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SPONTANEOUS REVEGETATION OF CUTWAWAY PEATLANDS OF NORTH AMERICA

Martha D. Graf, Line Rochefort, and Monique Poulin
Peatland Ecology Research Group and Centre d'études nordiques
Département de phytologie
Université Laval
Québec, QC, G1K 7P4, Canada
E-mail: martha-darling.graf.1@ulaval.ca

Abstract: Modern extraction methods permit peat to be extracted to the minerotrophic layer of ombrotrophic peatlands (bogs). As the environmental conditions of these harvested peatlands are similar to minerotrophic peatlands (fens), such sites should be restored towards a fen system. However, it is not known whether fen species would recolonize such harvested sites on their own. We surveyed vegetation and environmental variables in 28 harvested peatlands with minerotrophic residual peat across Canada and in Minnesota, USA, and compared them to 11 undisturbed fens. Compared to harvested bogs previously studied, the harvested fens sampled in this study revegetated remarkably quickly (50%–70% vegetation cover) when the hydrological conditions were suitable. However, revegetation was less extensive for sites that were still drained (25% vegetation cover). A high water table and a thin layer of residual peat were the most important factors contributing to rapid recolonization rates. Although the harvested fens were rapidly recolonized, species composition was not the same as observed on undisturbed fens. *Carex* and *Sphagnum*, dominant in undisturbed fens, generally did not recolonize harvested fens. Thus, whether the goal is to increase species richness or to ensure the return of peat accumulating functions, fen species may have to be actively introduced.

Key Words: fens, milled peatlands, restoration, succession, vacuum-harvest

INTRODUCTION

Fen restoration projects on harvested peatlands in North America aim to restore a fen plant community on sites that were previously bogs (Cooper and MacDonald 2000, Cobbaert et al. 2004). In North America, the dominant succession for peatlands begins with fens (minerotrophic peatlands) and gradually develops into bogs (ombrotrophic peatlands) (Kuhry et al. 1993). Thus, when the *Sphagnum* peat layer is completely removed, the successional clock is set back to the peatland's earlier minerotrophic state. Peatlands that have been harvested to the minerotrophic layer are richer in mineral peat content and have a higher pH than bogs, which creates conditions that are sub-optimal for bog community restoration (Wind-Mulder et al. 1996, Wind-Mulder and Vitt 2000). Restoration towards a fen system is therefore more appropriate for such sites.

Spontaneous revegetation resulting from natural succession may lead to more stable, better acclimated vegetation communities and cost less than active, imposed restoration strategies (Bradshaw 2000, Prach et al. 2001). However, when spontaneous revegetation does not meet restoration objectives, active restoration measures can 'fill in the gaps.' For example, plants that do not readily recolonize restoration sites can be reintroduced. Several studies have characterized the spontaneous colonization of harvested peatlands with ombrotrophic residual peat (harvested bogs) in northeastern Canada (Lavoie and Rochefort 1996, Girard et al. 2002, Lavoie et al. 2003, Poulin et al. 2005), but little research has addressed abandoned peatlands with minerotrophic residual peat. Such peatlands have been referred to as cutaway bogs with minerotrophic residual peat in Ireland (O'Connell 2000), but will be referred to as harvested fens in this paper. Studies on vacuum-harvested bogs have indicated that the vegetation cover of most vegetation strata was usually $< 25\%$, and that *Sphagnum* moss was rarely present (Girard et al. 2002, Salonen 1992, Lanta et al. 2004, Poulin et al. 2005). Famous et al. (1991) found that harvested fens revegetated more rapidly than harvested bogs. Their study showed that 75% of the harvested fens were completely revegetated within seven years; however, the identity of the recolonizing plants was not reported. Harvested fens in Ireland and Finland were mostly colonized by weedy, ruderal species (Salonen 1992, Rowlands 2001).

Abiotic factors such as water table level, residual peat thickness, and pH can strongly influence the succession of harvested fens and bogs (Famous et al. 1991, Girard et al. 2002). Bulk density and degree of decomposition increase after peatlands are drained and harvested, which, in turn, greatly impacts the hydrology and peat chemistry of the site (Price et al. 2003). Harvested peatlands are often phosphate-limited; vascular plants and pioneer mosses recolonize restored bogs more readily if a light phosphate fertilizer is applied (Rochefort et al. 2003). In undisturbed fens, variations in pH, electrical conductivity, and calcium, magnesium, and sodium concentrations are mainly responsible for vegetation gradients (Vitt and Chee 1990). Historical factors can also influence the succession of harvested peatlands. Girard et al. (2002) explained 44% of the variation of species occurrence with spatio-historical data, such as the duration of extraction activities, the time since abandonment of harvesting activities, the intensity of the harvesting activities, or the distance to the closest unharvested border. More information on the spontaneous recolonization of harvested fens and the environmental conditions associated with their recovery would be useful to tailor fen restoration strategies.

Our research was driven by the following questions: 1) do fen species return to the harvested fen sites spontaneously, 2) if so, which environmental conditions favor their return, and, finally, 3) which vegetation groups, otherwise common in undisturbed sites, are not successful in recolonizing bare surfaces after the abandonment of peat harvesting activities?

MATERIALS AND METHODS

Study Sites

Twenty-eight harvested fens and 11 undisturbed fens were sampled between June and August of 2004 and 2005 in the provinces of New Brunswick, Québec, Manitoba, and Alberta, Canada and the state of Minnesota, USA (Figure 1). These areas are the centers of peat harvesting in North America. The mean annual temperatures and precipitation, respectively, for the regions sampled are: 4.7°C and 1,115 mm in New Brunswick, 3.2°C and 963 mm in Québec, 2.6°C and 514 mm in Manitoba, and 2.4°C and 483 mm in Alberta (Environment Canada 2002), and 3.9°C and 787 mm in Minnesota (National Climatic Data Center 2001). For each potential site, pH and macrofossil data were used to confirm whether the residual peat was minerotrophic peat and the site could thus be considered a fen.

