# Net ecosystem CO$_2$ exchange of a cutover peatland rehabilitated with a transplanted acrotelm[1]

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*Abstract*: Natural peatlands are an important component of the global carbon cycle, representing a net long-term sink of atmospheric carbon dioxide (CO$_2$). The natural carbon storage function of these ecosystems can be severely impacted due to peatland drainage and peat extraction, leading to large and persistent sources of atmospheric CO$_2$ following peat extraction abandonment. Standard restoration techniques aim to restore the peatland to a carbon-accumulating system through various water management techniques to improve hydrological conditions and through reintroducing *Sphagnum* at the surface. However, restoring the hydrology of peatlands can be expensive due to the cost of implementing the various restoration techniques. This study examines the net ecosystem CO$_2$ exchange of a new extraction–restoration technique where the acrotelm is preserved and replaced directly on the cutover surface. Peat respiration at the experimental restored acrotelm (110.5 g C·m$^{-2}$ over the study period: May 20 – August 18) was significantly lower than at the natural peatland (144.8 and 203.7 g C·m$^{-2}$, wet and dry plots respectively). However, gross ecosystem production (GEP) at the experimental site was significantly reduced (–54.0 and –34.4 g C·m$^{-2}$) compared to the natural site (–179.2 and –162.0 g C·m$^{-2}$). Consequently, this was a growing season net emitter of CO$_2$ to the atmosphere over the season at the experimental site (78.5 and 56.5 g C·m$^{-2}$) and a growing season sink of CO$_2$ at the natural site (–17.6 and –22.8 g C·m$^{-2}$). Light response curves indicated that maximum GEP was significantly lower at the experimental site; however, it is likely that the percentage of living and dead vegetation at the plots post restoration had a large control on this lower productivity as plots with more living vegetation had higher overall productivity (GEP). Nevertheless, the experimental site did maintain limited productivity post-extraction, indicating that the carbon dynamics of the system was maintained due to this acrotelm restoration process, thereby likely returning the ecosystem toward a natural sink of atmospheric CO$_2$ faster than natural rehabilitation and current restoration techniques. As such, this approach to peat extraction may be an environmentally preferred approach to use.
*Keywords*: acrotelm, CO$_2$ exchange, moisture dynamics, peatland, restoration, water table.

*Résumé* : Les tourbières naturelles sont une composante majeure du cycle global du carbone représentant à long terme un puits net de dioxyde de carbone atmosphérique (CO$_2$). La fonction naturelle de séquestration traditionnelles du carbone de ces écosystèmes peut être sévèrement altérée par le drainage et l'extraction de la tourbe conduisant à d'importantes et persistantes pertes de CO$_2$ vers l'atmosphère après l'abandon de l'extraction de la tourbe. Les techniques traditionnelles de restauration visent à rétablir la fonction d'accumulation de carbone de la tourbière par diverses techniques de gestion de l'eau pour améliorer les conditions hydrologiques et par la réintroduction de *Sphagnum* à la surface. Cependant, restaurer l'hydrologie d'une tourbière peut être dispendieux en raison du coût d'implantation des différentes techniques de restauration. Cette étude examine les échanges nets de CO$_2$ d'une nouvelle technique d'extraction-restauration où l'acrotelme est préservé et replacé directement sur la surface d'où la tourbe a été extraite. La respiration de la tourbe de l'acrotelme restauré expérimentalement (110,5 g C·m$^{-2}$ durant la période d'étude : 20 mai – 18 août) était significativement plus faible que celle d'une tourbière naturelle (144,8 et 203,7 g C·m$^{-2}$ pour les sites humides et secs, respectivement). Cependant, la productivité brute de l'écosystème au site expérimental (**–54,0 et –34,4 g C·m$^{-2}$**) était significativement réduite en comparaison avec le site naturel (**–179,2 et –162,0 g C m$^{-2}$**). Par conséquent, le site expérimental était un émetteur net de CO$_2$ vers l'atmosphère pour la saison (78,5 et 56,5 g C·m$^{-2}$) et le site naturel, un puits de CO$_2$ durant la saison de croissance (**–17,6 et –22,8 g C·m$^{-2}$**). Les courbes de réponse à la lumière indiquaient que la productivité maximale brute de l'écosystème était significativement plus faible au site expérimental; cependant, il est probable que les pourcentages de végétation vivante et morte dans les parcelles restaurées exerçaient un contrôle important sur cette productivité réduite puisque les parcelles avec plus de végétation vivante avaient une productivité totale plus élevée. Néanmoins, le site expérimental gardait une faible productivité après extraction ce qui indique que la dynamique du carbone était maintenue dans le système en raison de ce processus de restauration de l'acrotelme rétablissant probablement ainsi la fonction naturelle de puits de CO$_2$ atmosphérique de l'écosystème plus rapidement que la récupération naturelle et les techniques traditionnelles de restauration. Ainsi, cette approche d'extraction de la tourbe pourrait être une voie à privilégier du point de vue environnemental.
*Mots-clés* : acrotelme, dynamique hydrologique, échange de CO$_2$, nappe phréatique, restauration, tourbière.

## Introduction

Natural peatlands are an important component of the global carbon cycle, contributing approximately one third

of the total soil carbon (Gorham, 1991). Peatland formation commonly leads to a 2-layered soil structure within the peat profile referred to as the acrotelm and catotelm (Ingram, 1978; 1992). The acrotelm is the upper layer of peat where water table fluctuations occur and is characterized by a high organic content that is poorly decomposed with high specific yield and porosity (Ingram, 1983). In natural peat-

lands, the large pore structure of the acrotelm contributes to a high water storage capacity (Boelter, 1968) and high $CO_2$ sequestration (McNeil & Waddington, 2003). The natural carbon storage function of these ecosystems can be severely impacted due to peatland drainage and peat extraction (*e.g.,* Waddington, Warner & Kennedy, 2002), These ecosystems are generally left abandoned for many years before any type of restoration occurs.

