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The Role of Sphagnum Fimbriatum in Secondary Succession in a Road-Salt Impacted Bog

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The role of *Sphagnum fimbriatum* in secondary succession in a road salt impacted bog

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Secondary succession of *Sphagnum* mosses was studied for 7 years along a belt transect in a bog that had been impacted by sodium chloride highway deicing salts. Laboratory studies on *Sphagnum fimbriatum* Wils., the dominant recolonizing species, were conducted to determine its salt tolerance level and ability to reproduce from spores and fragments across a salt gradient. Vegetative reproduction was also compared with that of four other recolonizing species. *Sphagnum fimbriatum* represented a high percentage of all recolonizing *Sphagnum* and generally began growing on low hummocks in quadrats where the salt content of the interstitial peat pore waters had dropped to about 300 mg/L as chloride. This salt concentration was also found to be the basic tolerance limit for mature plants and reproducing spores and fragments. The success of *Sphagnum fimbriatum* as a pioneer species seems to be associated with its prolific production and probable dispersal of spores, its superior vegetative reproduction, its tolerance of mineralized waters, and its ability to grow on hummocks out of direct contact with mineralized waters.

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Les auteurs ont étudié durant 7 ans, une succession secondaire de mousses *Sphagnum* le long d'un transect dans une tourbière ayant subi l'impact du chlorure de sodium utilisé dans le déglaçage d'une autoroute. Des études au laboratoire sur *S. fimbriatum* Wils., une espèce recolonisatrice dominante, furent conduites en vue de déterminer sa tolérance au sel et son potentiel de reproduction à partir de spores et de fragments, à travers un gradient de salinité. Sa reproduction végétative fut aussi comparée à celle de quatre autres espèces recolonisatrices. *Sphagnum fimbriatum* représente un pourcentage élevé de toutes les sphaignes recolonisatrices et, généralement, commence à croître sur des buttes peu élevées dans les quadrats où la teneur en sel des eaux interstitielles dans les pores de la tourbe est descendue à environ 300 mg/L de chlorure. Cette concentration en sel est la limite de base de la tolérance pour les plantes matures et pour les spores et fragments reproducteurs. Les succès de *S. fimbriatum*, en tant qu'espèce pionnière, semblent associés à la production abondante et à la dispersion probable des spores, à sa reproduction végétative supérieure, à sa tolérance aux eaux minéralisées et à sa capacité de croître sur des buttes sans contact direct avec les eaux minéralisées.

[Traduit par la revue]

Introduction

Studies of primary and secondary succession of *Sphagnum* mosses have assessed the role of environmental alterations or disturbance in the form of water chemistry changes (Grahn 1977), water level changes (Foster 1984), fire (Foster 1984), and physical disruptions such as tree falls (Noble *et al.* 1984) and peat mining (Elling and Knighton 1984). Other studies of the ecology of selected *Sphagnum* species have addressed the preferences or tolerances for environmental conditions such as moisture regime, water chemistry, shade, and microtopography (Green 1968; Clymo 1973; Vitt *et al.* 1975; Horton *et al.* 1979; Andrus *et al.* 1983; Hayward and Clymo 1983; Vitt and Slack 1984). These studies have not specifically addressed the fact that ecological and life-history characteristics of certain species may be important factors in determining the role of the species in succession (MacArthur and Wilson 1967; Gadgil and Solbrig 1972; Wilbur *et al.* 1974; Wilcox *et al.* 1985).

The purposes of this paper are to document secondary succession of *Sphagnum* in part of a bog that was severely affected by runoff of highway deicing salts (Wilcox 1986*a*, 1986*b*) and to assess some of the ecological characteristics of the dominant colonizing species (*Sphagnum fimbriatum* Wils.) that may allow it to serve as a pioneer in secondary succession.

Study area

Pinhook Bog is located in LaPorte County in northwestern Indiana and is included within the boundaries of Indiana Dunes National Lakeshore. The basin occupies an ice-block depression in the Valparaiso moraine and is effectively isolated from regional groundwater flow by sandy clay glacial till. The bog is characterized by acidic, weakly minerotrophic waters (mean pH 3.68; mean specific conductance, 64 μS/cm; mean Ca, 2.7 mg/L; mean Mg, 1.6 mg/L) and common bog vegetation that includes *Sphagnum*, sundew (*Drosera intermedia*), pitcherplant (*Sarracenia purpurea*), leatherleaf (*Chamaedaphne calyculata angustifolia*), highbush blueberry (*Vaccinium corymbosum*), and tamarack (*Larix laricina*) (Wilcox 1986*a*, 1986*b*).

