BLACK SPRUCE SEEDLING GROWTH AND NUTRITION ON SPHAGNUM AND FEATHER MOSS PEATS FROM A NORTHERN ONTARIO PEATLAND

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ABSTRACT

Growth of black spruce (*Picea mariana*) seedlings on moss-peat samples from a northern Ontario peatland was best on *Pleurozium schreberi*, and poorer (in order of decreasing crown lengths) on *Sphagnum magellanicum*, *S. angustifolium* and *S. fuscum*. Crown length was significantly and positively correlated with several site and peat measures--groundwater pH and calcium, nitrogen, potassium and phosphorus--and significantly and negatively correlated with loss on ignition and cation exchange capacity. Crown length was also significantly and positively correlated with foliar nitrogen, and significantly and negatively correlated with calcium and magnesium. Several silvicultural implications are discussed.

RÉSUMÉ

La meilleure croissance des semis d'Épinette noire (*Picea mariana*) sur des échantillons de mousse de tourbe provenant d'une tourbière du nord de l'Ontario a été obtenue sur *Pleurozium schreberi* et la plus médiocre (en ordre décroissant de la longeur des cimes), sur *Sphagnum magellanicum*, *S. angustifolium* et *S. fuscum*. La longueur des cimes était en corrélation positivement et significativement avec plusieurs paramètres de la station et des tourbes--pH et calcium de l'eau de surface, azote, potassium et phosphore--et significativement et négativement avec la perte après ignition et la capacité d'échange des cations. La longueur des cimes était aussi en corrélation significativement et positivement avec la teneur des feuilles en azote, et significativement et négativement avec la teneur en calcium et en magnésium. De nombreuses implications sylvicoles sont traitées dans le présent rapport.

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INTRODUCTION

Black spruce (*Picea mariana*[1]) swamps in the boreal forest are commonly characterized by irregular hummock and hollow topography created by numerous species of peat-forming mosses. The dominant mosses are species of *Sphagnum* and on drier, often well shaded mounds, feather mosses[2]. It is well known among foresters that *Sphagnum* moss and *Sphagnum* peat provide better substrates for black spruce seed germination and seedling survival than do feather moss and feather moss peat, mainly because of better moisture retention and supply (e.g., Heinselman 1957, Jarvis and Cayford 1960, Vincent 1966, Jeglum 1979). However, as the root systems of seedlings become established, nutrient supply becomes more important to seedling growth.

The importance of bryophytes as sensitive indicators of environmental factors has long been recognized by European phytosociologists (e.g., Sjörs 1963), and in recent years has become increasingly recognized in North America (e.g., Vitt and Slack 1975, Horton et al. 1979). The distribution of mosses has often been related to abiotic measures of important factor complexes, such as moisture and nutrient regime (e.g., Jeglum 1971, Horton et al. 1979). Another approach to the assessment of the nutrient regime is that of bioassay, in which the growth and nutrient uptake by one or more species are used to assess nutrient supply by various soil types or horizons (e.g., Winston 1974). This study utilizes black spruce seedling growth and nutrient uptake to assess the nutrient supply by the peats of four species of moss from a northern Ontario peatland.

The literature suggests that growth of black spruce and other conifers is better on feather moss peat than on *Sphagnum* peat. In a survey of soils and forest growth in the Algoma District, Wilde et al.

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[1] Nomenclature and author citations for vascular species follow Scoggan (1978-1979) and for mosses, Ireland et al. (1980).

[2] Feather mosses are a group of large mosses which occur together and have similar ecological characteristics. They often form continuous mats on the ground beneath upland black spruce, as well as beneath other coniferous forests. They also occur in swamps and bogs, in decreasing amounts as the *Sphagnum* mosses increase. They are favored by well shaded conditions, and do not retain moisture as well as *Sphagnum*. The main boreal feather moss is Schreber's feather moss (*Pleurozium schreberi*). Other common feather mosses are many-stalked broom moss (*Dicranum polysetum*), plume moss (*Ptilium crista-castrensis*), and step moss (*Hylocomium splendens*).

(1954) reported very high productive capacity of 'brown moss peat', comprised largely of the remains of *Pleurozium* and *Ptilium* with some fragments of wood and conifer leaf litter. They noted "high yields of 30 cords per acre [*ca.* 178 solid m^3/ha] at the age of 70 to 90 years", and observed: "The rate of growth is even higher on shallow peat, but drops off to about one-quarter of a cord per acre per year [*ca.* 1.5 solid m^3/ha/yr] on deep peat invaded by *Sphagnum* species." They went on to suggest that "under existing climatic conditions the removal of forest cover, or even a considerable opening of the canopy, will increase soil moisture in the surface layers and will accelerate the invasion of Sphagnaceae. This in turn, means increased anaerobiosis, irreversible fixation of nutrients, and adverse insulating effect of bog moss."

Only limited work has been done growing black spruce on various moss peats under controlled conditions. Arnott (1968) grew black spruce on *Pleurozium* and *Sphagnum nemoreum*. His study showed higher seedling shoot weights on *Pleurozium*, although the differences were not significant. Foliar analyses yielded higher levels of P and lower levels of K on *Pleurozium* than on *Sphagnum*; however, no obvious differences were obtained for N or other nutrients. (Tests of significance were not provided.) A recent study (Jeglum 1979) showed significantly better growth on *Pleurozium* than on *Sphagnum* when there was a daily watering. In that study, however, no information was obtained on peat chemistry or foliar nutrients as measures of nutrient supply.