Within North America approximately two thirds of the peat extraction for horticultural purposes occurs in Canada, and the demand for horticultural peat in Canada over the past century has led to the drainage and extraction of over 12 000 ha of peatlands (Cleary, Roulet & Moore, 2005). In areas such as the St. Lawrence lowlands in Québec losses of peatlands for peat extraction exceed 70% (Van Seters & Price, 2001). Drainage and extraction of peatlands create conditions that disturb the natural hydrological and carbon cycling regimes of the ecosystem. Block-cutting and vacuum extraction techniques have been used primarily for the peat horticulture industry in Canada. Early peat horticulture was typically performed by block-cutting, where drainage of the peatland occurred with a series of ditches and subsequent extraction trenches. The acrotelm was removed and discarded to the side, exposing the catotelmic peat used for horticulture. This deeper peat was cut by hand into blocks to an average of 60 cm depth (Girard, Lavoie & Thériault, 2002), leaving the landscape in an arrangement of alternating baulks (raised mounds) and trenches (*e.g.,* Robert, Rochefort & Garneau, 1999; Girard, Lavoie & Thériault, 2002). The remaining acrotelm material discarded to the side was generally moved to the centre of the extracted trench as more trenches were cut (Girard, Lavoie & Thériault, 2002). Rarely used commercially today, remnants of these systems still remain in both Europe and eastern North America (Price, Heathwaite & Baird, 2003). By the mid-1970s mechanized cutting became the dominant peat extraction practice for commercial use. Occurring at a larger areal scale than block-cutting, deeper and more frequent drainage ditches are used in order to facilitate adequate drainage to support heavy extraction machinery (Price, Heathwaite & Baird, 2003). Similarly to block-cutting, the acrotelm is removed; however, rather than discarding it adjacent to the extraction site, the stripped spoil or skag (*i.e.,* vegetation layer) is discarded completely (Heathwaite & Gottlich, 1993). The peat surface is then milled to facilitate drying, and peat fragments are typically vacuumed from the surface (*i.e.,* vacuum extraction) using heavy machinery to a depth of ~75 to 100 cm (Price, Heathwaite & Baird, 2003). Consequently, the peat extraction process creates unfavourable conditions at the peat surface, especially for species such as *Sphagnum* moss, the main peat-forming vegetation, to re-establish.

The extraction of peatlands leads to large and persistent sources of atmospheric $CO_2$ following abandonment (Waddington, Warner & Kennedy, 2002; Petrone, Waddington & Price, 2003) due to the decomposing peat and the unvegetated surface at the abandoned cutover site. Moreover, the longer a peatland remains abandoned the larger the atmospheric $CO_2$ source (Waddington & McNeil, 2002). However, it has been shown that extracted peat-

lands can return to a carbon-accumulating ecosystem at a plot scale (Tuittila *et al.,* 1999; Waddington & Warner, 2001), with recent evidence further demonstrating that ecosystem-scale restoration techniques can return cutover peatlands to a net sink of atmospheric $CO_2$ within 3 to 5 y (Greenwood, 2005), although they remain a net source of methane (Waddington & Day, 2007). Indeed, due to the water regulatory functions that acrotelm provides, it is hypothesized that preservation of the acrotelm would aid in maintaining close to natural hydrological conditions on the cutover surface post-extraction. More specifically, the water table position would be close to natural near-surface conditions, thereby stabilizing soil moisture content. By maintaining adequate water table, soil moisture, and soil tension conditions (Cagampan & Waddington, 2007), this would allow suitable conditions for *Sphagnum* mosses survival and growth at the surface. Consequently, the immediate presence of the acrotelm-vegetation cover over the cutover surface may return these ecosystems toward being net sinks of atmospheric $CO_2$ sooner than traditional restoration techniques. Here, we determine the controls and $CO_2$ exchange at a natural and acrotelm-transplanted cutover peatland by measuring spatial and temporal net ecosystem $CO_2$ exchange and determining the dominant ecohydrological processes controlling $CO_2$ exchange.

## Methods

STUDY AREA

This study was conducted at the Pointe-Lebel peatland, ~20 km south of the town of Baie Comeau, Québec (49° 7' N, 68° 12' W). The average annual temperature at the Baie Comeau airport (~3 km from the research site) is 1.5 °C, with mean January and July temperatures of –14.4 °C and 15.6 °C, respectively. The 30-y normal (1971–2000) annual precipitation is 1014.4 mm, of which 684.1 mm is rain (Environment Canada, 2006).

The Pointe-Lebel peatland is situated on top of deltaic sands adjacent to the St. Lawrence River forming a 92-ha shrub (*Chamaedaphne calyculata, Kalimia angustifolia, Picea mariana*, and *Ledum groenlandicum*), *Sphagnum* moss (*S. rubellum*, *S. fuscum*), and scattered open water pool bog complex. The peat depth in the peatland ranges from 5 to 6 m. At the southern end of this complex a small section of the peatland was subdivided into 2 sites for this study: natural and experimental. The natural site served as the control site and comprised a pristine section of the peatland that was not impacted by any peat extraction or peatland drainage. In June 2005, an experimental site (~6 × 12 m) set up parallel to a (~2 × 1 m) drainage ditch within the peat extraction zone was used to test the new acrotelm transplant procedure.

ACROTELM TRANSPLANT TECHNIQUE

The new acrotelm transplant and peat extraction–restoration technique was recently developed by Premier Tech Ltd. (Rivière-du-Loup, Québec) and is described in Cagampan and Waddington (2007). This technique increases peat extraction while attempting to minimize ecosystem impact by incorporating restoration (the acrotelm transplant) directly into the process. This trench extraction–restoration

technique removes peat in a manner similar to traditional block-cut methods (*e.g.,* Girard, Lavoie & Thériault, 2002). Extraction of the peat is performed mechanically with a back-hoe, creating extraction trenches parallel to a long and deeply (~4 × 3 m) cut drainage ditch (Figure 1a). Initially, the acrotelm and surface vegetation (mosses and shrubs) (~30 cm thick) within a ~5 × 5 m plot is removed and placed beside the extraction zone (Figure 1b). Peat is then mechanically removed to the depth of interest (~2 m) containing the viable peat for horticultural purposes (Figure 1c). The extracted peat is then transported to a processing facility. Once extraction is complete, the acrotelm that was retained is then transplanted over the older and more decomposed catotelm peat in the cutover peatland (Figure 1d). This creates a trench topography in which the surrounding natural peatland is higher than the extraction zone. The process is then repeated along the transect, thereby expanding the trench. Subsequent trenches are created parallel to the initial
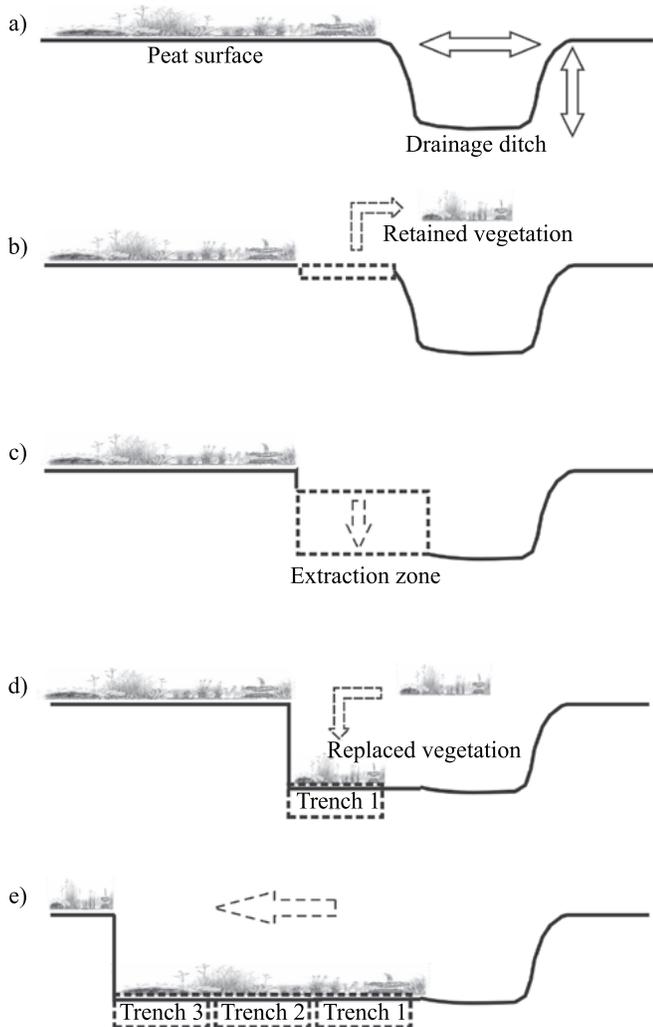