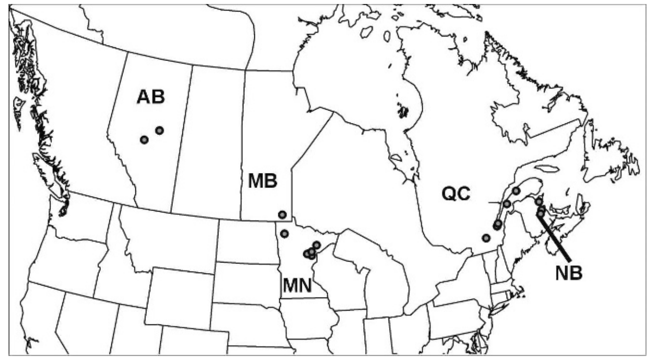

Figure 1. Location of the cities (see Table 1) near the studied peatlands in the Canadian provinces of Alberta (AB), Manitoba (MB), Québec (QC), and New Brunswick (NB) as well as the state of Minnesota (MN), USA.

Peat had been harvested from the sampled peatlands using either the bulldozer or the vacuum-harvesting method. Bulldozed peatlands were drained with small drainage ditches every 30 m across the peatland. When the hydraulic conditions permitted machines to enter the fields, the peat was bulldozed into stockpiles. Since the 1960s, the bulldozer method was largely replaced by the more cost-effective vacuum-harvesting method. For this method, peatland hydrology is altered by creating a large drainage canal around the periphery of the peatland and a network of smaller drainage canals (1 m × 1 m in a 'v' shape) every 30 m throughout the peatland (Price et al. 2003). The top layers of peat are allowed to air dry, thereby eliminating the costly drying process of the bulldozer method. After drying, the top few centimeters are removed with tractor-drawn vacuum machines. For a more detailed description of the vacuum-harvesting method, see Poulin et al. (2005).

The majority of the harvested fens studied no longer had intact drainage systems because canals usually collapse without active maintenance. The thin residual peat layer remaining on harvested fens is close to the water table, which quickly leads to the deterioration of drainage canals. Because bulldozed sites had been abandoned for a long period, none had intact drainage systems.

Each of the 28 harvested fens was characterized by the year it had been abandoned, the harvest method, and whether drainage canals were still active. Time since abandonment was determined by asking peatland site managers. The effectiveness of the drainage canals was determined visually by examining whether canals had collapsed or were still actively draining the site. Surveyed fens were grouped into the following disturbance classes: a) undisturbed sites, b) bulldozed sites, c) vacuum-harvested sites with non-functioning drainage canals (or undrained vacuumed), and d) vacuum-harvested sites with functioning drainage canals (or drained vacuumed). In total, 11 undisturbed sites, six bulldozed sites, 17 undrained vacuumed, and five drained vacuumed sites were sampled (Table 1).

Sampling Design and Measurements

Between 10 and 25 1-m^2 quadrats, depending on the size of the harvested fen, were equidistantly sampled across each site along transects arranged in a 'W' to ensure that borders as well as the center of the fens were sampled. Twenty-five quadrats were sampled for harvested fens $>$ 5 ha, and 10 or 15 quadrats were sampled for sites that were smaller. Eleven undisturbed fens (from 5–30 ha in size) were also surveyed with a 'W' transect (10 quadrats per site) to compare the vegetation of undisturbed fens with the spontaneous revegetation of the harvested fens. Each species and its percentage cover (to the nearest 2% for covers less than 10%, and to the nearest 5% for covers greater than 10%) were noted within each 1-m^2 quadrat. The nomenclature used for the vegetation follows Scoggan (1978) for vascular plants, Anderson (1990) for *Sphagnum* and, Anderson et al. (1990) for other mosses.

Physical variables were measured within or directly adjacent to each quadrat of the harvested fens. The measured variables were depth of peat (using a metal rod), depth to water table (a small hole was dug and the water table was given 15 minutes to stabilize), degree of decomposition of the residual peat using the von Post scale (Malterer et al. 1992), and the distance to the closest unharvested vegetated border. As plants can disperse from undisturbed peatland remnants adjacent to harvested peatlands, distance to the closest undisturbed vegetation could be important for recolonization.

A peat sample was taken from the top 5 cm of residual peat within each quadrat after the biological crust (first cm) of peat was removed. These samples were kept cool until analyses could be conducted, which was always within two weeks of collection. Peat samples were analyzed for pH, electrical conductivity, bulk density, and concentrations of Sodium (Na), Calcium (Ca), Magnesium (Mg), and soluble Phosphorus (P_{sol}) (which is the P directly available for plants). An Acumet Model 10 probe was used to measure pH (Fisher Scientific, Pittsburgh, Pennsylvania, USA). Electrical conductivity was measured with an Orion Model 122 conductivity meter (Thermo Electron Corporation Waltham, Massachusetts, USA), adjusted to 20°C and corrected for hydrogen ions (Sjörs 1952). These variables were measured in a 4:1 mixture of bi-distilled water and peat. Bulk density was calculated using the difference between the fresh mass and oven-dry mass of a known volume of peat (Hillel 1998). To minimize costs, every third peat sample was analyzed for chemistry. P_{sol} was extracted using the Bray 1 method (Bray and Kurtz 1945) and the extract was analyzed using flow injection analysis (Bogren and Hofer 2001). An inductively coupled argon plasma spectrophotometer (ICP-OES Optima 4300DV of Perkin Elmer) was used to determine Na, Ca, and Mg concentrations (Mehlich 1984). For undisturbed sites, a peat sample was taken from the middle of each undisturbed fen to characterize the same suite of chemical variables measured for the harvested fens.

Plant macrofossils of the residual peat were examined for three peat samples from each fen. These samples were chosen at random from the first third, second third, and last third of the peat samples to ensure that all samples were not from the same area of the sites. From each sample, 100 cm^3 of peat was prepared with a KOH solution and washed through a series of sieves (2 mm and 0.5 mm meshes), and then examined for fossils. A guide from Schoch (1988) was used to identify macrofossils.

