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Seasonal Net Ecosystem Carbon Exchange of a Regenerating Cutaway Bog: How Long Does it Take to Restore the C-Sequestration Function?

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Abstract

We measured the net ecosystem exchange (NEE) and respiration rates and modeled the photosynthesis and respiration dynamics in a cutover bog in the Swiss Jura Mountains during one growing season at three stages of regeneration (29, 42, and 51 years after peat cutting; coded sites A, B, and C) to determine if reestablishment of *Sphagnum* suffices to restore the C-sequestration function. From the younger to the older stage *Sphagnum* cover increased, while net primary *Sphagnum* production over the growing season decreased (139, 82, and, 67 g m^{-2} y^{-1} for A, B, and C respectively), and fen plant species were replaced by bog species. According to our NEE estimations, over the vegetation period site A was a net CO_2-C source emitting 40 g CO_2-C/m^2 while sites B and C were accumulating CO_2-C, on average 222 and 209 g CO_2-C/m^2, respectively. These differences are due to the higher respiration in site A during the summer, suggesting that early regeneration stages may be more sensitive to a warmer climate. Methane fluxes increased from site A to C in parallel with *Eriophorum vaginatum* cover and vascular plant leaf area. Our results show that reestablishing a *Sphagnum* cover is not sufficient to restore a CO_2-sequestrating function but that after circa 50 years the ecosystem may naturally regain this function over the growing season.

Key words: carbon sequestration, cutover bog, peatland restoration, photosynthesis, respiration, secondary succession.

Introduction

Northern peatlands are significant sinks and sources of atmospheric trace gases. They act as a sink for atmospheric C, because CO_2 fixation through primary production exceeds the CO_2 release due to the slow decomposition (Clymo 1984). But they also produce methane (CH_4), a much more effective greenhouse gas than CO_2, in the water-saturated, anaerobic peat. Therefore, they have both a warming and cooling effect on global climate (Frolking & Roulet 2007). Of the different types of peatlands, rain-water fed (ombrotrophic) *Sphagnum*-dominated peatlands (i.e. raised bogs) have especially high peat accumulation potential (Clymo et al. 1998).

In many areas, such as Western Europe and South-Eastern Canada, bogs have been extensively drained for agriculture or forestry, or exploited for peat (Joosten & Clarke 2002). Restoration of peatland remnants has become an important conservation issue and aims at increasing biodiversity, reestablishing characteristic vegetation, and restoring the C-sequestration function (Grosvernier et al. 1995; Chapman et al. 2003; Gorham & Rochefort 2003). It is generally believed that the C storage function of bogs can be restored through revegetation of the mined surface and especially by restoring a *Sphagnum* cover (Rochefort 2000; Waddington & Warner 2001).

However, reestablishing typical bog vegetation including *Sphagnum* is not straightforward and in most cases the long-term fate of the restored surfaces is unclear (Feldmeyer-Christe et al. 2001; Gorham & Rochefort 2003). Although some studies show that regenerating mined bogs may act as C sinks (Tuittila et al. 1999; Waddington & Warner 2001; McNeil & Waddington 2003; Tuittila et al. 2004; Bortoluzzi et al. 2006), there is also evidence that the reestablishment of a *Sphagnum* carpet may not be sufficient to restore the C-sequestration function of the ecosystem (Francez et al. 2000;

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Glatzel et al. 2004). To date, however, only one study has focused specifically on the C balance of regenerating cutover bogs in marginal regions for raised bog development as the French Jura Mountains and this study focused on the very early regeneration stages and not on fully vegetated surfaces (Bortoluzzi et al. 2006).

We studied the vegetation and carbon balance of a regenerating mined peatland in the Swiss Jura Mountains. We measured and modeled photosynthesis (P_{G}) and respiration (R_{tot}) fluxes and methane emissions during one growing season in three fully vegetated regeneration stages (respectively 29, 42, and 51 years after the abandonment of peat exploitation). The vegetation changed from a poor fen to a bog along the succession. We hypothesized that the C sink function would increase over the regeneration sequence owing to shifts in the balance between ecosystem respiration and net primary production (NPP). We expected such a shift to be related to the increased abundance of rootless cryptogamic plants and decreased abundance of vascular plants and associated root exudation along the gradient. This shift disconnects (physically and chemically) the productive acrotelm from the respiring catotelm. Likewise, we hypothesized that methane production would be stimulated by a higher abundance of vascular plants at the less advanced regeneration stage as methanogenesis is strongly dependent on decomposition products. Our models were designed to identify the origin (CO_2, CH_4) and magnitude of these carbon losses as a function of simple biotic and abiotic variables.

Methods

Study site and Experimental Design

The study site is a 14.5-ha cutover bog in the Swiss Jura Mountains (La Chaux d'Abel; 47°10′N, 6°57′E; 1,040 m a.s.l.). The mean annual temperature and precipitation (1980–2004) are 6.4°C and 1,463 mm/yr. Exploitation began during World War II (WWII) and was interrupted progressively. Three zones (coded sites A, B, and C) were chosen as representative of different regeneration stages (A representing the youngest and C the oldest). In site C, clear cuts were stopped just after WWII, while in site B the clear cuts stopped in 1963 (Grünig et al. 1986). Site A was exploited last until around 1976 and mowed until 1995. A few scattered birch trees are growing in sites A and B, while the tree density and height are higher in site C. The three sites are situated in the same peatland complex in the same geomorphological depression and underlying geological basement and likely share the same or similar developmental history. The area is flat with no visible surface runoffs. The peat depth is on average: 1.43 m in site A, 1.30 m in site B, and 2.19 m in site C. In each site, four plot-replicates of 1.5 × 1.5-m in size (coded 1–4) were randomly selected. The sites were representative of the succession gradient present and that was attested through historical data, dendrochronology of tree stands as well as the recovering vegetation. Within each plot one 30-cm diameter aluminum collar was inserted 10 cm in the surface for gas analyses.

