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Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO_2 exchange to ecosystem-scale restoration

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[1]   Northern peatlands represent a globally important stock of soil carbon and have acted as a net sink of atmospheric CO_2 throughout the Holocene. Disturbance for horticultural peat extraction disrupts ecosystem function and converts these ecosystems to large, persistent sources of carbon dioxide (CO_2). This study investigates the effect of ecosystem-scale restoration on growing season CO_2 exchange in a peatland by comparing a restored site to a neighboring nonrestored section for 1 year prerestoration (1999) and 3 years postrestoration (2000–2002). Prior to restoration, less than 23% of the site was vegetated, and it was a source of 245 g C m^{-2} to the atmosphere during the growing season (May to early October). Following restoration, the water table remained deep, and soil moisture was significantly higher than the nonrestored section. By the third year postrestoration, vegetation covered 50% of the restored peatland. Moss covered 90% of this vegetated area. Vegetation productivity at the restored site was also enhanced with gross ecosystem photosynthesis under full light conditions significantly higher at the restored site at both moss and herbaceous plots by 2002. While this increase in vegetation productivity provided fresh substrate and resulted in higher CO_2 production potential for restored site peat, ecosystem respiration was similar to or lower than that at the nonrestored site for both bare peat and vegetated areas because of the generally wetter site conditions resulting from restoration. By upscaling chamber CO_2 exchange measurements to the ecosystem level, on the basis of the relative proportion of each surface cover type, we determined the site was a net sink of ~20 ± 5 g C m^{-2} during the growing season only 2 years postrestoration. Combining our results with previous work on CH_4 emissions and dissolved organic carbon export, we suggest that this degraded peatland ecosystem will likely return to a net carbon sink in 6 to 10 years postrestoration.

1. Introduction

[2] Peatland ecosystems represent a net long-term sink (23–28 g C m^{-2} yr^{-1}) of atmospheric carbon dioxide (CO_2) [*Gorham*, 1991; *Roulet et al.*, 2007]; however, drainage and peat extraction are impacting this important biogeochemical and ecosystem function [*Waddington et al.*, 2002]. Extracted peatlands become a large and persistent source of atmospheric carbon dioxide (CO_2) following industrial abandonment [*Petrone et al.*, 2003; *Waddington et al.*, 2002]. However, plot-scale evidence suggests that peatland restoration is able to return an extracted peatland to a net carbon-accumulating ecosystem [*Tuittila et al.*, 1999; *Waddington and Warner*, 2001]. If restoration can be successfully applied at the landscape scale, then it is possible to

minimize the impact of peatland drainage and extraction. The aim of this paper is to examine changes in growing season CO_2 exchange in the first 3 years following the full ecosystem restoration of a degraded peatland.

[3] Peatland drainage and peat extraction result in an increase in CO_2 emissions to the atmosphere because of the removal of vegetation and a decrease in the position of the water table, which, in turn, increases aerobic decomposition and shuts down photosynthesis [*Waddington and Price*, 2000]. After approximately 20–50 years of peat extraction the site is abandoned, and the bare peat on the cutover peatland surface is often left to regenerate. However, these degraded cutover sites rarely return to functional peatland ecosystems because in most cases the physical and hydrological conditions that are necessary for *Sphagnum* moss reestablishment have been eliminated [*Price*, 1997]. Consequently, these dry and bare peat surfaces become persistent sources of atmospheric carbon dioxide (CO_2) [*Petrone et al.*, 2003; *Waddington and Warner*, 2001]. For example, *Waddington et al.* [2002] determined that a cutover peatland released over 360 g C m^{-2} 2 to 7 years

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after abandonment, while *Waddington and McNeil* [2002] found that peat oxidation rates remained high even after 2 decades of postextraction abandonment. However, other studies have found that peat extraction decreased total bacterial and microbial biomass [*Croft et al.*, 2001], which ultimately reduced peat decomposition rates at these sites.

[4] In order to return the natural carbon sink function of these impacted peatland ecosystems, a large restoration effort is taking place in Canada [*Cleary et al.*, 2005]. The long-term goal of these peatland restoration efforts in North America is to return a natural, functioning, carbon-accumulating ecosystem [*Rochefort et al.*, 2003] by raising the water table to promote *Sphagnum* peat-forming species [*Quinty and Rochefort*, 1997]. This is carried out by blocking drainage ditches to reduce runoff [*Quinty and Rochefort*, 1997; *Rochefort*, 2000], building peat dykes to retain spring snowmelt water, and sometimes constructing open water ponds [*Quinty and Rochefort*, 1997]. *Sphagnum* fragments are spread onto the site from a natural donor peatland in a 1:10 ratio [*Rochefort et al.*, 2003] and are protected by a straw mulch applied at a rate of $\sim$3000 kg ha^{-1}. Straw mulch improves the soil hydroclimate conditions by reducing evapotranspiration, which, in turn, reduces soil water tension and increases soil moisture in the surface layer [*Price et al.*, 1998]. In some cases, phosphorus fertilizer is applied to enhance rapid colonization by vascular plants, which act as companion species to *Sphagnum* mosses [*Rochefort et al.*, 2003]. Peatland restoration has the opportunity to return the peatland to a carbon-accumulating system [*Waddington and Price*, 2000] and maybe even to a net carbon sink [*Tuittila et al.*, 1999; *Yli-Petäys et al.*, 2007].

[5] Most studies conducted in restored peatland ecosystems have shown a decreased release of CO_2 to the atmosphere with active rewetting [*Komulainen et al.*, 1999; *Tuittila et al.*, 1999; *Waddington and Warner*, 2001]. A plot-scale study conducted by *Waddington and Warner* [2001] concluded that small-scale (15 m^2) restoration reduced CO_2 emissions by a factor of 2 compared to a cutover peatland. Approximately 70% of this decrease in CO_2 emissions postrestoration was due to an increase in restored peatland productivity, and 30% was due to a decrease in soil respiration [*Waddington and Warner*, 2001]. European studies that adopt a different approach to peatland restoration have also shown a reduction in CO_2 efflux postrestoration. For example, *Tuittila et al.* [1999] found that peatland rewetting decreased respiration as well as increased productivity at the site, specifically from *Eriophorum* spp. Similarly, *Komulainen et al.* [1999] found that rewetting drained peatlands increased *Eriophorum* cover and ultimately changed the seasonal carbon balance toward an increase in CO_2 sequestration. However, the strength of the annual carbon sink may decline after many decades as *Eriophorum* dominance declines [*Yli-Petäys et al.*, 2007].

[6] An important consideration from a restoration and ecosystem ecology perspective is the rate at which ecosystem respiration and gross ecosystem productivity change postrestoration. The objectives of this study were to examine changes in carbon exchange at a cutover peatland in the first 3 years postrestoration. A paired ecosystem catchment approach was adopted where 85% of a former cutover peatland was restored and the remaining 15% was not restored. We measured CO_2 exchange in both catchments over several years to establish the effect of restoration and hypothesized that CO_2 efflux would decrease at the restored peatland, independent of interannual variability, as determined by the control (i.e., unrestored) catchment.