The present work is a more detailed study of nutrient supply by *Pleurozium* peat, and by the moss peat of three species of *Sphagnum*, to black spruce seedlings. Growth of seedlings on moss peats collected from several plots, and analyses of peats and seedling needles, allow for a detailed assessment of the relative nutrient supply capabilities of the peats of the four moss species.

STUDY AREA

The study was based on peat samples collected from three 0.04-ha plots located in the Wally Creek Experimental Area of the Canadian Forestry Service, a peatland located approximately 30 km east of Cochrane near Wade Lake, in the Northern Clay Section of the Boreal Forest (Rowe 1972). Figure 1 is a stereo-pair of the area with the location of the plots. Plots I and II were located on black spruce/labrador-tea (*Ledum groenlandicum*) sites, while Plot III was on a black spruce/few-seeded sedge (*Carex oligosperma*)/*Sphagnum angustifolium*[3]

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[3]*Sphagnum angustifolium* = *S. fallax* var. *angustifolium* is part of a species complex that has been termed the *S. recurvum* group in North American literature. In recent work in North America, this group has been regarded as consisting of three or four species (Horton et al. 1979, Ireland et al. 1980), one of which is *S. angustifolium*.

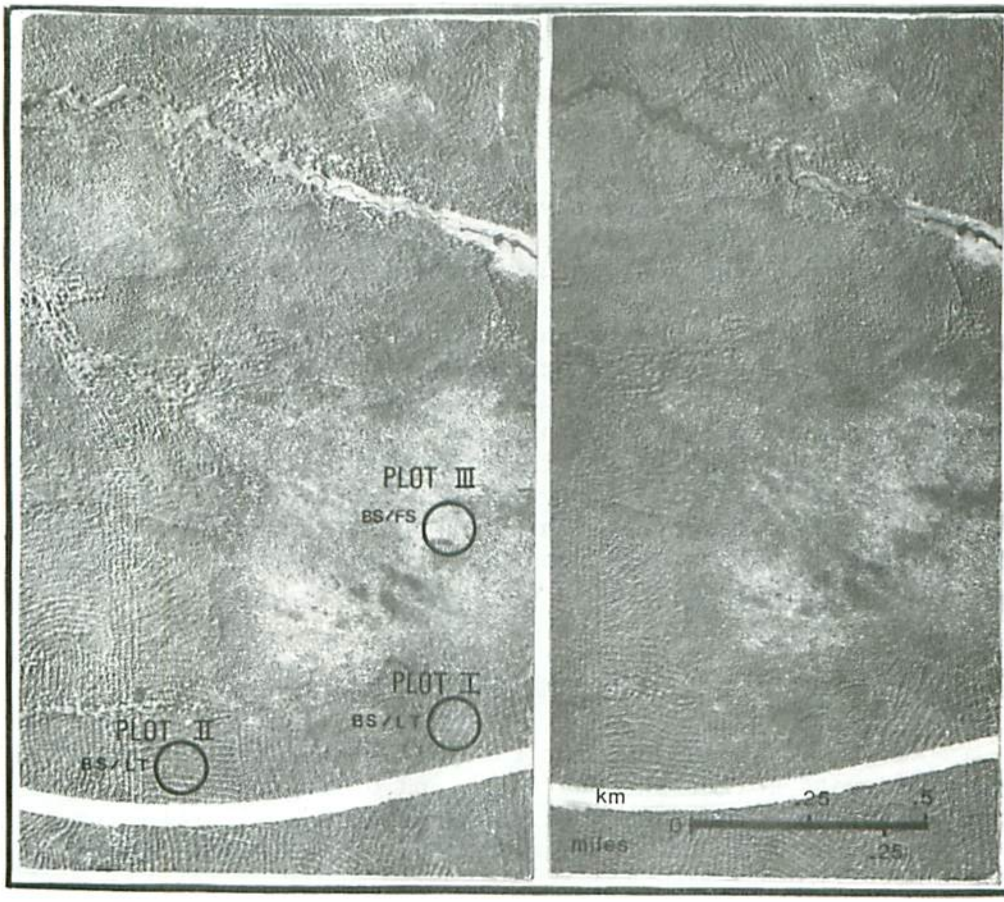

Figure 1. The peatland area near Wade Lake (Wally Creek) with the location of the plots. Plots I and II were black spruce/labrador-tea (BS/LT) and Plot III was black spruce/few-seeded sedge (BS/FS).

Figure 2. Pan containing a moss-peat seedbed from which living mosses have been removed, with black spruce seedlings.

site (*cf.* Jeglum et al. 1974). These two site types will be referred to as BS/LT and BS/FS, respectively. Vegetation and habitat data for the plots in Figure 1 as well as other plots along transects through the peatland have been published by Jeglum and Boissonneau (1977).