FIGURE 1. The acrotelm transplant technique. a) A natural peatland prior to extraction adjacent to a large drainage ditch. b) The acrotelm and surface vegetation is removed and retained. c) Extracted peat. d) Retained acrotelm and vegetation is transplanted onto cutover peat surface. e) Extraction–restoration continues parallel and away from the ditch and moves into the peatland as subsequent trenches are created.

trench, decreasing the overall elevation of the peatland over time (Figure 1e). The transplanting of the acrotelm vegetation onto the cutover peatland in the trench is considered to be the "restoration" or rehabilitation process since the acrotelm structure is retained. It should be noted that while this technique is referred to as the acrotelm transplant technique (see Cagampan & Waddington, 2007), the upper peat layer removed is not always the exact thickness of the pre-extraction acrotelm (but it is very close). Moreover, once transplanted, the acrotelm may technically no longer be considered as such since the water table dynamics of the rehabilitated peatland are altered (Cagampan & Waddington, 2007).

### ENVIRONMENTAL VARIABLES

Air temperature was measured using a Campbell Scientific T107 air temperature probe (Edmonton, Alberta, Canada) and a series of thermocouples (Type E) installed at various depths (5, 10, 15, 30, and 60 cm). Precipitation was measured using a Texas Electronic (Campbell Scientific) tipping bucket rain gauge at the natural site, and additional precipitation data was collected from the adjacent Baie Comeau airport weather station (Environment Canada, 2006). PAR was measured using a Li-COR (Lincoln, Nebraska, USA) quantum light sensor ($\mu$mol·m$^{-2}$·s$^{-1}$). These variables, logged every 20 min at both the natural and experimental sites using Campbell Scientific CR10X dataloggers, were used to establish empirical relationships with $CO_2$ flux over the season.

Water table levels were measured at 2 locations (natural and experimental) using a pulley system potentiometric water level recorder, logged every minute, and averaged every 20 min using the dataloggers. Additional manual point water table measurements were taken at 12 permanent slotted PVC wells located adjacent to $CO_2$ flux plots in each of the natural and experimental sites on a weekly basis for determining relationships with the $CO_2$ measurements.

Campbell Scientific CS615 water content reflectometers were used to measure volumetric moisture content (VMC) at the 10-cm mid-acrotelm depth at each site. The probe consists of two 30-cm-long steel probes using time-domain measurement methods that are sensitive to dielectric permittivity to calculate moisture content (Campbell Scientific, Edmonton, Alberta, Canada).

### $CO_2$ EXCHANGE MEASUREMENTS

Measurements of $CO_2$ exchange were undertaken from May 20th to August 18th (day of year 140–230), representing the spring and summer growing periods. The static chamber technique (*e.g.,* Griffis, Rouse & Waddington, 2000) was used to measure the net ecosystem exchange of $CO_2$. Twelve sampling locations were installed at each site (24 total) to ensure representativeness of the flux measurements and characterization of the vegetative structure. Each location included both shrub and *Sphagnum* moss species, the dominant plant functional types. Square metal collars (60 × 60 cm) were inserted into the peat and maintained as permanent sampling stations (plots). A clear square Plexiglas chamber (area = 1200 cm$^2$, volume = 120 L) was placed and sealed over the collars to measure net ecosystem exchange (NEE). Temperature within the chamber was

monitored and an internal cooling system maintained ambient temperature conditions during light periods. Respiration ($R_{TOT}$) was measured by placing an opaque plastic tarp over the chamber. Gross ecosystem production (GEP) was determined as the difference between measured NEE and $R_{TOT}$ values from the plot over the same sampling period. NEE and PAR relationships were established using a series of mesh shrouds of various sizes placed over the clear chamber to measure NEE under reduced light conditions. The concentration of $CO_2$ in the chamber headspace was measured using a portable infrared gas analyzer (EGM-2 PP-Systems, Amesbury, Massachusetts, USA) at 30-second intervals over a 3-min period. Instantaneous measurements of peat temperature, volumetric moisture content (VMC), water table, and photosynthetic active radiation (PAR-1) were recorded at each collar during chamber sampling. Peat temperature (°C) was measured using a Barnant temperature probe (Barnant, Barrington, Illinois, USA), and VMC of underlying peat was measured using a Campbell Scientific Hydrosense TDR. Temperature, VMC, and water table were used to establish empirical relationships with $CO_2$ flux. $CO_2$ fluxes were calculated from the slope of the gas concentration over time, and quality control of fluxes was performed. Slopes with $r^2$ values of less than 0.70 were excluded from calculations except for the case of zero flux. Regression analysis was conducted to determine relationships between the measured environmental variables and $CO_2$ flux. A statistical analysis package was used (SPSS Inc., Chicago, Illinois, USA) for multiple regression analysis and ANOVA testing of measured data at each site to determine empirical relationships and significance of fluxes, respectively.