2. Methods

2.1. Study Site

[7] This study took place at the Bois-des-Bel peatland located in the Bas-Saint-Laurent region of Québec, $\sim$14 km east of Rivière-du-Loup (47°53$'$N, 69°27$'$W). The mean annual temperature for the region is 3°C, with mean January and July temperatures of -12°C and 18°C, respectively. The mean annual precipitation is 926 mm with 27% falling as snow. The Bois-des-Bel peatland is a $\sim$200 ha treed bog; an 11.5 ha section of the peatland was drained in 1972 and subsequently vacuum extracted from 1973 to 1980, after which it was abandoned until 1999 (Figure 1). The abandoned peatland was divided into 11 fields (30 $\times$ 300 m) and separated by drainage ditches running parallel (north-south) to the long axis of the fields. In the autumn of 1999, ecosystem-scale restoration commenced using the standard North American restoration techniques as outlined in section 1 and also by *Rochefort et al.* [2003]. Initially, the surface was cleared of all vegetation and woody material that was present after abandonment. Drainage ditches were blocked, and several dykes (low-lying peat walls) were created to retain snowmelt. *Sphagnum* fragments were also introduced from a natural donor peatland, after which they were protected by a straw mulch cover applied at a rate of 3000 kg ha^{-1}. Last, phosphorus fertilizer was applied at a rate of 15 g m^{-2} to enhance vascular plant colonization [*Rochefort et al.*, 2003]. The extracted peatland was separated into two catchments: a 7.5 ha restored section (westernmost peat fields 1$-$8) and a 1.8 ha cutover section (easternmost fields 10 and 11) with a buffer strip left in between the two catchments (field 9). The restored section of the Bois-des-Bel peatland was further divided into four zones (1$-$4) and separated by dykes. Zones 2, 3, and 4 were restored in the fall of 1999, while zone 1 was restored in the fall of 2000. The average peat depths of the restored and cutover sites are 1.5 and 1.6 m, respectively, which is typical of residual peat depths for cutover peatlands in Canada. The dominant species found at Bois-des-Bel postrestoration include *Polytrichum* spp., Ericaceous shrubs (including *Chamaedaphne calyculata*, *Vaccinium angustifolium*, and *Ledum groenlandicum*), *Eriophorum vaginatum*, and *Typha latifolia*. Furthermore, *Sphagnum* spp., mainly *Sphagnum rubellum*, was present at the restored site, while *Picea mariana* and *Betula* spp. were present at the cutover site.

[8] Research was undertaken during the growing season between May and early October at the restored and cutover sites in 1999 (the baseline prerestoration year) and in the first 3 years postrestoration (2000, 2001, and 2002).

2.2. Laboratory CO_2 Production Potential

[9] Three cores of peat were removed from each of the natural, cutover, and restored sections of the Bois-des-Bel peatland on 30 August 2001 and returned to the laboratory
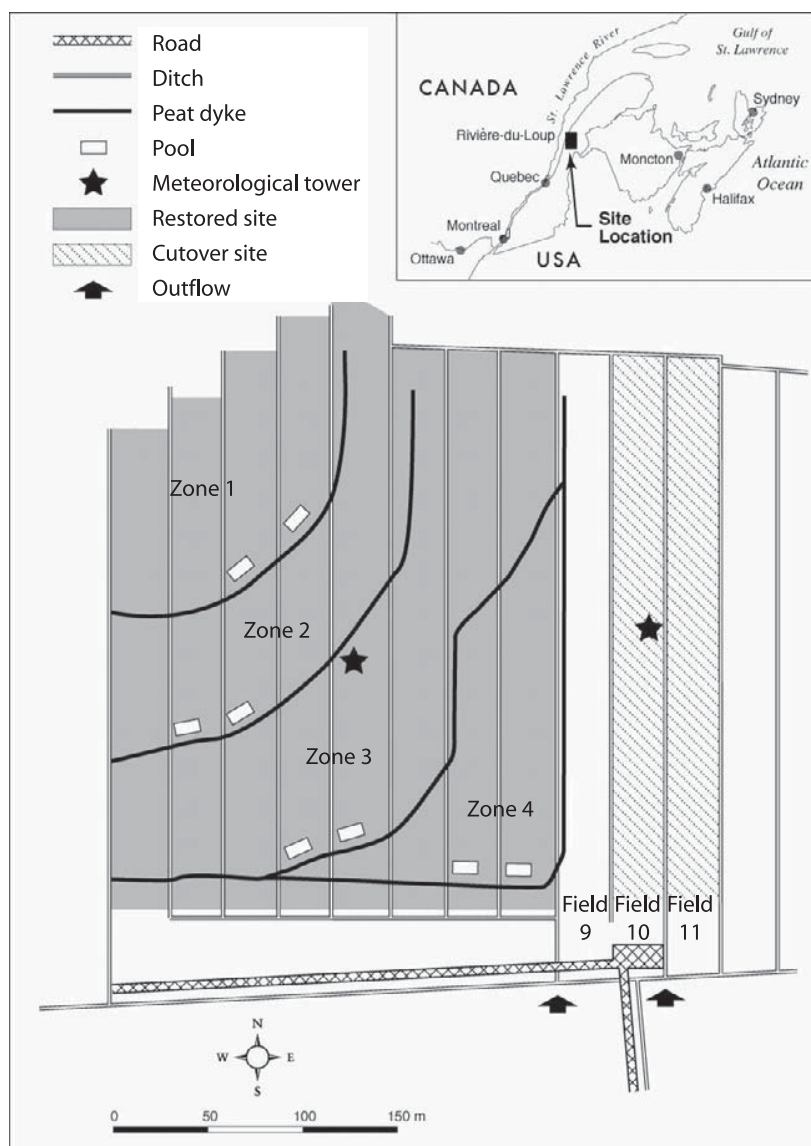
Figure 1. Bois-des-Bel peatland study area (47°53′N, 69°27′W) showing the restored (gray) and cutover (hatched) sites.

on ice for analysis. Subsamples of the cores were taken at depths with a focus around the average water table position for each core. Approximately $10-15$ g of peat were taken from each depth interval and placed into 250 mL incubation jars. The incubation of the samples was conducted under aerobic and anaerobic conditions at 4°C, 12°C, and 20°C. For the aerobic samples the jars of peat were closed and placed into a growth chamber at the different incubation temperatures. For the anaerobic incubation the samples were flushed with nitrogen gas for 15 min in an anaerobic glove bag prior to incubation. Before each gas-sampling process, the samples were mechanically agitated for 20 min. For both the aerobic and anaerobic experiments, 3 mL of headspace were initially removed from the jars using a syringe. The jars were then backfilled with an equivalent amount of nitrogen gas to keep the volume of headspace consistent. This procedure was repeated every 12 h for 48 h. Gas samples were analyzed on a Varian 3800 gas chro-

matograph equipped with a thermal conductivity detector and Porapak N column for CO_2 analysis. Changes in concentration in the jars were converted to production potential (g CO_2 m^{-2} d^{-1}) on the basis of headspace volume and dry weight of peat. Production values were expressed on a per-area basis by integrating production potential over the entire peat profile, weighing each production value on the basis of the depth interval sampled and bulk density of the peat. An analysis of variance (ANOVA) test was performed comparing these total profile production values at each site under the three incubation temperatures.

2.3. Field Carbon Dioxide Flux

[10] Net ecosystem (CO_2) exchange (NEE) was measured using the chamber technique several times a week during each field season. Measurements were made at 3 to 13 sites of each of the dominant vegetation surface covers, including moss species (*Sphagnum* and *Polytrichum*) and herbaceous

species (*Eriophorum*) in both the cutover and restored sites. The number of measurement sites for each type of vegetation cover was initially limited because of the lack of establishment of vegetation postrestoration.

[11] The chamber technique is described in detail by *Griffis et al.* [2000]. Briefly, a cylindrical chamber of a known surface area (0.05 m^2) and volume (20 L) was placed and sealed over permanent PVC collars inserted into the peat to a depth of $\sim$10–15 cm at each sampling location. A dark chamber was used to measure ecosystem respiration (ER), and a clear Plexiglas chamber was used to measure NEE. All chambers were equipped with a fan to ensure air was well mixed during the sampling period. Clear chambers were equipped with a cooling device to maintain ambient temperature conditions [*Griffis et al.*, 2000]. Gross ecosystem photosynthesis (GEP) was determined as the difference between NEE and ER measurements obtained from the same measurement site in the same sampling period. To establish relationships between GEP and photosynthetically active radiation (PAR) (light response curves), a series of shrouds of various mesh sizes were placed over the clear chamber to measure NEE under reduced light conditions. The concentration of CO_2 in the chamber headspace was measured using an infrared gas analyzer (PP systems EGM-2) at 30 s intervals over a duration of 5 min. CO_2 flux was calculated from the change in concentration over the 5 min interval and was corrected for volume and temperature variations. CO_2 fluxes with R^2 values of 0.70 or less were removed (<3% of measurements), expect for the cases of zero flux (change in chamber CO_2 headspace concentration of <1 ppm). We adopted the ecological sign convention for CO_2 exchange, with negative values representing a net loss of CO_2 from the peatland (gain to the atmosphere).