Plots I and II were richer than Plot III, as indicated by various measures for nutrient status, the presence of various plant indicators of minerotrophic conditions (*cf.* Sjörs 1963), floristic richness, and site index. Plots I and II had been partially cut in the 1930s during the horse-logging era, and the parallel trails used to skid out the logs are plainly visible in Figure 1. Enough advance growth was left to regenerate the area fully, and numerous trees have grown to merchantable size since the first cutting. Plot III is non-merchantable and has never been cut.

METHODS

Moss-peat substrates for the predominant mosses in each of the three plots were collected toward the end of September at each of 10 collection sites. The moss species for the 10 collection sites sampled were: Plot I -- (1) *Pleurozium schreberi*, (2) *Sphagnum magellanicum*, (3) *S. angustifolium*, and (4) *S. fuscum*; Plot II -- (5) *Pleurozium schreberi*, (6) *Sphagnum magellanicum*, (7) *S. angustifolium* and (8) *S. fuscum*; and Plot III -- (9) *Sphagnum angustifolium*, and (10) *S. fuscum*. *Pleurozium* and *Sphagnum magellanicum* were present only in small patches or in mixtures with other species in Plot III; hence, these species were not sampled in this plot.

At each collection site two blocks of moss plus the underlying peat were carefully cut out to fit snugly into plastic dish pans (Fig. 2). The two blocks for each collection site were located contiguously in a mat or mound dominated by one moss species and underlain by the peat laid down by that species. One of the pans of each pair had all of the living moss plants plucked by hand from the surface to simulate shearblading, a technique of site preparation on peatlands (Haavisto 1979); the other pan of the pair was the control with living moss surfaces left intact. An additional peat sample was collected at each site from the upper 0 to 5 cm, living moss excluded, for determining field water content of the peat at the start of the experiment, and also to obtain von Post humification ratings (Canada Soil Survey Committee, Subcommittee on Soil Classification 1978).

At each collection site, depth to groundwater was measured and a groundwater sample collected, usually from a shallowly dug hole in a depression but sometimes from a shallow open water pool located close by. The samples were collected in polyethylene bottles treated with iodine to reduce biological activity, stored frozen in the dark, and filtered before analysis. Water pH (electronic meter) and calcium (Ca) (atomic absorption spectrophotometry) were measured for these samples.

The pans were transported to benches in a fiberglass-covered greenhouse, in which temperatures were maintained at 21°C and humidity was usually well above 50%. Fluorescent and incandescent lights were on for 16 hours each day to augment and lengthen the natural photoperiod during the fall and winter months.

Pans were watered daily with distilled water sprinkled uniformly over the surface of the moss or exposed peat. Rate of watering was the mean daily precipitation for Cochrane, Ontario, 2.12 mm (Chapman and Thomas 1968), which translated into 195 mL to cover the 28 x 32 cm of moss-peat surface. Holes were punched in the pan bottoms so that any excess water would drain out. A mixed lot of black spruce seed collected from Site Regions 3E and 3W (Hills 1960) was sown on the surface of each pan in early October. When seedlings were well established, they were thinned to 10, well spaced, healthy individuals per pan. The seedlings were excavated and measured for various growth parameters in late March, about 5½ months after seed germination.

The needles of the seedlings from each of the 20 treatment combinations were combined, and analyzed for nutrient contents. For nitrogen (N) a semimicro-Kjeldahl method was used. Samples were dry-ashed at 500°C, the ash extracted with concentrated HCl and the extract analyzed for phosphorus (P) (molybdo-phosphoric acid method using Spectronic 20), potassium (K) (flame-emission spectrophotometry), and Ca and magnesium (Mg) (atomic absorption spectrophotometry).

At the end of the experiment, peat samples were taken from the upper 0 to 5 cm, excluding living moss, for both plucked and living treatments, for gravimetric moisture content determinations. After these determinations, samples from plucked and living pans were combined for each site, and analyzed for loss on ignition (LOI, 500°C) and for 'total' and 'exchangeable' nutrients. Analysis for N was again by the Kjeldahl method. Total concentrations for P, K, Ca and Mg were obtained with two methods--acid digestion and dry ashing. For acid digestion (wet ashing) samples were dissolved with strong acids--nitric, sulfuric, perchloric and hydrofluoric. For dry ashing, samples were treated as in the foliar analyses. For both methods the same instruments were used to obtain concentrations as in foliar analyses.

Cation exchange capacity (CEC) was measured by the neutral normal ammonium acetate method. Exchangeable P was determined on a Spectronic 20 after a sample had been extracted with Bray and Kurtz Solution Number 1. Exchangeable K, Ca and Mg were determined, after a sample had been extracted with neutral normal ammonium acetate by the same methods as in foliar analyses.

Analysis of variance (AOV), Tukey's w procedure and simple correlation analysis (Steel and Torrie 1960) were used to judge differences between and among treatments, or correlations between parameters.

RESULTS

Seedling Growth

For the two BS/LT plots (I and II) seedling crowns were longest on *Pleurozium* and significantly different from those on *S. angustifolium* and *S. fuscum*, which were the shortest (Table 1). *Sphagnum magellanicum* produced seedling crown lengths more similar to those on *Pleurozium* than to those on the other two *Sphagnum* species. The seedling crown lengths on *Sphagnum angustifolium* and *S. fuscum* in the BS/FS plot (III) were not significantly different from those in the BS/LT plots (I and II).