Part of the bog was contaminated by NaCl deicing salts that originated from an uncovered road-salt storage pile near its southern boundary. Details of the sequence of events from construction of the salt storage area in 1963 to covering of the salt in 1972 to abandonment of the site in 1981 can be found in Wilcox (1986*a*). Salt concentrations in the interstitial waters of the peat mat declined gradually from 1979 to 1983 as the salt was leached into the deeper peats (Wilcox 1986*a*). Partial recovery of the bog plant community, including *Sphagnum*, also occurred (Wilcox 1986*b*). The magnitude of the changes in salt concentration between 1980 and 1986 is shown by the chloride data of Fig. 1. The pH and alkalinity of waters in the salt-

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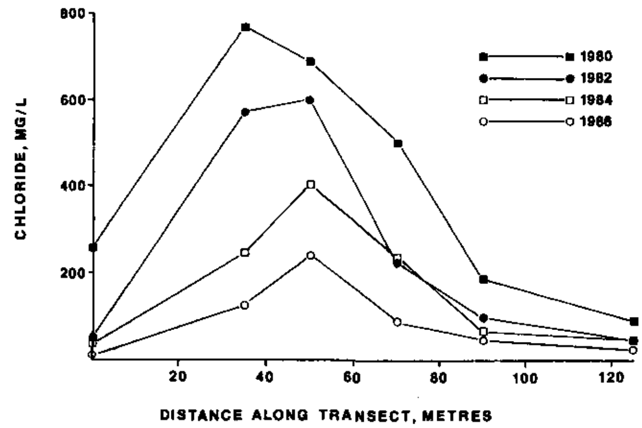

FIG. 1. Mean chloride concentrations in wells sampling surface interstitial peat pore waters along salt-impacted transect, Pinhook Bog, 1980–1986 (derived from Wilcox 1986*a*; D. A. Wilcox, unpublished data).

impacted zone were elevated also, but there were no clear trends in the differences between years. The mean pH at sampling sites relevant to this study ranged from 5.3 to 5.8 between 1980 and 1986. The pH dropped sharply at the edge of the impacted area to the pH of 3.5–4.0 typical of the unimpacted mat (Wilcox 1986*a*; D. A. Wilcox, unpublished data).

Methods

Field surveys

Direct gradient surveys for individual colonies (contiguous, monospecific patches) of *Sphagnum* were conducted in early August 1980–1986 along a portion of the permanently marked belt transect that had been established for surveys of all vegetation (Wilcox 1986*b*). The belt transect consisted of contiguous 2 × 10 m quadrats extending 220 m from the base of the salt storage area into the unimpacted bog. The quadrats were numbered consecutively from the bog perimeter inward and correspond to 10-m distance units (e.g., quadrat 4 = 30–40 m). Only quadrats 1–10 were used for *Sphagnum* surveys because *Sphagnum* was too plentiful to distinguish individual colonies beyond the 100-m point on the transect. Species identification was made for each colony found, and the distance along the transect and approximate ground cover (in square centimetres) were noted. Taxonomy is according to Andrus (1980).

Salt tolerance

The salt tolerance of *Sphagnum fimbriatum*, the dominant species in quadrats 1–10, was tested in a manner similar to that used by Wilcox (1984) for *S. recurvum* P. Beauv. Groups of 20 randomly selected individual plants were cut to 5-cm lengths and placed in polyvinylchloride screen cylinders. These were incubated in solutions of bog water (from an uncontaminated site) with salt added in varying concentrations (two cylinders or 40 plants per solution). The plants were grown at 19°C under artificial light in a 16-h photoperiod for 75 days (see Wilcox, 1984, for details). The salt solutions used were NaCl concentrations of 0, 300, 500, 900, 1500, 3000, and 5000 mg/L as chloride (0, 8.5, 14.1, 25.4, 42.3, 85, and 141 m*M* NaCl), $CaCl_2$ at 1500 mg/L as chloride (21.1 m*M* Ca, 42.3 m*M* Cl), Na_2SO_4 at 976.3 mg/L as sodium (42.3 m*M* Na, 21.1 m*M* SO_4), and $CaSO_4$ (21.1 m*M*). The non-NaCl salts were used for comparisons with the 1500 mg/L chloride NaCl solution to determine the relative effect of each ion.