Environmental Data

Air and peat temperature, ground water level, and solar irradiance were measured in each plot every week from May to October 2005. Air temperature (T) was measured at 30-cm height and the soil temperature at 5- ($t5$), 10- ($t10$), and 30-cm ($t30$) depth. The ground water level (wt) was measured in piezometers. Solar radiation was measured using a photosynthesis active radiation (PAR) probe (model PAR-1; PP Systems, Hitchin, United Kingdom), directly connected to the portable Infrared Gas Analyser (IRGA). The radiation was measured in mol m^{-2} second^{-1}, proportional to the number of incident photons between 400 and 700 nm.

Regeneration Age and Vegetation

The minimal time since the end of the peat exploitation and the beginning of regeneration was determined by tree ring analysis of 11 birches. Since site A was mowed until 1995, trees growing in the vicinity and in comparable situation in terms of vegetation and topography were chosen for coring. For sites B and C, trees growing nearby the plots were selected. Birch tree ages were significantly different among sites (Kruskal–Wallis χ^2, $df = 2$, $p < 0.001$), with means of, respectively, 22.0 (SD = 2.7), 35.0 (SD = 7.8), and 42.7 (SD = 4.6) years. In site B, exploitation was stopped in 1963 (information from local farmers) and so we conclude that there is a lag of 7 or 8 years between the end of peat harvesting and the establishment of the first birch trees. Applying this lag to all sites we get ages of 29, 42, and 51 years.

The vegetation was analyzed in each plot with the "point-quadrat" method (Goodall 1952) in August using a 37.5 × 25-cm grid of 150 points fixed at 20-cm height. Nomenclature for plants follows Tutin et al. (1964–1980) for vascular plants and Corley et al. (1981) for bryophytes. *Sphagnum* NPP was measured using the "bottle brushes wires" method as in a previous study (Mitchell et al. 2002). Four wires per plot were inserted into the moss carpet and measured at the beginning and end of the growing season. The difference of length measured on the wires represents the seasonal vertical growth of the *Sphagnum* carpet (L). To estimate *Sphagnum* carpet density (D), a 7-cm diameter core was collected around every wire at the end of the growing season. Mosses were counted and the stem (section 1–3 cm) was weighted (W). *Sphagnum* NPP was determined as:

$$\mathrm{NPP}(\mathrm{g\ m^{-2}\ yr^{-1}}) = W(\mathrm{g/m}) \times L(\mathrm{m/yr}) \times D\,[\mathrm{individuals/m^2}] \qquad (1)$$

Vascular plants leaf area index (LAI) was determined based on the number of individuals and leaves per plant for each dominant species in up to three 5-cm diameter rings per gas measurements collar. The length of 10 leaves per ring was measured four times during the season. Moreover, 10 leaves of each species were collected outside the rings at the beginning of July. These leaves were scanned, and the surface and length were measured using the ImageJ software (Abramoff et al.

2004). The relation between area and length was determined by linear regression. The LAI was obtained as:

$$\text{LAI} = \text{mean length} \times \text{regression coefficient} \times \text{cover} \quad (2)$$

Gas Flux Measurements

Net ecosystem exchange (NEE) of CO_2 and respiration (R_{tot}) rates were estimated by measuring CO_2 fluxes. Measurements were taken every second week during the growing season using the static chamber technique. Calculating NEE for a site or peatland type from chamber measurements is challenging because the existing spatial heterogeneity is not taken into account. Other methods such as eddy covariance measurements would be needed to support chamber measurements but this method is not applicable to the small peatlands with complex spatial patterns over relatively small surfaces and different histories of exploitation and subsequent recovery such as the bogs located in the southern margin of raised bog distribution in Europe and North America. However, our primary goal was to compare the NEE among three sites of different ages and, for this purpose, chamber measurements are adequate. We used a transparent Plexiglas chamber of 24 dm^3 in volume and 30 cm in diameter connected to an IRGA (EGM-1; PP Systems, Hitchin, United Kingdom). Gas fluxes were measured on collars inserted within the plots in microsites representative for the site (i.e. lawns, excluding hummocks or depressions). To complete the measurements under a wide light range, shroud shades of varying transparency were put above the plot and the measurements were repeated. The air was mixed with a fan and the air temperature was monitored. Measurements were not used if the variation of PAR was greater than 50 mol m^{-2} second^{-1} during measurement. Net ecosystem exchange was measured in daylight, while respiration (R_{tot}) was measured by covering the chamber with a dark, insulating sleeve and allowing the system to adapt for 5 minutes. The CO_2 concentration was noted every 15 seconds until the critical points of 300 and 400 ppm were reached (usually after about 1 minute for photosynthesis and 4–6 minutes for respiration). Gross photosynthesis (P_G) was calculated as the difference between NEE and $R_{\text{tot.}}$

$$P_G = \text{NEE} - R_{\text{tot}} \quad (3)$$

We did not measure gas fluxes during the winter period. Winter gas fluxes are primarily C losses from the ecosystem and may cause the net annual C balance to be negative (Yli-Petays et al. 2007). However, unless the pattern of winter C losses is opposite to the summer pattern and of greater amplitude the intersite differences we observe should remain valid (e.g. Alm et al. 1999*a*).