For *Sphagnum* substrates there were consistently shorter seedling crowns on living moss than on peat surfaces (Table 1). The crowns of seedlings growing on living *Sphagnum* were often partially, and sometimes completely, covered by *Sphagnum* moss by the end of the experiment. In one of the two *Pleurozium* comparisons, seedlings on living moss had significantly longer crowns than those on peat.

General Habitat Features for Plots and Moss-Peat Types

Simple measures of moisture and nutrient regime (Table 2) suggested that the BS/FS plot was wetter and poorer than the BS/LT plot. For both site types, *Sphagnum fuscum* mounds were elevated the highest above the groundwater level, *S. angustifolium*, the least (Table 3). By the end of the experiment, with application of the regular daily watering regime, the majority of peats from BS/LT had gained moisture, whereas those from BS/FS had lost moisture. The *Sphagnum* peats contained between two and three times as much moisture as the *Pleurozium* peats.

The sampled peats were all fibric (poorly decomposed) (Table 2). Moist-peat pH means for moss-peat types were all quite low, less than 3.9. *Pleurozium* and *Sphagnum magellanicum* had the highest pH means, whereas *S. fuscum* had the lowest means. The highest water pH and water Ca means were for water collections taken near the *Pleurozium* and *Sphagnum magellanicum* moss-peat collections in BS/LT, the lowest for *S. angustifolium* and *S. fuscum* in BS/FS. Loss on ignition was least for *Pleurozium*, greatest for *Sphagnum fuscum* and intermediate for *S. magellanicum* and *S. angustifolium*.

Table 1. Crown length means ($\bar{x}$) and coefficients of variation (CV) for black spruce on ten moss-peat substrates from three plots.

	Mean Crown Length (mm)				
	Peat		Living moss		All
No. of measures	10		10		20
Plot I (BS/LT)	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$
Pleurozium schreberi	14.5^{x}	45	41.8^{y}	52	28.2^{d}
Sphagnum magellanicum	39.9^{x}	31	11.8^{y}	111	25.9^{cd}
Sphagnum angustifolium	14.6^{x}	52	9.8^{x}	34	12.2^{ab}
Sphagnum fuscum	16.3^{x}	36	12.8^{x}	57	14.6^{abc}
Plot II (BS/LT)					
Pleurozium schreberi	25.3^{x}	60	23.0^{x}	66	24.2^{bcd}
Sphagnum magellanicum	18.1^{x}	56	17.6^{x}	40	17.9^{abcd}
Sphagnum angustifolium	12.7^{x}	40	6.7^{y}	73	9.7^{a}
Sphagnum fuscum	8.3^{x}	55	5.9^{x}	62	7.1^{a}
Plot III (BS/FS)					
Sphagnum angustifolium	18.4^{x}	78	3.8^{y}	78	11.1^{a}
Sphagnum fuscum	9.8^{x}	57	8.2^{x}	55	9.0^{a}

x, y Comparisons in rows between the means for peat and living moss. Values with different letters are significantly different at the 95% level of probability.

a, b, c, d Comparisons in the last column among 11 means. Values with different letters are significantly different at the 95% level of probability.

Table 2. General habitat features of the plots and moss-peat types. Parentheses enclose number of values in mean. Determinations carried out for the 0 to 5 cm of peat just beneath living moss.

	Black Spruce/Labrador-tea (Plots I and II)								Black Spruce/Few-seeded Sedge (Plot III)			
	Pleurozium schreberi		*Sphagnum magellanicum*		*Sphagnum angustifolium*		*Sphagnum fuscum*		*Sphagnum angustifolium*		*Sphagnum fuscum*	
Depth to ground-water (cm)	35	(2)	33	(2)	25	(2)	50	(2)	15	(1)	35	(1)
Peat moisture (% dry wt)												
- exp. start	369	(6)[a]	877	(6)[bc]	882	(6)[bc]	772	(6)[b]	1731	(3)[d]	1054	(3)[c]
- exp. end	544	(4)[a]	762	(4)[ab]	1155	(4)[b]	1394	(4)[b]	1412	(2)[b]	804	(2)[ab]
Humification (1-10)	2.0	(2)	2.5	(2)	2.0	(2)	2.0	(2)	2.0	(1)	2.0	(1)
Moist-peat pH	3.87	(10)[c]	3.86	(10)[c]	3.53	(10)[b]	3.11	(10)[a]	3.61	(5)[bc]	3.20	(5)[a]
Water pH	5.8	(2)	5.3	(2)	5.2	(2)	4.9	(2)	4.1	(1)	4.1	(1)
Water Ca (ppm)	7.07	(2)	6.54	(2)	5.41	(2)	5.95	(2)	3.18	(1)	3.40	(1)
Loss on ignition (% dry wt)	93.9	(4)[a]	96.4	(4)[b]	96.9	(4)[b]	98.1	(4)[b]	96.5	(2)[b]	98.1	(2)[b]

[a,b,c,d] Values in rows with different letters are significantly different at the 95% level of probability. Statistical comparisons were made when there were enough values to permit it.