At the end of the experiment, each individual plant length was measured to determine growth in length, and the growth in biomass was determined by the capitulum correction method of Clymo (1970) (see Wilcox 1984). The regression equation for *Sphagnum fimbriatum* was

$$[1] \quad \text{capitulum weight} = 4.9606(\text{stem weight}) - 0.0006 \quad (r^2 = 0.889)$$

Biomass increases were converted to percentage increases based on the original weight of the 1 cm long capitulum. Statistical analyses consisted of one-way analysis of variance (ANOVA) and Student–Newman–Keuls sequential range tests. Data transformations necessary to improve the homogeneity of variance were arcsin $(p)^{1/2}$ transformations for percent growth in biomass and a log transformation for growth in length versus salt concentration.

Reproduction from spores

The differential ability of *Sphagnum fimbriatum* to reproduce from spores at different salt concentrations was tested. *Sphagnum fimbriatum* with abundant spore capsules was collected from Pinhook Bog in early July and cultured in 10 × 10 × 6 cm plastic containers with bog water (about 200 spore capsules per container). Two containers each were placed in 60 × 20 × 60 cm enclosures constructed of plastic film and built into north-facing windows. Temperatures were maintained at about 19°C. Two 15 × 15 × 3 cm perforated trays containing autoclaved peat were also placed in each enclosure to serve as the medium for growth from spores. These trays were each placed in 20 × 20 × 4 cm containers to which salt water solutions were added (0, 300, 500, 900 mg/L as chloride). One control enclosure at 0 mg/L Cl^- contained commercial potting soil as the growth medium. Another control enclosure contained autoclaved peat at 0 mg/L Cl^-, but no *Sphagnum* spore capsules were introduced. After 150 days, the numbers of gametophores were counted in each of 49 cells of a 7 × 7 grid placed over each tray. Half of the cells for each treatment were randomly selected to be used in comparisons between treatments by one-way ANOVA.

Regeneration from fragments

The ability of each of the five *Sphagnum* species encountered in the field surveys to form vegetative innovations (Lane 1977) was assessed by placing 40 capitula and 40 branch fascicles of each onto 20 × 20 × 4 cm trays containing autoclaved peat. The trays were incubated at 19°C in north-facing windows for 110 days and observed weekly for vegetative growth. In addition to *S. fallax* (Klinggr.) Klinggr., *S. bartlettianum* Warnst., *S. magellanicum* Brid., *S. recurvum* P. Beauv., and *S. fimbriatum* cultured in 0 mg/L Cl^- waters, *Sphagnum fimbriatum* was also cultured at 300, 500, and 900 mg/L Cl^- and a control treatment contained autoclaved peat but no *Sphagnum* fragments. At the end of the experiment, the total numbers of innovations for each treatment were counted.

Results

Field surveys

A very high percentage of the *Sphagnum* that recolonized quadrats in the salt-impacted zone of Pinhook Bog was *S. fimbriatum* (Table 1). This was especially true for quadrats 2–9. The area covered by *S. fimbriatum* increased on a yearly basis between 1981 and 1986 in nearly all quadrats. The number of individual colonies also increased in each quadrat but then generally decreased as colonies merged. The *S. fimbriatum* colonies were almost always found on low hummocks at the bases of shrubs or on other slightly elevated surfaces. Casual observations of *Sphagnum* throughout the salt-impacted zone confirmed the species and habitat results from the transect.

The only other species of *Sphagnum* found in quadrats 1–10 were *S. fallax*, *S. bartlettianum*, *S. magellanicum*, and *S. recurvum*. With the exception of quadrat 10, nearly all of the *Sphagnum* occurred as separate, monospecific colonies, suggesting common ancestry. In quadrat 10, colonies of different species were often adjacent to each other. All colonies of species other than *S. fimbriatum* in all years in quadrats 2 and 4 of Table 2 were *S. recurvum*, all in quadrats 7 and 8 and nearly all in quadrat 9 were *S. fallax*, and quadrat 10 contained all

TABLE 1. Number of colonies and area covered (cm^2, in parentheses) by *Sphagnum fimbriatum* in 2 × 10 m quadrats of belt transect, Pinhook Bog, 1980–1986