Ecophysiological parameters of $CO_2$ fluxes were characterized by creating light response curves for each of the collar locations. These curves model the relationship between the GEP and PAR and are fitted using an equation for a rectangular hyperbola:

$$\text{GEP} = \frac{(\alpha \times \text{PAR} \times \text{GP}_{MAX})}{(\alpha \times \text{PAR}) + \text{GP}_{MAX}} - R_{TOT} \qquad [1]$$

where PAR is measured PAR ($\mu mol \cdot m^{-2} \cdot s^{-1}$), $GP_{MAX}$ is the empirically derived gross photosynthetic exchange of $CO_2$, and $\alpha$ is the initial slope of GEP *versus* PAR. Total ecosystem respiration ($R_{TOT}$) was modeled separately using a simple linear or multiple regression relationship from chamber-based measurements with peat temperature, water table, and/or moisture at some sites.

The growing season was divided into 3 growing season periods: early (May 20th to June 2nd), mid (June 10th to July 31st), and late (August 4th to August 18th). The light response curve relationships for each period and each plot were applied to continuous daily PAR measurements (days 140–230) and averaged over a 24-h period to obtain daily averages for GEP. $R_{TOT}$ was calculated similarly using the environmental controls stated above, and NEE was calculated as the addition of GEP and $R_{TOT}$. Growing season flux total estimates were calculated by summing the hourly modeled data.

VEGETATION SURVEYS

Vegetation surveys at each plot were performed to identify the dominant individual vegetation species at both the natural and experimental sites in mid August, 2005. Moreover, relative percent cover within the plots was determined to classify dominant vegetation type. From the vegetation surveys it was apparent that vegetation had experienced some disturbance at some of the transplanted acrotelm plots. Vegetation survey results were correlated to the $GP_{max}$ to determine the gross productivity differences between disturbed and non-disturbed plots.

## Results

PLOT CLASSIFICATION

For $CO_2$ exchange analysis (measured and modeled) each plot at the natural (N) and experimental (E) sites was categorized into "wet" or "dry" plots based on relative VMC measurements. Once categorized, VMC at natural dry plots ($N_{DRY}$) averaged $41.3 \pm 6.0\%$ (SD) and natural wet plots ($N_{WET}$) $83.9 \pm 9.5\%$ over the season. For experimental site plots, VMC averaged $74.7 \pm 13.3\%$ and $92.2 \pm 2.8\%$ for dry ($E_{DRY}$) and wet ($E_{WET}$), respectively (Figure 2). A clear difference in VMC for wet and dry plots existed, and therefore $CO_2$ exchange measurements used the same classification for analysis and comparison of sites and plots.

MEASURED $CO_2$ EXCHANGE

At the natural site, the daily response of $CO_2$ exchange differed between wet and dry plots ($N_{WET}$ and $N_{DRY}$) (Figure 3a). GEP ranged from –5.0 to –22.6 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ at $N_{DRY}$ and from –2.6 to –18.9 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ at $N_{WET}$. GEP at the beginning of the season was low, and the highest fluxes occurred during mid-summer (days 175–205). Over the season GEP at $N_{DRY}$ was greater than $N_{WET}$; however, responses in fluxes were similar and variability was low at each site.

The experimental site GEP was significantly lower ($P < 0.05$) than the natural site over the season (Figure 3b). Measured GEP ranged from –8.4 to –1.2 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ at experimental dry ($E_{DRY}$) and –0.8 to –4.8 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ at experimental wet ($E_{WET}$). Overall, GEP at $E_{DRY}$ was greater than $E_{WET}$, with variability being low and responses of fluxes
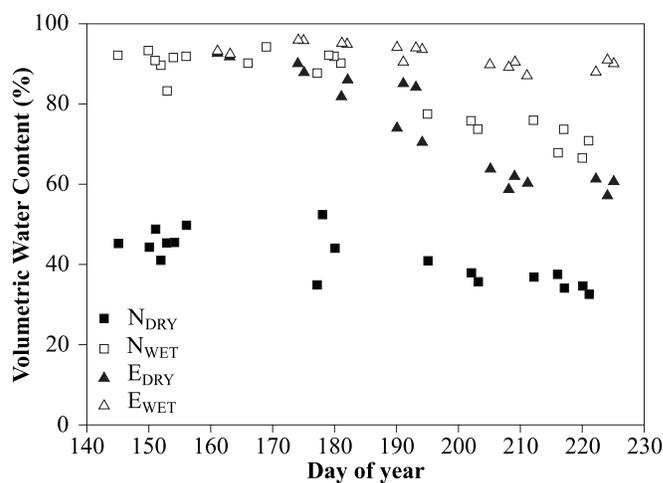


FIGURE 2. Volumetric Moisture Content (VMC) for wet and dry plots at the natural (N) and experimental (E) sites, exhibiting the differences in moisture both within and between sites.

similar between sites. Peak GEP at these sites occurred from mid to late summer (days 180–230).

Total ecosystem respiration ($R_{TOT}$) at $N_{DRY}$ and $N_{WET}$ ranged from 4.7 to 12.8 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ and 1.7 to 11.8 g $CO_2 \cdot m^{-2} \cdot d^{-1}$, respectively (Figure 3a). $R_{TOT}$ at each site responded similarly, with fluxes at the beginning (days 145–160) and at end of the season (days 210–228) being very similar. Variability in flux was low at the wet and dry sites; however, $N_{WET}$ was moderately lower over the peak summer (days 175–205) period compared to $N_{DRY}$.

$R_{TOT}$ at $E_{DRY}$ and $E_{WET}$ ranged from 3.4 to 9.5 g $CO_2 \cdot d^{-1}$ and 2.4 to 5.9 g $CO_2 \cdot m^{-2} \cdot d^{-1}$, respectively (Figure 3b). The response of $CO_2$ flux was similar at each site; however, $E_{DRY}$ had greater overall $R_{TOT}$ than $E_{WET}$. Peak $R_{TOT}$ occurred during mid to late summer (days 180–210) and remained stable over this period. In comparison to the natural site, $E_{DRY}$ responded similarly to $N_{DRY}$; however, $E_{WET}$ had lower $R_{TOT}$ compared to $N_{WET}$.