Table 3. Chemical determinations for the peat substrates, 0-5 cm.

	Black Spruce/Labrador-tea				Black Spruce/Few-seeded Sedge		
	Pleurozium schreberi	*Sphagnum magellanicum*	*Sphagnum angustifolium*	*Sphagnum fuscum*	*Sphagnum angustifolium*	*Sphagnum fuscum*	F-ratio
No. of determinations[1]	6	6	6	6	3	3	
Cation exchange capacity (m.eq./100 g)							
$\bar{x}$	67.1^{a}	79.3^{ab}	87.7^{bc}	109.0^{d}	94.6^{cd}	98.5^{cd}	26.46**
CV	10	3	5	9	5	6	
N							
Kjeldahl-N (%)							
$\bar{x}$	0.801^{c}	0.652^{b}	0.492^{a}	0.441^{a}	0.732^{bc}	0.502^{a}	29.86**
CV	6	11	13	14	9	6	
P							
Acid digestion (%)							
$\bar{x}$	0.078^{c}	0.056^{bc}	0.036^{ab}	0.025^{a}	0.073^{c}	0.070^{c}	11.00**
CV	13	44	39	41	5	14	
Dry ashing (%)							
$\bar{x}$	0.058	0.052	0.049	0.036	0.036	0.037	1.44^{NS}
CV	39	27	45	28	28	10	
Exch. (%)							
$\bar{x}$	0.024^{ab}	0.026^{b}	0.023^{ab}	0.010^{a}	0.032^{b}	0.013^{ab}	2.97*
CV	96	39	61	27	32	12	
K							
Acid digestion (%)							
$\bar{x}$	0.304^{b}	0.215^{a}	0.208^{a}	0.138^{a}	0.127^{a}	0.193^{a}	10.10**
CV	17	13	24	38	11	16	
Dry ashing							
$\bar{x}$	0.156	0.187	0.137	0.126	0.114	0.163	1.25^{NS}
CV	41	37	42	11	23	21	
Exch. (%)							
$\bar{x}$	0.090^{b}	0.086^{b}	0.045^{a}	.030^{a}	.048^{ab}	.065^{ab}	6.34**
CV	37	20	22	47	69	34	
Ca							
Acid digestion (%)							
$\bar{x}$	0.336^{ab}	0.484^{ab}	0.559^{b}	0.456^{ab}	0.135^{ab}	0.105^{a}	3.48*
CV	35	57	12	25	35	7	
Dry ashing (%)							
$\bar{x}$	0.314	0.420	0.337	0.316	0.344	0.167	1.20^{NS}
CV	49	34	58	46	10	17	
Exch. (%)							
$\bar{x}$	0.133	0.179	0.125	0.091	0.211	0.115	1.96^{NS}
CV	57	41	14	35	65	2	
Mg							
Acid digestion (%)							
$\bar{x}$	0.108^{bc}	0.092^{abc}	0.120^{c}	0.109^{bc}	0.057^{a}	0.061^{ab}	5.03**
CV	33	22	8	24	25	3	
Dry ashing (%)							
$\bar{x}$	0.065	0.062	0.082	0.083	0.042	0.042	2.30^{NS}
CV	34	23	38	40	34	7	
Exch. (%)							
$\bar{x}$	0.047^{ab}	0.049^{b}	0.046^{ab}	0.024^{a}	0.043^{ab}	0.031^{ab}	2.59^{NS}
CV	43	20	31	25	40	17	

[1] Three determinations for each moss-peat collection site.

^{a,b,c,d} Values in rows with different letters are significantly different at the 95% level of probability.

* Significant at 95% level.

** Significant at 99% level.

Chemical Analyses for the Moss-Peat Substrates

AOVs--10 (collection sites) x 3 (analysis methods)--were performed for P, K, Ca, and Mg. In each AOV, there were highly significant differences among collection sites and analysis methods, the latter factor consistently obtaining much larger F values than the former factor. Tests of differences among means for analysis methods showed that for K and Mg, means from each of the three methods were significantly different. For P and Ca, acid extraction and dry ashing values were similar, but these were significantly different from exchangeable values. Tests of differences among collection sites revealed no significant differences between means for the replicate collections for each moss-peat type from each of the two BS/LT plots.

AOVs among means for the six moss-peat/site type combinations were performed for all chemical determinations (Table 3). Significant F values (P > 95 or 99%) were obtained for, from greatest to least, N, CEC, P and K (acid dig.), K (exch.), Mg and Ca (acid dig.), and P (exch.). The lowest F values for P, K, Ca and Mg were always for the dry ashing method, and these F values were always non-significant.

The acid digestion method usually yielded higher values of P, K, Ca and Mg than did dry ashing (Table 3). Exchangeable values were almost always lowest. Coefficients of variation were quite variable, and no consistent patterns were observed which would favor one analytical procedure over the other on the basis of variance.

Foliar Analyses

The highest means for N were associated with *Pleurozium* substrates, whereas the highest means for P, K, Ca and Mg were associated with either *Sphagnum angustifolium* or *S. fuscum* (Table 4).

