

Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec

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Summary

1. As an aid for restoration projects, the relative potential for plants to immigrate to sites after severe disturbance was investigated and an index developed to determine their relative immigration potential. The goal was to establish baseline knowledge for the species pool in severely disturbed sites prior to restoration. The method was based on the identification of potential colonists, inventories of populations in surrounding vegetation and autecological information on their maximum fecundity and dispersal by wind, water or animals.
2. The method was applied to milled peatlands in south-eastern Quebec, Canada, after the cessation of peat extraction activities. Thirty-two species, ranging from mosses to trees, which are common in natural or abandoned milled peatlands in southern Quebec, were selected as potential colonists.
3. Populations of study species differed markedly in edges of milled peatlands in terms of their abundance, presence and presence of fertile plants. An edge effect was apparent where the populations of many species varied as a function of distance from milled surfaces, caused, in part, by drainage.
4. Mosses had relatively high potential to immigrate to milled bogs because of their high fecundity and the wind-dispersal ability of their spores. The scarcity of mosses in abandoned milled bogs did not appear to be a result of the lack of immigrant propagules. Herbs had relatively low immigration potential, due to their rarity in edges, but herbs such as *Eriophorum vaginatum* were able to recolonize milled bogs in spite of this low potential. Shrub species generally had high immigration potential because of their abundance at edges and the high dispersal ability of propagules by wind, water and animals. Trees had high immigration potential due to their abundance at edges and their wind-dispersal abilities.
5. *Synthesis and applications.* An index of immigration potential provides information on the probable initial species pool after severe disturbance, against which the effects of local habitat suitability and establishment factors can be added to assess probable successional patterns. Its flexibility and applicability to varied life forms should make it useful for diagnosing recolonization bottlenecks in a wide variety of disturbance and restoration situations. It also allows for an assessment of the relative need for introducing species during the restoration of severely disturbed environments.

Keywords: bog, cut-over peatland, disturbance, plant dispersal, primary succession, restoration ecology, species pool.

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Introduction

The main goal of most projects in ecosystem restoration is to shorten the successional pathways towards plant

communities that are functionally similar, if not structurally similar, to the pre-disturbance state (Lockwood & Pimm 1999). One approach taken to achieve this goal is similar to that proposed for determining assembly rules of plant communities (Keddy 1992, 1999). Managers must first define the species pool available for recolonization, secondly determine the main abiotic and biotic filters operating during the recolonization

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process, thirdly determine how species respond to these filters, and finally manipulate these filters in an efficient manner until the community is restored. The initial information required is the composition of the post-disturbance species pool available for recolonization. This species pool consists of adult plants and propagules that persist through the disturbance and propagules that immigrate from surrounding sites (Noble & Slatyer 1980). Following a severe disturbance, the species pool is entirely dependent on the immigration of propagules and recolonization, in the absence of introductions, is propagule-limited (del Moral & Wood 1993; Ash, Gemmell & Bradshaw 1994).

Milled peatlands are examples of severely disturbed environments that rely entirely on immigration or active introductions for recolonization. Ombrotrophic peatlands in eastern Canada are exploited for their peat over several decades using the method of milling and vacuum collection (Crum 1988). Once abandoned, milled surfaces are flat and large (up to 5 km²) with a dense network of ditches. Fibric to sapric, *Sphagnum* peat substrates usually remain (> 1 m thick) that are acid (pH 3–5) and nutrient-poor (Wind-Mulder, Rochefort & Vitt 1996). There is no residual plant cover nor a seed bank (Salonen 1987). Subsequent recolonization is slow and many typical ombrotrophic peatland species are absent, notably *Sphagnum* species (Curran & MacNaoidhe 1986; Salonen 1990; Salonen & Setälä 1992; Salonen, Penttinen & Särkkä 1992; Desrochers, Rochefort & Savard 1998). The poor recolonization has been attributed to the paucity of immigrant propagules and harsh edaphic conditions for plant establishment (Salonen & Setälä 1992) but the relative importance of each is poorly understood.

The immigration of plants into disturbed ecosystems can be determined in a straightforward manner by trapping the diaspore rain. However, such determinations are labour-intensive and forcibly site-specific (Salonen 1987; Poschod 1995). Furthermore, traps in milled peatlands are often filled by wind-blown peat (D.R. Campbell, personal observation). Immigration may also be quantified using physical models such as those developed for determining wind dispersal of tree seeds from forest edges to clearings (Greene & Johnson 1996) or from isolated stands (Nathan, Safriel & Noy-Meir 2001). But, if the vegetation structure surrounding the disturbance is variable, as is the case for milled peatlands, the consequent wind environments will be as well, making predictions difficult (Nathan, Safriel & Noy-Meir 2001). A more general approach has been proposed to define local and regional species pools of target communities, which in effect defines immigration potential (Zobel, van der Maarel & Dupré 1998). A series of key autecological factors for immigration are considered for each species; a factor with a low value reduces the overall probability of a species of belonging to a species pool of a particular target community. The approach cannot provide quantitative information on dispersal distances, but it allows for

a general determination of probable immigrants to a community from a large suite of potential species.

In this study, a method was developed to assess the relative immigration potential of plants colonizing milled peatlands based on the approach proposed for determining local species pools (Zobel, van der Maarel & Dupré 1998). Immigration is considered strictly as the arrival of potential colonists to a milled surface; establishment and subsequent community dynamics affected by restoration conditions are not considered here. A comparative approach is used, and an index of immigration potential is determined for each species relative to other species considered. This method allows for an evaluation of the role of immigration in determining recolonization. Poor recolonization success despite good immigration potential would suggest that other steps after immigration control recolonization. Moreover, it allows for the identification of species that must be introduced prior to restoration. Although this approach can easily be applied to individual sites, it is applied here to the general case of milled peatlands in south-eastern Quebec, Canada.

Methods

IDENTIFICATION OF POTENTIAL COLONISTS

Study species were chosen a priori as the most frequent species of vascular plants and mosses occurring in natural ombrotrophic peatlands or abandoned milled peatlands in southern Quebec (L. Rochefort & F. Quinty, unpublished data; Appendix 1). Species common in natural peatlands are the target species to be restored, while those species that actually recolonize milled bogs include many unwanted opportunistic species. Similar substrate, pH and nutrient conditions are found in milled peatlands and natural ombrotrophic peatlands, although milled peatlands are substantially drier (Wind-Mulder, Rochefort & Vitt 1996; Price, Rochefort & Quinty 1998). As such, milled peatlands should provide suitable habitat conditions for both groups of species, once hydrological conditions are restored. The moss *Dicranella cerviculata* and the trees *Pinus banksiana* and *Larix laricina* were also included because they appear to be underrepresented in our surveys of milled peatlands. *Dicranella cerviculata* may have been missed as a result of its small size, while the tree species are occasionally important colonists in some milled peatlands. In total, 23 species of vascular plants and nine species of mosses were included for study. Nomenclature follows Anderson, Crum & Buck (1990) for mosses, except for *Sphagnum*, which follows Anderson (1990). For vascular plants, nomenclature follows Scoggan (1978–79), except for *Vaccinium oxycoccus* L.