Average daily ground temperature at 5 cm depth generally corresponded well with $R_{TOT}$ over the season at the natural site. Similarly, the experimental site plots corresponded with the 10-cm ground temperature (Figure 4a). As the daily 5- and 10-cm average ground temperature increased over the season at the natural site, respiration flux responded accordingly. High ground temperatures at the natural site (*e.g.,* days 190 and 217) corresponded with the highest respiration, whereas lower temperature days (*e.g.,*
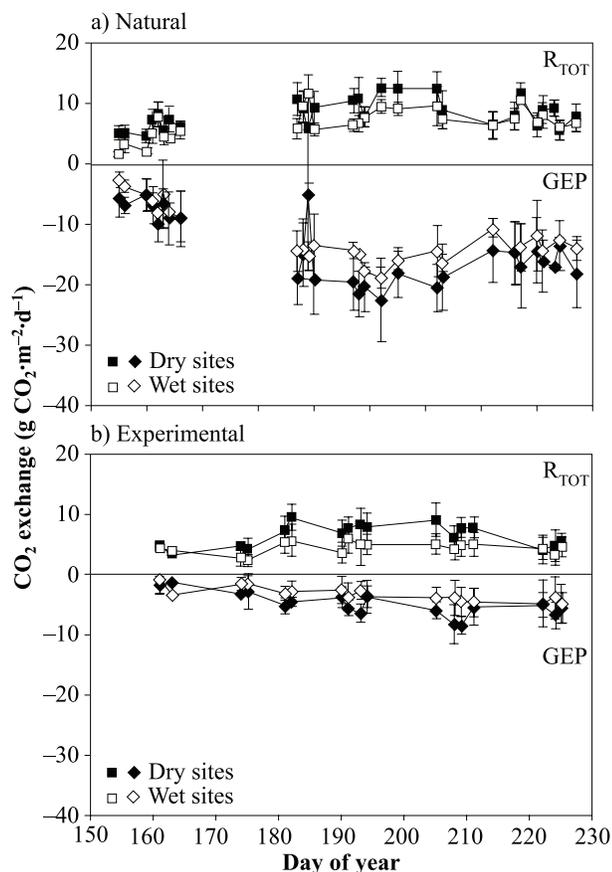
140 and 212) had decreased respiration. At the experimental site, increased respiration also occurred during high temperatures (*e.g.,* days 182 and 209), with lower fluxes during low temperatures (*e.g.,* days 175 and 205). Peak respiration at the natural site occurred during the late summer (days 190–200), whereas the experimental site peak respiration occurred from mid to late summer (days 180–210). Furthermore, water table corresponded more strongly with $R_{TOT}$ at the experimental site, where wetter plots had an observed increase in respiration as water table position decreased (Figure 4b).

On a seasonal basis, NEE at $N_{WET}$ and $N_{DRY}$ plots was $-5.2 \pm 4.0$ and $-5.9 \pm 5.4$ g $CO_2 \cdot m^{-2} \cdot d^{-1}$ and $1.1 \pm 3.0$ and $1.5 \pm 2.4$ g $CO_2 \cdot m^{-2} \cdot d^{-1}$ for $E_{WET}$ and $E_{DRY}$ (Figure 5). Average NEE showed significantly more uptake ($P < 0.05$) at the natural site than the experimental site, although no significant differences existed between the wet and dry plots at each site.

MODELED $CO_2$ EXCHANGE

The natural site modeled $R_{TOT}$ averaged 8.3 and 5.9 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ for dry and wet plots, respectively. Conversely, $E_{DRY}$ and $E_{WET}$ averaged 4.5 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ each, respectively. GEP at $N_{DRY}$ and $N_{WET}$ averaged $-7.3$



FIGURE 3. Daily $CO_2$ exchange ($R_{TOT}$ and GEP) at wet and dry plots for a) natural and b) experimental sites over the season.
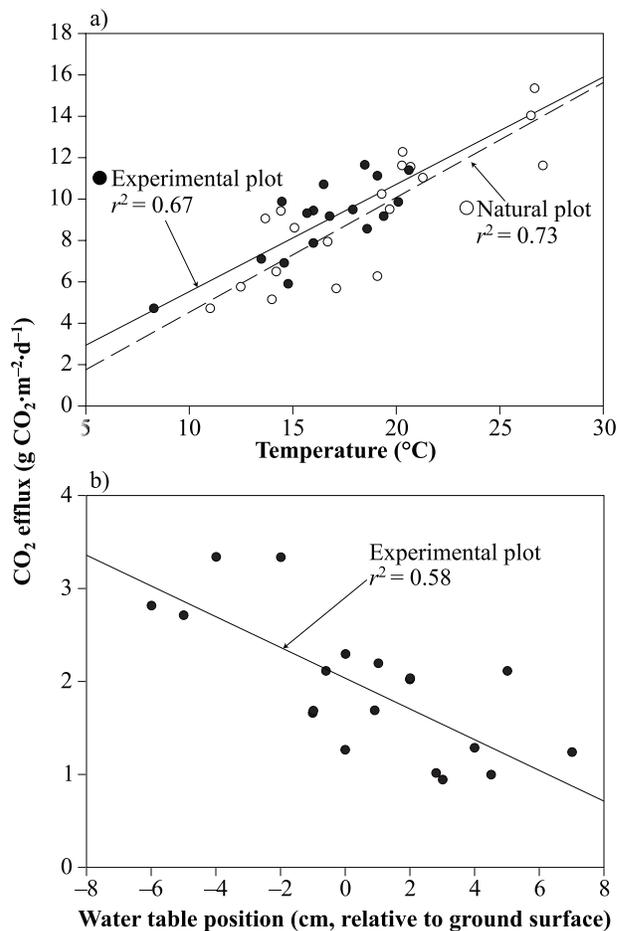


FIGURE 4. Respiration relationships with a) ground temperature for natural (5 cm depth) and experimental (10 cm depth) plots and with b) water table at experimental plots. Negative water table values refer to below the peat surface.

and $-6.6$ g $CO_2 \cdot m^{-2} \cdot d^{-1}$, however, the experimental site GEP was much lower, averaging $-2.2$ and $-1.4$ g $CO_2 \cdot m^{-2} \cdot d^{-1}$ for dry and wet, respectively. Overall, NEE at $N_{DRY}$ and $N_{WET}$ was 0.93 and $-0.72$ g $CO_2 \cdot m^{-2} \cdot d^{-1}$ and at $E_{DRY}$ and $E_{WET}$ 2.3 and 3.2 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ (Figure 6). In general, $R_{TOT}$ was highest at the natural site compared to the experimental site. Similarly, GEP was greater at the natural site, suggesting greater productivity in the vegetative composition compared to the experimental site. Due to the differences in production and respiration at each site, the overall NEE indicates that the natural site was not significantly different from zero; however, the experimental site was a moderate source of $CO_2$ to the atmosphere over the season.