To measure CH_4 emissions, we used a dark PVC static chamber of 21.2-dm^3 volume and 30-cm diameter protected by thermo insulation also reflecting the light. Samples were taken using 9-mL S-Monovettes® syringes. Three samples were taken after a constant accumulation time of 20 minutes, starting 5 minutes after the enclosure was deployed. The CH_4 emission rates were determined by linear regression on the time series as these were as good as expressed through exponential or Gaussian functions. The syringes were sealed by hot glue and stored at 5°C and analyzed within 48 hours. Analyses were made using a TCD gas chromatograph (Varian, micro-GC). The operating range was 1 ppm to 100%. The first column was a Poraplot PPQ 10 m heated at 65°C with an initial pressure of 100 kPa and an injection time of 200 milliseconds. The second column was a Molsieve M5Å 4 m heated at 45°C with an initial pressure of 140 kPa and an injection time of 200 milliseconds. Both columns had helium 60 as carrier gas (purity of 99.9999%). Samples 2.5 mL in volume were pumped into the loop. External multilevel calibrations were made on a broad range of concentrations (in ppm: 1.25 ± 0.0612, 2.5 ± 0.725, 25 ± 0.3525, 500 ± 0.55, 5000 ± 3.345) and adjusted to a straight line with $r^2 = 0.9997$. We added a "free air" median reference point to the three field measures: the zero value of 1.717 ppm (the average value for Switzerland).

NEE Modeling

We used peat, air temperature, water table depth, and PAR (photosynthetic active radiation) as explanatory variables to fit models for respiration and photosynthesis rates. To estimate the seasonal NEE patterns, linear and nonlinear models were built on ln-transformed R_{tot} and P_G, respectively. Total respiration (R_{tot}) and gross photosynthesis (P_G) were modeled using the following equations:

$$\ln R_{\text{tot}} = a_0 + a_1 \times \text{wt} + a_2 \times \text{t30} + a_3 \times T \quad (4)$$

$$P_G = \text{Q} \times \text{PAR}/(k + \text{PAR}) \times \text{wt} + c \times T \quad (5)$$

where wt indicates the water table depth, measured in cm, $t30$ is the peat temperature in °C at 30-cm depth, and T is the air temperature in °C measured 30-cm above the moss carpet. The hourly NEE was estimated over the growing season incorporating the climatic data collected in the nearest meteorological station in Bettlerstock (10 km from the site) in the fitted models. The climate station measured light intensity in sunlight and in the forest. For sites A and B the sunlight values were retained, for site C, which had a tree cover of about one-third, the sunlight values were diminished by one-third of the difference between forest and sunlight values. Hourly water table (wt) and peat temperature at 30-cm depth ($t30$) were extrapolated from the model constructed on the measured data. To estimate the stability of each model, 500 new datasets were obtained by bootstraps. R_{tot} and P_G were modeled for each pseudoreplicate.

For NEE calculation, the model parameter values inferred from the original dataset were used. In addition, R_{tot} and P_G were calculated for each set of pseudoreplicated parameters. The first and third quartiles of these pseudoreplicates are illustrated on the figures as error bars and provide a reasonable indication of the validity of R_{tot} and P_G values. Predicted NEE was finally calculated as the sum of R_{tot} and P_G, while the confidence interval was estimated as the sum of the confidence intervals of R_{tot} plus P_{G}.

Numerical Analyses

Differences among sites in abiotic and biotic environmental data were tested by Kruskal–Wallis tests. In order to estimate the CO_2 and CH_4 rates, linear regressions were fitted on the CO_2 and CH_4 concentrations time series using software R (R Development Core Team, 2006) (Table S1). For the CO_2 rates, linear regressions with adjusted $r^2 < 0.85$ were eliminated (none for respiration rates and 4% of the regression data for photosynthesis). For the CH_4 rates, linear regressions with adjusted $r^2 < 0.6$ were eliminated (13% of the total). The eliminated regressions had anomalies such as a second value lower than the first, but there was no indication of bubbling. To fit linear and nonlinear models for respiration and photosynthesis rates, respectively, peat and air temperature, water table depth, LAI, and PAR were used as explanatory variables.

Results

Environmental Data

Both peat temperature and water level depth did not differ among sites (Kruskal–Wallis χ^2, $df = 2$, $p > 0.05$) (not illustrated). Peat temperatures ranged between 4.5 and 21.8°C at 5 cm, between 5.2 and 16.4°C at 10 cm, and between 6.9 and 15.0°C at 30 cm and showed the same trend at each depth, increasing until August and decreasing afterward. Water table depth ranged between 4.5 and 41 cm, with the minimum depth at the end of June.

Vegetation

Sites A, B, and C have contrasted vegetation (Table 1). *Sphagnum* cf. *fallax* covered 71, 88, and 91% of the surface in sites A, B, and C, respectively (Fig. 1a) and was significantly different among sites (Kruskal–Wallis χ^2, $df = 2$, $p < 0.05$). *Sphagnum* NPP decreased from site A to C (respectively 139, 82, and 67 g m^{-2} yr^{-1}) and was significantly different among sites (Kruskal–Wallis χ^2 test, $df = 2$, $p < 0.05$) (Fig. 1b). The LAI differed significantly among sites (Kruskal–Wallis χ^2, $df = 2$, $p < 0.001$). In all sites, peak biomass was reached by early August with an average of 1.01 in site A excluding plot A2, 4.60 in plot A2, 1.13 in site B, and 1.18 in site C. Leaf area index values were highest in site C throughout the growing season. However, in August, plot A2 biomass was more than double the average of site C.

The vegetation was clearly different among sites (Table 1). Stage A is characterized by a high diversity of fen (e.g. *Carex*

Table 1. Relative abundance (average percentage cover over four plots estimated by point-quadrat) of plant species in three study sites of La Chaux d'Abel cutover bog and average distance based on the Steinhaus similarity index on percentage cover data between pairs of plots within each site.