SOURCE POPULATIONS IN EDGES OF MILLED PEATLANDS

Populations of study species in edges of milled peatlands were evaluated in the summer of 1998 through

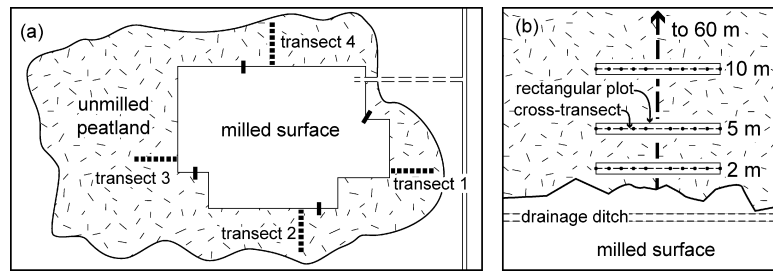


Fig. 1. (a) Placement of main transects in the edges of milled bogs and (b) close-up plan view of a portion of a transect showing the placement of rectangular plots and cross-transects.

random surveys of edges of 12 active or abandoned milled peatlands in south-eastern Quebec (area 11–236 ha, mean \pm SD 88 ± 74 ha; perimeter 1.3–8.9 km, mean \pm SD 4.3 ± 2.2 km). For each milled surface, the perimeter was identified, and sections adjacent to processing mills and recently cut-over areas were excluded. The remaining perimeter was divided into four equal segments, and a starting point for the transects was determined randomly within each perimeter segment (Fig. 1a). In total, four transects were surveyed per peatland. Each transect ran perpendicular to the edge and began where vegetative cover began (Fig. 1b). Study species were surveyed at distances of 2, 5, 10, 20, 30, 40, 50 and 60 m from the edge using three techniques. First, a 10-m long cross-transect was placed perpendicular to the main transect at each distance. The presence of study species touching a 2-cm diameter point was noted at 10 1-m distant points. This technique allowed for quantitative estimations of percentage cover of most study species but was inadequate to detect small or infrequent species. Secondly, 1×10 -m rectangular plots were also placed perpendicular to the main transect at each distance and the presence of each study species was determined. Thirdly, the presence of flower- or fruit-bearing individuals was determined in the same rectangular plots. Sampling was arbitrarily limited to 60 m from edges, partly based on the impact of drainage on edges studied by Poulin, Rochefort & Desrochers (1999). Propagules may disperse from longer distances but they should be rare relative to those originating close to milled edges.

Aerial photographs (1948–94) were examined to estimate the age of the closest drainage ditch to the sampling point. Drainage age was set as the midpoint age between the aerial photograph when a ditch appears and the previous photograph. If a ditch was present at the date of the earliest photograph, this date was taken as the drainage age.

MAXIMUM FECUNDITY

The fecundity of a given species varies widely in space and time, making estimation difficult. The maximum fecundity of a species, however, is more easily determined and allows for a discrimination between species at least on a log scale. The maximum fruiting body density of each species was therefore determined in the

1999 growing season by deliberately searching peatlands in south-eastern Quebec for individuals with large concentrations of fruiting bodies. Fruiting bodies were considered as berries, drupelet aggregates, spikes, cones or capsules, depending on the species. Maximum density was determined at two separate sites for most species. Habitats searched included edges of milled peatlands, as well as natural peatlands and abandoned milled peatlands for species that fruited infrequently in edges. Counts were made by placing quadrats of 50×50 cm for vascular plants or 25×25 cm for mosses over areas of high concentration and counting the number of fruiting bodies. Five quadrats were counted per species per site and, where possible, quadrats were placed more than 2 m apart. Four undispersed fruiting bodies were collected per quadrat.

For vascular plants, the number of propagules in 20 fruiting bodies was counted in the laboratory under a dissecting microscope. For mosses, spore number in five capsules was determined using the haemocytometer technique of Sundberg & Rydin (1998), except that spore aggregates were separated by repeated shaking of the vial in a wide arc. Spores in four 1-mm^2 squares on the diagonal of a Fuchs-Rosenthal haemocytometer (Hausser Scientific, Horsaam, PA) were counted, and four subsamples were counted for each vial. For vascular plants and mosses, the number of propagules per dm^2 was determined by multiplying the density of fruiting bodies by the average seed or spore count at that site. The highest number of propagules per dm^2 was selected as the maximum fecundity.

WIND-DISPERSAL ABILITY

Three variables were used to estimate the wind-dispersal ability of study species: (i) propagule release height; (ii) fall time (propagule release height/settling velocity); and (iii) propagule wing loading (mass area^{-1}). Propagules released from higher elevation are generally exposed to greater wind velocities (Greene & Johnson 1996) and consequently have a greater probability of being carried further by wind. Likewise, propagules with a longer fall time (higher release height and/or slower settling velocity) are also more likely to be exposed to wind and carried away. Wing loading is a key dispersal variable because its square root predicts settling velocity and hence horizontal dispersal distance

of wind-dispersed species (Augsburger 1986; Augspurger & Franson 1987). It also predicts entrainment wind velocity during secondary dispersal (Johnson & Fryer 1992; Greene & Johnson 1997). Only dispersal ability of moss spores was evaluated. Dispersal by vegetative fragments is possible (Poschlod 1995); however, they are not adapted to long-distance dispersal in the same way as spores (Kimmerer 1991; Sundberg 2000) and should therefore contribute little to the post-milled species pool.

Propagule release height

The median propagule release height for each species was measured along transects in edges of milled peatlands, described above (variable *n*; Appendix 2). Individuals were chosen randomly within rectangular plots closest to the milled edge, for a maximum of three individuals per species per transect. Because *Sphagnum* species possess an air gun-release mechanism that shoots their spores 15 cm or more above the capsules (Ingold 1965), this height was taken as the release height.

Fall time

Fall time was determined by dividing propagule release height by settling velocity. Settling velocity was evaluated for vascular plant propagules by collecting propagules in the field, air-drying them in the laboratory for at least 2 weeks prior to testing, dropping them in still air from a height of 2 m and measuring mean settling time over 20 trials. The settling velocity for small-seeded species, namely *Kalmia* spp., *Ledum groenlandicum* and *Drosera rotundifolia*, was measured from a release height of 1 m. For moss spores, terminal velocity was calculated from spore diameter using Stokes' law for spheres at low Reynold's numbers and assuming spores to be unit density spheres (Gregory 1973). Although few measurements of spore density are available for bryophytes, this assumption generally holds for most pollen and fungi spores (Gregory 1973). Spore diameter was taken from the literature (Crum & Anderson 1981; Daniels & Eddy 1985).

Wing loading

Wing loading was calculated by dividing propagule mass by area. For vascular plants, propagules were dried at 70 °C for 48 h then weighed to 10 µg precision. For species with large propagules, 20 propagules, collected from natural peatlands and edges of milled peatlands, were weighed individually. For species with smaller propagules, 10 groups of 20–100 propagules were weighed. The surface area of smaller propagules was photographed digitally, larger propagules were scanned with an image scanner, and for *Eriophorum* species photographs were taken then digitized. The area of propagules was then determined using Scion image analysis software (Scion Corporation 2000). For

Eriophorum species, effective propagule area was estimated by measuring bristle length in four directions and calculating the area of a circle, using mean bristle length as the radius. For mosses, spores were again considered to be unit density spheres. Spore diameter was used to calculate sphere area and volume. From volume, mass was then determined. Spore diameter was taken from the literature, as indicated above.

FLOATABILITY

The ability of propagules of vascular plants to float was evaluated by individually placing air-dried propagules of each species in microcentrifuge tubes or beakers of distilled water at 21 °C for 72 h and shaking containers for 5 s each 8–12 h. The proportion of 10 viable propagules, which remained afloat, was then determined for each species. The floatability of moss spores was not evaluated.

CAPACITY FOR ANIMAL DISPERSAL

The dispersal ability of propagules of vascular plants by animals was evaluated by simply determining the presence of fleshy fruit. Fleshy-fruited propagules will be actively sought for their pulp and not their seeds. Therefore, their seeds are likely to survive the ingestion and digestion processes. No species had any obvious adaptations to adhere to animals (hooks or barbs). Such structures are not necessarily required for epizoochory to occur (Fischer, Poschlod & Beinlich 1996; Kiviniemi & Telenius 1998) although dispersal distances are usually shorter. Neither did species have propagules with elaiosomes. The dispersal capacity of moss spores by animals was not evaluated.