ECOPHYSIOLOGICAL PARAMETERS

Light response curves for the median plot at both the natural and experimental sites illustrate the differences in productivity over the season (Figure 7). Generally, the modeled curves at the natural site maintained robust well-fitted
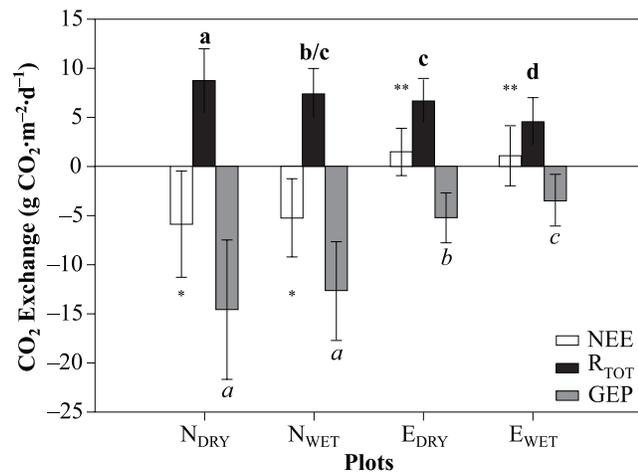


FIGURE 5. Average ($\pm$ SD) seasonal $CO_2$ exchange (NEE, GEP, and $R_{TOT}$) at the natural (N) and experimental (E) sites for wet and dry plots. Significant differences ($P < 0.05$) existed between and within sites and are designated by bold letters (a–d) for $R_{TOT}$, italic letters (a–c) for GEP, and asterisks (*) for NEE.
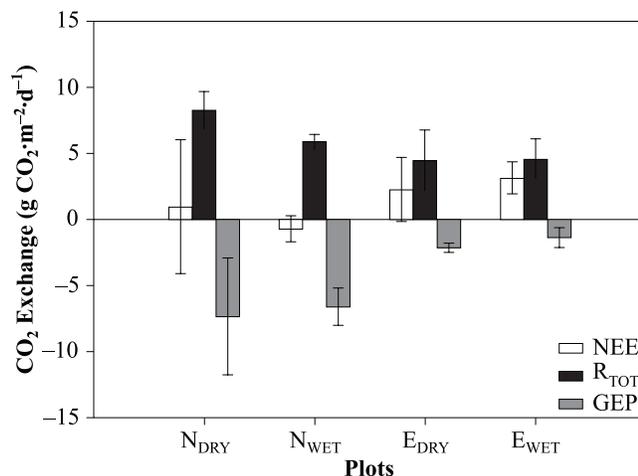


FIGURE 6. Modeled $CO_2$ averages ($\pm$ SD) for the natural (N) and experimental (E) sites at both wet and dry plots.

($r^2$ value) curves over the 3 periods ($r^2$ values: early, 0.71; mid, 0.90; late, 0.96), and variability in GEP around the curves was minimal with high $GP_{MAX}$ values. However, the experimental plot experienced greater variability in GEP, with weaker fits around the curves ($r^2$ values: early, 0.26; mid, 0.68; late, 0.22) with greatly reduced $GP_{MAX}$ values. The median $GP_{MAX}$ at the natural plot ranged from 8.8 to 19.9 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ over the 3 periods, whereas the median $GP_{MAX}$ at the experimental plot ranged from 2.2 to 6.6 g $CO_2 \cdot m^{-2} \cdot d^{-1}$. Furthermore, $GP_{MAX}$ values at the natural site were generally the greatest during the mid-period (July), whereas the experimental site had maximum productivity over the late period (August).

PHYSIOLOGICAL CONDITIONS OF VEGETATION

Vegetation coverage at the natural site ranged between 20 and 90% for mosses and 5 and 50% for shrubs. Conversely, the relative coverage of mosses and shrubs at the experimental site was moderately higher, ranging from 40 to 95% and 5 to 60%, respectively. Mosses and shrubs at the natural site were undisturbed and the vegetation was generally healthy throughout most of the season, experiencing moderate desiccation at a number of plots, particularly in the hummock microforms over the latter half of the season (mid-July to August). At the experimental site, the plots were installed in vegetation that had experienced disturbance from the acrotelm transplant process. Consequently, the plots at the experimental site visually had varying degrees of disturbance, ranging from compaction to highly stressed desiccated moss and shrub covers relative to the undisturbed natural site. Moreover, a number of plots had highly disturbed moss and shrub vegetation with relatively low living biomass. These disturbances can affect the overall productivity of the plots due to the relative amounts of living and dead vegetation present. Measured $GP_{MAX}$ from daily measurements (where PAR > 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) over the season revealed that a moderately disturbed plot generally had higher GEP than a highly disturbed plot at the experimental site (Figure 8). $GP_{MAX}$ at a highly disturbed plot was 4.2 g $CO_2 \cdot m^{-2} \cdot d^{-1}$, whereas a moderately disturbed plot had a significantly higher maximum GEP of 10.9 g $CO_2 \cdot m^{-2} \cdot d^{-1}$. Furthermore, the variability in $GP_{MAX}$ over the season was greatest at the highly disturbed plot, whereas the moderately disturbed plot had a moderately steady increase in $GP_{MAX}$ over the season.