One-way AOVs among the six moss-peat/site type combinations revealed significant (P > 95 or 99%) differences for foliar K, Ca and Mg. However, a three-way AOV for only the BS/LT plots (4 moss-peat types x 2 treatments x 2 plots) indicated significant (P > 95 or 99%) differences among the moss-peat types for all five elements.

The three-way AOV also indicated significantly (P > 95 or 99%) higher values of all foliar elements for seedlings growing on living moss than for those growing on peat substrates. There were significant (P > 95 or 99%) differences between BS/LT plots for P and K, but not for N, Ca or Mg. Because BS/LT plot differences were not as important as moss-peat and treatment differences, they were not segregated in Table 4.

Table 4. Mean foliar nutrient concentrations, for the six moss-peat/site types, and for peat and living moss treatments.

	Black Spruce/Labrador-tea (BS/LT)					Black Spruce/Few-seeded Sedge (BS/FS)	
	Pleurozium schreberi	*Sphagnum magellanicum*	*Sphagnum angustifolium*	*Sphagnum fuscum*	*Sphagnum angustifolium*	*Sphagnum fuscum*	F-ratio
n	4	4	4	4	2	2	
N							
peat	1.582	1.379	1.150	1.296	1.363	1.358	1.08^{NS}
living	2.284	1.617	1.853	1.221	1.156	1.490	2.03^{NS}
P							
peat	0.210	0.152	0.224	0.166	0.258	0.206	0.85^{NS}
living	0.236	0.166	0.381	0.247	0.313	0.401	3.55^{NS}
K							
peat	0.930^{ab}	0.740^{a}	0.905^{ab}	0.942^{ab}	1.035^{ab}	1.071^{b}	3.18^{*}
living	1.117^{ab}	0.691^{a}	1.478^{b}	0.791^{a}	0.984^{ab}	1.521^{b}	6.39^{**}
Ca							
peat	0.615	0:557	0.709	0.562	0.444	0.549	1.49^{NS}
living	0.441^{a}	0.720^{a}	1.263^{a}	0.603^{a}	1.258^{a}	1.113^{a}	3.27^{*}
Mg							
peat	0.155^{ab}	0.119^{a}	0.168^{b}	0.149^{ab}	0.187^{b}	0.142^{ab}	3.73^{*}
living	0.158^{ab}	0.146^{a}	0.311^{ab}	0.158^{ab}	0.361^{b}	0.236^{ab}	4.55^{*}

^{a,b} Means with different letters are significantly different at the 95% level of probability.

* Significant at 95% level.

** Significant at 99% level.

NS Not significant.

Interrelationships of Seedling Growth, Foliar Nutrients, and Habitat Measures

Several simple correlation matrices were prepared to elucidate interrelationships among various measures. Correlations among foliar nutrient concentrations and crown length were based on 20 sets of values--the two treatments (peat, living moss) for each of the 10 moss-peat collection sites (Table 5). N was directly and significantly ($P > 99\%$) correlated with crown length. All the other foliar nutrients were inversely correlated with crown length, Ca and Mg significantly so ($P > 95$ or 99%). N was not significantly correlated with any other element. All possible combinations for P, K, Ca and Mg, however, were directly and significantly ($P > 95$ or 99%) correlated.

Table 5. Matrix of correlation coefficients(r) among foliar nutrients and crown length, based on 20 sets of mean values.

	N	P	K	Ca	Mg
P	0.31				
K	0.22	0.46*			
Ca	-0.12	0.58**	0.61**		
Mg	-0.05	0.53*	0.77**	0.88**	
Crown length	0.59**	-0.21	-0.20	-0.60**	-0.48*

* Significant at 95% level of probability.

** Significant at 99% level of probability.

Another set of correlations, based on 30 sets of individual determinations, was prepared (Table 6), to determine how well the results from the three methods of analyzing peat were related. Significant ($P > 99\%$) correlations were obtained only between acid digestion and exchangeable concentrations for P and K. None of the correlations of values from dry ashing with acid digestion, or dry ashing with the exchangeable method, were significantly correlated.

Another set of correlations (Table 7) was developed to assess which of the nutrient-related measures were the best indicators of nutrient regime. Only acid digestion values for peat chemistry were used for this, and when these were correlated among themselves, the correlations were based on 30 sets of individual determinations. When correlations involved at least one measure other than an acid digestion value, then correlations were based on means for each of the 10 collection sites. Of the nine correlations between each measure and the other measures, six were significant (P > 95 or 99%) for LOI, CEC and N; five for P and K; and three or fewer for other measures.

Table 6. Correlation coefficients(r) between nutrient concentrations obtained from three methods of chemical analysis--acid digestion, dry ashing, and exchangeable--based on 30 individual determinations.

	Acid + Ash	Acid + Exch.	Ash + Exch.
P	0.15	0.58**	0.31
K	0.25	0.49**	0.09
Ca	-0.20	-0.32	0.30
Mg	0.09	0.11	0.36

Correlations of each of the measures for moisture and nutrient regime with seedling crown length were based on 10 sets of mean values (Table 8). There were significant (P > 95 or 99%) positive correlations for groundwater pH and Ca, N, K (acid dig. and exch.), and P (dry ash.) Significant (P > 95%) negative correlations were obtained for LOI and CEC.