DATA ANALYSES

Multiple logistic regression analyses were performed using the GENMOD procedure of SAS statistical analysis software (SAS Institute 1996–99) to determine the effects of distance from edge and drainage age on the presence of the study species, as well as on the presence of fertile plants of the study species. Because adjacent plots within a main transect may have been autocorrelated, repeated-measures analyses were used within main transects using the autocorrelation option. Similarly, simple Poisson regression analyses were performed with GENMOD to determine the effects of these same variables separately on species abundance, again using repeated-measures analyses and the autocorrelation option. In all regressions, type 3 contrasts were used and the dispersion parameter was scaled to deviance.

A composite variable for 'importance in edges' was calculated for each species from (i) its mean presence across all distances, (ii) its mean abundance, (iii) its mean presence of fertile plants and (iv) a trend variable indicating its bias with respect to the distance from the edge. This fourth variable was constructed using the

regression slopes with respect to distance from the edges as determined from the three regression analyses above. Species whose regression slopes were significantly positive with respect to distance (more abundant or present further from the edge) were given a score of 0, while those with a significantly negative slope with respect to distance (more abundant or present closer to the edge) were given a score of 2. Those without a significant slope were given a score of 1. Scores were added for the three regressions (abundance, presence and fertile plants) for a possible total score of 6. All variables were then rescaled using the technique of ranging (Sneath & Sokal 1973), so that minimum and maximum values of each variable ranged between 0 and 1, respectively. The arithmetic mean of these four variables was taken. This composite variable was again rescaled from 0 to 1 using the same ranging technique.

A composite variable for 'dispersal ability by wind' was also constructed for each species from (i) release height, (ii) fall time and (iii) log wing loading. Log_{10} wing loading was used instead of square-root wing loading because a far greater range of values was obtained in this study than those in previous studies (Augsburger & Franson 1987; Greene & Johnson 1997) as a result of the inclusion of species with heavy propagules (wingless seeds, berries). Each variable was again rescaled using the ranging technique. The reciprocal of wing loading was used so that smaller wing loading had greater value. As such, species with a combination of high release height, long fall time and small wing loading were considered as the best wind dispersers. The composite wind-dispersal ability was determined from the arithmetic mean of these three variables, which was rescaled again using the ranging technique.

Remaining variables (log maximum fecundity, floatability and fleshy fruits) were also rescaled using the ranging technique. The relative immigration potential of each species by wind, water or animals was calculated as the geometric mean of (i) their importance in edges of milled peatlands, (ii) their maximum fecundity and (iii) their dispersal ability by either wind, water or animals. This value was again rescaled using the ranging procedure. The geometric mean was used because overall immigration ability is the product and not the sum of these three variables. To avoid over-penalizing species that fell last for edge importance, fecundity or dispersal ability, 0.01 was added to all ranged values prior to geometric averaging. Consequently, such species may have low but non-negligible immigration potential.

Results

POPULATIONS IN EDGES OF MILLED PEATLANDS

Populations of study species differed markedly in the edges of milled peatlands in terms of abundance, presence and fertile plants, and many also varied with distance to edge (Table 1 and Fig. 2). Among mosses,

Polytrichum strictum was widespread and showed no significant trends with distance. *Pleurozium schreberi*, *Sphagnum capillifolium* and *Sphagnum fuscum* only became frequent further from edges (> 20 m). *Dicranella cerviculata* was generally infrequent but, contrary to other mosses, increased within 10–20 m from edges. Herbaceous plants were uncommon in general, with few fertile plants. *Eriophorum vaginatum* was the most common herb. Shrubs were by far the most frequent species in edges of milled peatlands. Relatively few trends with respect to distance were found amongst shrubs, although *Aronia melanocarpa* and *Vaccinium angustifolium* increased in abundance or presence of fertile plants near edges, while *Vaccinium oxycoccus* declined. *Picea mariana* was the most frequent tree species, but declined within 30 m of edges. Conversely, *Betula papyrifera* and *Betula populifolia* were present more often within 30 m of edges. *Larix laricina* was also frequent but showed no trends with respect to distance from edges.

Drainage ditches were 1.7 ± 1.1 m (mean \pm SD) deep with respect to main transects. Distance of plots and cross-transects to the nearest drainage ditch was only moderately correlated with the distance to milled edges ($r = 0.72$), because many ditches occurred further from edges or ran parallel to main transects. Most ditches were dug in the 1970s and 1980s, although some sites were drained earlier in the 1930–50s and a few sites in the early 1990s. On average, drainage occurred 26.8 ± 12.8 years ago (mean \pm SD) across all sampling points. The abundance, presence and presence of fertile plants of most species decreased with increasing drainage age (Table 1).

MAXIMUM FECUNDITY

Mosses, especially *Polytrichum strictum* and *Pohlia nutans*, were by far the most fecund of the study species (Fig. 2; Appendix 2). Amongst vascular plants, the shrubs *Kalmia angustifolia* and *Ledum groenlandicum* were the most fecund. *Rubus chamaemorus* was by far the least fecund species. Maximum fecundity was not determined for *Scirpus cespitosus* because of the lack of fruiting plants in 1999.

DISPERSAL ABILITY

The study species had a wide variety of propagule types, including spores, variously winged seeds, seeds with long pappus and fleshy fruits (Appendix 2). Tree species had the highest release heights as well as winged seeds with low wing loading. Consequently they had the highest composite wind-dispersal abilities, especially *Betula papyrifera* (Fig. 2). Mosses had low release heights; however, they also had very low wing loadings and long fall times as a result of the small size of spores. As a result, the composite wind-dispersal ability of mosses was also high, especially for *Polytrichum strictum*, which has very small spores. Amongst herbaceous plants, both species of *Eriophorum* have high

Table 1. Populations of study species in the edges of milled bogs in terms of abundance, presence and fertile plants, and their trends as functions of distance from the edge (Dist) and drainage age (Age). For abundance data, the number of cross-transects (n) where a species was found is shown along with its percentage occurrence (%) across all cross-transects ($n = 380$). For presence and fertile plants, the number and percentage of all plots where present is shown ($n = 380$). Trends for distance or age were determined from signs of significant slopes from multiple Poisson and logistic regression analyses ($P < 0.05$, $n = 48$ main transects; see text for details)

Species	Abundance				Presence				Fertile plants			
	n	%	Dist	Age	n	%	Dist	Age	n	%	Dist	Age
Mosses												
<i>Dicranella cerviculata</i>	7	0.3	–	–	18	5	–	–	9	2	–	–
<i>Pleurozium schreberi</i>	98	6.5	+		123	33	+		13	3	+	
<i>Pohlia nutans</i>	48	2.7			70	18		–	12	3		
<i>Polytrichum strictum</i>	84	6.6			131	34			44	12		
<i>Sphagnum angustifolium</i>	43	2.9	+	–	61	16	+	–	0	0		
<i>Sphagnum capillifolium</i>	124	10.2	+	–	167	44	+	–	19	5		–
<i>Sphagnum fallax</i>	3	0.1			6	2			0	0		
<i>Sphagnum fuscum</i>	83	6.8	+	–	122	32	+	–	23	6	+	–
<i>Sphagnum magellanicum</i>	47	2.1	+	–	83	22	+	–	2	1		
Herbaceous plants												
<i>Carex limosa</i>	20	1.1		–	23	6		–	6	2		
<i>Carex oligosperma</i>	16	1			26	7			9	2		
<i>Carex stricta</i>	9	0.6		+	12	3			3	1		
<i>Drosera rotundifolia</i>	12	0.5			31	8	+	–	13	3		
<i>Eriophorum angustifolium</i>	6	0.2		–	11	3		–	3	1		
<i>Eriophorum vaginatum</i>	25	1.3		–	50	13		–	20	5		–
<i>Rubus chamaemorus</i>	20	0.7			50	13			6	2		
<i>Sarracenia purpurea</i>	4	0.1			20	5			1	0		
<i>Scirpus cespitosus</i>	4	0.2			6	2			6	2		
Shrubs												
<i>Andromeda glaucophylla</i>	29	1.1		–	55	14		–	30	8		–
<i>Aronia melanocarpa</i>	37	2.1			57	15			18	5	–	
<i>Chamaedaphne calyculata</i>	191	16.3		–	224	59		–	205	54		–
<i>Kalmia angustifolia</i>	219	26.7			260	68		–	207	54		–
<i>Kalmia polifolia</i>	79	3.3		–	135	36		–	102	27		–
<i>Ledum groenlandicum</i>	196	17.1			237	62		–	191	50		
<i>Rhododendron canadense</i>	67	4.6			93	24			72	19		
<i>Vaccinium angustifolium</i>	155	11.1		–	202	53			58	15	–	
<i>Vaccinium oxycoccus</i>	78	5	+	–	97	26	+	–	35	9	+	–
Trees												
<i>Betula papyrifera</i>	51	4.6		–	67	18		–	21	6		–
<i>Betula populifolia</i>	37	2.8		–	40	10		–	30	8		
<i>Larix laricina</i>	86	5.5			112	29			50	13		
<i>Picea mariana</i>	144	17.2	+	–	173	46	+	–	101	27	+	
<i>Pinus banksiana</i>	30	1.9			39	10			35	9		