[12] Bare peat respiration was determined in the field by taking peat CO_2 efflux measurements from bare peat plots from mid-May to early October in 1999, 2000, and 2001 using the static chamber technique described above. In 1999, prior to restoration, CO_2 fluxes from both bare peat and ditches were measured at a 30 m ditch-to-ditch transect in the middle of the to-be-restored field 4 and cutover peat field 10 (see Figure 1). Measurements were made at 0, 2, 5, 10, 15, 20, 25, 28, and 30 m from the western ditch. Two additional transects located 100 m north and south of the central transects had permanent measurement plots at 5, 15, and 25 m from the western ditch. This sample design was maintained at the cutover site in 2000 and 2001; however, sampling locations at the restored site were randomly distributed onto at least 17 bare peat patches following restoration because of the infilling of ditches and alteration of the peat surface during the restoration process (i.e., previous bare peat areas on the transect became vegetated postrestoration). CO_2 was initially sampled at these locations; however, as the vegetation community changed with time postrestoration, collars were moved so that distinct vegetation communities could be monitored through time.

2.4. Environmental Variables

[13] Two micrometeorological towers were located in both the restored and cutover sites (Figure 1) for the continuous measurement of precipitation, temperature, peat moisture, water table position, and photosynthetically active radiation (PAR). Precipitation was measured every half hour using a tipping bucket rain gauge (Campbell Scientific, Utah) as well as from two manual gauges. Air temperature was measured using a thermocouple, and peat temperatures were obtained using a series of thermocouples installed in the peat at various depths (0, 2, 5, 10, 25, 50, and 75 cm). Peat volumetric moisture content (VMC) was measured with Campbell CS615 moisture probes at both 5 and 50 cm depths (Campbell Scientific, Utah), and water table levels were monitored hourly using remote data system wells in addition to manual measurements. PAR was measured continuously using a LI-COR quantum light sensor (LI-COR Inc., Nebraska). All tower measurements were recorded using a CR21X data logger (Campbell Scientific, Utah) every 10 s and were then averaged to give half-hourly values. In addition, instantaneous measurements of air temperature, peat temperature, VMC, and PAR were made during chamber CO_2 sampling. Air temperature and peat temperature at 2, 5, 10, and 15 cm depths were recorded at each site during sampling using a Comark KM43 temperature probe (±0.3°C). VMC for the upper 10 cm of the underlying peat was measured using a Campbell Scientific HydroSense (CD620) soil moisture time domain reflectometry probe, with a probe length of 12 cm and a ±3% accuracy.

2.5. Data Analysis

[14] Each growing season was divided into three periods: period 1 ("pregreen") from 17 May to 8 June, period 2 ("green") from 19 June to 2 September, and, lastly, period 3 ("postgreen") from 2 September to 11 October [*Petrone et al.*, 2003]. In 2002, measurements were made only in pregreen and green periods. Although seasonal CO_2 exchange can be modeled on the basis of growing season shifts in vegetation cover [e.g., *Tuittila et al.*, 1999] or leaf area–vegetated green area [e.g., *Wilson et al.*, 2007], the vegetated periods described above have also been used widely in the literature [e.g., *Griffis et al.*, 2000; *Strack et al.*, 2006] and reduce the number of variables incorporated into the models. Thus, we have adopted this more simplified method in this study.

[15] Within each period, GEP was modeled using a nonrectangular hyperbola relationship between PAR and GEP data using modeling software (Photosyn Assistant, Dundee Scientific, United Kingdom) and the following equation:

$$A = \frac{\Phi Q + A_{\max} - \sqrt{((\Phi Q + A_{\max})^2 - 4\Phi Q k A_{\max})}}{2k}, \quad (1)$$

where A is net leaf photosynthesis, Q is PAR, Φ is the apparent quantum efficiency (initial slope), $A_{\max}$ is the maximum gross photosynthetic exchange of CO_2, and k is the convexity value. Models were created separately for each vegetation type in each period. Empirical relationships between ER and environmental variables (peat temperature at 2, 5, and 10 cm depth and volumetric soil moisture content) were determined using multiple linear regression. Continuously modeled ER fluxes were calculated using the empirical relationships with the best R^2 value determined separately for each vegetation type in each period. NEE for each vegetation type was determined as the sum of modeled
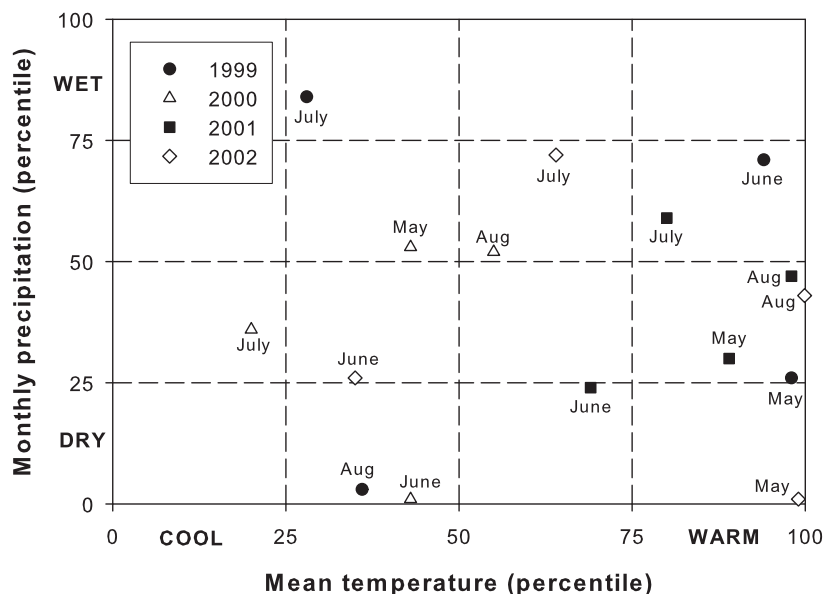
Figure 2. Monthly precipitation and temperature data for each study season (1999–2002) compared to 30 year normals.

GEP and ER over the growing season. Total ecosystem NEE was calculated using a weighted average in which the carbon flux from each surface cover was multiplied by the total surface area occupied by this vegetation type. While a complete uncertainty analysis is beyond the scope of this paper, we adopted an approach similar to that of *Waddington and Roulet* [2000] to provide an estimate of the uncertainty (∼25% of the season flux) of our growing season estimates.

[16] In order to assess shifts in carbon exchange in response to restoration, a general linear model (Minitab statistical software) was applied for each surface cover type with restoration, year, and restoration times year as factors. We assessed variance in carbon exchange under full light conditions (photosynthetic photon flux density (PPFD) > 1000 μmol m^{-2} s^{-1}) [*see Bubier et al.*, 2003; *Strack et al.*, 2006] referred to as GEP$_{max}$ and NEE$_{max}$. Variance in ER following restoration was also assessed. Differences between groups were then assessed with a one-way analysis of variance with Tukey's pairwise comparisons. Nonnormally distributed data were transformed using the Box-Cox power transformation prior to analysis of variance; however, untransformed data are presented throughout for clarity.

3. Results

3.1. Interannual Variability of Environmental Variables

[17] In all years, both prerestoration and postrestoration, Bois-des-Bel experienced mainly drier and warmer conditions compared to the 30 year (1971–2000) normal (Figure 2), with exceptionally drought-like conditions during August 2002. The mean water table depth for both the restored (−54.5 cm) and the cutover (−51.4 cm) sites was similar prerestoration (1999). Mean water table position for the first 3 years postrestoration was −46.0, −39.5, and −43.8 cm at the cutover site in 2000, 2001, and 2002, respectively, while

at the restored site an increase in the water table position occurred (−31.5, −30.4, and −35.9 cm in 2000, 2001, and 2002, respectively). Each year postrestoration the restored site water table position was significantly ($p < 0.05$) higher than the cutover site.