With respect to the correlation of the nutrient contents in the peat with those in the black spruce needles, of all the elements, only N showed a significant, and positive, correlation (Table 8).

DISCUSSION

This study showed that moss-peat types (species) accounted for the greatest differences in seedling growth. The best black spruce seedling growth was on *Pleurozium schreberi*; growth was only slightly reduced on *Sphagnum magellanicum*, and was poorest on *Sphagnum angustifolium* and *S. fuscum*.

Much smaller differences were obtained among plots, and growth on each of the four moss-peat types was similar and not significantly different among the three plots.

Table 7. Matrix of correlation coefficients(r) among nutrient regime measures obtained from the plots or from peat analyses. Values to left of the line in the table are based on 10 sets of means, those to the right on 30 sets of individual determinations.

	pH, moist-peat	pH, water	Ca, water	LOI	CEC	N	P	K	Ca
pH, groundwater	0.50								
Ca, groundwater	0.34	0.85**							
LOI	-0.75*	-0.59	-0.55						
CEC	-0.91**	-0.65*	-0.40	0.83**					
N	0.78**	0.36	0.22	-0.85**	-0.47**				
P-acid dig.	0.61	0.01	-0.04	-0.79*	-0.46*	0.76**			
K-acid dig.	0.55	0.75*	0.48	-0.72*	-0.53**	0.48**	-0.48**		
Ca-acid dig.	0.01	0.44	0.23	0.32	0.15	-0.33	-0.68**	-0.02	
Mg-acid dig.	0.29	0.51	0.65*	-0.75*	-0.12	0.38*	0.25	0.29	-0.14

* Significant at 95% level of probability.

** Significant at 99% level of probablity.

Table 8. Correlations of site and peat measures with crown length and with corresponding foliar nutrient concentrations, based on means for 10 sets of values (peat and living moss foliar values combined).

	Correlations(r) of peat measures	
	With crown length	With corresponding foliar nutrient
Moisture regime		
Depth to groundwater	-0.10	-
Peat moisture		
- exp. start	-0.57	-
- exp. end	-0.30	
Nutrient regime		
Moist-peat pH	0.60	-
Water pH	0.80**	-
Water Ca	0.64*	-
Loss on ignition	-0.63*	-
CEC	-0.72*	-
N	0.65*	0.61*
Acid digestion		
P	0.37	0.02
K	0.75*	0.01
Ca	0.17	0.15
Mg	0.25	-0.10
Dry ashing		
P	0.64*	0.04
K	0.54	-0.41
Ca	0.07	-0.16
Mg	0.04	-0.04
Exchangeable methods		
P	0.55	0.10
K	0.64*	-0.19
Ca	0.26	-0.18
Mg	0.37	0.23

* Significant at 95% level of probability.

** Significant at 99% level of probability.

Even though differences in growth on each moss-peat type among plots were not significant, nonetheless, growth of mature trees showed considerable differences among plots. The site index on Plot I (BS/LT) was 9.2 m, that on Plot II (BS/LT) was 3.6 m, and that on Plot III (BS/FS) was 1.5 m. The relatively low value in Plot II is probably due to the fact that height and age were obtained from very old trees which survived the cutting in the 1930s, and had ages in excess of 150 years and much reduced growth rates in later years. One factor that could explain the reduction in growth across Plots I to III is increasing water content in the peat. Another important change from Plots I to III is in the relative proportions of moss-peat types. *Pleurozium* and *Sphagnum magellanicum* decreased across this sequence, whereas *S. angustifolium* and *S. fuscum* increased.

The shorter length of crowns on *Sphagnum* moss than on *Sphagnum* peat is probably related to the growth of living *Sphagnum* around and sometimes over seedlings. This did not happen in the case of *Pleurozium* moss, which grows much more slowly. In one of the two *Pleurozium* comparisons seedlings on living moss had significantly longer crowns than did those on peat. In this sample the peat had the greatest moisture content of all the *Pleurozium* moss-peat pans, and this could account for the excellent seedling growth. It has been demonstrated that different watering frequencies effect different growth responses on *Pleurozium* (Jeglum 1979). If a large number of *Pleurozium* peat samples covering a wide range of bulk densities were used in another experiment, with constant watering as in this study, it is probable that good moisture content-growth relationships would be found, and that these would be influenced by the different rates of drying by peats of different densities.

The strongest differences for habitat measures, including both site measures and peat chemical analyses, were among moss-peat types. It was also clear that the BS/LT plots were richer and less wet than the BS/FS plot.

Comparisons of three techniques of peat analysis for P, K, Ca, and Mg showed highest values for acid extraction, lower for dry ashing, and lowest for the exchangeable technique. Significant differences were frequently obtained, although acid extraction and dry ashing values were somewhat more similar than were those of dry ashing and the exchangeable technique. For a number of reasons acid extraction seemed to be a better method than dry ashing for obtaining totals. In the first place, acid extraction yielded somewhat higher total concentrations. It may be that some of the nutrients were lost in fly ash during the ashing process. In the second place, in several of the AOVs where differences among moss-peat types or plots were being tested, acid digestion values frequently yielded significant differences, whereas dry ashing did so only infrequently. Finally, when the concentrations from the three techniques were compared, correlations between acid digestion and dry ashing values for all four elements--P, K, Ca and Mg--were non-significant, whereas those between acid digestion and the exchangeable method for P and K were significant. These observations suggest that acid digestion may be preferable to dry ashing for obtaining total values for the main elements. It may be that the same applies to foliar analysis, although in this study only dry ashing values were obtained.