wind-dispersal ability because propagules had abundant long pappus bristles and very low wing loading. Several shrub species have small, winged propagules with low wing loading favouring their dispersal by wind.

Propagules of several vascular plant species were able to float for 72 h (Appendix 2). All propagules of *Carex* species, *Drosera rotundifolia*, *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Kalmia polifolia* and, to a lesser extent, *Kalmia angustifolia* remained afloat as a result of trapped air bubbles. The large berries of *Vaccinium oxycoccus* and to a lesser extent *Vaccinium angustifolium* also remained afloat, but fleshy fruits of other shrubs did not. Amongst trees, only a small proportion of *Betula* seeds remained afloat.

The only species of vascular plants with fleshy

fruits were *Rubus chamaemorus*, and the shrubs *Aronia melanocarpa*, *Vaccinium oxycoccus* and *Vaccinium angustifolium* (Appendix 2). As such, only these species were considered to have high potential for animal dispersal.

IMMIGRATION POTENTIAL

Immigration via wind dispersal

The moss *Polytrichum strictum* showed the highest overall immigration potential as a result of moderate frequency in edges and high fecundity and dispersal ability by wind (Fig. 2). Other mosses had relatively high immigration potential because of their fecundity

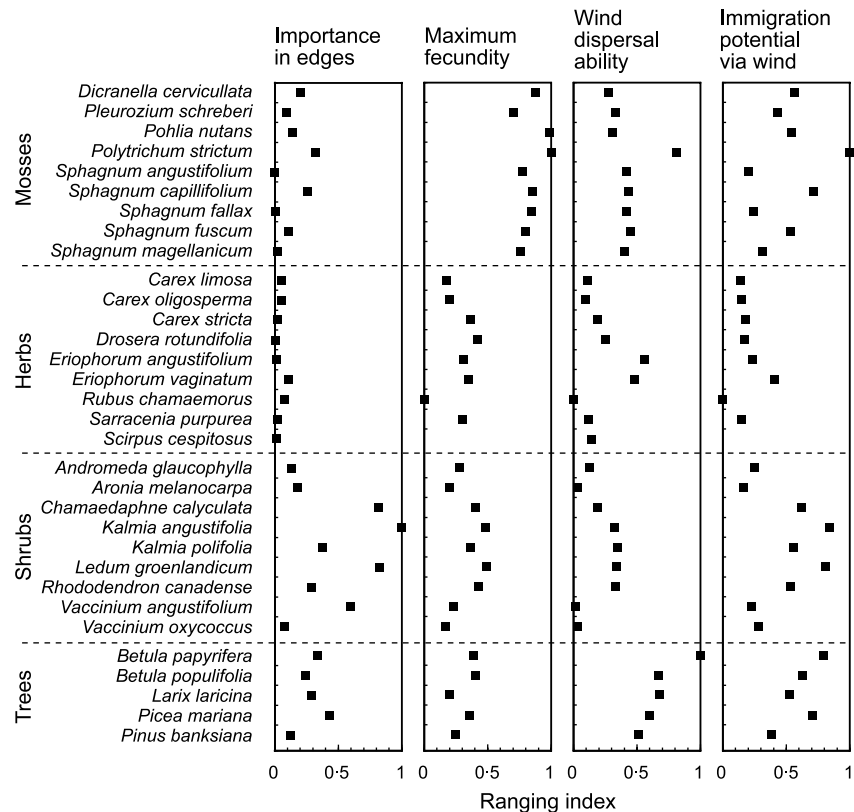


Fig. 2. Importance in edges, log maximum fecundity, wind-dispersal ability and overall immigration potential via wind dispersal by study species of mosses and vascular plants. The axes were rescaled to set the range for each variable between 0 and 1.

and dispersal ability. Herbaceous plants showed lower immigration potential via wind dispersal, largely as a result of their rarity in edges. *Eriophorum vaginatum* was the most likely herbaceous species, which would immigrate by wind to milled peatlands. *Kalmia angustifolia* and *Ledum groenlandicum* were the vascular plants with the highest immigration potential, closely followed by *Betula papyrifera* and *Picea mariana*.

Immigration via water dispersal

Many species of shrubs showed a high potential of immigration into milled peatlands via water dispersal (Fig. 3). The immigration potential of herbaceous plants via water dispersal was higher than via wind dispersal, yet still remained low relative to other species, as a result of their rarity in edges. Trees showed low potential for water dispersal.

Immigration via animal dispersal

Shrub species with fleshy fruits showed a high potential for immigrating into milled peatlands via animal dispersal (Fig. 3). *Rubus chamaemorus* had fleshy fruit but it had a low overall score because of its rarity in edges and low fecundity. Several species without fleshy fruits had low but non-negligible potentials to be dispersed by animals (e.g. *Kalmia*) because they were frequent in edges and fecund.

IMMIGRATION POTENTIALS VS. ACTUAL RECOLONIZATION

The estimation of immigration potential can be compared to survey data of frequent colonists of abandoned milled peatlands in Quebec (Appendix 1) to determine the role of immigration on actual recolonization. The comparison is crude because successful colonists differ in their ability to survive and spread in milled peatlands, but it permits an evaluation of the role of immigration in determining actual recolonization. Although mosses have high immigration potential by wind, they are greatly underrepresented on abandoned milled peatlands compared with vascular plants (Fig. 4a). Mosses with higher immigration potential by wind are generally more frequent colonists on milled peatlands. However, *Sphagnum capillifolium* and *Sphagnum fuscum* are rare on milled peatlands (< 1% occurrence) even though they have relatively high immigration potential. For vascular plants, species that have high immigration potential by wind, water or animal dispersal are generally the most frequent colonists on abandoned milled peatlands (Fig. 4b). Several exceptions exist, as is the case for *Kalmia polifolia*, which shows high potential to immigrate via both wind and water dispersal but has very low presence on milled surfaces. Conversely, *Rubus chamaemorus* and *Eriophorum vaginatum* are both more frequent in milled peatlands than predicted by their immigration potential.