	Site A (29 yrs)		*Site B (42 yrs)*		*Site C (51 yrs)*	
Species	*Average*	*SE*	*Average*	*SE*	*Average*	*SE*
Anthoxanthum odoratum	5.2	4.9	0.0	0.0	0.0	0.0
Aulacomnium palustre[a]	2.5	1.9	2.2	0.8	4.5	1.7
Avenella flexuosa	0.0	0.0	0.0	0.0	0.2	0.2
Betula nana	3.5	2.1	0.0	0.0	0.0	0.0
Calluna vulgaris	3.2	1.4	0.0	0.0	0.0	0.0
Carex nigra	13.2	5.4	1.2	0.8	0.0	0.0
Comarum palustre	9.7	6.7	2.3	2.3	0.0	0.0
Deschampsia caespitosa	1.3	0.9	0.0	0.0	0.0	0.0
Epilobium palustre	0.0	0.0	0.0	0.0	0.5	0.5
Equisetum palustris	0.2	0.2	0.0	0.0	0.0	0.0
Eriophorum vaginatum[a]	28.0	8.3	32.2	5.8	25.0	3.3
Luzula nivea	0.0	0.0	0.0	0.0	0.5	0.5
Molinia caerulea	0.2	0.2	4.3	1.7	0.0	0.0
Poa pratensis	0.0	0.0	0.0	0.0	0.2	0.2
Polygonum bistorta	1.2	0.7	0.0	0.0	0.0	0.0
Polytrichum commune	5.8	3.8	0.0	0.0	8.0	4.8
Polytrichum strictum	0.5	0.5	0.2	0.2	0.8	0.5
Potentilla erecta	11.5	3.6	6.7	1.9	0.0	0.0
Sphagnum cf. fallax	71.8	2.5	88.0	0.7	88.2	3.7
Trichophorum caespitosum	0.8	0.8	0.0	0.0	0.0	0.0
Vaccinium oxycoccos[a]	0.0	0.0	0.0	0.0	6.0	4.0
Viola palustris	1.0	0.8	2.7	1.2	0.0	0.0
Total cover of bog species in the plots	30.5		34.3		35.5	
Within site heterogeneity[b]	0.36		0.15		0.18	

Time after peat cutting was estimated from birch tree ages and information from local farmers.

Sphagnum magellanicum[a], *Sphagnum rubellum, Sphagnum fuscum*[a] locally present in site C outside the surveyed plots.

[a] Characteristic species of open raised bogs (*Sphagnion magellanici*) (Delarze et al. 1998).

[b] Distance = 1 − Steinhaus similarity (Legendre & Legendre 1998).

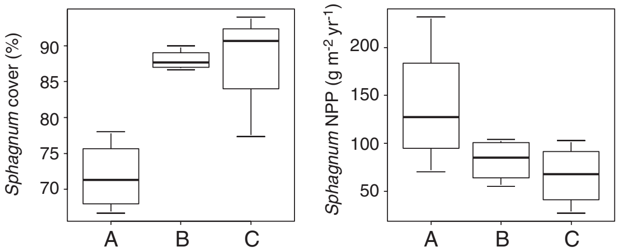

Figure 1. *Sphagnum* cover and NPP in the three regeneration sites. (a) *Sphagnum* cover percentages in sites A (29 years of regeneration), B (42 years), and C (51 years). The central bars indicate the median values, the box limits indicate the first and third quartiles and the whiskers the minimum and maximum values. (b) *Sphagnum* NPP, in g m^{-2} yr^{-1}, produced during the growing season 2005 (calendar weeks) in each site.

nigra, *Comarum palustre*, and *Potentilla erecta*) and meadow species (e.g. *Anthoxantum odoratum*), and also a high interplot variability as assessed by Steinhaus similarity (Legendre & Legendre 1998) (Table 1). Site B has a lower diversity, fewer generalist and fen species, but no characteristic bog species. *Sphagnum* cover is significantly higher in site B than in site A, and not significantly different between sites B and C. This suggests that the regeneration is more advanced, but has not yet reached typical bog conditions (Grosvernier et al. 1995; Matthey 1996). Site C is more diverse than site B and contains more and a higher total cover of characteristic bog species (Delarze et al. 1998) than sites A and B (Table 1).

Measured CO_2 Fluxes

Figure 2 shows the P_G and R_{tot} measurements over the growing season in sites A, B, and C. The seasonal differences were more marked for R_{tot} than for P_G. Furthermore the seasonal variability was less marked in site C than in sites A and B. Site B stood out by having very few low values for P_G in the first half of the growing season.

NEE Balance

For modeling of respiration (Table 2), the contribution of water table depth (a_1) and peat temperature at 30-cm depth (a_2) decreased from site A to site C, where it was negligible. By contrast, the effect of air temperature (a_3) was not significant in sites A and B, but significant in site C. Gross photosynthesis (P_G) variance was mostly explained by PAR combined with water table depth (wt) and air temperature (T) (Table 3). Plot A2 was excluded from the models because of the exceptionally high value of its LAI.

The relationship between observed versus modeled P_G and R_{tot} is shown in Figure 3. P_G values tended to be overestimated for low values and underestimated for high values. For R_{tot}, the errors of estimates are lower and comparable among the three sites.