Data Analyses

Physicochemical and vegetation measurements for each undisturbed and each harvested fen were averaged. Percent cover information was categorized into the following groups: total vegetation, bare peat, Cyperaceae, Gramineae, true mosses, and *Sphagnum*. *Carex* and *Scirpus*, as subsets from the Cyperaceae family, were included as additional vegetation subgroups. The physicochemical measurements and grouped vegetation data were compared between disturbance classes (undisturbed, bulldozed, undrained vacuumed, and drained vacuumed) using analyses of variance (ANOVA) and multiple comparison tests (protected LSD). Analyses were conducted using SAS (SAS Statistical System software, v. 9.1, SAS Institute Inc., Cary, North Carolina, USA). Chemical data and all vegetation groups except total vegetation and bare peat were log transformed to normalize data. Statistical results were considered significant at $\alpha = 0.05$.

A principal components analysis (PCA) was conducted in Canoco (ter Braak and Smilauer, v. 4.5, Biometris - Plant Research International, Wageningen, The Netherlands) using the species

Table 1. A general description of each abandoned, harvested fen sampled. The abbreviations used to describe the plant composition of the residual peat are the following: *Aln* (*Alnus*), *Aul* (*Aulacomnium*), *Bet* (*Betula*), *Cal* (*Calliergon*), *Car* (*Carex*), *Cha* (*Chamaedaphne*), Cyp (Cyperaceae), *Dre* (*Drepanocladus*), *Lar* (*Larix*), lig (ligneous residue), *Pol* (*Polytrichum*), rhi (rhizome), rt (roots and rootlets), *Sci* (*Scirpus*), and *Sph* (*Sphagnum*).

Peat-land	City, Province/State	Location	Disturbance Class	Area (ha)	Year Aban-doned	Plants and % Cover in Residual Peat
1	Inkerman, NB	47°37′N 64°50′W	Drained vacuumed	2	2001	*Sph* 70, lig 20, *Cha* 5, *Lar* 2, rt 2
2	Rexton, NB*	46°38′N 64°53′W	Drained vacuumed	20	1992	*Sph* 45, rt 45, Cyp 5, lig 3, *Aul* 3
3	Kent, NB*	46°37′N 65°08′W	Undrained vacuumed	2	1998	rt 40, *Sph* 35, lig 10, Cyp 10, *Pol* 5
4	St. Fabien, QC	48°18′N 68°52′W	Undrained vacuumed	12	2000	lig 35, *Dre* 35, *Cal* 10, *Lar* 10, rt 5, Cyp 5
5	St. Fabien, QC	48°19′N 68°50′W	Undrained vacuumed	8	1995	rt 40, Cyp 20, lig 15, *Sph* 12, *Sci* 5 *Cha* 2
6	St. Fabien, QC	48°19′N 68°50′W	Undrained vacuumed	7	1998	rt 60, lig 20, *Sph* 10, *Aln* 3
7	St. Fabien, QC	48°18′N 68°51′W	Undrained vacuumed	10	1999	*Sph* 35, rt 30, lig 12, Cyp 12, *Car* 3
8	Rivière-du- Loup, QC*	47°45′N 69°30′W	Undrained vacuumed	6	1988	lig 85, rt 6, Cyp 3, *Car* 3, *Cha* 3
9	Rivière-du-Loup, QC*	47°45′N 69°30′W	Undrained vacuumed	5	1993	lig 50, Cyp 15, rt 12, *Sph* 7, *Dre* 7 , *Lar* 3
10	St. Charles, QC	46°40′N 71°10′W	Undrained vacuumed	5	1999	rt 65, lig 17, Cyp 13, *Car* 7, *Sph* 4
11	St. Henri, QC	46°42′N 71°03′W	Undrained vacuumed	14	1982	rt 50, lig 20, *Car* 17, Cyp 5, *Sph* 4, *Dre* 3, *Lar* 2
12	St. Bonaventure, QC	45°57′N 79°42′W	Bulldozed	12	1984	rt 40, *Car* 20, *Sph* 13, lig 12, Cyp 10, *Bet* 5
13	Cromwell, MN*	46°40′N 92°44′W	Drained vacuumed	16	2002	lin 50, rt 20, *Sph* 20, *Car* 5, *Alu* 3, *Cha* 2
14	Cromwell, MN*	46°40′N 92°46′W	Drained vacuumed	12	2001	lin 45, Cyp 40, rt 15
15	Cromwell, MN*	46°40′N 92°44′W	Undrained vacuumed	20	2002	lin 55, rt 33, Cyp 10, *Sph* 2
16	McGregor, MN*	46°38′N 96°19′W	Undrained vacuumed	4	1998	rt 25, lin 25, Cyp 25, *Car* 10, *Cal* 7, *Dre* 3
17	Central Lakes, MN*	47°17′N 92°28′W	Bulldozed	4	1997	rt 55, lin 12, Cyp 10, rhi 10, *Car* 7, *Sph* 5
18	Central Lakes, MN*	47°17′N 92°28′W	Bulldozed	6	1997	*Sph* 70, lin 15, rt 10, Cyp 5
19	Floodwood, MN*	46°55′N 92°41′W	Bulldozed	4	1975	rt 50, lin 20, rhi 8, *Lar* 8, *Car* 5, *Sph* 5, *Cha* 5
20	Newfolden, MN*	48°24′N 96°10′W	Undrained vacuumed	4	2003	Cyp 40, rt 35, lin 15, *Car* 7, *Aln* 3
21	Newfolden, MN*	48°24′N 96°10′W	Undrained vacuumed	16	2000	lin 45, *Car* 22, rt 15, *Sph* 5, *Cal* 5, *Cam* 7, *Aul* 2
22	Newfolden, MN*	48°24′N 96°10′W	Undrained vacuumed	16	2004	rt 30, lin 25, *Cal* 20, Cyp 15, *Car* 5, *Sph* 5
23	Giroux, MB*	49°35′N 96°30′W	Undrained vacuumed	18	1999	lin 27, rt 25, *Dre* 15, *Cam* 10, Cyp 10, *Cal* 3, *Sph* 2
24	Giroux, MB*	49°35′N 96°30′W	Undrained vacuumed	14	1999	*Sph* 40, Cyp 25, lin 20, rt 13, *Cal* 2
25	Newbrook, AB*	54°20′N 112°55′W	Bulldozed	85	1975	rt 32, *Sph* 23, lin 20, Cyp 12, *Car* 10
26	Newbrook, AB*	54°21′N 112°53′W	Bulldozed	16	1987	*Sph* 65, lin 13, Cyp 7
27	Evansburg, AB*	53°37′N 115°04′W	Undrained vacuumed	28	1993	*Sph* 50, lin 25, rt 12, *Car* 7, Cyp 5
28	Evansburg, AB*	53°38′N 115°06′W	Drained vacuumed	70	1999	lig 37, *Dre* 32, *Sph* 18, rt 10, Cyp 3