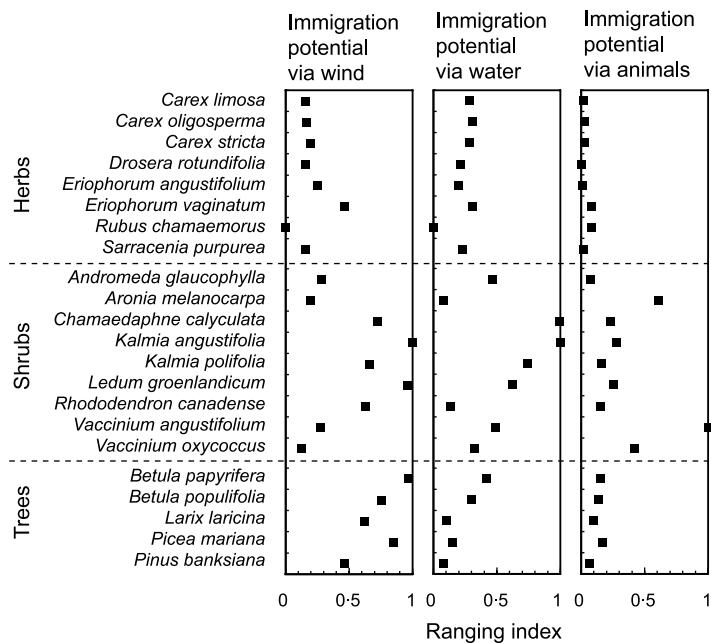


Fig. 3. Overall relative immigration potential via wind dispersal, water dispersal and animal dispersal for study species of vascular plants. The axes were rescaled as in Fig. 2.

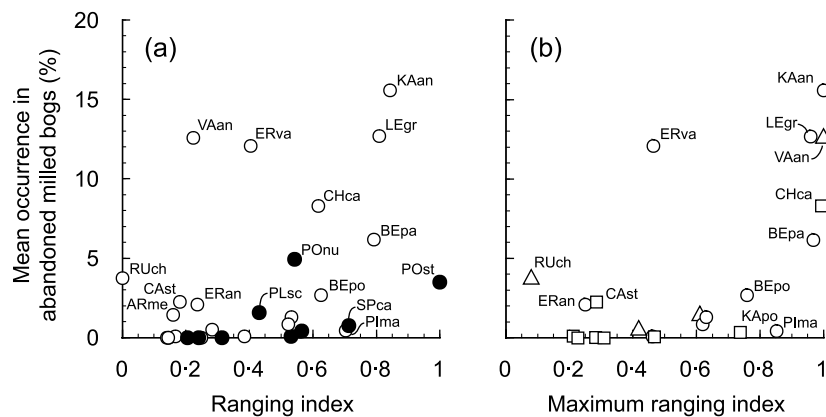


Fig. 4. Comparison of the mean occurrence of study species in abandoned milled peatlands in Quebec vs. (a) the immigration potential of all species by wind dispersal (mosses: solid circles; vascular plants: hollow circles) and vs. (b) the mean immigration potential of vascular plant species by wind (circles), water (squares) and animal dispersal (triangles). Mean occurrences of study species in abandoned milled peatlands are from Appendix 1. Species codes are constructed using the first two letters of the genus and the species.

Discussion

The immigration of potential colonists to milled peatlands depends on the occurrence of residual populations in edges, their fecundity and their ability to disperse by an available vector. The disparity between species is evident just from their residual populations in milled edges. Many typical peatland species are rare (e.g. herbs) while other species that are absent from natural peatlands have become frequent in edges (e.g. birches). A pronounced edge effect is also evident where many species vary in abundance as a function of distance from the edge. The dissimilarity of the vegetation between milled edges and natural peatlands in part reflects decades of disturbance from drainage and extraction activities. Direct drainage effects appear to

have an impact because drainage age predicts the occurrence of many species. Drainage in peatlands affects species composition as a result of altered hydrologic conditions and consequent effects on soil aeration and nutrient dynamics (Laine, Vasander & Laiho 1995; Poulin, Rochefort & Desrochers 1999). However, it is unclear to what extent drainage vs. other disturbances associated with peat extraction are responsible for this edge effect. For instance, the decline of *Picea mariana* near edges may be caused by the practice of clearing trees prior to exploitation.

Differences in immigration ability between study species become even more evident when edge populations are coupled with their maximum fecundity and dispersal ability by wind, water and animals. Species differ dramatically in their ability to disperse by a

particular dispersal agent, and several are not limited to a single agent. However, wind is the key dispersal agent in all milled peatlands because of their large, open and aerodynamically smooth substrates (Campbell, Lavoie & Rochefort 2002). Several studies have determined the prevalence of wind-dispersed diaspores in the seed rain (Curran & MacNaeidhe 1986; Salonen 1987; Salonen, Penttinen & Särkkä 1992; Poschlod 1995). For instance, *Betula* species are known to be entrained for long distances over smooth surfaces (Matlack 1989; Greene & Johnson 1997). In Europe, *Betula pubescens* dispersed up to 1061 viable seeds $\text{m}^{-2} \text{year}^{-1}$ in milled peatlands from a distance of 250 m from the closest vegetated edges (Salonen 1987).

Surface water is present in milled peatlands during snow melt and for longer periods in parts of the drainage ditch network. Water can therefore act as a seasonal dispersal agent for diaspores. However, in comparison with wind dispersal, water dispersal is more site-specific and depends on the duration, location and flow direction of surface water in the drainage network with respect to the edges of the milled zones.

Remnant peatland fragments in milled peatlands have more abundant and diverse assemblages of songbirds than natural peatlands (Delage, Fortin & Desrochers 2000). Small mammals are also more diverse in these fragments than in natural peatlands (Mazerolle, Drolet & Desrochers 2001). Their effectiveness as seed dispersal agents, however, is unknown. The lack of vegetation on milled peatlands restricts the use of milled surfaces by animals and any consequent seed dispersal. However, the prevalence of *Vaccinium angustifolium* in abandoned milled surfaces appears to indicate that animals do disperse seeds on milled peatlands. In addition, occasional tracks of large mammals in milled bogs indicate that epizoochory of propagules may occur.

This study provides evidence that a potential exists for moss spores to immigrate to milled surfaces. Moss species are only moderately common and fertile in edges of milled peatlands but are very fecund and have great wind-dispersal abilities. Previous studies have shown that dispersal of moss spores is concentrated within short distances of adult plants (1–2 m; McQueen 1985; Kimmerer 1991; Miles & Longton 1992). However, only one study compared spore release vs. observed deposition patterns (Miles & Longton 1992). Less than 13% of released spores were deposited within 2 m in forested and less in open habitats. Mosses appear to have highly leptokurtic dispersal distributions with long, fat tails (*sensu* Clark *et al.* 1998) that favours long-distance dispersal.

The discrepancies between immigration potential and actual recolonization for several species suggest that other factors control their colonization success after immigration. The recolonization failure of mosses must primarily be a result of problems during establishment on milled peat surfaces. *Sphagnum* species are especially vulnerable to drought and substrate instability during the establishment phase (Rochefort 2000).

Picea mariana is also frequent in edges, relatively fecund and has high wind-dispersal ability, but is a rare component of the vegetation in abandoned milled peatlands. Harsh substrate conditions, possibly summer drought or needle ice, could prevent its establishment and survival. Conversely, *Eriophorum vaginatum* is infrequent in edges but relatively fecund with high wind-dispersal ability, and frequently colonizes milled peatlands. Similarly, *Rubus chamaemorus* is infrequent in edges, has low fecundity and only disperses by animals, yet is more frequent in milled peatlands than many species. Its presence in abandoned milled peatlands infers that the remainder of its life cycle, namely their germination, establishment, clonal growth or sexual reproduction, is favoured on milled peatlands relative to other species.

APPLICATIONS

The colonization of disturbed environments is often limited by the availability of immigrant propagules (del Moral & Wood 1993; Ash, Gemmill & Bradshaw 1994; Pywell *et al.* 2002). Knowledge of the immigration potential of species should be useful for planning the restoration of these environments. Decisions could then be made on the need for introducing species.