**Discussion**

As mentioned earlier, natural peatlands are a net long-term sink of atmospheric $CO_2$. However, cutover peatlands represent a persistent source of atmospheric $CO_2$, with carbon loss estimated at 300 to 400 g $C \cdot m^{-2} \cdot y^{-1}$ (Waddington & Price, 2000; Waddington & McNeil, 2002; Petrone, Waddington & Price, 2003) due to enhanced peat oxidation (Greenwood, 2005). While Schothorst (1977) suggested that oxidation should decrease with time since abandonment due to a decrease in substrate quality, most measurements of $CO_2$ exchange in cutover peatlands suggest otherwise. For example, Waddington, Warner, and Kennedy (2002) found that older cutover peatlands lost more carbon than
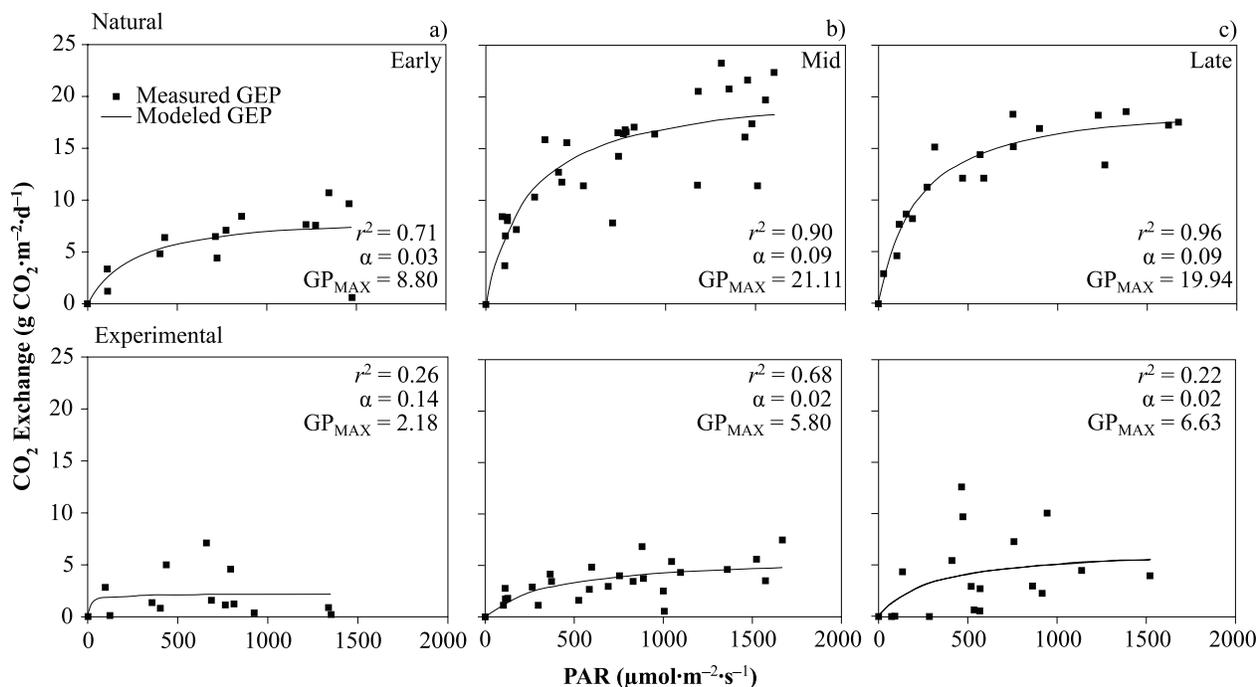
FIGURE 7. Modeled light response curves for a natural and experimental plot, showing the differences in GP$_{MAX}$ at a) early (June), b) mid (July), and c) late periods (August).
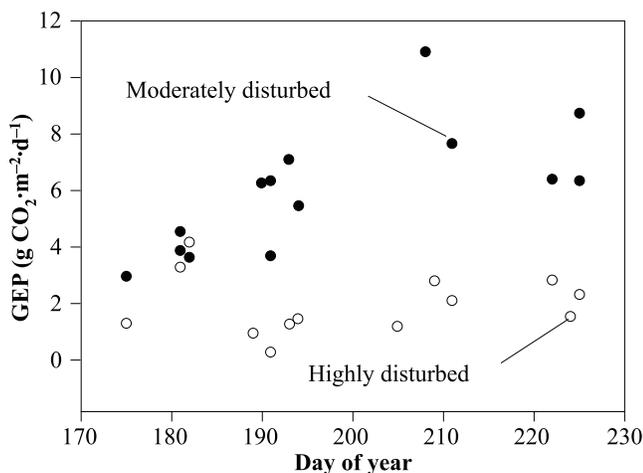


FIGURE 8. GP$_{MAX}$ (PAR > 1000 μmol·m$^{-2}$·s$^{-1}$) at moderately disturbed (dark circles) and highly disturbed (open circles) plots at the experimental site.

recent cutover sites. and Greenwood (2005) demonstrated that a cutover peatland was still a large source of CO$_2$ over 20 y post abandonment, releasing between 83 and 136.8 g C·m$^{-2}$ over a 2-y period. Hence, the longer a cutover peatland remains in an unrestored state the greater the total release of CO$_2$ to the atmosphere. Waddington and McNeil (2002) estimated that an 11.5-ha peatland lost 730 t C due to peat oxidation in the first 19 y post extraction because of enhanced decomposition from a low water table and low VMC (Waddington, Warner & Kennedy, 2002). Komulainen *et al.* (1999) showed that CO$_2$ efflux from peatlands can decrease when plots are rewetted. Consequently, it was hypothesized that acrotelm transplanting would result in a decrease in respiration due to wetter conditions and the

removal of the high-quality peat in the lower acrotelm and upper catotelm. Indeed, respiration at the natural site was significantly higher than at the experimental site, with CO$_2$ emissions totalling 144.8 and 203.7 g C·m$^{-2}$ (wet and dry plots) over the study period (May 20 – August 18), while the experimental site emitted only 110.5 g C·m$^{-2}$, representing a large reduction (50–80%) in emissions compared to the natural site over the season. This suggests that transplanting the acrotelm on the cutover surface immediately after extraction may directly benefit restoration through an immediate reduction in respiration. The decrease in respiration at the experimental site can be partly explained by changes in peat VMC dynamics as VMC of the acrotelm has a major control on the gas exchange process (*e.g.,* Silvola, 1986; 1990; Komulainen *et al.,* 1999; McNeil & Waddington, 2003). The experimental site maintained a moderately higher water table over the season and generally wetter surface moisture conditions than the natural site post restoration. CO$_2$ efflux at the experimental site was predominately subject to moisture controls, particularly water table depth, with temperature as a secondary control. As water table position decreased at plots with high VMC (*i.e.,* lawns), CO$_2$ efflux increased with the drawdown, revealing moderately strong negative relationships with plots having $r^2$ values ranging from 0.48 to 0.78. Drier plots (*i.e.,* hummocks) were mainly controlled by moderately strong positive correlations to temperature ($r^2 = 0.59$–0.67), indicating increased efflux with higher temperatures. Lafleur *et al.* (2005) found that a dry peatland was strongly correlated to peat temperature; however, their results suggest that wetter peatlands may have stronger respiration controls with water table depth.

The extraction–restoration process likely influences reduced respiration at the experimental site since a pre-

served portion of the acrotelm is replaced directly on the cutover surface immediately after extraction. Price and Whitehead (2004) showed that VMC under *Sphagnum* cushions was generally 5–14% greater than on adjacent bare cutover peat, which suggests that mosses can regulate local substrate water storage and therefore aid in retaining moisture in peat. Waddington and Warner (2001) noticed a reduction in peat respiration from peat with *Sphagnum* cover *versus* cutover bare peat, indicating that the differences in $CO_2$ efflux from the sites are potentially due to moisture dynamics between cutover and natural sites.

Increasing VMC on cutover peatlands is particularly important for *Sphagnum* moss regeneration and productivity as both can increase with high water levels (Campeau & Rochefort, 1996). As such, it was hypothesized that GEP would be higher at the experimental site and higher than at recently restored peatlands. However, the experimental site experienced significantly lower production over the season. Moreover, the differences in GEP accounted for the greatest influence on the overall net $CO_2$ exchange between the natural and experimental site. Over the study season the natural site (wet and dry) had an overall uptake of −179.2 and −162.0 g C·m$^{-2}$ compared to −54.0 and −34.4 g C·m$^{-2}$ at the experimental plots (wet and dry), representing a reduction of 20–30% in total productivity. The low productivity at the experimental site (despite the reduction in respiration) shifted the site towards a net source of $CO_2$ over the season. Consequently, the net carbon flux over the season at the experimental site (wet and dry) was 78.5 and 56.5 g C·m$^{-2}$, while the natural plots (wet and dry) stored −17.6 and −22.8 g C·m$^{-2}$, respectively.