Quadrat	1980	1981	1982	1983	1984	1985	1986
1	—	—	—	—	—	—	—
2	—	3 (3 500)	3 (3 800)	5 (6 850)	9 (9 194)	8 (11 057)	6 (16 362)
3	—	2 (200)	2 (500)	2 (625)	3 (2 100)	4 (5 809)	4 (11 420)
4	—	—	—	1 (25)	1 (100)	1 (100)	4 (775)
5	—	—	—	—	1 (150)	1 (300)	1 (800)
6	—	—	—	4 (100)	2 (150)	3 (354)	2 (1 050)
7	—	1 (10)	2 (100)	5 (183)	6 (304)	11 (1 032)	9 (3 325)
8	—	1 (10)	1 (10)	6 (443)	5 (509)	7 (1 310)	11 (3 107)
9	—	1 (10)	2 (19)	5 (169)	4 (250)	6 (412)	7 (850)
10	—	2 (75)	3 (225)	9 (893)	15 (2 548)	13 (3 506)	12 (5 240)

TABLE 2. Number of colonies and area covered (cm^2, in parentheses) by *Sphagnum* other than *S. fimbriatum* in 2 × 10 m quadrats of belt transect, Pinhook Bog, 1980–1986

Quadrat	1980	1981	1982	1983	1984	1985	1986
1	—	—	—	—	—	—	—
2	—	—	1 (10)	1 (100)	1 (200)	1 (4 200)	1 (6 000)
3	—	—	—	—	—	—	—
4	—	—	—	—	—	—	1 (150)
5	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—
7	—	—	—	1 (10)	—	—	—
8	—	—	—	1 (10)	—	—	—
9	1 (10)	1 (10)	1 (10)	2 (14)	1 (24)	3 (231)	2 (475)
10	—	4 (130)	11 (265)	28 (1 178)	48 (3 632)	58 (6 926)	53 (13 301)

four species. In quadrat 10, *S. fallax* represented 100% of the total (on an area basis) in 1981 but only 42% of the total in 1986. *Sphagnum bartlettianum* increased from 32% of the total in 1982 to 53% in 1986. *Sphagnum magellanicum* represented about 4% of the quadrat 10 total from 1982 to 1986, and *S. recurvum* represented about 1% of the 1985 and 1986 totals.

Salt tolerance

The growth in length of *S. fimbriatum* was reduced significantly ($p = 0.05$) versus the control at concentrations of NaCl greater than 300 mg/L Cl^- (Table 3). The pattern of reduction in length followed the pattern of increasing salt concentration. A major length reduction occurred at 500 mg/L Cl^-, and there was virtually no growth at 3000 and 5000 mg/L Cl^-. Growth in biomass was substantially reduced at salt concentrations greater than 900 mg/L Cl^-, this growth reduction being statistically significant, also (Table 3).

Comparisons of growth in equimolar concentrations of $CaSO_4$, Na_2SO_4, NaCl, and $CaCl_2$ indicate that chloride salts reduce both length and biomass growth to a greater degree than sulfate salts, regardless of the cation (Table 4). Sodium salts reduce growth in length to a greater degree than their counterpart calcium salts, but the results for growth in biomass are ambiguous with regard to cation (Table 4). Overall, the relative toxicity of ions toward *S. fimbriatum* seems to be $Cl^- >> Na^+ > Ca^{2+} > SO_4^{2-}$. In fact, SO_4^{2-} shows potential for growth stimulation over and above the control.

Reproduction from spores

Sphagnum fimbriatum gametophores were abundant on the autoclaved peat at low salt concentrations. There were significantly ($p = 0.05$) more gametophores per cell in the 0 mg/L salt treatment (equivalent to 6.7 gametophores/cm^2) than in the 300-mg/L treatment (5.7/cm^2) (Table 5). Very few gametophores grew at 500 mg/L (0.3/cm^2) and none grew at 900 mg/L Cl^-. No gametophores were found in the control enclosure where *S. fimbriatum* (spores) were not introduced, so the autoclaving process seemed to be successful in sterilizing the peat media. Gametophores were found on the potting soil, further substantiating that the peat was not the source of the new plants. Plant growth (protonemata) was first noted in the 0 and 300 mg/L Cl^- treatments after 53 days.