According to our models (Fig. 4), in summer C-sequestration increased with increasing site age: site A was a net carbon source, site B alternated between sink and source, while site C was a carbon sink. Little or no difference was observed during spring and autumn when all sites accumulated carbon,

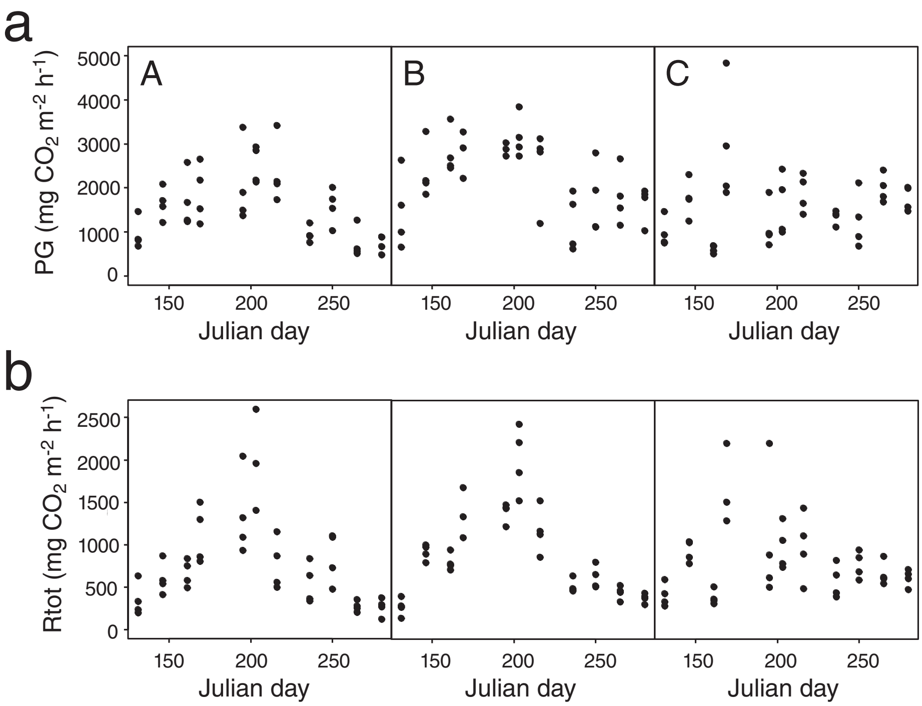

Figure 2. Field measurements of (a) gross photosynthesis (P_G) and (b) total respiration (R_{tot}) for the three study sites A (29 years old), B (42 years old), and C (51 years old). The fluxes are in mg CO_2 m^{-2} h^{-1}.

Table 2. Models coefficients for total respiration (R_{tot}).

	Coefficients for the R_{tot} model: $ln(R_{tot}) = a_0 + a_1 \times wt + a_2 \times t30 + a_3 \times T$				
Site	*a_0*	*a_1*	*a_2*	*a_3*	*Adjusted r^2*
A	**1.877**	**0.058**	**0.295**	—	0.77
	1.860 [1.577:2.141]	0.059 [0.053:0.064]	0.294 [0.272:0.320]		
B	**3.241**	**0.042**	**0.224**	—	0.83
	3.232 [3.094:3.360]	0.042 [0.039:0.045]	0.227 [0.213:0.238]		
C	**4.674**	—	**0.092**	**0.045**	0.45
	4.686 [4.529:4.866]		0.093 [0.079:0.106]	0.05 [0.043:0.055]	

R_{tot} is a function of water table level (wt), peat temperature at 30-cm depth ($t30$), and air temperature (T). The coefficients estimated on the measured data are indicated in bold. Also indicated are the median and the first and third quartiles (in square brackets) estimated on 500 nonparametric bootstrap replicates.

Table 3. Models coefficients for gross photosynthesis (P_G).

	Coefficients for the P_G model: $P_G = Q \times PAR/(k + PAR) \times wt + c \times T$			
	Q	*k*	*c*	*Adjusted r^2*
A	**98.25**	**746.08**	**23.62**	0.58
	98.60 [82.27:127.74]	697.52 [350.03:1456.69]	23.63 [18.23:28.56]	
B	**123.67**	**632.29**	**41.04**	0.61
	126.76 [115.36:142.86]	642.04 [418.62:1019.28]	40.04 [35.09:45.28]	
C	**60.58**	**588.89**	**48.46**	0.30
	66.22 [51.93:84.74]	616.11 [416.72:995.80]	48.06 [42.93:53.71]	

P_G is a function of PAR, wt, and T. The coefficients estimated on the measured data are indicated in bold. Also indicated are the median and the first and third quartiles (in square brackets) estimated on 500 nonparametric bootstrap replicates.

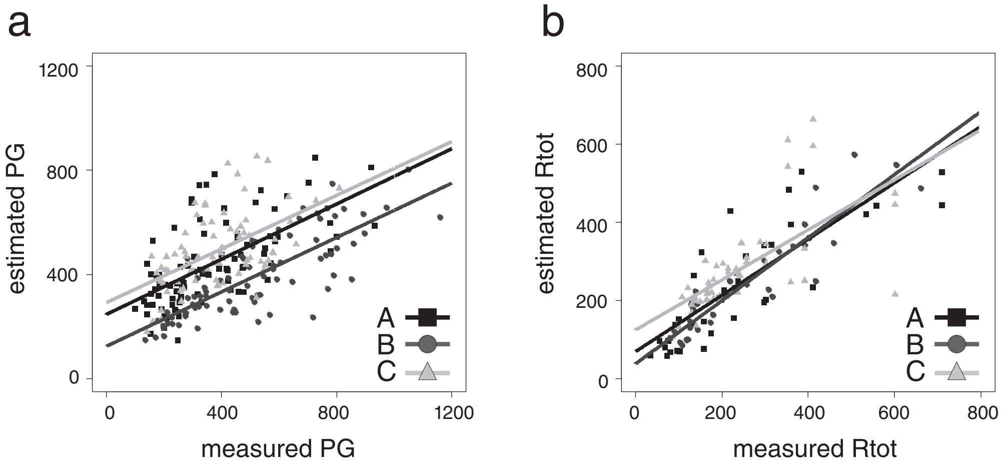

Figure 3. Comparison of field measurements and estimated values in the same environmental conditions for (a) gross photosynthesis and (b) total respiration for the three study sites A (29 years old, black squares), B (42 years old, dark gray circles), and C (51 years old, light gray triangles). The fluxes are in mg CO_2-C m^{-2} h^{-1}.