[18] Mean VMC at 5 cm depth at the restored site meteorological tower was 62%, 49%, and 38% for the 2000, 2001, and 2002 study seasons, respectively. In contrast, the cutover site had generally lower seasonal average volumetric soil moisture values of 34%, 20%, and 39% for the 2000, 2001, and 2002 seasons. Considering all data from the 3 years postrestoration, the restored site had significantly higher VMC than the cutover site ($F = 5079.2$; $df = 1$, $p < 0.001$). However, interannual variability was high, and while the restored site had significantly higher VMC than the cutover site in 2000 and 2001, there was no difference between sites in 2002.

[19] The restored site showed a general increase in peat temperature at 5 cm depth with time postrestoration with seasonal average peat temperatures of 13.8°C, 15.4°C, and 16.1°C for the 2000, 2001, and 2002 study seasons, respectively. In contrast, the cutover site showed no clear differences in peat temperature at 5 cm depth over the three postrestoration study seasons, where the seasonal average peat temperatures were 14.4°C, 14.9°C, and 14.4°C for 2000, 2001, and 2002, respectively.

3.2. Peat Respiration: CO$_2$ Efflux From Bare Peat

[20] Both the cutover and the restored sites showed large spatial variability in CO$_2$ efflux during the 1999 (prerestoration) study season, with average ditch respiration generally higher than average peat respiration fluxes along the ditch-to-ditch transects. Specifically, the average plus or minus standard deviation ditch respirations for the restored and cutover sites were −6.4 ± 4.9 and −8.2 ± 6.8 g CO$_2$ m^{-2} d^{-1} compared to the average bare peat fluxes over the same transects of −6.4 ± 6.8 and −5.2 ± 4.2 g CO$_2$ m^{-2}
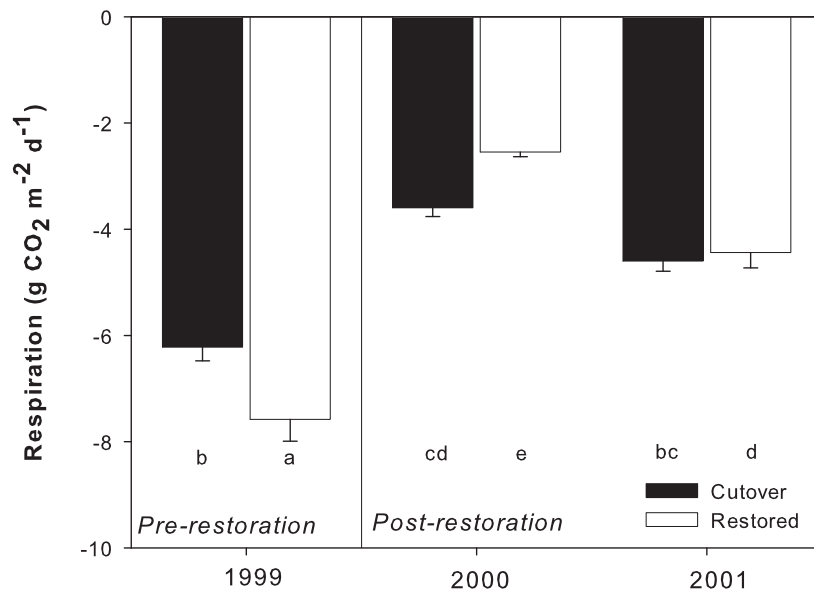
Figure 3. Seasonal average peat respiration from the cutover (black) and restored (white) sites in 1999, 2000, and 2001. The ecological sign convention has been adopted where a negative flux refers to a loss from the ecosystem. Bars with no letters in common are significantly different from each other (ANOVA, $F = 70.0$, $df = 5$, $p < 0.001$; Tukey's pairwise comparisons, $\alpha = 0.05$).

d^{-1}. The seasonal mean bare peat respiration was significantly higher at the restored site than at the cutover site in 1999, and respiration in 1999 was higher than in any other year measured (Figure 3). Following restoration, mean CO_2 fluxes from the restored site were consistently and significantly lower than those from the cutover site (Figure 3). Because of this shift, both year ($F = 110.9$, $df = 2$, $p < 0.001$) and restoration ($F = 24.5$, $df = 1$, $p < 0.001$) were significant factors controlling the variance in peat respiration. There was also a significant year times restoration interaction ($F = 26.7$, $df = 2$, $p < 0.001$).

3.3. Peat Respiration: Laboratory CO_2 Production Potentials

[21] Aerobic CO_2 production potential followed the trend natural > restored > cutover site at all temperatures (Figure 4a) with CO_2 production increasing significantly at each site with each increase in incubation temperature. Cutover CO_2 production was significantly (ANOVA, $p < 0.05$) lower than the restored and natural sites at 12°C and 20°C, whereas the natural and restored sites were not significantly different from each other at all incubation temperatures. All sites were similar at 4°C. Q_{10} values (percentage change in production rate with a 10°C change in temperature) followed the trend restored (6.4) > natural (5.3) > cutover (5.2) for the 4°C–12°C range and cutover (3.3) > restored (2.6) > natural (2.5) for the 12°C–20°C range.

[22] Anaerobic CO_2 production potential was similar at all sites at 4°C and 12°C (Figure 4b), while at 20°C, CO_2 production was significantly (ANOVA, $p < 0.05$) greater at the restored site than at the cutover and natural sites that were similar. Total production increased at all sites with an increase in incubation temperature. Q_{10} for the 4°C–12°C range and 12°C–20°C range followed the trend cutover (2.2, 2.6) > restored (2.1, 2.4) > natural (1.9, 2.1).

Anaerobic/aerobic CO_2 production potential ratios at 20°C also followed the trend cutover (0.96) > restored (0.63) > natural (0.41).

3.4. Vegetation Cover Prerestoration and Postrestoration

[23] Rapid changes in the percent vegetation cover were observed at the restored site; however, the percent vegetation cover of the cutover site did not change between years (Figure 5). The restored site showed a large decrease in the percentage of bare peat cover from 77.7 in 1999, to 56.7 in 2000, to 18.7 in 2001, and, finally, to 9.4 in 2002 (Figure 5). However, there was no change in the percent cover of ditches over the study periods. There were large increases in the percent cover of both mosses and herbaceous vegetation with time postrestoration at the restored site. Specifically, the percent cover of mosses, mainly *Polytrichum* spp., increased from 4.5% in 1999 to ~50% in 2002. Herbaceous vegetation cover at the restored site increased from 3% in 1999, to 14% in 2000, to 32% in 2001, and to 35% in 2002.