Regeneration from fragments

Sphagnum fimbriatum (without salt additions) produced more innovations from both branch fascicles and capitula than any of the other four species tested (Table 6). However, when NaCl was added to the culture solutions, the numbers of innovations were greatly reduced. By species, the numbers of innovations from branch fascicles increased in the order *S. recurvum, S. magellanicum, S. bartlettianum, S. fallax,* and *S. fimbriatum*. Innovations from capitula increased in the order *S. magellanicum, S. fallax, S. recurvum, S. bartlettianum*, and *S. fimbriatum*. Apical growth of the original capitula was observed for all species and was first noted after 19 days of culturing. The first innovations from branch fascicles were noted after 26 days and the first innovations from capitula after 54 days.

Discussion

Sphagnum *succession*

Secondary succession of *Sphagnum* in the salt-impacted zone of Pinhook Bog from 1980 to 1986 included 5 of the 16 species known to grow in the bog (Andrus and Wilcox 1985).

TABLE 3. Results of Student–Newman–Keuls sequential range tests ($\alpha = 0.05$) based on one-way ANOVAs for growth in length and biomass of *Sphagnum fimbriatum* by chloride concentration

Chloride (mg/L)	0	300	500	900	1500	3000	5000
Mean increase in length (cm)[a]	2.61	2.03	0.91	0.88	0.41	0.10	0.03

Chloride (mg/L)	300	0	900	500	1500	5000	3000
Mean increase in biomass (%)[b]	233.6	207.3	199.3	165.8	88.7	65.2	62.6

NOTE: Values sharing common underscoring do not differ significantly ($\alpha = 0.05$).
[a] $F_{0.05(6,\ 279)} = 53.75$, $p = 0.0000$ based on log transformation of length.
[b] $F_{0.05(6,\ 279)} = 19.26$, $p = 0.0000$ based on arcsin $(p)^{1/2}$ transformation of percent growth.

TABLE 4. Results of Student–Newman–Keuls sequential range tests ($\alpha = 0.05$) based on one-way ANOVAs for growth in length and biomass of *Sphagnum fimbriatum* by type of salt

Salt[a]	$CaSO_4$	Control	Na_2O_4	$CaCl_2$	NaCl
Mean increase in length (cm)[b]	2.61	2.60	1.90	0.52	0.40

Salt[a]	$CaSO_4$	Na_2SO_4	Control	NaCl	$CaCl_2$
Mean increase in biomass (%)[c]	499.1	337.1	207.3	88.7	42.4

NOTE: Values sharing common underscoring do not differ significantly ($\alpha = 0.05$).
[a] Concentrations are equimolar to 1500 mg/L Cl^- treatment (42.3 m*M* Na^+, 42.3 m*M* Cl^-, 21.1 m*M* Ca^{2+}, 21.1 m*M* SO_4^{2-}).
[b] $F_{0.05(4,\ 199)} = 45.46$, $p = 0.0000$.
[c] $F_{0.05(4,\ 199)} = 99.88$, $p = 0.0000$ based on arcsin $(p)^{1/2}$ transformation of percent growth.

TABLE 5. Results of Student–Newman–Keuls sequential range tests ($\alpha = 0.05$) based on one-way ANOVA for numbers of *Sphagnum fimbriatum* gametophores per grid cell of growth media by chloride concentration

Chloride (mg/L)	0	300	500	900
Mean no. of gametophores/4 cm^2 cell[a]	27.0	22.8	1.2	0.0

NOTE: Values sharing common underscoring do not differ significantly ($\alpha = 0.05$).
[a] $F_{0.05(3,\ 195)} = 114.47$, $p = 0.0000$ (autoclaved peat media).

Of these 5 species, 2 are generally found in ombrotrophic to weakly minerotrophic peatlands (*S. magellanicum* and *S. fallax*), 2 are found in weakly minerotrophic conditions (*S. recurvum* and *S. bartlettianum*), and 1 (*S. fimbriatum*) is usually found in minerotrophic peatlands (Andrus 1980). It might then be expected that *S. fimbriatum* would be more prevalent than the other species in an area subject to mineralization from road salt. However, other minerotrophic species of Pinhook Bog were not found in the impacted zone (*S. riparium* Angstr., *S. squarrosum* Crome, *S. teres* (Schimp.) Angstr., *S. flexuosum* Dozy & Molk., *S. imbricatum* Russow, and *S. henryense* (Warnst.). The first four of these are primarily carpet formers (Andrus 1980) and could thus be affected by being in greater contact with the salt-laden water than a hummock former such as *S. fimbriatum*. The latter two of these six species may form hummocks, but they are not found in abundance in the area of the bog studied.