Determining the relative immigration potential of species is relatively straightforward given a list of colonists with suitable habitat requirements, data on source populations of propagules, and autecological information on fecundity and dispersal characteristics of species. It is also possible to compare species with a wide range of life forms, from mosses to trees. Bottlenecks during the immigration sequence can be pinpointed. It should be especially useful where the relative immigration of desirable vs. undesirable species to restoration sites is unknown. If desirable species can be shown to immigrate, restoration efforts can concentrate on encouraging their establishment. The main disadvantage of this approach is the lack of quantitative determination of dispersal distance. The probable concentrations of diaspores on disturbed sites at different distances from edges cannot be determined. However, actual immigration varies greatly between sites and years as a result of many factors. Any quantitative determinations of immigration would vary likewise. A qualitative determination of immigration potential using a relative index does not suffer from this problem, yet provides useful determinations of the likely initial species pool following disturbance.

For milled peatlands in southern Quebec, immigration *per se* appears to be a recolonization constraint for the herbaceous species studied, but does not appear to be as great a constraint for most mosses, ericaceous shrubs or trees. The poor recolonization of many of the latter species is probably a result of establishment failure, especially in the case of mosses. Restoration efforts in milled bogs should therefore concentrate on introducing species with low immigration potential (e.g.

herbaceous species) while promoting microenvironments suitable for the establishment of other species. However, the introduction of species with good immigration potential may still be required as a result of the large size of milled peatlands.

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References

- Anderson, L.E. (1990) A checklist of *Sphagnum* in North America north of Mexico. *Bryologist*, **93**, 500–501.
- Anderson, L.E., Crum, H.A. & Buck, W.R. (1990) List of the mosses of North America north of Mexico. *Bryologist*, **93**, 448–499.
- Ash, H.J., Gemmell, R.P. & Bradshaw, A.D. (1994) The introduction of native plant species on industrial waste heaps: a test of immigration and other factors affecting primary succession. *Journal of Applied Ecology*, **31**, 74–84.
- Augspurger, C.K. (1986) Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany*, **73**, 353–363.
- Augspurger, C.K. & Franson, S.E. (1987) Wind dispersal of artificial fruits varying in mass, area and morphology. *Ecology*, **68**, 27–42.
- Campbell, D.R., Lavoie, C. & Rochefort, L. (2002) Wind erosion and surface stability in abandoned milled peatlands. *Canadian Journal of Soil Science*, **82**, 85–95.
- Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G., Lewis, M., Lynch, J., Pacala, S., Prentice, I.C., Schupp, E.W., Webb, T. III & Wyckoff, P. (1998) Reid's paradox of rapid plant migration: dispersal theory and interpretation of palaeoecological records. *Bioscience*, **48**, 13–24.
- Crum, H.A. (1988) *A Focus on Peatlands and Peat Mosses*. University of Michigan Press, Ann Arbor, MI.
- Crum, H.A. & Anderson, L.E. (1981) *Mosses of Eastern North America*. Columbia University Press, New York, NY.
- Curran, P.L. & MacNaeidhe, F.S. (1986) Weed invasion of milled-over bog. *Weed Research*, **26**, 45–50.
- Daniels, R.E. & Eddy, A. (1985) *Handbook of European Sphagna*. Abbots Ripton, Huntington, UK.
- Delage, V., Fortin, M.-J. & Desrochers, A. (2000) Effets de lisi ere et d'isolement des habitats d'oiseaux chanteurs dans les tourbi eres exploit ees. * coscience*, **7**, 149–156.
- Desrochers, A., Rochefort, L. & Savard, J.-P.L. (1998) Avian recolonization of eastern Canadian bogs after peat mining. *Canadian Journal of Zoology*, **76**, 989–997.
- Fischer, S.F., Poschlod, P. & Beinlich, B. (1996) Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology*, **33**, 1206–1222.

- Greene, D.F. & Johnson, E.A. (1996) Wind dispersal of seeds from a forest into a clearing. *Ecology*, **77**, 595–609.
- Greene, D.F. & Johnson, E.A. (1997) Secondary dispersal of tree seeds on snow. *Journal of Ecology*, **85**, 329–340.
- Gregory, P.H. (1973) *The Microbiology of the Atmosphere*, 2nd edn. Leonard Hill, London, UK.
- Ingold, C.T. (1965) *Spore Liberation*. Clarendon Press, Oxford, UK.
- Johnson, E.A. & Fryer, G.I. (1992) Physical characterization of seed microsites – movement on the ground. *Journal of Ecology*, **80**, 823–836.
- Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157–164.
- Keddy, P. (1999) Wetland restoration: the potential for assembly rules in the service of conservation. *Wetlands*, **19**, 716–732.
- Kimmerer, R.W. (1991) Reproductive ecology of *Tetraphis pellucida*. II. Differential success of sexual and asexual propagules. *Bryologist*, **94**, 284–288.
- Kiviniemi, K. & Telenius, A. (1998) Experiments on adhesive dispersal by wood mouse: seed shadows and dispersal distances of 13 plant species from cultivated areas in southern Sweden. *Ecography*, **21**, 108–116.
- Laine, J., Vasander, H. & Laiho, R. (1995) Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology*, **32**, 785–802.
- Lockwood, J.L. & Pimm, S.L. (1999) When does restoration succeed? *Ecological Assembly Rules: Perspectives, Advances, Retreats* (eds E. Weiher & P. Keddy), pp. 363–392. Cambridge University Press, Cambridge, UK.
- McQueen, C.B. (1985) Spatial pattern and gene flow distances in *Sphagnum subtile*. *Bryologist*, **88**, 333–336.
- Matlack, G.R. (1989) Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. *Journal of Ecology*, **77**, 853–869.
- Mazerolle, M.J., Drolet, B. & Desrochers, A. (2001) Small-mammal responses to peat mining of southeastern Canadian bogs. *Canadian Journal of Zoology*, **79**, 296–302.
- Miles, C.J. & Longton, R.E. (1992) Deposition of moss spores in relation to distance from parent gametophytes. *Journal of Bryology*, **17**, 355–368.
- del Moral, R. & Wood, D.M. (1993) Early primary succession on the volcano Mount St Helens. *Journal of Vegetation Science*, **4**, 223–234.
- Nathan, R., Safriel, U.N. & Noy-Meir, I. (2001) Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology*, **82**, 374–388.
- Noble, I.R. & Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5–21.
- Poschlod, P. (1995) Diaspore rain and diaspore bank in raised bogs and implications for the restoration of peat-mined sites. *Restoration of Temperate Wetlands* (eds B.D. Wheeler, S.C. Shaw, W.J. Fojt & R.A. Robertson), pp. 471–494. John Wiley & Sons, Chichester, UK.
- Poulin, M., Rochefort, L. & Desrochers, A. (1999) Conservation of bog plant species assemblages: assessing the role of natural remnants in mined sites. *Applied Vegetation Science*, **2**, 169–180.
- Price, J., Rochefort, L. & Quinty, F. (1998) Energy and moisture considerations on cutover peatlands: surface microtopography, mulch cover and *Sphagnum* regeneration. *Ecological Engineering*, **10**, 293–312.
- Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294–309.
- Rochefort, L. (2000) *Sphagnum* – a keystone genus in habitat restoration. *Bryologist*, **103**, 503–508.