3.5. Response of Moss NEE Postrestoration

[24] Restoration ($F = 61.4$, $df = 1$, $p < 0.001$), year ($F = 9.8$, $df = 3$, $p < 0.001$), and restoration times year interaction ($F = 10.9$, $df = 3$, $p < 0.001$) were all significant descriptors of variance in moss NEE_{max}. In 1999, NEE_{max} was similar at both cutover and restored sites. Following restoration, mean cutover moss NEE_{max} plus or minus standard deviation was -3.85 ± 7.05, 1.16 ± 4.54, and -4.15 ± 9.38 g CO_2 m^{-2} d^{-1} in 2000, 2001, and 2002, respectively. At the restored site, NEE_{max} was 1.67 ± 4.68, 6.20 ± 4.80, and 7.29 ± 7.75 g CO_2 m^{-2} d^{-1} in 2000, 2001, and 2002, respectively. Thus, while moss at the cutover site was a net source of atmospheric CO_2 under full light conditions in 2000 and 2002, the restored site was consistently a sink of
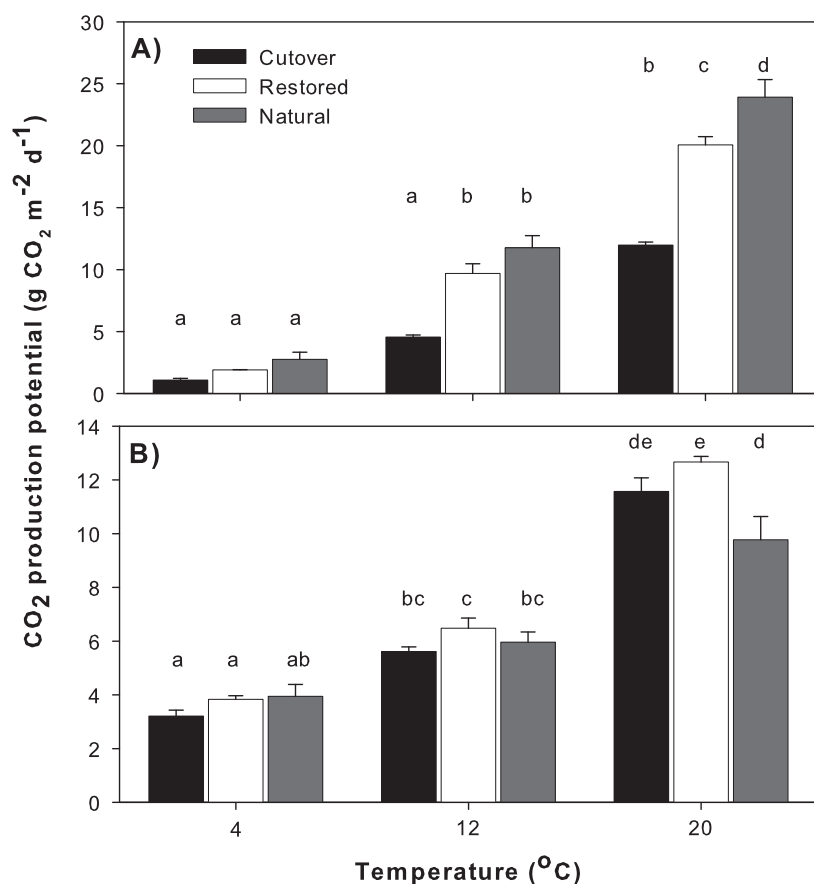
Figure 4. (a) Total aerobic and (b) total anaerobic CO_2 production rates at incubation temperatures of 4°C, 12°C, and 20°C for the cutover (black), restored (white), and natural (gray) sites. Bars with no letters in common are significantly different from each other (ANOVA; $F = 133.5$, $df = 8$, $p < 0.001$; Tukey's pairwise comparisons, $\alpha = 0.05$). Data were not normally distributed; therefore, statistical tests were performed on Box-Cox transformed data. Nontransformed data are shown here for ease of interpretation. Letters should only be compared within each plot.
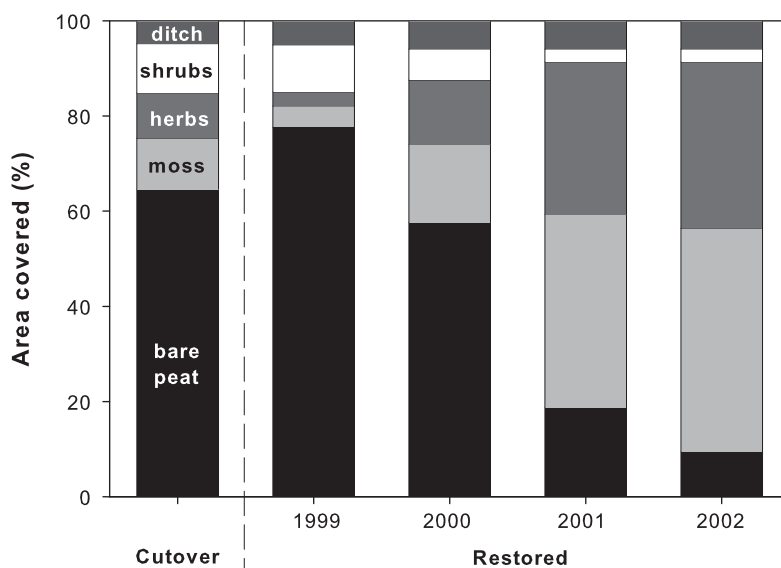

Figure 5. Surface cover (percent) at the cutover site (all years) and restored site (1999–2002).
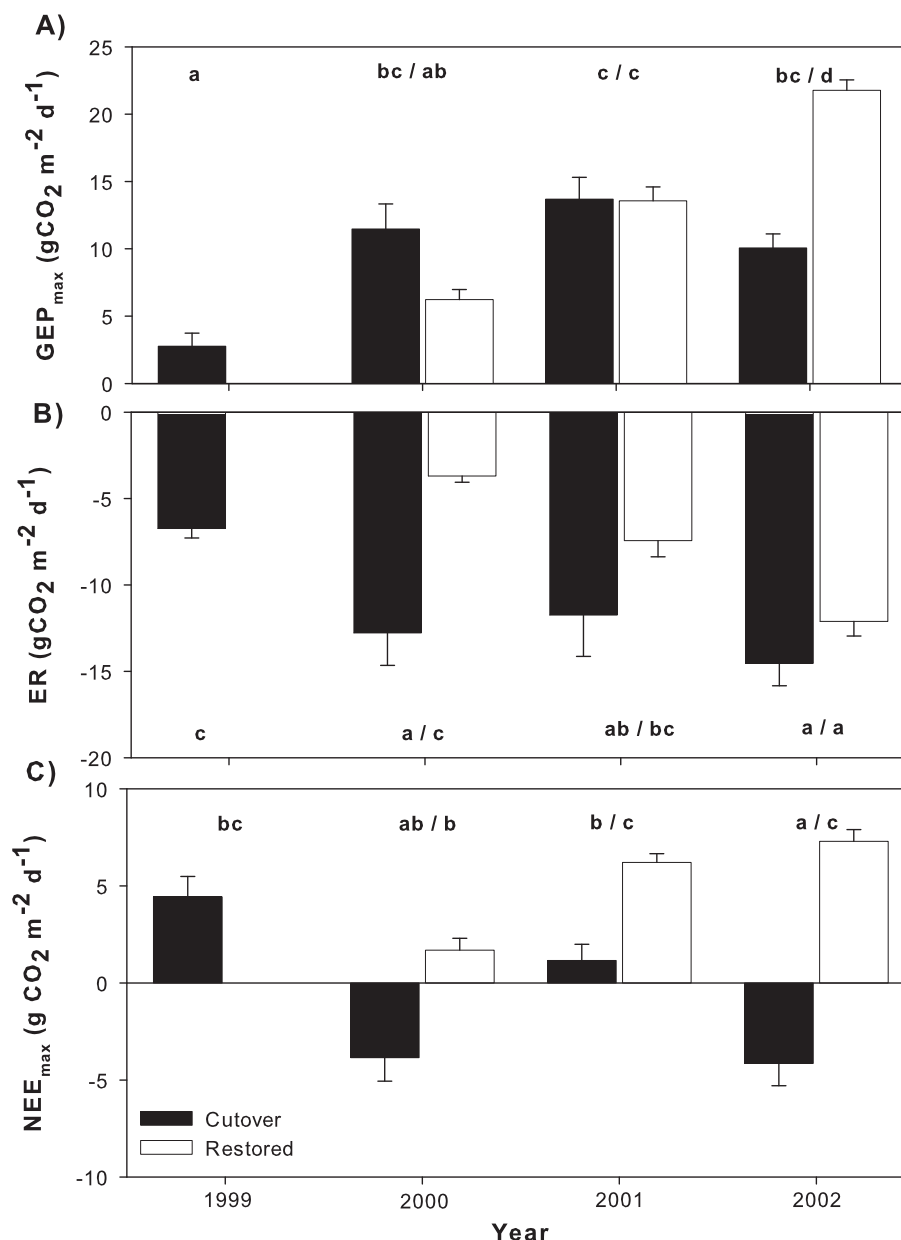
Figure 6. Growing season average carbon exchange for moss: (a) gross ecosystem photosynthesis when PPFD > 1000 μmol m^{-2} s^{-1} (GEP$_{max}$), (b) ecosystem respiration (ER), and (c) net ecosystem exchange when PPFD > 1000 μmol m^{-2} s^{-1} (NEE$_{max}$) for cutover (black bars) and restored (white bars) sites. In 1999, measurements were made prior to restoration but only at locations on the future restored site, so only one bar is shown; it is colored as cutover to indicate that it has not yet been restored. Bars with no letters in common are significantly different from each other (ANOVA, $df = 6$, $p < 0.001$; Tukey's pairwise comparisons, $\alpha = 0.05$). Letters should only be compared within each plot.