Primary and secondary succession of *Sphagnum* has been observed and reported by others (Grahn 1977; Elling and Knighton 1984). Noble *et al.* (1984) found *S. girgensohnii* Russow to be the first colonizer of coniferous forest floors in Alaska, and Foster (1984) found the same species to be the first colonizer following fire in upland forests of Labrador. Other early colonizers are reported to be *S. mendocinum* Sull. & Lesq. and *S. squarrosum* in wet depressions and ponds of coniferous forests (Noble *et al.* 1984) and *S. lindbergii* Lindb. in hollows and *S. fuscum* (Schimp.) Klinggr. on hummocks following changes in moisture regime (Foster 1984).

Sphagnum fimbriatum was 1 of 8 species found to be invading an alkaline, lakeside marsh in lower Michigan (Glime *et al.* 1982) and 1 of 3 species invading an abandoned beaver meadow in New York (Breden 1984). In Indiana, it has also been found on hummocks in an intradunal pond following cessation of industry-related flooding (Andrus and Wilcox 1985). There is evidence, then, that *S. fimbriatum* may possess certain attributes that allow it to succeed as a successional pioneer species in wetlands of north-temperate North America.

Ecological characteristics of Sphagnum fimbriatum

Sphagnum fimbriatum is a minerotrophic species that can grow in moderately calcareous waters (Clymo and Hayward 1982). It is common at the mineral soil edges of bogs and poor fens and also in poor to medium open and wooded fens, habitats similar to early colonizer *S. girgensohnii* (Andrus 1980). Its distribution is circumpolar and bipolar, and in North America, it extends from the arctic to West Virginia, Ohio, Indiana, Illinois, Iowa, South Dakota, Colorado, Idaho, and California (Andrus 1980). It is a fast-growing, slender plant with a small capitulum and may grow on low hummocks or dense carpet patches (Andrus 1980). As a hummock former, *Sphagnum fimbriatum* can grow without direct contact with mineralized or contaminated waters such as those found in the peat mat of the salt-impacted zone of Pinhook Bog. Its water is obtained by both precipitation and water from below drawn up by capillary action. The moderately dense hummocks of *S. fimbriatum* do not resist desiccation well, and this species is

TABLE 6. Maximum numbers of new innovations observed growing from *Sphagnum* branch fascicles and capitula during 112-day incubation on autoclaved peat at differing NaCl concentrations

		Source of innovations	
Species	Salt concn.[a]	Branch fascicles	Capitula
Control	0	0	0
Sphagnum fallax	0	42	14
S. bartlettianum	0	33	70
S. magellanicum	0	24	12
S. recurvum	0	8	34
S. fimbriatum	0	105	98
S. fimbriatum	300	15	36
S. fimbriatum	500	9	4
S. fimbriatum	900	0	0

[a]Salt concentration in milligrams per litre as chloride.

not desiccation tolerant (Green 1968). Therefore, *S. fimbriatum* is more or less restricted to moist sites that do not dry out completely.

Sphagnum fimbriatum is relatively tolerant of pollutants such as Pb, Cd, As, Hg, Cu, and F (Simola 1977*a*, 1977*b*) and is also relatively tolerant of NaCl. As with *S. recurvum* (Wilcox 1984), Cl^- salts are greater growth inhibitors of *S. fimbriatum* than are SO_4^{2-} salts.

Sphagnum fimbriatum was described by Andrus (1980) as often having abundant sporophytes and fruiting more freely than any other *Sphagnum* species. In Pinhook Bog, the hummocks of *S. fimbriatum* are covered with black spore capsules in early July; other species are only occasionally observed fruiting. *Sphagnum fimbriatum* can reproduce vegetatively from fragments much better than the other species growing in the salt-impacted zone of Pinhook Bog, and it can do so, to a limited extent, in salt concentrations up to 500 mg/L Cl^-.

