brown tissue in phosphate nutrition of mosses and presumably explains the translocation of carbohydrates from green to brown tissue in all of these and other moss species (Collins and Oechel 1974; Sveinbjornsson and Oechel 1981; Skre et al. 1983b).

The differences in phosphate absorption among the four moss species studied are consistent with other aspects of their ecology. *Polytrichum*, which depends primarily upon soil for cations (Streeter 1970) and water (Proctor 1981; Skre et al. 1983a), had highest phosphate absorption rates by stems in mineral soil. Moving groundwater flowing over permafrost may bring substantial phosphate and other minerals to the surface of rhizoids of these moss stems. In contrast, *Sphagnum*, *Hylocomium*, and *Pleurozium* acquire both water (Proctor 1981; Skre et al. 1983a) and cations (Tamm 1953, 1964; Weetman and Timmer 1967; Ruhling and Tyler 1970; Rieley et al. 1979; Pakarinen 1978; Binkley and Graham 1981) from precipitation and leachates from

the vascular canopy; these mosses showed highest phosphate absorption potential in green leaves.

Our measurement of uptake from solutions provides a measure of the *potential* of mosses to absorb phosphate, where concentration at the moss surface is carefully controlled. Average phosphate concentrations in soil solution and throughfall (average of 5 μM ; Van Cleve and Dyrness 1983) are in the midrange of the phosphate concentrations that we tested. Actual phosphate concentrations experienced by moss tissue in the field are probably near the low end of the concentration range that we tested because of diffusion to the moss surface.

Mosses dominate the productivity and nutrient cycling of black spruce forests (Tamm 1953; Weetman and Timmer 1967; Skre and Oechel 1979), because this forest type provides moisture conditions favorable for moss growth (Skre and Oechel 1981; Skre et al. 1983a) and a relatively low input of vascular litter compared to adjacent hardwood stands; heavy litter could completely cover the moss layer and greatly retard moss growth. In the Washington Creek black spruce forest, mosses have a green-plus-brown biomass (645 g/m^2) similar to that of the absorptive roots of black spruce (685 g/m^2 ; Chapin 1983). Given that almost all (99%) of the black spruce roots are situated beneath the moss layer (Tyron and Chapin 1983), the position of mosses confers a considerable advantage over spruce roots in intercepting nutrients brought to the forest floor in litter, throughfall, and precipitation. Moreover, the moss layer has a high potential to absorb or adsorb cations (Clymo 1963; Ruhling and Tyler 1970) and to absorb phosphate (this study).

Vascular plants growing in a black spruce forest minimize their nutrient requirement by efficiently retaining nutrients through prolonged leaf retention and effective reabsorption from senescing leaves (Chapin 1983; Hom and Oechel 1983). Nevertheless, they must absorb some phosphate to support growth and replenish losses due to litterfall. One possibility is that the needs of vascular plants are met by decomposing moss at the base of the moss mat (Weetman and Timmer 1967). This pathway of nutrient transfer through dead moss tissue may be relatively slow, because the decomposition rate of moss tissue is inherently low and is further reduced by the low temperature and pH prevailing at the base of the moss mat (Coulson and Butterfield 1978; Heal et al. 1978; but see Bernier and Roberge 1962). Leaching may also explain some of the ^{32}P movement that we observed from mosses to underlying soil, although the high phosphate absorption capacities of mosses make this pathway unlikely, and our field experiments show that very little phosphate penetrates more than 2 cm into the forest floor.

A third path of nutrient movement from the moss mat may be via decomposer or mycorrhizal hyphae which are abundant in litter in the moss layer and are loosely associated with moss fronds (Parke and Linderman 1980; Proctor 1981; Brown 1982; PW Flanagan, unpublished work). The increase in retention of ^{32}P by mosses when fungicide was applied (non-significant trend) or when roots were cut ($P < 0.05$) beneath the mosses suggests that this latter avenue may be important. It is unlikely that roots could directly compete with mosses for phosphate, because there are no spruce roots in the moss layer. Thus, spruce trees may actively compete with mosses by supporting mycorrhizal hyphae that penetrate the moss layer. This direct cycling

of nutrients from litter and throughfall back to vascular plants is similar to that demonstrated for tropical forests (Stark and Jordan 1978) and may be a common process in moss-dominated boreal and other nutrient-limited ecosystems.

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