CO_2 under the same condition. The restored moss NEE$_{max}$ was significantly different from the cutover site in each year following restoration, always acting as a larger sink for CO_2 and with the largest difference being between the sites observed in 2002 (Figure 6c).

[25] The shifts in NEE$_{max}$ postrestoration resulted from both increased moss productivity and ER that remained below that of the cutover site. Although moss ER was only significantly lower at the restored site compared to the cutover site in 2000, in each year postrestoration, ER was consistently lower at the restored site (Figure 6b). Moss GEP$_{max}$ increased following restoration and was significantly higher than the cutover site in 2002. This increase in moss productivity is reflected in the change in parameters for the light response curves. For example, restored site moss A_{max} ranged from 7.9 g CO_2 m^{-2} d^{-1} in 2000, only 1 year postrestoration, to 35.5 g CO_2 m^{-2} d^{-1} in 2002 (Table 1). Moreover, changes in the initial slope of the light response curve (Φ), which indicates the rate of GEP increase at low light levels, also increased with time post-

Table 1. GEP-Modeling Parameters for Moss and Herbaceous Vegetation at the Restored and Cutover Sites for 1999–2002

	Moss Vegetation				Herbaceous Vegetation			
	n	Φ	A_{max}	k	n	Φ	A_{max}	k
Restored								
1999	199	0.0276	9.63	1.13×10^{-8}	203	0.14	45.4	8.11×10^{-15}
2000	182	0.0259	7.87	0.9062	44	0.133	43.2	1.84×10^{-4}
2001	149	0.0324	18.7	2.54×10^{-15}	43	0.0772	17.3	1.77×10^{-15}
2002	296	0.0459	35.5	0.0459	288	0.0806	40	1.09×10^{-14}
Cutover								
1999	199	0.0276	9.63	1.13×10^{-8}	203	0.14	45.4	8.11×10^{-15}
2000	84	0.0125	11.1	0.993	84	0.0137	30.1	9.24×10^{-5}
2001	88	0.0208	19.7	1.12×10^{-4}	84	0.0162	6.84	3.73×10^{-8}
2002	134	0.111	10.5	1	164	0.0522	20.2	2.8×10^{-15}

restoration. Restored site moss slope values ranged from 0.03 in 2000 to 0.05 in 2002 (Table 1). Both A_{max} and Φ were lower at the cutover site in each year postrestoration.

3.6. Response of Herbaceous Vegetation NEE Postrestoration

[26] Mean herbaceous vegetation (mainly consisting of *Eriophorum* spp.) NEE_{max} was much larger than that at moss-covered locations (Figure 7). Mean plus or minus standard deviation NEE in 1999 was 7.9 ± 6.6 g CO_2 m^{-2} d^{-1}, a net sink of atmospheric CO_2. Postrestoration, the restored site was always a net CO_2 sink and showed large interannual variability with NEE_{max} ranging from 8.7 ± 1.1 g CO_2 m^{-2} d^{-1} in 2001 to 20.6 ± 1.4 g CO_2 m^{-2} d^{-1} in 2000. In contrast, the cutover site herbaceous vegetation had a net release of CO_2 under full light during both the 2001 and 2002 study seasons, with seasonal average fluxes of -0.4 ± 0.6 and -2.2 ± 0.7 g CO_2 m^{-2} d^{-1}, respectively (Figure 7). However, during the 1999 and 2000 study seasons, cutover herbaceous vegetation was an overall net sink of atmospheric CO_2. During all years postrestoration (2000–2002) the restored site herbaceous vegetation was a significantly larger sink of CO_2 under full light than the cutover site.

[27] Similar to moss vegetation, shifts in NEE_{max} at herbaceous plots resulted from increased vegetation productivity following restoration. However, ER also increased following restoration. Following restoration, ER was consistently higher at restored plots than at cutover plots, but this difference was only significant in 2001. In each year postrestoration, GEP_{max} was significantly greater at restored herbaceous plots than at cutover plots. Restored GEP_{max} was similar to prerestoration 1999 values, while cutover plots were consistently lower in 2000–2002 than 1999 GEP_{max} (Figure 7). As for moss plots, this increased productivity was reflected in consistently higher A_{max} and Φ for restored herbaceous plots compared to cutover plots. A_{max} ranged from 17.3 g CO_2 m^{-2} d^{-1} in 2001 to 43.2 g CO_2 m^{-2} d^{-1} in 2000, while restored site herbaceous vegetation had much steeper initial slopes compared to the moss locations with a range of 0.08 in 2001 to 0.13 in 2000 (Table 1).

3.7. Ecosystem Growing Season CO_2 Balance

[28] When comparing the seasonal totals of NEE for both the restored and cutover sites as determined by upscaled chamber estimates, the restored site is a small sink of CO_2 during the 2000 growing season (9.9 g C m^{-2}) and a

slightly larger sink during the 2001 season (19.9 g C m^{-2}) (Table 2), although these values are likely not different given errors in the estimation. Again, it should be noted that the 2002 seasonal total NEE was not calculated, as data were not collected during period 3 ("postgreen") of that study season. However, to investigate interannual comparison, total NEE during the "green" period (period 2) can be compared between prerestoration and all years postrestoration. The green period represents the period of peak vegetative growth, especially for herbaceous species, which can lead to a period of maximum uptake of CO_2 for the restored site. At the cutover site, green period NEE was -130.9, -89.2, -66.0, and -25.7 g C m^{-2} for the years 1999, 2000, 2001, and 2002, respectively. For the same years the green period NEE at the restored site was -134.7, -52.3, -2.0, and 16.3 g C m^{-2}. Thus, the restored site increased its net carbon sink strength during the green period with time postrestoration because of the substantial increase in vegetative cover and an overall reduction of bare peat, while the cutover site remained a source of CO_2 over the same time period.

4. Discussion

[29] Applying the North American peatland restoration technique (outlined by *Rochefort et al.* [2003]) resulted in a substantial increase in vegetation cover. This alone should enhance CO_2 uptake, but it was also observed that the vegetation at the restored site was more productive than patches established on the neighboring unrestored peat surface. Despite observed increases in potential CO_2 production in laboratory incubations, restoration resulted in an overall reduction in CO_2 efflux from bare peat areas. These effects resulted from improved hydrological conditions and the development of vegetation cover following restoration.

4.1. Development of Vegetation Cover

[30] Restoration resulted in a decline in bare peat cover from close to 78% prerestoration (1999) to less than 10% in the third year following restoration (2002). Studies of abandoned vacuum-harvested peatlands have shown poor revegetation when no active restoration is applied [*Poulin et al.*, 2005; *Graf et al.*, 2008], linked to poor hydrologic conditions and a limited seed bank. Restoration ameliorates these conditions by applying *Sphagnum* fragments and mulch and blocking drainage ditches, and these methods have been shown to enhance vegetation cover at both the plot scale and the ecosystem scale [*Waddington and Warner*, 2001; *Petrone*, 2002]. The establishment of this vegetation cover is essential for returning the peatland carbon sink function by providing a mechanism for GEP. At the restored site, there was also a shift in the dominance of moss species present over time, with a 22% increase in *Sphagnum* moss cover between 1999 and 2001, where the site contained no *Sphagnum* cover prior to restoration.