Mechanism of invasion

The recolonization of the salt-impacted zone of Pinhook Bog by *Sphagnum fimbriatum* follows the pattern of the salt tolerance and field salt concentration data presented. The tolerance level of *S. fimbriatum* plants is about 300 mg/L Cl^- (Table 3), and growth from spores is poor at concentrations greater than 300 mg/L Cl^- (Table 5). Vegetative regeneration is greatly reduced at 300 mg/L Cl^- (Table 6), but it declines even more at higher concentrations. If a composite tolerance level of 300 mg/L is assumed, colonization in 1980 would have been possible only in quadrats 1, 9, 10 (however, quadrat 1 was unsuitable because of standing water). In 1980, colonization was not observed in any quadrat. By the next year, however, Cl^- concentrations were less than 300 mg/L in quadrats 1, 2, and 7–10, and they were near that level in quadrat 3. All of these quadrats, except for the flooded quadrat 1, had some colonization in 1981. The trend then continued through 1986, with colonization expanding along the transect and colonies growing in size as Cl^- concentrations declined.

There were no significant changes in pH between years (Wilcox 1986*a*), therefore, pH in individual quadrats was not a factor in determining when *Sphagnum* could recolonize. However, it is possible that the four less-minerotrophic species would be able to grow better in quadrats 8–10, where the mean pH was about 5.3, as opposed to values as high as 5.8 in the other quadrats.

There is strong secondary evidence that *Sphagnum fimbriatum* could have used wind dispersal of spores to spread to new sites in Pinhook Bog that were quite distant from existing colonies. However, no protonemata or gametophores of this prolific spore producer were observed in the field. Failure to find spore reproduction in the field is not unusual (e.g., Ferguson and Lee 1983), but the assumption has been made that such reproduction must occur (Clymo and Hayward 1982). McQueen (1985*a*, 1985*b*) was successful in finding germinating spores, protonemata, and gametophores of *S. subtile* (Russow) Warnst. in the field, but his work required very close examination of a lot of material and was timed to coincide with development in laboratory simulations. This approach might result in documenting spore reproduction of *S. fimbriatum* in Pinhook Bog, especially since laboratory growth has been successful (see also Simola 1977*a*).

Reintroduction of *Sphagnum* into the salt-impacted zone could also have been by transportation of fragments by animals, birds, or high waters. This mechanism is especially plausible in quadrat 10 for the four species other than *S. fimbriatum* (see Table 2). However, it would not explain the dominance of *S. fimbriatum* in the other quadrats. Even a few fragments could recolonize an area quite rapidly (Elling and Knighton 1984). Whether the first new *Sphagnum* plants were derived from spores or fragments, vegetative reproduction would be expected to dominate continued colonization (Sobotka 1976; Lane 1977).

Sphagnum can be expected to continue recolonizing the salt-impacted area of Pinhook Bog as salt levels decline. Secondary succession will be affected by the remaining salt, and the elevated alkalinity and pH (Wilcox 1986*a*), the declining numbers of colonization sites above the salt-containing water, and possibly by site preemption (Grace 1987) by dense stands of *Vaccinium oxycoccos* and *Typha angustifolia* (Wilcox 1986*b*; Wilcox and Buchholz 1986).

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ANDRUS, R. E. 1980. Sphagnaceae of New York State. N.Y. State Mus. Bull. 422.

ANDRUS, R. E., and WILCOX, D. A. 1985. New records for *Sphagnum* in Indiana. Mich. Bot. **24**: 147–152.

ANDRUS, R. E., WAGNER, D. J., and TITUS, J. E. 1983. Vertical zonation of *Sphagnum* mosses along hummock–hollow gradients. Can. J. Bot. **61**: 3128–3139.

BREDEN, T. F. 1984. Colonization patterns of red maple (*Acer rubrum*) in an abandoned beaver meadow. M.S. thesis, Rutgers University, New Brunswick, NJ.

CLYMO, R. S. 1970. The growth of *Sphagnum*: methods of measurement. J. Ecol. **58**: 13–49.

——— 1973. The growth of *Sphagnum*: some effects of environment. J. Ecol. **61**: 849–869.

CLYMO, R. S., and HAYWARD, P. M. 1982. The ecology of *Sphagnum*. *In* Bryophyte ecology. *Edited by* A. J. E. Smith. Chapman and Hall, London. pp. 229–289.

ELLING, A. E., and KNIGHTON, M. D. 1984. Sphagnum moss recovery after harvest in a Minnesota bog. J. Soil Water Conserv. **39**: 209–211.