* Locations where a natural fen within a 10 km radius was sampled.

data from all quadrats to assess whether species compositions were similar among regions and/or disturbance classes. Two ordination plots were created where sample scores were coded for either region or disturbance class. The environmental variables that had the largest impact on the species composition were determined using redundancy analysis (RDA) in Canoco (ter Braak and Smilauer, v. 4.5, Biometris - Plant Research International, Wageningen, The Netherlands). Only data from vacuum-harvested fens were used for the RDA analysis because future fen restoration projects will likely only deal with such sites. Species data for the PCA and RDA analyses were log transformed to achieve normality. A Hellinger transformation was also applied to the data. This transformation permitted the use of linear models (PCA and RDA) for community composition data with long gradients (Legendre and Gallagher 2001). Sample scores were used to create confidence ellipses for the different regions and disturbance classes using Systat (Systat Software, Inc., Richmond, California, USA). Each ellipse was centered around the sample mean for each class; the standard deviations of the sample scores from axes 1 and 2 determined the major axes and the sample covariance determined the orientation. Vegetation classes (fen, bog, marsh, and ruderal species) were identified using the habitat descriptions from various plant identification guides (Johnson et al. 1995, Marie-Victorin 1995, Newmaster et al. 1996).

Species richness (average number of species per 1-m^2 quadrats within each fen) was compared among disturbance classes. The species turnover rate among all quadrats within each fen was calculated as Whittaker's overall β diversity as modified by Harrison et al. (1992). This measure ranges from 0 for no turnover to 100 for complete turnover (Magurran 2003). Whittaker's β diversity was chosen as both allow sites with different sample sizes to be compared (Magurran 2003). Mean species richness and mean overall β diversity of each fen were compared using ANOVA and protected LSD procedure in SAS with $\alpha = 0.05$. Beta diversity was log transformed to achieve normality.

RESULTS

Environmental Conditions

Although harvested fens varied in harvest method or hydrology, only a few environmental variables differed among harvested sites (Table 2). The water table for bulldozed sites was higher than both drained and undrained vacuumed sites ($F_{3,24} = 3.48$; $P = 0.031$). The degree of peat decomposition was higher in undrained than drained sites ($F_{3,24} = 3.62$; $P = 0.026$), but did not differ from bulldozed sites (Table 2). Finally, time since abandonment of bulldozed sites was longer than for vacuum-harvested sites ($F_{3,24} = 6.11$; $P < 0.001$).

The undisturbed and harvested fens can be considered transitional poor fens due to their peat chemical properties and plant compositions (Tables 1 and 3) (Gorham and Janssens 1992, Vitt 2006). When macrofossil plant composition was averaged across all sites, residual peat consisted of 27% roots/rootlets, 27% wood, 19% *Sphagnum*, 16% Cyperacea, and 5% brown mosses. The pH, conductivity, and Ca, Mg, and Na content of peat did not differ among the disturbance classes. P_{sol} concentration of undisturbed sites was higher ($F_{3,37} = 8.17$; $P < 0.001$) than that of harvested sites.

Vegetation Cover

Despite minimal variation in environmental conditions among disturbance classes, revegetation patterns varied greatly (Figure 2). Undisturbed sites supported the greatest vegetation cover (close to 100%). Vegetation cover was 70%, 50%, and 25% for bulldozed sites, undrained vacuumed sites, and drained vacuumed sites, respectively. Bare peat

Table 2. Environmental parameters (means ± SE) for bulldozed, undrained vacuumed, and drained vacuumed fens in Canada and Minnesota, USA. An ANOVA and protected LSD analysis tested for the differences among disturbance classes. Different lowercase letters in a column indicate significant differences among means (P < 0.05). Undisturbed fens were not included because variables were not measured.

Disturbance Class	n	Water Table (cm)	Peat Depth (cm)	Degree of Decomposition (von Post scale)	Bulk Density g cm^{-3}	Years since abandonment
Bulldozed	6	−6.7 (± 10.0) a	124.8 (± 32.5) a	6.18 (± 0.09) ab	0.13 (± 0.01) a	21.2 (± 4.1) a
Undrained Vacuumed	17	−23.2 (± 5.9) b	71.4 (± 11.1) a	6.57 (± 0.13) a	0.22 (± 0.03) a	7.4 (± 1.1) b
Drained Vacuumed	5	−41.1 (± 14.4) b	123.0 (± 40.3) a	5.54 (± 0.48) b	0.31 (± 0.11) a	5.4 (± 1.7) b

Table 3. Mean peat chemistry data (± SE) of the residual peat for each disturbance class. ANOVA and protected LSD analyses were used to test for differences among disturbance classes. Different lowercase letters in a column indicate significant differences among means ($P < 0.05$).

Disturbance Class	n	pH	Conductivity (m/cm)	P_{sol} [mg kg^{-1}]	Ca [mg^{-1}]	Mg [mg g^{-1}]	Na [mg g^{-1}]
Undisturbed	11	5.30 (± 0.9) a	34.5 (± 36.0) a	62.7 (± 8.1) a	6.0 (± 1.5) a	1.1 (± 0.3) a	0.34 (± 0.02) a
Bulldozed	6	4.77 (± 0.4) a	34.7 (± 11.6) a	34.7 (± 5.0) b	6.4 (± 0.9) a	0.9 (± 0.1) a	0.31 (± 0.02) a
Undrained Vacuumed	17	5.30 (± 0.2) a	85.4 (± 26.1) a	27.4 (± 2.4) b	8.1 (± 5.4) a	1.7 (± 0.1) a	0.32 (± 0.02) a
Drained Vacuumed	5	4.46 (± 0.2) a	92.4 (± 66.8) a	28.1 (± 4.3) b	5.8 (± 9.4) a	1.2 (± 0.3) a	0.43 (± 0.08) a

showed a complementary picture with the highest percent unvegetated (73%) recorded for the drained vacuumed sites.