4.2. Enhanced Vegetation Productivity

[31] Prior to restoration, peat cover and moss cover constituted a net seasonal source of CO_2 to the atmosphere. This net release of CO_2 to the atmosphere prerestoration was likely due to the poor hydrological conditions present at the cutover site with significantly high soil water tensions
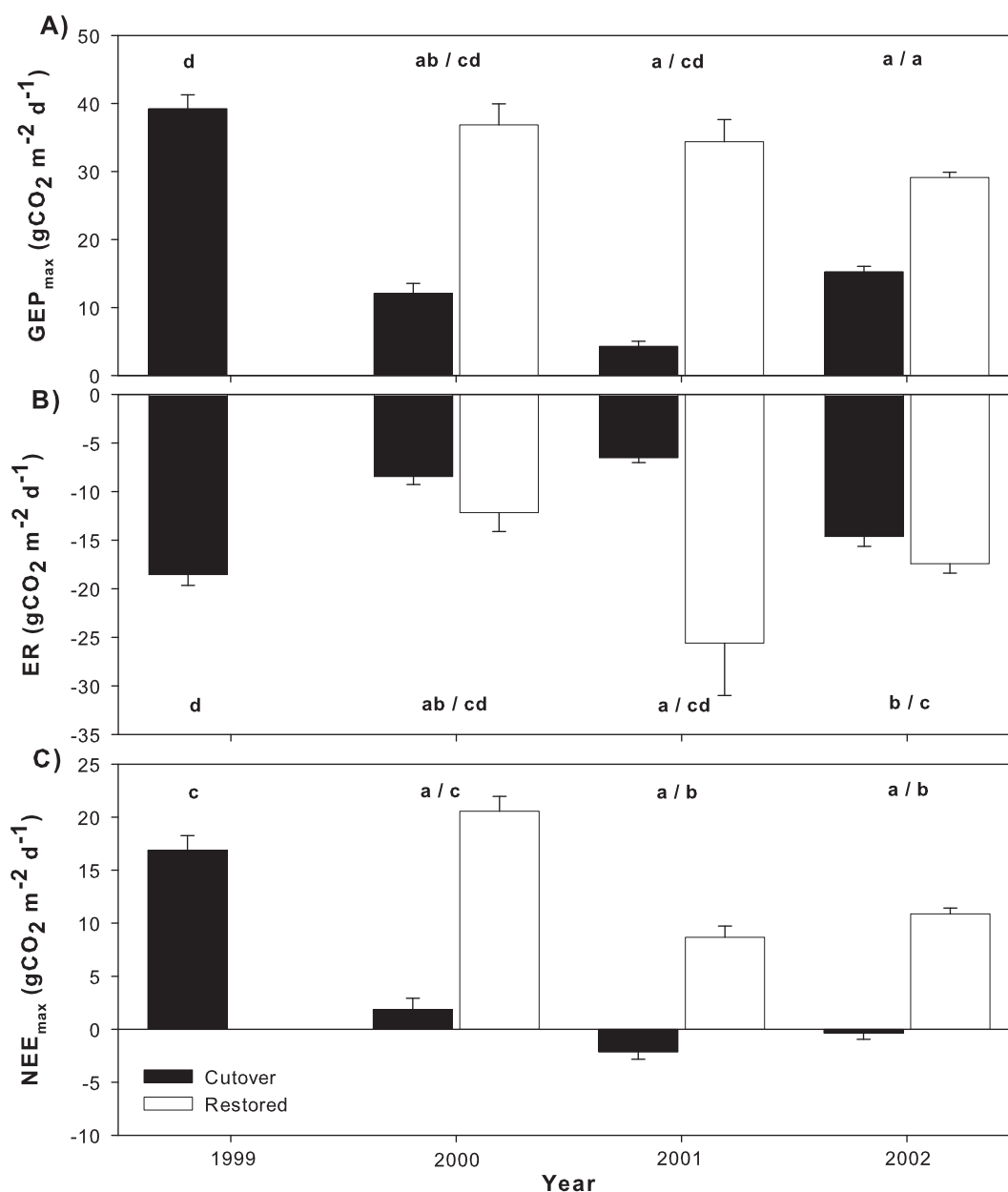
Figure 7. Growing season average carbon exchange for herbaceous plots (mainly *Eriophorum* sp.):
(a) gross ecosystem photosynthesis when PPFD > 1000 μmol m^{-2} s^{-1} (GEP$_{max}$), (b) ecosystem
respiration (ER), and (c) net ecosystem exchange when PPFD > 1000 μmol m^{-2} s^{-1} (NEE$_{max}$) for
cutover (black bars) and restored (white bars) sites. In 1999, measurements were made prior to restoration
but only at locations on the future restored site, so only one bar is shown; it is colored as cutover to
indicate that it has not yet been restored. Bars with no letters in common are significantly different from
each other (ANOVA, *df* = 6, *p* < 0.001; Tukey's pairwise comparisons, α = 0.05). Letters should only be
compared within each plot.

and reduced soil moisture [*Shantz and Price*, 2006a].
Moreover, prerestoration, *Sphagnum* moss was not present
at either the cutover site or the restored site. The only moss
vegetation present was *Polytrichum strictum*, a pioneer
species that has the ability to grow abundantly on cutover
sites [*Groeneveld and Rochefort*, 2005]. This species has a
high tolerance to desiccation and aids in establishment and
recovery of *Sphagnum* [*Groeneveld and Rochefort*, 2005].

[32] Postrestoration, the restored site moss seasonal NEE
significantly increased, with an overall increase by ~220%
in only 3 years, increasing the net CO$_2$ sink function at these
sites. The increased productivity with time postrestoration
can be attributed to substantial improvements in hydrolog-
ical conditions necessary for moss establishment due to
active rewetting in the restoration process. For example, the
restoration process maintained soil moisture above 50% and

Table 2. Modeled Growing Season NEE for the Cutover and Restored Sites[a]

	Cutover			Restored		
	Area (%)	NEE (g CO_2^-C m^{-2})	Contribution	Area (%)	NEE (g CO_2^-C m^{-2})	Contribution
1999						
Ditches and pools	4.8	−407.5	−19.6	5.1	−352.8	−18.0
Bare peat	64.6	−280.5	−181.2	77.7	−260.7	−202.6
Mosses	10.8	−180.4	−19.5	4.4	−180.4	−7.9
Herbaceous	9.5	−399.0	−37.9	2.9	−399.0	−11.6
Shrubs	10.3	−54.8[b]	−5.6	9.9	−54.8[b]	−5.4
Seasonal NEE (g CO_2^-C m^{-2})			−263.6 ± 65.9			−245.5 ± 61.4
2000						
Ditches and pools	4.8	−164.7	−7.9	5.9	−112.0	−6.6
Bare peat	64.6	−108.5	−70.1	57.6	−79.5	−45.8
Mosses	10.8	−411.8	−44.5	16.5	12.3	2.0
Herbaceous	9.5	−95.8	−9.1	13.5	473.7	63.9
Shrubs	10.3	−54.8	−5.6	6.5	−54.8	−3.6
Seasonal NEE (g CO_2^-C m^{-2})			−137.2 ± 34.3			9.9 ± 2.5
2001						
Ditches and pools	4.8	−106.4	−5.1	6.0	−144.2	−8.6
Bare peat	64.1	−85.6	−54.9	18.7	−73.7	−13.8
Mosses	10.5	−56.8	−6.0	40.6	67.2	27.3
Herbaceous	10.3	−84.2	−8.7	32.0	48.0	15.4
Shrubs	10.3	−13.4	−1.4	2.7	−13.4	−0.4
Seasonal NEE (g CO_2^-C m^{-2})			−76.1 ± 19.0			19.9 ± 5.0

[a]Growing season length was 136, 149, and 150 days in 1999, 2000, and 2001, respectively.
[b]Shrub plots were not measured in 1999. Modeled NEE values from 2000 were used. We adopted an approach similar to that of *Waddington and Roulet* [2000] to provide an estimate of the uncertainty (∼25% of the growing season flux).

soil water pressures above −100 mbar, required for adequate *Sphagnum* growth despite limited precipitation 3 years postrestoration [*Shantz and Price*, 2006b]. A study conducted by *Campeau and Rochefort* [2000] also found a deviation between growth rates of mosses (*Sphagnum*) at both natural and restored peatlands. They suggested that in restored sites, *Sphagnum* mosses had a greater density and number of capitula present compared to natural peatlands, which ultimately allows the developing *Sphagnum* species to maintain a higher moisture content as well as to increase productivity [*Campeau and Rochefort*, 2000].