although site B the most. Our models show that over the growing season, sites A and C had lower respiration rates than site B, while photosynthetic activity was highest in B and lowest in A. As a result, site A was a carbon source, emitting 40 g CO_2-C/m^2, while both sites B and C were carbon sinks (respectively of 220 and 209 g CO_2-C/m^2) (Fig. 5).

CH_4 Emissions

Methane emissions did not show any seasonal trend, but fluxes differed significantly among sites (Kruskal–Wallis χ^2, $df = 2$, $p < 0.001$), increasing from site A to C (respectively 0.42 ± 0.26, 0.52 ± 0.33, and 1.36 ± 0.75 mg CH_4-C m^{-2} h^{-1} in sites A, B, and C) (Fig. 6). Throughout the growing season sites A, B, and C released 1.84, 2.30, and 5.98 g CH_4-C/m^2, respectively.

Discussion

The secondary succession in mined bogs parallels the switch from fen to bog observed during the development of northern bogs where the system changes from sedge-dominated to

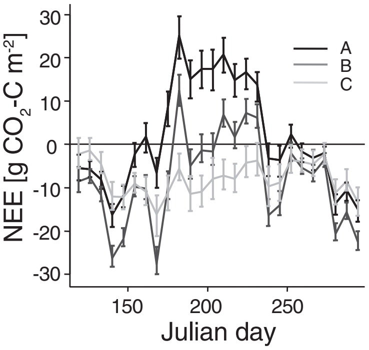

Figure 4. Modeled weekly NEE in g CO_2-C m^{-2} week^{-1} in the three sites A (29 years old, black), B (42 years old, dark grey), and C (51 years old, light grey), during the growing season 2005. Positive signs indicate C losses from the peatland. Error bars indicate the first and third quartiles values obtained by bootstrapping.

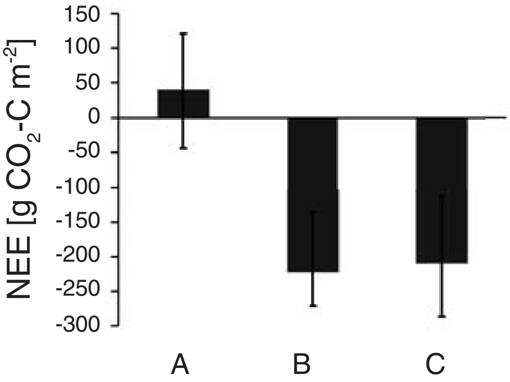

Figure 5. Modeled NEE in g CO_2-C m^{-2} over the 2005 growing season in the three sites A (29 years old), B (42 years old), and C (51 years old). Positive values indicate C losses from the peatland. Error bars indicate the first and third quartiles values obtained by bootstrapping.

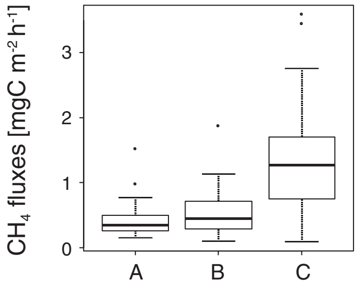

Figure 6. Methane fluxes (mg CH_4-C m^{-2} h^{-1}) measured in the three sites A, B, and C during the growing season 2005. The central bar indicates the median value, the box limits indicate the first and third quartiles and the whiskers the minimum and maximum values if there are.

Sphagnum-dominated communities (Rydin et al. 2006). There is paleoecological evidence for climatic influences on past peatland dynamics: succession from fen toward bog conditions, a process similar to the secondary succession we studied in mined bogs, was slower for peatlands located at the southern fringe of the boreal forest than for those located further north (Kuhry et al. 1993). Our modeling results agree with this: As hypothesized, the three regeneration stages differed in their functioning as well as in the effects of abiotic variables on respiration and photosynthesis.

Environmental Data Regeneration Age and Vegetation

Climatically, the year 2005 was not especially hot or cold. For example, the number of very hot days (above the 80th percentile) measured at low elevation (Neuchâtel) was slightly below the trend calculated from 1900 onward (Rebetez 2004) (updated data, M. Rebetez 2004, Swiss Federal Research Institute WSL, Lausanne, Switzerland, personal communication). The year 2005 was thus representative for the general climate of the early 21st century for the region. We therefore consider our measurements as representative for the functioning of the studied sites under the present climatic conditions.

None of the abiotic environmental variables were different among sites and plots. By contrast, all biological variables differed significantly among sites. The gradient of trees recolonization age agrees with historical information (from local farmers) and the site history inferred from the vegetation. The consistent trends observed for vegetation (e.g. increase of bog indicators) and gas exchange (increasing C sink) from site A to C confirm that the selected sites correspond to a regeneration sequence. Thus our results can be interpreted as revealing the effect of vegetation changes along a regeneration gradient on the functioning of the ecosystem, and not those of changes in abiotic conditions along this sequence. This is important in a management perspective because vegetation surveys are much cheaper and easier than monitoring of abiotic variables.