The productivity and growth of *Sphagnum* in cutover peatlands is limited not only by water availability, but also by drying and wetting cycles (McNeil & Waddington, 2003). Large variability in VMC in the capitula and acrotelm (Cagampan & Waddington, 2007) likely contributed to the low (and variable) GEP at the experimental site due to large changes in moisture, which can suppress photosynthesis and enhance respiration. The diurnal variation in surface moisture was especially high at the experimental plots, with observed wetting and drying cycles of up to 30% in change of moisture (~10 mm) on a daily basis (Cagampan & Waddington, 2007). Consequently, the variability in GEP observed at the experimental site may have been related to the diurnal cycles at the peat surface. Indeed, the scatter in experimental site light response curves was much greater than at the natural site, where moisture conditions were much more stable. Photosynthetic rates of *Sphagnum* mosses can increase with higher water contents (Rydin & McDonald, 1985), suggesting that water availability is important for moss growth and productivity. The drying and subsequent rewetting of the peat can produce an immediate increase of respiration but more importantly shut down photosynthesis for a prolonged period of time (20 d) (McNeil & Waddington, 2003). As a result, the diurnal wetting and drying at the experimental plots may have suppressed the photosynthetic ability (*i.e.,* GEP) of *Sphagnum* for the majority of the season, in turn affecting the carbon balance through enhanced respiration.

While moisture is generally the main control of gas exchange, the disturbance of the vegetation with the trans-

planting process likely had a considerable effect (and possibly the greatest effect) on productivity. The cutting and transplanting of the acrotelm can cause disturbance to the vegetative structure, causing death and desiccation, especially to *Sphagnum* mosses. This in turn can lower GEP significantly due to the lack of photosynthesis, thereby shifting the experimental site towards a net source of $CO_2$. Vegetation at both the natural and the experimental site was comparable in terms of moss and shrub community; however, the physiological "health" of the vegetation, in particular the disturbance to the vegetative structure, may have had a significant effect on photosynthesis. As the acrotelm vegetation is initially removed and subsequently replaced over the cutover surface, the vegetation can be compressed, cracked (macropores and fissures), and even placed on its side or upside down. As a result, the vegetation likely became stressed due to changes in the acrotelm structure, causing some of the vegetation to desiccate and eventually die. This was reflected in productivity, with the results for maximum GEP (PAR > 1000 μmol·m$^{-2}$·s$^{-1}$) at a highly disturbed moss-dominated plot (4.2 g $CO_2$·m$^{-2}$·d$^{-1}$) representing a 40% decrease in maximum productivity compared to a moderately disturbed moss-dominated plot (10.9 g $CO_2$·m$^{-2}$·d$^{-1}$). The percentage of living and dead vegetation at the plots controlled productivity, with plots that had more living vegetation having higher overall productivity. Therefore, the generally low productivity of the plots was offset by higher respiration, shifting the site toward being a source of atmospheric $CO_2$. Interestingly, the greatest productivity was observed during the latter part of the season, corresponding to the growth of new capitula of *Sphagnum* moss. Regeneration of mosses post disturbance appears to increase productivity, and it is expected as the vegetation resettles post disturbance that productivity at the site should increase due to the growth and regeneration of both new and old vegetation. As in traditional restoration, re-establishment and survival of key vegetative species such as *Sphagnum* (the main peat-forming vegetation) will be the indicator in measuring successful restoration, and on-going vegetation surveys by other researchers will allow for the confirmation of this hypothesis in the near future.

Traditional restoration efforts have shown that $GP_{MAX}$ can increase post restoration. Waddington and Warner (2001) showed that a restored peatland at a plot scale (−17.5 g $CO_2$·m$^{-2}$·d$^{-1}$) had 2 times greater maximum production than a natural site (−8.2 g $CO_2$·m$^{-2}$·d$^{-1}$) and almost 3 times that of naturally regenerated cutover peatland (−6.5 g $CO_2$·m$^{-2}$·d$^{-1}$). Similarly, Greenwood (2005) found that $GP_{MAX}$ had an increasing trend over a 3-y period (−7.9 to −35.5 g $CO_2$·m$^{-2}$·d$^{-1}$) at the ecosystem restoration scale. Furthermore, Frolking et al. (1998) obtained modeled $GP_{MAX}$ for natural northern boreal peatlands has ranged from 4.1 ± 0.1 to 7.1 ± 0.5, with an average of 5.2 ± 0.1. Results from this study suggest that while experimental $GP_{MAX}$ was significantly lower on average than that of standard restored sites, it was comparable to the mean maximum for natural northern boreal peatlands. However, $GP_{MAX}$ is likely enhanced at standard restored sites because of the changing and emerging vegetation. Herbaceous vegetation can colonize rapidly after restoration, acting as

pioneer species prior to *Sphagnum* moss re-establishment (Lavoie *et al.,* 2003). This herbaceous vegetation has higher photosynthetic rates compared to moss species such as *Sphagnum* (Griffis, Rouse & Waddington, 2000), which can account for the large differences in $GP_{MAX}$ between natural and standard restored peatlands.

## Conclusion and implications for restoration

Waddington and Price (2000) suggest that it is important to restore an extracted peatland as soon as possible post abandonment to reduce total carbon losses (Waddington & McNeil, 2002) and limit irreversible changes to the peat structure (Price, 1996; 1997; Schlotzhauer & Price, 1999). The acrotelm transplant onto cutover peat approach adopted at the experimental site was successful in maintaining moisture conditions similar to the natural site (Cagampan & Waddington, 2007), but it was still a net emitter of $CO_2$ to the atmosphere during the growing season.

The experimental site in this study did not maintain carbon-accumulating processes at the level of natural or standard restored sites, due to differences in productivity. Nevertheless, the experimental site did maintain limited productivity post-extraction, indicating that the carbon cycling of the system was still functional post disturbance, which suggests that the acrotelm restoration technique has potential to return the ecosystem toward being a natural sink of atmospheric $CO_2$ over a longer period of time. Therefore, it is suggested that the extraction–restoration process use more care in both the removal of the upper peat layers and their replacement on the cutover surface. Limiting surface damage (*e.g.,* compression) and spaces (gaps/fissures) between the transplanted acrotelm blocks may limit moisture variability (see Cagampan & Waddington, 2007 for details) by decreasing lateral expansion and increase survival of the vegetation (*i.e., Sphagnum* moss), thereby increasing overall productivity.

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