Species of the Cyperaceae and Gramineae families were especially successful in recolonizing undrained harvested sites. Cover of Cyperaceae on undisturbed, bulldozed, and undrained vacuumed sites was similar, but was much lower for drained vacuumed sites (Figure 2). Closer examination of the Cyperaceae family shows that undisturbed sites were dominated by *Carex* species (Figure 2), while undrained vacuumed sites were dominated by *Scirpus cyperinus*. Bulldozed sites were mainly recolonized by *Rhynchospora alba* and *Carex* species (unpub. data).

Bryophytes were much less successful at recolonizing vacuumed sites. The percentage of *Sphagnum* was high on undisturbed and bulldozed sites (30% and 20%, respectively), but *Sphagnum* was virtually absent from drained and undrained vacuumed sites (Figure 2). The percent cover of true mosses was lower for both classes of vacuumed sites than for undisturbed or bulldozed sites (Figure 2). However, percent cover of true mosses was relatively low even on undisturbed and bulldozed sites (8% cover).

Plant Species Richness

Species richness was greater in undisturbed and bulldozed sites than vacuum-harvested sites (Figure 3). No difference in β diversity could be detected among the disturbance classes (Figure 3). As sampling effort of the undisturbed fens was smaller than that of harvested fens, diversity estimates for undisturbed fens are conservative.

Vegetation Composition

The ordination plots generated from PCA axis scores did not generate strong patterns when samples were coded by region (Figure 4a), despite the immense geographic distance between some regions (Figure 1). When samples were coded by drainage and harvest method, a much stronger pattern emerged (Figure 4b). Undisturbed fens exhibited the tightest grouping. Undisturbed and drained vacuum-harvested sites were markedly different due to the high percentage of bare peat at drained vacuumed sites (Figures 2 and 5). The vegetation of bulldozed sites most resembled that of undisturbed sites (Figure 4b), with both being dominated by typical fen species (Figure 5). The samples from undrained vacuumed sites were the most variable in terms of species composition as shown by the large ellipses on the ordination plots (Figures 4b and 5). In general, most undrained vacuumed sites were dominated by bare peat, *Scirpus cyperinus* and, to a lesser extent, other common wetland plants (i.e., *Juncus tenuis*, *Juncus effusus*, *Solidago graminifolia*, and *Spiraea latifolia*) (Figure 5).

The recolonization of marsh and fen species was correlated with high water tables (Figure 6). Fen species were associated with long abandonment times, whereas marsh species were associated with high pH and higher peat decomposition. Several ruderal species were correlated with high electrical conductivity, medium to high pH values, and high Ca and Mg concentrations. Bog species were correlated with a thick residual peat layer and low pH values. The occurrence of bare peat on vacuum harvested sites was associated with a thick residual peat layer, dry conditions (deeper water tables), and a short time since abandonment.

DISCUSSION

Cutaway peatlands with residual minerotrophic peat, or harvested fens, were quickly recolonized by vegetation. Despite a short time since abandonment, 5–7 years on average, vacuum-harvested fens in this study showed relatively high percentages of vegetation cover when compared to vacuum-harvested bogs of Eastern Canada (Poulin et al. 2005). We found that harvested fens supported a vegetation cover between 25% and 60%, whereas other studies show that harvested bogs usually supported vegeta-