FERGUSON, P., and LEE, J. A. 1983. The growth of *Sphagnum* species in the southern Pennines. J. Bryol. **12**: 579–586.

FOSTER, D. R. 1984. The dynamics of *Sphagnum* in forest and peatland communities in southeastern Labrador, Canada. Arctic, **37**:

133–140.

GADGIL, M. D., and SOLBRIG, O. T. 1972. The concept of *r*- and *K*-selection: evidence from wild flowers and some theoretical considerations. Am. Nat. **106**: 14–31.

GLIME, J. M., WETZEL, R. G., and KENNEDY, B. J. 1982. The effects of bryophytes on succession from alkaline marsh to *Sphagnum* bog. Am. Midl. Nat. **108**: 209–223.

GRACE, J. B. 1987. The importance of preemption and founder effects on the zonation of *Typha* species along lakeshores. Ecol. Monogr. In press.

GRAHN, O. 1977. Macrophyte succession in Swedish lakes caused by deposition of airborne substances. Water Air Soil Pollut. **7**: 295–305.

GREEN, B. H. 1968. Factors influencing the spatial and temporal distribution of *Sphagnum imbricatum* Hornsch. ex Russ. in the British Isles. J. Ecol. **56**: 47–58.

HAYWARD, P. M., and CLYMO, R. S. 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. J. Ecol. **71**: 845–863.

HORTON, D. G., VITT, D. H., and SLACK, N. G. 1979. Habitats of circumboreal-subarctic sphagna. I. A quantitative analysis and review of species in the Caribou Mountains, northern Alberta. Can. J. Bot. **57**: 2283–2317.

LANE, D. M. 1977. Extent of vegetative reproduction in eleven species of *Sphagnum* from northern Michigan. Mich. Bot. **16**: 83–89.

MACARTHUR, R. H., and WILSON, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

MCQUEEN, C. B. 1985*a*. A technique for raising and maintaining cultures of *Sphagnum* from spores. Evansia, **2**: 15–16.

——— 1985*b*. Spatial pattern and gene flow distances in *Sphagnum subtile*. Bryologist, **88**: 333–336.

NOBLE, M. G., LAWRENCE, D. B., and STREVELER, G. P. 1984. *Sphagnum* invasion beneath an evergreen forest canopy in southeastern Alaska. Bryologist, **87**: 119–127.

SIMOLA, L. K. 1977*a*. The tolerance of *Sphagnum fimbriatum* towards lead and cadmium. Ann. Bot. Fenn. **14**: 1–5.

——— 1977*b*. Growth and ultrastructure of *Sphagnum fimbriatum* cultured with arsenate, fluoride, mercury, and copper ions. J. Hattori Bot. Lab. **43**: 365–377.

SOBOTKA, D. 1976. Regeneration and vegetative propagation of *Sphagnum palustre* as a factor of population stability. Acta Soc. Bot. Pol. **45**: 357–367.

VITT, D. H., and SLACK, N. G. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. Can. J. Bot. **62**: 1409–1430.

VITT, D. H., CRUM, H., and SNIDER, J. A. 1975. The vertical zonation of *Sphagnum* species in hummock–hollow complexes in northern Michigan. Mich. Bot. **14**: 190–200.

WILBUR, H. M., TINKLE, D. W., and COLLINS, J. P. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Am. Nat. **108**: 805–817.

WILCOX, D. A. 1984. The effects of NaCl deicing salts on *Sphagnum recurvum* P. Beauv. Environ. Exp. Bot. **24**: 295–304.

——— 1986*a*. The effects of deicing salts on water chemistry in Pinhook Bog, Indiana. Water Resour. Bull. (Pa. Dep. Environ. Resour.), **22**: 57–65.

——— 1986*b*. The effects of deicing salts on vegetation in Pinhook Bog, Indiana. Can. J. Bot. **64**: 865–874.

WILCOX, D. A., and BUCHHOLZ, R. W. 1986. Vegetation restoration in a road-salt impacted bog. Restoration Manage. Notes, **4**(1): 28.

WILCOX, D. A., PAVLOVIC, N. B., and MUEGGLER, M. L. 1985. Selected ecological characteristics of *Scirpus cyperinus* and its role as an invader of disturbed wetlands. Wetlands, **5**: 87–98.