- Salonen, V. (1987) Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Holarctic Ecology*, **10**, 171–174.
- Salonen, V. (1990) Early plant succession in two abandoned cut-over peatland areas. *Holarctic Ecology*, **13**, 217–223.
- Salonen, V. & Setälä, H. (1992) Plant colonization of bare peat surface – relative importance of seed availability and soil. *Ecography*, **15**, 199–204.
- Salonen, V., Penttinen, A. & Särkkä, A. (1992) Plant colonization of a bare peat surface: population changes and spatial patterns. *Journal of Vegetation Science*, **3**, 113–118.
- SAS Institute (1996–99) *SAS Release 6.12*. SAS Institute Inc., Cary, NC.
- Scion Corporation (2000) *Scion Image for Windows*. Scion Corporation, Frederick, MD.
- Scoggan, H. (1978–79) *The Flora of Canada*. National Museums of Canada, Ottawa, Canada.
- Sneath, P.H.A. & Sokal, R.R. (1973) *Numerical Taxonomy: The Principles and Practice of Numerical Classification*. W.H. Freeman, San Francisco, CA.
- Sundberg, S. (2000) *The ecological significance of sexual reproduction in peat mosses (Sphagnum)*. PhD Thesis. Uppsala University, Uppsala, Sweden.
- Sundberg, S. & Rydin, H. (1998) Spore number in *Sphagnum* and its dependence on spore and capsule size. *Journal of Bryology*, **20**, 1–16.
- Wind-Mulder, H.L., Rochefort, L. & Vitt, D.H. (1996) Water and peat chemistry comparisons of natural and post-harvested peatlands across Canada and their relevance to peatland restoration. *Ecological Engineering*, **7**, 161–181.
- Young, J.A. & Young, C.G. (1992) *Seeds of Woody Plants in North America*. Dioscorides Press, Portland, ME.
- Zobel, M., van der Maarel, E. & Dupré, C. (1998) Species pool: the concept, its determination and significance for community restoration. *Applied Vegetation Science*, **1**, 55–66.

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Appendix 1

Most frequent species of mosses and vascular plants in natural ombrotrophic peatlands or abandoned milled peatlands in Quebec (natural peatlands: $n = 31$, L. Rochefort, unpublished data; abandoned milled peatlands: $n = 11$, abandoned for 6–20 years, L. Rochefort & F. Quinty, unpublished data)

Species	Family	Natural peatlands		Milled peatlands	
		% occurrence (mean \pm SD)	n	% occurrence (mean \pm SD)	n
Mosses					
<i>Dicranella cerviculata</i>	Dicranaceae	0	0	< 1	3
<i>Pleurozium schreberi</i>	Hylocomiaceae	4 \pm 12	5	2 \pm 3	3
<i>Pohlia nutans</i>	Bryaceae	0	0	5 \pm 17	3
<i>Polytrichum strictum</i>	Polytrichaceae	15 \pm 21	18	3 \pm 5	5
<i>Sphagnum angustifolium</i>	Sphagnaceae	33 \pm 32	21	0	0
<i>Sphagnum capillifolium</i>	Sphagnaceae	55 \pm 32	27	1 \pm 2	2
<i>Sphagnum fallax</i>	Sphagnaceae	22 \pm 28	17	0	0
<i>Sphagnum fuscum</i>	Sphagnaceae	49 \pm 33	26	< 1	1
<i>Sphagnum magellanicum</i>	Sphagnaceae	46 \pm 28	29	0	0
Herbaceous plants					
<i>Carex limosa</i>	Cyperaceae	24 \pm 26	20	0	0
<i>Carex oligosperma</i>	Cyperaceae	35 \pm 31	19	0	0
<i>Carex stricta</i>	Cyperaceae	0	0	2 \pm 8	1
<i>Drosera rotundifolia</i>	Droseraceae	35 \pm 35	24	0	0
<i>Eriophorum angustifolium</i>	Cyperaceae	2 \pm 5	4	2 \pm 5	3
<i>Eriophorum vaginatum</i>	Cyperaceae	19 \pm 20	21	11 \pm 21	8
<i>Rubus chamaemorus</i>	Rosaceae	17 \pm 32	9	4 \pm 6	7
<i>Sarracenia purpurea</i>	Sarraceniaceae	17 \pm 21	16	0	0
<i>Scirpus cespitosus</i>	Cyperaceae	17 \pm 30	10	0	0
Shrubs					
<i>Andromeda glaucophylla</i>	Ericaceae	32 \pm 22	26	0	0
<i>Aronia melanocarpa</i>	Rosaceae	5 \pm 12	6	2 \pm 2	5
<i>Chamaedaphne calyculata</i>	Ericaceae	71 \pm 31	31	9 \pm 9	10
<i>Kalmia angustifolia</i>	Ericaceae	39 \pm 28	26	17 \pm 26	8
<i>Kalmia polifolia</i>	Ericaceae	49 \pm 33	28	< 1	4
<i>Ledum groenlandicum</i>	Ericaceae	36 \pm 31	23	14 \pm 17	10
<i>Rhododendron canadense</i>	Ericaceae	0	0	1 \pm 2	5
<i>Vaccinium angustifolium</i>	Ericaceae	7 \pm 12	11	14 \pm 13	9
<i>Vaccinium oxycoccus</i>	Ericaceae	74 \pm 26	31	< 1	3
Trees					
<i>Betula papyrifera</i>	Betulaceae	0	0	5 \pm 10	6
<i>Betula populifolia</i>	Betulaceae	0	0	3 \pm 6	4
<i>Larix laricina</i>	Pinaceae	5 \pm 9	12	1 \pm 1	6
<i>Picea mariana</i>	Pinaceae	21 \pm 22	20	< 1	4
<i>Pinus banksiana</i>	Pinaceae	0	0	< 1	1

Appendix 2

Detailed data on maximum fecundity and dispersal variables for study species

Species	Propagule type	Max. fruiting body density (dm ⁻²)	Number of propagules per fruiting body		Log max. fecundity (dm ⁻²)	Median release height (m)	
			<i>n</i>	Mean ± SE		<i>n</i>	Mean ± SE
Mosses							
<i>Dicranella cerviculata</i>	Spore (16–21 µm)	581	5	35300 ± 13100	7.31	39	0.008 ± 0.000
<i>Pleurozium schreberi</i>	Spore (11–20 µm)	9	5	81900 ± 26900	5.87	7	0.019 ± 0.001
<i>Pohlia nutans</i>	Spore (16–21 µm)	432	5	416000 ± 18000	8.26	37	0.022 ± 0.001
<i>Polytrichum strictum</i>	Spore (8–9 µm)	60	5	4240000 ± 200000	8.41	65	0.046 ± 0.002
<i>Sphagnum angustifolium</i>	Spore (22–24 µm)	33	5	89300 ± 13100	5.47	0	0.15
<i>Sphagnum capillifolium</i>	Spore (24–28 µm)	182	5	71600 ± 12400	7.12	42	0.15
<i>Sphagnum fallax</i>	Spore (25–28 µm)	176	5	73100 ± 22900	7.11	0	0.15
<i>Sphagnum fuscum</i>	Spore (23–27 µm)	54	5	81600 ± 15000	6.64	38	0.15
<i>Sphagnum magellanicum</i>	Spore (26–30 µm)	26	5	89300 ± 14000	6.36	8	0.15
Herbaceous plants							
<i>Carex limosa</i>	Achene in periginium	2	20	14 ± 1	1.34	20	0.20 ± 0.02
<i>Carex oligosperma</i>	Achene in periginium	5	20	7 ± 1	1.49	6	0.49 ± 0.05
<i>Carex stricta</i>	Achene in periginium	5	16	177 ± 9	2.98	3	0.41 ± 0.02
<i>Drosera rotundifolia</i>	Seed with fusiform tips	23	8	111 ± 8	3.41	29	0.09 ± 0.01
<i>Eriophorum angustifolium</i>	Achene with silky bristles	17	20	18 ± 3	2.49	6	0.47 ± 0.04
<i>Eriophorum vaginatum</i>	Achene with silky bristles	19	20	37 ± 2	2.84	24	0.30 ± 0.01
<i>Rubus chamaemorus</i>	Large fleshy drupe	1	20	1	-0.15	15	0.09 ± 0.01
<i>Sarracenia purpurea</i>	Wingless seed	0	18	1330 ± 78	2.42	1	0.25
<i>Scirpus cespitosus</i>	Short-bristled achene	NS*	0	NS*	NS*	8	0.20 ± 0.01
Shrubs							
<i>Andromeda glaucophylla</i>	Wingless seed	9	20	20 ± 1	2.24	30	0.21 ± 0.02
<i>Aronia melanocarpa</i>	Berry-like pomes	34	20	1	1.53	28	0.85 ± 0.05
<i>Chamaedaphne calyculata</i>	Wingless seed	32	20	60 ± 2	3.29	118	0.44 ± 0.02
<i>Kalmia angustifolia</i>	Terminally winged seed	69	20	130 ± 15	3.95	122	0.48 ± 0.02
<i>Kalmia polifolia</i>	Terminally winged seed	5	20	176 ± 20	2.98	84	0.39 ± 0.02
<i>Iedum groenlandicum</i>	Terminally winged seed	83	20	133 ± 11	4.04	106	0.47 ± 0.02
<i>Rhododendron canadense</i>	Terminally winged seed	17	20	184 ± 15	3.48	48	0.58 ± 0.02
<i>Vaccinium angustifolium</i>	Berry	64	16	1	1.81	62	0.30 ± 0.02
<i>Vaccinium oxycoccus</i>	Berry	20	20	1	1.3	39	0.01 ± 0.00