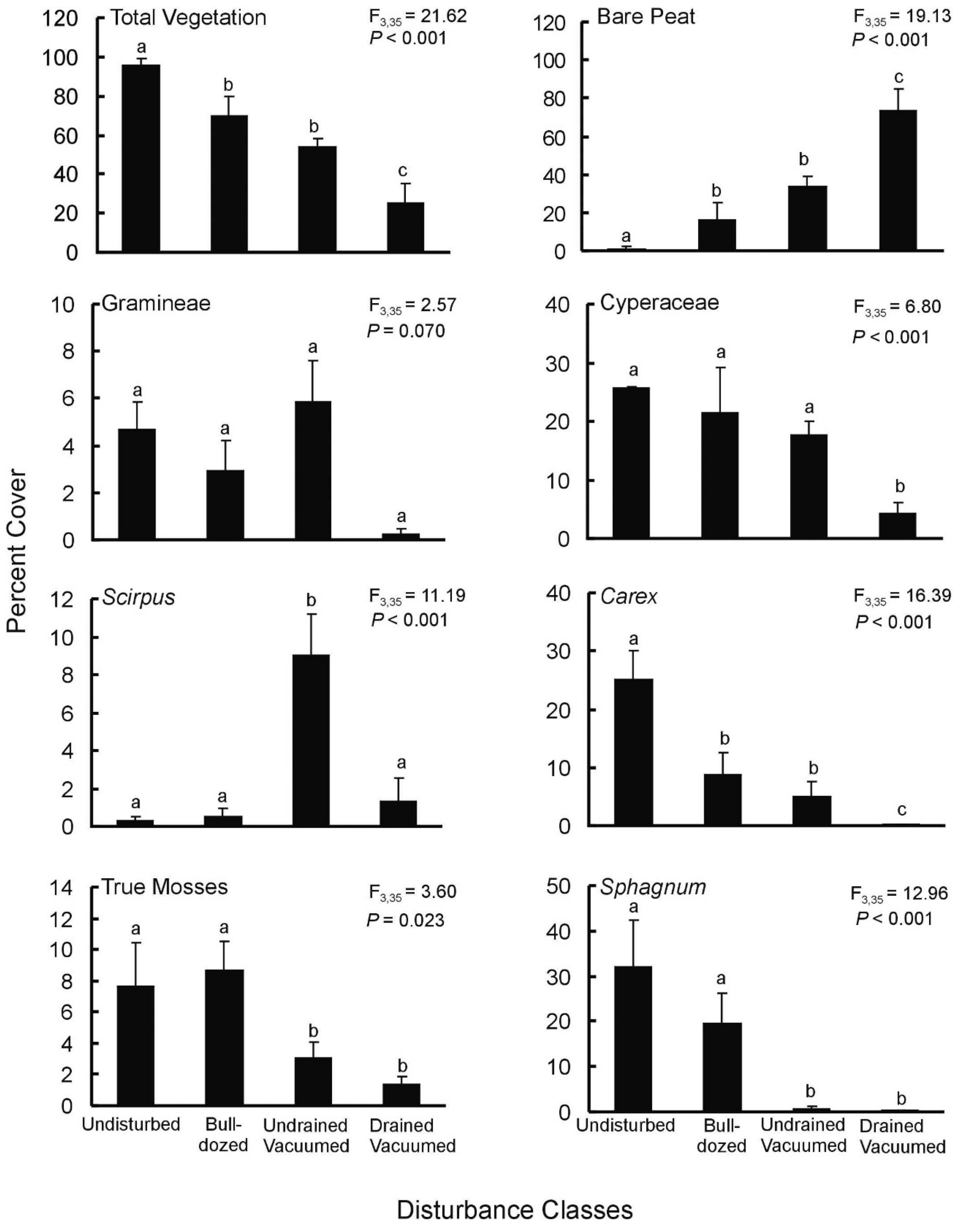

Figure 2. Mean vegetation cover, bare peat, and various important vegetation groups for the 28 harvested and 11 undisturbed fens. ANOVAs tested for differences among disturbance classes. Lowercase letters signify significant differences ($\alpha = 0.05$) among classes.

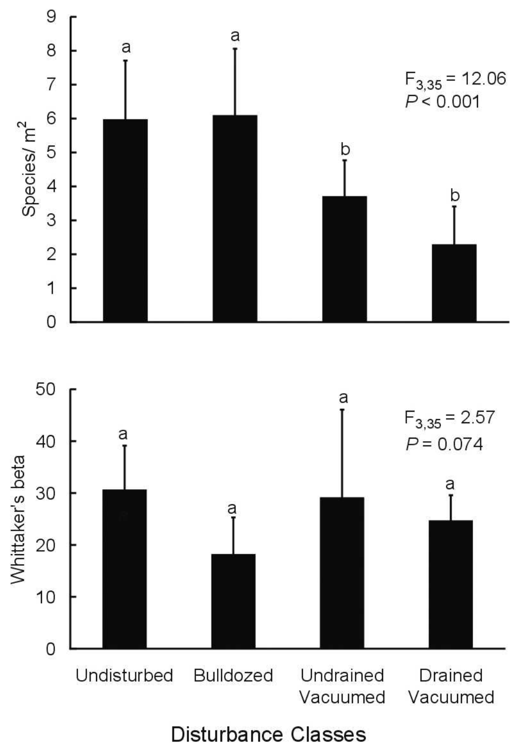

Figure 3. Mean species richness per quadrat and Whittaker's β for each disturbance class. The lowercase letters show significant differences ($\alpha = 0.05$) among classes.

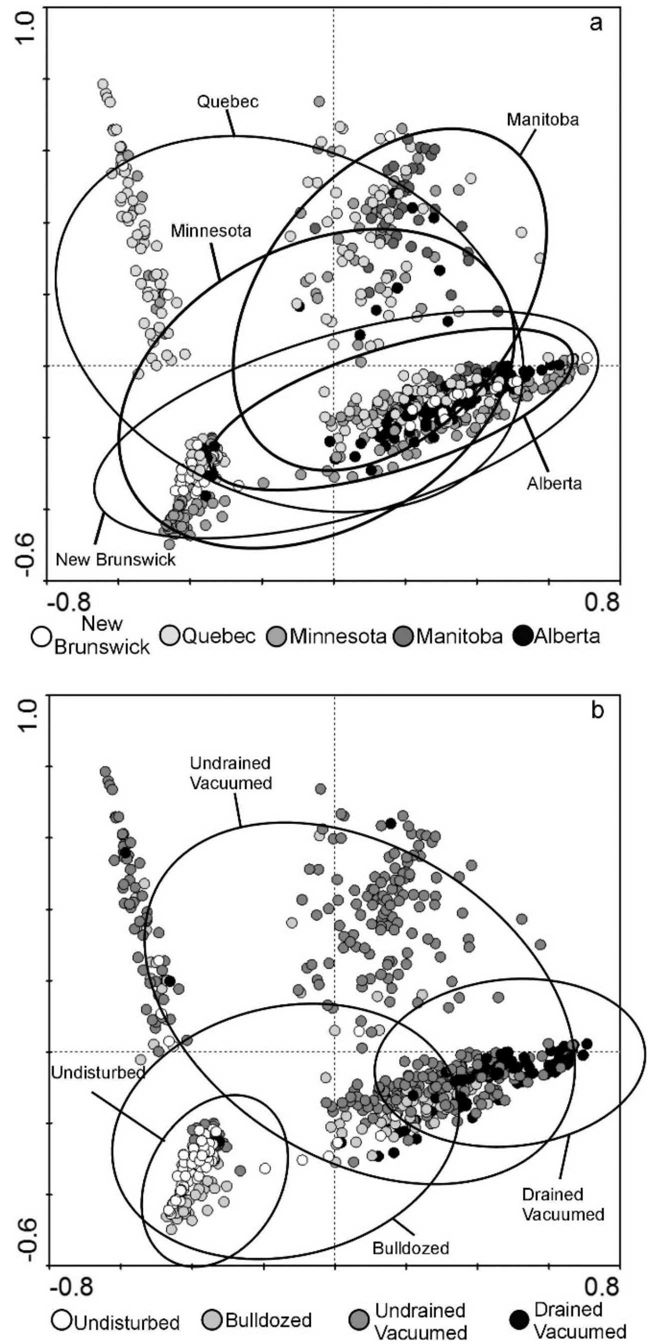

Figure 4. PCA ordination plot of site scores for vegetation recorded in 1-m^2 quadrats of 28 harvested and 11 undisturbed fens coded according to (a) geographic region and (b) to the disturbance class (harvesting type and drainage). Confidence ellipses are shown for the sample scores from each region. Each confidence ellipse is centered around the sample mean. The standard deviations determine the major axes and the sample covariances the orientation.

tion cover below 25% cover for most vascular plant groups (Famous et al. 1991, Poulin et al. 2005). The hydrology of the sites we sampled played a crucial role in revegetation success; sites where drainage canals had collapsed revegetated to a greater extent with wetland plants than sites with active drainage canals. Thus, this study shows that recolonization of harvested fens is not limited by dispersal for many, but not all, wetland species. However, environmental conditions for species establishment and survival need to be met for rapid colonization.