Sphagnum NPP values are within the range reported by Gunnarsson (2005). The trend for *Sphagnum* NPP was opposite to that of *Sphagnum* cover. A lower *Sphagnum* NPP may be caused by the higher biomass of vascular plants in the later regeneration stages, causing shading (Berendse et al. 2001). Another possible cause is a change in species composition: early stages were dominated by the more minerotrophic species *Sphagnum fallax*, while other ombrotrophic species such as *Sphagnum magellanicum*, *Sphagnum rubellum*, and *Sphagnum fuscum* also occurred locally in site C. These changes in species composition also suggest a decrease in nutrient availability from site A to site C (Hajek & Adamec 2009; Grosvernier et al. 1997).

Contrary to the point-quadrat results, *Eriophorum vaginatum* was the only vascular species present in the gas analyzer collars in site C. This difference is due to the higher vegetation patchiness in site C (data not shown). The larger point-quadrat plots captured more of this diversity than the gas exchange collars, which were in addition inserted in the most homogeneous microsites (flat lawns). This fact has implications for the CO_2 balance (see further).

NEE Models

Gross photosynthesis (P_G) variance was mostly explained by PAR combined with water table depth (wt) and air temperature (T). This agrees with previous studies (Alm et al. 1999*b*; Komulainen et al. 1999). The influence of LAI was negligible, compared to that of wt and T. It should be noted that LAI does not include mosses. *Sphagnum* grows mostly in spring and fall and often suffers from drought in summer. By contrast, vascular plants and mosses such as *Polytrichum strictum* grow mostly in summer (Mitchell et al. 2002). Leaf area index only captures part of these patterns and this may explain why T, PAR, and wt were selected in the models but LAI not.

For modeling of respiration, $t30$ and wt were more important for sites A and B than for site C. This means that variations in water table depth and peat temperature have a strong effect on respiration in younger sites but less so for the more advanced site. This suggest that in a climate change perspective, the C-sequestration function of advanced regeneration stages may be more resistant to future increase of temperature and/or a high variation of pluviometry while early regeneration stages may lose C at a higher rate. The influence of temperature and water table on respiration rates can be easily explained since it has been shown that the water table determines the boundary between aerobic and anaerobic conditions (Kettunen et al. 1999), while the temperature influences the metabolic rate of organisms.

Furthermore, the observed differences in vegetation, biomass (LAI), and the type and abundance of plant roots among the sites determine the amount of nutrients and moisture available to the microbes (Silvola et al. 1996; Artz et al. 2008), the organic matter available to microorganisms (Crow & Wieder 2005) and ultimately their response to abiotic factors.

NEE in the Three Regenerating Sites

The average rates we measured are comparable to those observed in Canada (Bellisario et al. 1998; McNeil & Waddington 2003) and Finland (Alm et al. 1999*a*; Komulainen et al. 1999; Tuittila et al. 1999; Yli-Petays et al. 2007).

Our data show that although the C-sequestration capacity increases from early to late succession, reestablishing a *Sphagnum* cover is not sufficient to restore C-sequestration in mined peatlands. The early regeneration stage was still a C source despite a 71% *Sphagnum* cover. The intermediate regeneration stage had a higher (88%) *Sphagnum* cover and was more efficient in sequestering C. Sites A and C had lower respiration rates than site B while photosynthetic activity was highest in B and lowest in A. These differences mainly appeared during summer when the model-estimated C-sequestration augmented with increasing age of regeneration. Only little or no difference was observed during spring and autumn (Figs. 3 & 4). The resulting NEE shows that site A is a carbon source while sites B and C both act as significant carbon sinks over the growing period. The higher *Sphagnum* cover and LAI in sites B and C may explain their stronger CO_2-C uptake. *Sphagnum* necromass decomposes slower than that of graminoids in bogs (Coulson & Butterfield 1978; Aerts et al. 1999). Even though carbon accumulation is similar in sites B and C, site B is more active than site C (i.e. higher P_G as well as R_{tot}). This is in agreement with vegetation differences between the two sites: site B still has poor fen vegetation with highest *Eriophorum* cover, while site C had bog-like vegetation. The growth form and biomass allocation pattern of *E. vaginatum* optimizes its productivity and CO_2 sequestration capacity (Chapin et al. 1979; Kummerow et al. 1988; Alm et al. 1999*b*; Komulainen et al. 1999; Tuittila et al. 1999). Furthermore, root exudates from vascular plants stimulate soil biological activity (Silvola et al. 1996; Crow & Wieder 2005) and thus respiration.

As we did not observe any significant differences in abiotic factors among the sites, the differences in ecosystem functioning are most likely caused by unmeasured factors linked to the vegetation and/or the peat properties. This suggests that changes in the vegetation modify the functioning of the ecosystem by changing how abiotic factors affect the C balance. Vegetation changes may also directly influence ecosystem functioning by affecting the quality of organic matter both in litter and root exudates.

Over the regeneration sequence, the modeled influence of temperature and water table on respiration decreased. This suggests that the C-sequestration capacity of the most advanced regeneration stage will be more resistant to temperature and/or water table changes, at least within the range of observed values for these two variables.