[33] Herbaceous vegetation displayed a larger variability in NEE with time postrestoration. Similar to moss vegetation, the restored site had a positive NEE in all years postrestoration and therefore represented a net seasonal uptake of atmospheric CO_2. Previous studies conducted in European restored peatlands show similar increases in net CO_2 uptake with time postrestoration, generally as a result of increased herbaceous vegetation cover. *Tuittila et al.* [1999] found that active rewetting decreased ER as well as increased GEP at the site, specifically from *Eriophorum* spp. They determined that the site became a net sink of atmospheric CO_2 from a dense *Eriophorum* cover only 2 years postrestoration. Similarly, *Komulainen et al.* [1999] found that rewetting drained peatlands increased *Eriophorum* spp. cover and ultimately changed the seasonal carbon balance toward an increase in CO_2 sequestration, where the seasonal CO_2 balance ranged between 54 and 101 g C m^{-2} at the rewetted site. In the present study, while a seasonal net sink at the restored site is evident, it is likely not a net annual sink given losses of carbon via wintertime ER.

[34] Herbaceous species are not only important in storing organic matter in newly restored peatlands, but they also provide improved microclimatic conditions for other bog species, namely, *Sphagnum* mosses, to establish on these cutover sites [*McNeil and Waddington*, 2003]. Herbaceous vegetation such as *Eriophorum vaginatum* establishes rapidly after restoration, and subsequently, its colonization improves the microhabitat for the initiation and growth of other vascular plants and mosses [*Lavoie et al.*, 2003] and can enhance carbon storage in restored peatlands [*Tuittila et al.*, 1999]. However, *Waddington and Day* [2007] determined that herbaceous vegetation increased the rates of CH_4 emissions in restored peatlands by providing a conduit for CH_4 to escape to the atmosphere without oxidation as well as providing an additional source of labile carbon for microbial activity from root exudates. Consequently, while herbaceous species represent a net seasonal uptake of CO_2 postrestoration at Bois-des-Bel and provide adequate conditions for moss establishment, they also represent a net source of CH_4 postrestoration [*Waddington and Day*, 2007], which has larger implications in the net greenhouse gas sink function of restored peatland ecosystems, since it has a global warming potential 23 times greater than CO_2 on a 100 year time scale.

4.3. Effects on Ecosystem Respiration

[35] Prior to restoration the largest CO_2 fluxes observed were from locations with the highest water table position, whereas the lowest fluxes observed for both the cutover and restored transects were from sites located at the relative midpoint of each transect (greatest depth to the water table). These results suggest that the microbial community may be moisture limited at the driest sections of the peatland [*Lomander et al.*, 1998; *Subke et al.*, 2003]. High fluxes adjacent to the ditches suggest that the ditches supply moisture to stimulate microbial activity in nearby locations and also likely provide a source of labile carbon for microbial consumption in the form of dissolved organic carbon [*Waddington et al.*, 2008].

[36] With time postrestoration, restored site fluxes decreased significantly. The decrease in CO_2 flux after restoration may be attributed to a reduction in aerobic decomposition from a shallower water table position as well as a significant increase in soil moisture conditions at the restored site postrewetting. Therefore, active rewetting at the restored site created a reduction in the aerobic zone and ultimately a reduction of peat oxidation. This decrease occurred despite an increase in peat CO_2 production potential. *Croft et al.* [2001] and *Marinier et al.* [2004] determined that microbial activity was stimulated with restoration as a result of increased labile carbon present from emerging vegetation inputs at these sites compared to those that remain abandoned. *Basiliko et al.* [2007] also observed increased microbial biomass and CO_2 production following restoration of a block-cut peatland. While a block-cut extract peatland differs from the vacuum-extracted approach used at Bois-des-Bel, it is interesting to note that *Basiliko et al.* [2007] observed significant relationships between aerobic and anaerobic CO_2 production and peat humification, carbon substrate quality, microbial biomass, and nutrient concentrations. It has also been observed that vegetation succession following restoration results in changes in the microbial community [*Artz et al.*, 2008] that, in turn, could alter rates of CO_2 production. Thus, improved peat quality linked to an emerging, productive vegetation community results in the observed enhanced aerobic and anaerobic potential CO_2 production postrestoration; however, hydrological conditions in the field result in measured ER below that of the cutover site. In general, aerobic production potential was higher than anaerobic potential; however, at 4°C, anaerobic production potentials were actually slightly higher (Figure 4). This is likely due to differences in the incubation setup between the aerobic and anaerobic runs as the anaerobic samples were first flushed with nitrogen and thus started with minimal headspace CO_2 concentrations. *Basiliko et al.* [2007] suggest that changes in incubation procedure can lead to differences in the resultant production potentials.

[37] Ecosystem respiration was enhanced at vegetated areas following restoration. Seasonal moss ER at the restored site increased significantly between the 2001 and 2002 study seasons (Figure 6). This increase in respiration can be attributed to climatic variability, as 2002 was a dry year compared to all other previous study seasons as well as the long-term average. Similarly, ER at herbaceous plots was consistently higher on the restored site than on the cutover site (Figure 7). The increase in seasonal ER from vegetated plots postrestoration is likely also related to a "priming effect" [*Kuzyakov et al.*, 2000, 2001], where the accumulation of both aboveground and belowground biomass ultimately becomes a source of labile carbon for microbial activity during senescence and by the excretion of root exudates [*Marinier et al.*, 2004]. Finally, increasing ER likely results from increasing autotrophic restoration as vegetation productivity increases.

4.4. Toward Restoring the Peatland Carbon Sink Function

[38] Upscaling chamber estimates of NEE to the ecosystem level at Bois-des-Bel peatland showed a dramatic shift from an ecosystem that was a net source of CO_2 to the atmosphere -245.5 g C m^{-2} prerestoration to a system only 2 years postrestoration that is a net growing season sink for atmospheric CO_2 of $\sim 20 \pm 5$ g C m^{-2}. Over the same period, the unrestored cutover site was a source of CO_2 in each study year, although substantial interannual variability was apparent. Given that the focus of this study was to compare CO_2 exchange between restored and cutover sites, controls on this interannual variability were not investigated in detail. Previous studies determining NEE of the restored site of this ecosystem on the basis of micrometeorological techniques suggest the restored site is an even larger source of CO_2 to the atmosphere postrestoration [*Petrone et al.*, 2003]. However, simulated NEE exchange estimates based on these initial eddy covariance micrometeorological measurements indicate that the site has the potential to return to a net carbon sink by the end of the sixth year postrestoration [*Petrone*, 2002]. Encouragingly, this study provides promising evidence that ecosystem-scale restoration projects of cutover peatlands do have the potential to return to a net carbon sink due in part to a decrease in peat respiration linked to active rewetting from the restoration process itself in addition to an emerging, productive vegetation cover within 3 years postrestoration. Two of the main goals of successful peatland restoration are to have an established *Sphagnum* moss cover as well as to return the net carbon sink function of the system. In the case of Bois-des-Bel, the percent cover of *Sphagnum* moss is increasing, and the results of this study suggest that at least during the growing season, the site has become a net sink of CO_2. However, on an annual basis the restored site is likely a weak source of CO_2 given that our study only took place during the growing season, and wintertime fluxes are likely not insignificant. *Waddington and Day* [2007] determined that the Bois-des-Bel cutover site loses 0 to 0.6 g CH_4-C m^{-2} during the growing season, and the restored site CH_4 emissions are increasing with time postrestoration (up to 3.1 g CH_4-C m^{-2}). Given that the cutover and restored sites also lose 6.2 to 10.3 and 3.4 to 3.8 g C m^{-2}, respectively, as dissolved organic carbon [*Waddington et al.*, 2008], we suggest that this degraded peatland ecosystem has not yet returned to a net carbon sink but will likely return to a net carbon sink in 6 to 10 years postrestoration [*Petrone*, 2002].

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