Appendix 2 Continued

Species	Propagule type	Max. fruiting body density (dm ⁻²)	Number of propagules per fruiting body		Log max. fecundity (dm ⁻²)	Median release height (m)		
			<i>n</i>	Mean ± SE		<i>n</i>	Mean ± SE	
Trees								
<i>Betula papyrifera</i>	Bilateral winged seed	5	20	264 ± 20	3.13	23	6.45 ± 0.56	
<i>Betula populifolia</i>	Bilateral winged seed	5	20	392 ± 11	3.31	27	3.13 ± 0.27	
<i>Larix laricina</i>	Asymmetrical winged seed	1	–	32†	1.51	49	4.83 ± 0.36	
<i>Picea mariana</i>	Asymmetrical winged seed	16	20	51 ± 4	2.91	62	3.85 ± 0.25	
<i>Pinus banksiana</i>	Asymmetrical winged seed	3	20	30 ± 3	1.93	27	2.86 ± 0.24	
Species	Settling velocity (m s ⁻¹)‡	Fall time (s)	Propagule area (mm ⁻²)	Propagule mass (mg)§		Wing loading (mg cm ⁻²)	Floatability (%)	Fleshy fruits¶
				<i>n</i>	Mean ± SE			
Mosses								
<i>Dicranella cerviculata</i>	0.012	0.69	0.0011	–	2.7 × 10 ⁻⁵	2.5	–	–
<i>Pleurozium schreberi</i>	0.009	2.19	0.00075	–	1.6 × 10 ⁻⁵	2.1	–	–
<i>Pohlia nutans</i>	0.012	1.86	0.0011	–	2.7 × 10 ⁻⁵	2.5	–	–
<i>Polytrichum strictum</i>	0.003	17.38	0.00023	–	3.0 × 10 ⁻⁶	1.1	–	–
<i>Sphagnum angustifolium</i>	0.026	5.70	0.0017	–	5.1 × 10 ⁻⁵	3.1	–	–
<i>Sphagnum capillifolium</i>	0.023	6.44	0.0021	–	7.4 × 10 ⁻⁵	3.5	–	–
<i>Sphagnum fallax</i>	0.024	6.20	0.0022	–	7.8 × 10 ⁻⁵	3.5	–	–
<i>Sphagnum fuscum</i>	0.022	6.94	0.002	–	6.5 × 10 ⁻⁵	3.3	–	–
<i>Sphagnum magellanicum</i>	0.027	5.57	0.0025	–	9.2 × 10 ⁻⁵	3.7	–	–
Herbaceous plants								
<i>Carex limosa</i>	2.03 ± 0.01	0.10	4.5 ± 0.1	20 (1)	1.42 ± 0.1	31.7	100	0
<i>Carex oligosperma</i>	2.64 ± 0.01	0.19	9.7 ± 0.5	16 (1)	5.47 ± 0.15	58.4	100	0
<i>Carex stricta</i>	1.48 ± 0.01	0.27	3 ± 0.2	20 (1)	0.4 ± 0.06	13	100	0
<i>Drosera rotundifolia</i>	0.39 ± 0.00	0.23	0.26 ± 0.01	10 (100)	0.008	3.1	100	0
<i>Eriophorum angustifolium</i>	0.24 ± 0.00	1.94	1262 ± 78	20 (1)	0.95 ± 0.07	0.08	60	0
<i>Eriophorum vaginatum</i>	0.26 ± 0.00	1.14	1119 ± 51	20 (1)	1.84 ± 0.07	0.17	30	0
<i>Rubus chamaemorus</i>	3.43 ± 0.02	0.03	31.4 ± 2.3	20 (1)	50.51 ± 5.72	149.7	0	1
<i>Sarracenia purpurea</i>	2.14 ± 0.02	0.11	1.8 ± 0.1	16 (1)	0.52 ± 0.03	28.4	60	0
<i>Scirpus cespitosus</i>	1.15 ± 0.01	0.17	1.2 ± 0.1	10 (20)	0.24	19.8	0	0

Appendix 2 Continued

Species	Settling velocity (m s ⁻¹)‡	Fall time (s)	Propagule area (mm ⁻²)	Propagule mass (mg)§		Wing loading (mg cm ⁻²)	Floatability (%)	Fleshy fruits¶
				n	Mean ± SE			
Shrubs								
<i>Andromeda glaucophylla</i>	1.87 ± 0.02	0.11	0.75 ± 0.03	10 (20)	0.18	23.8	100	0
<i>Aronia melanocarpa</i>	3.72 ± 0.02	0.23	30.8 ± 1.1	20 (1)	73.11 ± 3.86	238.9	0	1
<i>Chamaedaphne calyculata</i>	1.09 ± 0.01	0.41	0.51 ± 0.02	10 (20)	0.071	13.9	100	0
<i>Kalmia angustifolia</i>	0.33 ± 0.00	1.46	0.17 ± 0.01	10 (100)	0.0047	2.7	70	0
<i>Kalmia polifolia</i>	0.23 ± 0.00	1.69	0.29 ± 0.01	10 (100)	0.0059	2	100	0
<i>Ledum groenlandicum</i>	0.31 ± 0.01	1.51	0.27 ± 0.01	10 (100)	0.0057	2.1	20	0
<i>Rhododendron canadense</i>	0.39 ± 0.01	1.49	0.65 ± 0.03	10 (100)	0.0177	2.7	0	0
<i>Vaccinium angustifolium</i>	3.45 ± 0.02	0.09	14.1 ± 0.7	20 (1)	21.32 ± 1.86	148.1	30	1
<i>Vaccinium oxycoccus</i>	3.46 ± 0.02	0.003	79 ± 3.6	20 (1)	63.69 ± 4.27	80.2	100	1
Trees								
<i>Betula papyrifera</i>	0.72 ± 0.01	9.01	6.9 ± 0.5	20 (1)	0.22 ± 0.02	3.4	20	0
<i>Betula populifolia</i>	0.58 ± 0.01	5.37	5 ± 0.3	10 (20)	0.096	1.9	10	0
<i>Larix laricina</i>	1.34 ± 0.04	3.60	22.8 ± 0.9	20 (1)	1.5 ± 0.1	6.5	0	0
<i>Picea mariana</i>	0.86 ± 0.01	4.47	15.1 ± 0.8	20 (1)	1.49 ± 0.09	10.1	0	0
<i>Pinus banksiana</i>	0.73 ± 0.00	3.94	39.6 ± 1.7	20 (1)	3.32 ± 0.26	8.3	0	0

*Fecundity for *Scirpus cespitosus* was not sampled.

†From Young & Young (1992).

‡Mean ± SE for vascular plants, n = 16–20.

§The number of propagules from which each mass determination is measured is shown in parentheses.

¶For fleshy fruits, 0 = no; 1 = yes.