Vegetation composition varied considerably among disturbance classes even though few differences were observed in environmental conditions. Only available P concentration was higher in undisturbed sites compared to harvested sites, as has also been observed when comparing harvested and undisturbed bogs (Andersen et al. 2006). Thus, recolonization may be limited by the availability of resources for plant establishment.

The bulldozed sites supported vegetation that most resembled that of the undisturbed fens. This could be because the hydraulic conditions of bulldozed sites most resembled natural conditions and because bulldozed sites were older, allowing for a longer recovery time. *Sphagnum* species were especially successful at recolonizing bulldozed sites, a pattern also observed in trenches of harvested block-cut peatlands (Poulin et al. 2005). The successful recolonization of the bulldozed sites is

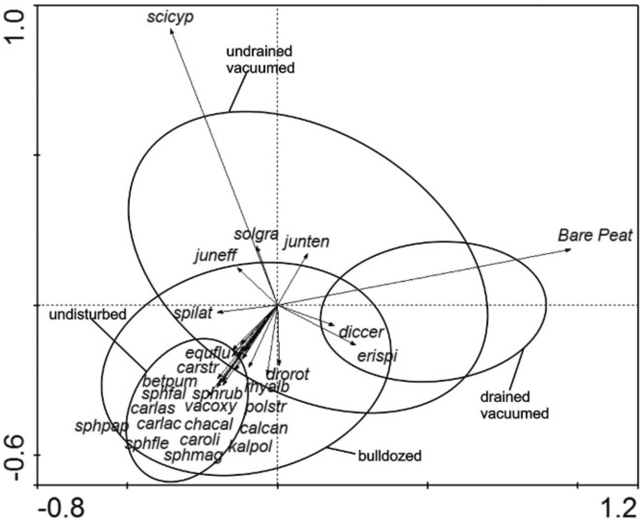

Figure 5. PCA ordination plot of species scores for all vegetation samples from 28 harvested and 11 undisturbed fens including the confidence ellipses for the disturbance classes shown in Figure 5. The species abbreviations are the first three letters of the genus and species names of each species; the full names are provided in Appendix 1.

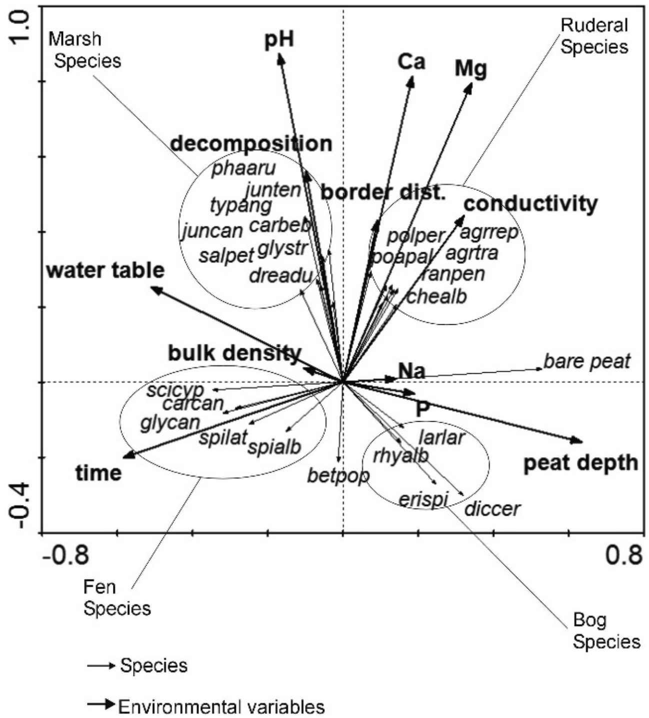

Figure 6. Redundancy analysis (RDA) biplot for samples from the vacuum-harvested sites where drainage canals were no longer functioning. The species abbreviations are the first three letters of the genus and species names; the full names are listed in Appendix 1. The environmental variable 'time' refers to the time since abandonment of peat harvesting and 'border dist.' refers to the distance between the sampled quadrat and the closest unharvested, vegetated border. Environmental variables explained 16.6% of total variation in species data with 7.4% explained by Axis 1 and 2.4% by Axis 2.

of secondary importance from a restoration perspective, as this peat harvesting method is no longer used and will most likely not be used in the future due to its costly drying process. For the remainder of this discussion, we will focus on the spontaneous revegetation of the vacuum-harvested fens because future restoration projects will mitigate this type of harvested peatland.

Vascular plants were more successful than bryophytes at recolonizing vacuum-harvested fens. In particular, *Scirpus cyperinus* was very successful, presumably due to its easily dispersed seeds. Although *Scirpus* species are found on undisturbed fens, *Carex* is generally the dominant genus. In European fen restoration projects, *Carex* species are reintroduced because they are generally dispersal limited and because undisturbed remnants, which could serve as diaspore sources, are scarce (van Duren et al. 1998, Roth et al. 1999, Patzelt et al. 2001). Because harvested fens were originally bogs, the undisturbed remnants adjacent to the harvested surface are unlikely to be fens. Therefore, the local species pool may not even contain *Carex* species. Thus, while the harvested fens were quickly colonized, the lack of some genera suggests that the chances of spontaneous colonization of some key fen species are limited. However, the success of *Scirpus* and other wetland plants is a good indication that the conditions should be adequate for reintroducing fen species.