CH_4 Emissions

The CH_4 emission rates we measured are comparable to rates observed in southern Québec (Moore & Knowles 1990; Bubier et al. 1993; Strack et al. 2006) and Central Finland (Minkkinen & Laine 2006). Methane fluxes were two to three times higher in site C than in the other two sites. This can be related to the larger LAI observed in site C and especially the abundance of *E. vaginatum* in the measuring collars. Indeed aerenchyma pathways through vascular plants can reduce CH_4 oxidation from 90% to no more than 55% by bypassing the diffusion through the peat and allowing methane to reach the surface faster and avoiding oxidation (Ding et al. 2005), and *E. vaginatum* is particularly effective in channeling CH_4 (Schimel 1995; Strand 2002). Finally, the heterogeneity in the distribution of *Sphagnum* species can also influence the amount of CH_4 reaching the surface, since CH_4 oxidation can differ among *Sphagnum* species owing to differences in the structure of the moss carpet (Basiliko et al. 2004).

We did not find any seasonal variation in CH_4 emission rates. This was surprising given that CH_4 emission rates are generally correlated to water table position, at least within *Sphagnum*-dominated vegetation (i.e. excluding rich fens) (Bubier et al. 1995). However, the gradient of methane emissions we observed corresponds to a gradient of LAI, and such relationships have previously been reported in *Sphagnum*-dominated peatlands (Greenup et al. 2000). The CH_4 cycle in peatlands is governed by peat type, surface vegetation, climate, and hydrology, but there are still many open questions about the controls over methane production and release from these wetlands (Alm et al. 1999*b*; Vann & Megonigal 2003; Whalen 2005; Hines et al. 2008).

Conclusions

Our main goal was to determine if reestablishment of *Sphagnum* suffices to restore the C-sequestration function in regenerating cutover bogs located at midlatitude in Europe. According to our NEE estimations, over the vegetation period the youngest site (29 years of regeneration) was a net CO_2-C source emitting 40 g CO_2-C m^{-2} while the intermediate and older sites (42 and 51 years) were accumulating CO_2-C, on average 222 and 209 g CO_2-C m^{-2}, respectively. Methane fluxes increased from site A to C in parallel with *Eriophorum vaginatum* cover and vascular plant leaf area in the gas measurement collars. Our results show that reestablishing a *Sphagnum* cover is not sufficient to restoring a CO_2-sequestrating function but that after circa 50 years the ecosystem may regain this function, at least over the growing season.

Our model results show that the strongest differences among regeneration stages are observed during the warmer period; the lower C-sequestration capacity of the early regeneration stage is due to the higher values of total respiration during the summer. This could suggest that under a warmer climate bog regeneration may be more difficult or even impossible. Experimental studies are, however, required to assess this more precisely.

Implications for Practice

- The study of a regenerating cutaway bog in the Swiss Jura Mountains showed that the restoration of continuous *Sphagnum*-dominated vegetation similar to natural peatlands does not necessarily indicate that the C-sequestration function is restored.
- C-sequestration is mostly governed by respiration rates, which in early regeneration phases respond strongly to temperature and water table depth and is thus high in the summer.
- C-sequestration increases from early to advanced regeneration stages and the advanced stage with vegetation most similar to that of pristine bogs was a C sink over the growing season.
- The C sequestering function of advanced regeneration stages is less affected by changes in temperature and water table depth. These ecosystems may thus resist better to changes in climate while the succession of early regeneration stages toward more advanced stages may become increasingly difficult.

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Table S1. Relative abundance of plant species in each plot of the three study sites in La Chaux d'Abel peatland (Swiss Jura).

Supplementary Table 1. Relative abundance of plant species in each plot of the three study sites in La Chaux d'Abel peatland (Swiss Jura).

Species	Site A – 29 yrs Plot 1	Plot 2	Plot 3	Plot 4	Site B – 42 yrs Plot 1	Plot 2	Plot 3	Plot 4	Site C – 51 yrs Plot 1	Plot 2	Plot 3	Plot 4
Anthoxanthum odoratum	20.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aulacomnium palustre *	0.0	0.0	2.0	8.0	3.3	2.0	0.0	3.3	5.3	4.7	0.0	8.0
Avenella flexuosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Betula nana	0.0	5.3	8.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calluna vulgaris	0.0	2.7	3.3	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carex nigra	27.3	6.7	3.3	15.3	0.0	3.3	0.0	1.3	0.0	0.0	0.0	0.0
Comarum palustre	9.3	0.7	28.7	0.0	9.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Deschampsia caespitosa	1.3	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epilobium palustre	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Equisetum palustris	0.0	0.0	0.67	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eriophorum vaginatum *	16.7	49.3	32.7	13.3	20.0	24.7	42.7	41.3	28.0	15.3	26.7	30.0
Luzula nivea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Molinia caerulea	0.0	0.0	0.7	0.0	9.3	3.3	2.0	2.7	0.0	0.0	0.0	0.0
Poa pratensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Polygonum bistorta	0.0	2.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polytrichum commune	0.0	0.0	7.3	16.0	0.0	0.0	0.0	0.0	0.0	0.0	19.3	12.7
Polytrichum strictum	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.67	1.33	0.0	0.0	2.0
Potentilla erecta	5.3	16.0	5.3	19.3	2.7	8.0	11.3	4.7	0.0	0.0	0.0	0.0
Sphagnum cf. fallax	78.0	69.3	73.3	66.7	86.7	87.3	88.0	90.0	90.7	90.7	94.0	77.3
Trichophorum caespitosum	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vaccinium oxycoccos *	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7	0.0	7.3
Viola palustris	3.3	0.7	0.0	0.0	6.0	0.0	2.0	2.7	0.0	0.0	0.0	0.0
Total cover of bog species	16.7	49.3	34.7	21.3	23.3	26.7	42.7	44.7	33.3	36.7	26.7	45.3

Note: *S. magellanicum* *, *S. rubellum, S. fuscum* * locally present in site C outside the surveyed plots.
* Characteristic species of open raised bogs (*Sphagnion magellanici*) (Delarze et al. 1998)