The site and soil measures that were significantly correlated with crown length--groundwater pH and Ca, LOI, CEC, N, P and K--may all be regarded as components of nutrient regime, and none of the measures of moisture regime were significantly correlated with crown length. However, there were only a few simple measures taken for moisture regime, and it cannot be stated from this evidence that moisture regime, including the interrelated aeration component of moisture regime, had no limiting influence on seedling growth in the *Sphagnum*.

Foliar concentrations of N, Ca and Mg were significantly or highly significantly correlated with growth--N directly, and Ca and Mg inversely. It appears that N was the main nutrient controlling growth rates among the four moss-peat types, and that Ca, and Mg, as well as P and K (also inversely though not significantly related), became less concentrated (diluted) in the leaf tissues as seedling growth increased and leaf tissues expanded. It is not clear why the peat substrates produced seedlings with lower foliar nutrient concentrations than those on living moss. The most apparent explanation is that of dilution of the nutrient concentration in the larger seedlings on the peats.

During searches for large enough moss blocks to fit the sample pans it was observed that *Pleurozium schreberi* peat was often underlying *Sphagnum magellanicum* and *S. angustifolium*. This suggests a recent trend in *Sphagnum* encroachment, which could have been brought on by the cutting in the 1930s followed by a rise in water table. Spread of *Sphagnum* after cutting has been documented previously (e.g., Losee 1961, Keller and Watterston 1962). Wilde et al. (1954) and Keller and Watterston (1962) suggested that in localities vulnerable to invasion by *Sphagnum* moss, choice of cutting method may influence rate of *Sphagnum* encroachment. The latter authors suggested that conservative partial cuttings could preclude or slow down the spread of *Sphagnum*, and would likely be compensated by a higher increment.

The different rates of growth of black spruce seedlings on the moss-peat types sampled are those that would be predicted from what is known about the occurrence of these species along a nutrient regime gradient (e.g., Jeglum 1971, Horton et al. 1979). *Pleurozium* has been indicated for a long time as a better nutrient supplier than *Sphagnum* (e.g., Wilde et al. 1954) but in this study it is made clear that *Pleurozium* and *Sphagnum* mosses from the same plot provide quite different levels of nutrient supply to black spruce seedlings. Within the peatland studied here, the *Pleurozium* tended to occur as mats, often in the shade of black spruce and well above the groundwater level. The *Sphagnum* species tended to be in more open locations, in the cut lines in the BS/LT or in natural openings. *Sphagnum angustifolium* and *S. magellanicum* were usually closest to the groundwater level in mats or low mounds, and as such were influenced by the mineral soil water. *Sphagnum fuscum* occurred in the highest mounds above the groundwater, and hence was most isolated from the mineral soil water and most influenced by the nutrient-poor water of incoming precipitation.

Even though all three *Sphagnum* species occur over a broad range of nutrient regimes (Horton et al. 1979), field observations suggest that *Sphagnum magellanicum* is often most abundant in swamps with intermediate nutrient regimes, *S. angustifolium* in swamps with poor (weakly minerotrophic) conditions, and *S. fuscum* in very poor (ombrotrophic) conditions. Since black spruce seedling growth is related to the moss-peat types in the same way that the moss-peat types are positioned along the nutrient gradient, it is therefore quite probable that the relative proportions of the four moss species, and others not tested here, could be used to predict the nutrient regime of a site in relation to black spruce growth and, undoubtedly, other species on the site.

SILVICULTURAL IMPLICATIONS

1. When cutover black spruce swamps are being planted, black spruce seedlings should be planted whenever possible in feather moss rather than *Sphagnum* peat, because *Sphagnum* does not provide as good a supply of N and also tends to grow up around the seedling, partially covering lower leaves and branches. In swamps the feather moss microsites will usually have adequate moisture to ensure seedling establishment.

2. Harvesting of black spruce swamps may, by causing a rise of water levels, hasten the natural process of *Sphagnum* encroachment in swamps, thereby promoting natural deterioration of site quality and eventual conversion of productive swamps into nonmerchantable swamps or treed bogs. This process is probably more rapid following clearcutting than following partial or modified harvesting, because of higher and more rapid rises of water levels following the more complete removal of the evapotranspiration stream. Partial cutting will cause lesser rises of water levels, and also maintain more of the shade-loving feather mosses. However, in order fully to arrest and reverse the natural process of water level rise and *Sphagnum* encroachment, peatland drainage must be employed. This will lower water levels, discourage *Sphagnum* development, and promote more rapid nutrient release by improving the aeration of the surface layers of the peat.

3. In describing and analyzing peats it is important to note the botanical origin of the peat, since nutrient regime is highly related to the species of moss from which the peat is derived. Moss species, and their relative abundances, can be used as indicators of the relative nutrient status of swamps, and hence their relative wood growing capabilities.

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