Bryophytes, especially *Sphagnum*, were virtually absent from the vacuum-harvested sites, despite *Sphagnum* diaspores being present in nearby undisturbed bog remnants. *Sphagnum* species establish on bare peat surfaces much more effectively if vegetative propagules are reintroduced and a mulch layer is spread for protection during the first few years (Rochefort et al. 2003). We expect the same is true for true mosses, which may explain why bryophyte colonization was a rare event at our study sites.

Similar to observations by Soro et al. (1999), the drained and undrained vacuumed sites supported fewer species per square meter than the undisturbed sites even though the sampling effort of undisturbed sites was smaller than for harvested sites. However, the turnover rate was similar among all disturbance classes because fewer species observed on the drained and undrained vacuumed sites increased the chance that turnover rate would be high. The average time since abandonment was very short for the vacuum-harvested sites. Thus, with time, vacuum-harvested sites will probably become more diverse. However, even after 50 years, the vegetation of harvested bogs had not yet recovered to its original composition (Soro et al. 1999). Reintroducing species is an option to accelerate community recovery.

In vacuum-harvested sites, recolonization rates were higher when residual peat layers were thin. A similar trend was observed on block-cut, harvested bogs where *Sphagnum* recolonization was higher in trenches with a thin residual peat layer than those with a thick residual peat layer (Poulin et al. 2005). Vacuum-harvested fens with a thick residual peat layer were drier, as was also found for the trenches of harvested, block-cut peatlands (Poulin et al. 2005). The relationships among a thin residual peat depth, improved hydrology, and higher cover of spontaneous revegetation could have implications not only for fen restoration, but also for bog restoration. In cases of bog restoration where recreation of the proper hydrology is impossible, one option might be to remove more of the residual peat layer. The removal of the *Sphagnum* residual peat layer has been suggested to improve the hydrology of a harvested peatland in Germany (Sliva and Pfadenhauer 1999). As radical as this might seem, removing peat to create better hydrological conditions might be an interesting alternative. Thus, when bog restoration is not an option, the creation of a fen or a marsh will increase landscape diversity and create a better habitat for wildlife than forest plantations or berry farms, which are other proposed land use alternatives for harvested peatlands.

CONCLUSIONS

This research suggests that reintroducing fen species would increase the biological value of harvested peatlands with minerotrophic residual peat. However, it is not known which vegetation groups should be emphasized because the goals of fen restoration largely remain undefined. Rochefort (2000) defines the goals of peatland restoration in North America as focusing on the return of ecosystem function, especially peat accumulation. If this is the goal, the return of *Sphagnum* species, which inhabit transitional and poor fens, should be emphasized (Rochefort 2000). Sliva (1997) and Wind-Mulder et al. (1996) both advocate the reintroduction of *Sphagnum* species to direct and accelerate the succession towards a bog condition.

The question remains whether the return of fen ecosystem functioning should be the goal of fen restoration or whether it might be beneficial to put more emphasis on their possible contribution to regional diversity. Fens are notorious as 'hot spots' of diversity (Bedford and Godwin 2003) and are rare in southeastern Canada (Kuhry et al. 1993). The reintroduction of fen species to cutaway peatlands with minerotrophic residual peat could create a biological gem out of lackluster non-restored sites, dominated by a few, ubiquitous species.

To date, North American fen restoration research has focused entirely on reintroducing vascular plants (Cooper and MacDonald 2000, Cobbaert et. al. 2004). By including bryophytes in restoration projects, the diversity and perhaps the peat-accumulating function of the restored peatlands would be improved. Before target vegetation communities for fen restoration can be identified, more research is needed to understand the respective roles of mosses and vascular plants in the ecosystem functions of restored fens.

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Appendix 1. A complete list of species and codes for those species indicated in Figures 5 and 6.

Mosses and Liverworts	Code
Dicranella cerviculata (Hedw.) Schimp.	diccer
Drepanocladus aduncus (Hedw.) Warnst.	dreadu
Polytrichum strictum Brid.	polstr
Sphagnum	
Sphagnum fallax (Klinggr.) Klinggr.	sphfal
Sphagnum flexuosum Dozy & Molk. var. *flexuosum* var. *ramosissimum* Andrus	sphfle
Sphagnum magellanicum Brid.	sphmag
Sphagnum papillosum Lindb.	sphpap
Sphagnum rubellum Wils.	sphrub
Sedges, Rushes and Grasses	
Agropyron repens (L.) P. Beauv.	agrrep
Agropyron trachycaulum (Link) Malte	agrtra
Calamagrostis canadensis (Mich.) Nutt.	calcan
Carex bebbii Olney (Bailey) Fern	carbeb
Carex canescens L.	carcan
Carex lacustris Willd.	carlac
Carex lasiocarpa Ehrh.	carlas
Carex oligosperma Michx.	caroli
Carex stricta Lam.	carstr
Eriophorum vaginatum L. var. *spissum* (Fern.) Boivin	erispi
Glyceria canadensis (Michx.) Trin.	glycan
Glyceria striata (Lam.) Hitchc.	glystr
Juncus canadensis Gay	juncan
Juncus effusus L.	juneff
Juncus tenuis Willd.	junten
Phalaris arundinacea L.	phaaru
Poa palustris L.	poapal
Rhynchospora alba (L.) Vahl.	rhyalb
Scirpus cyperinus (L.) Kunth	scicyp
Forbs	
Chenopodium album L.	chealb
Drosera rotundifolia L.	drorot
Equisetum fluviatile L.	equflu
Polygonum persicaria L.	polper
Ranunculus pensylvanicus L. f.	ranpen
Solidago graminifolia (L.) Salisb.	solgra
Typha angustifolia L.	typang
Shrubs	
Chamaedaphne calyculata L. Moench	chacal
Kalmia polifolia L.	kalpol
Salix petiolaris Sm.	salpet
Spirea alba Du Roi	spialb
Spiraea latifolia (Ait.) Ahles	spilat
Vaccinium oxycoccos L.	vacoxy
Trees	
*Betula populifoli*a Marsh.	betpop
Betula pumila L.	betpum
Larix laricina (Du Roi) K. Koch	larlar