The importance of groundwater-derived carbon dioxide in the restoration of small *Sphagnum* bogs

Význam oxidu uhličitého ve vodě při obnově vrchovišť

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Dedicated to Kamil Rybníček and Eliška Rybníčková on the occasion of their 80th birthdays

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Essential for successful bog restoration is the reestablishment of *Sphagnum* mosses. High carbon dioxide availability has been shown to be of great importance for the growth of *Sphagnum* mosses. In well-developed *Sphagnum* bogs large amounts of carbon dioxide are produced by (an)aerobic decomposition of the peat layer. In cut-over *Sphagnum* bogs this carbon source is often greatly reduced. In this study the importance of groundwater-derived carbon dioxide is demonstrated in aquatic environments, where *Sphagnum* species have started to form floating mats after former cut-over activities by farmers. We discuss the results of measures taken to restore one of the largest wet heathland reserves in western Europe. After rewetting, some bogs developed markedly well, whereas others did not. The developmental success of 10 small bogs was quantified by analysing aerial photographs and sampling of surface and groundwater. The analysis of the ground- and surface water samples revealed that in the well-developed bogs there were significantly higher TIC/CO_2 concentrations than in poorly developed bogs. It is concluded that in the early stages of bog formation the growth of *Sphagnum* is better in bog systems that are fed by an inflow of carbon-rich groundwater from outside the bog. The present findings suggest that high carbon dioxide availability is a prerequisite for the successful reestablishment of *Sphagnum* mosses in peat-bog restoration projects and that carbon-rich groundwater can substitute for the carbon dioxide from decomposing peat.

Keywords: bog restoration, CO_2, groundwater, hydrology, photosynthesis, rewetting

Introduction

Due to the important role of mires in the global carbon cycle (Joosten & Clark 2002) and their unique ecological value, much effort is dedicated globally to the restoration of damaged bogs. However, the restoration of many bogs has proven to be fairly complicated and not always successful (Vermeer & Joosten 1992, Money & Wheeler 1999, Rochefort & Price 2003, Grootjans et al. 2012).

Essential for successful bog restoration is the reestablishment of *Sphagnum* mosses followed by the redevelopment of a functional acrotelm, leading to a self-sustaining peat-forming system (Money & Wheeler 1999, Smolders et al. 2003, Money et al. 2009). Since wet conditions, a high water table and precipitation are essential if *Sphagnum* is to thrive (e.g. Robroek et al. 2009), the creation of suitable wet conditions is a prerequisite in restoring peatlands. Often rewetting is realized by inundating large areas to ensure wet conditions throughout the year (Money & Wheeler 1999, Smolders et al. 2003). The water layer can be colonized by aquatic *Sphagnum* species, especially *Sphagnum cuspidatum*, which form dense mats on which acrotelm-forming species like *S. magellanicum* and *S. papillosum* might become established (Money & Wheeler 1999). However, inundating large areas of peat often results in large water bodies, in which *Sphagnum* growth is severely hampered. The lack of success in recolonization by aquatic *Sphagnum* species in rewetted bog remnants is ascribed to the limited availability of light and/or CO_2 (Money & Wheeler 1999, Smolders et al. 2001, Tomassen et al. 2010).

Sphagnum mosses are known to be obligate CO_2 users (Bain & Proctor 1980) and therefore limited by the diffusive supply of CO_2 to the site of carbon fixation. In very wet conditions the *Sphagnum* mosses are surrounded by a thick water layer, which lowers CO_2 conductivity resulting in a reduced photosynthetic rate (Silvola 1990, Williams & Flanagan 1996). Consequently, high rates of underwater photosynthesis can only be sustained when the leaves are surrounded by water with high levels of CO_2 (Silvola 1990, Paffen & Roelofs 1991, Jauhiainen & Silvola 1999, Smolders et al. 2003).

In well-developed bogs CO_2 is produced in large quantities by the decomposition of peat (Bridgham & Richardson 1992, Smolders et al. 2001, Waddington et al. 2001, Glatzel et al. 2004). Carbon dioxide concentrations in the pore water can reach up to several millimoles per liter (Smolders et al. 2003), which compensates for the low diffusion rates and ensures sufficient photosynthetic carbon fixation (Silvola 1990, Maberly & Madsen 2002). This so-called substrate-derived CO_2 is an important carbon source for aquatic and also emergent *Sphagnum* mosses (Baker & Boatman 1990, Paffen & Roelofs 1991, Riis & Sand-Jensen 1997, Smolders et al. 2001). Under anoxic conditions, the methane production in the catotelm may exceed that of CO_2. Methanotrophic bacteria can oxidize this methane to CO_2, which can be used as a carbon source by *Sphagnum* mosses (Raghoebarsing et al. 2005, Kip et al. 2010).

However, after peat extraction little of the organic material remains and as a consequence CO_2 release by decomposition is greatly reduced or ceases altogether. The highly decomposed, humified peat that is left behind, can only sustain a limited production of CO_2 (and methane) (Bridgham & Richardson 1992, Waddington et al. 2001, Glatzel et al. 2004, Tomassen et al. 2010). For successful restoration of bogs in which most of the peat has been removed, as well as for the initial establishment of peat mosses on mineral substrates, an additional source of carbon might be essential for the reestablishment of *Sphagnum* mosses.

This study focuses on the potential role of CO_2 in the development of small *Sphagnum* bogs in a field situation in the Dwingelderveld reserve. This reserve is characterized by numerous small *Sphagnum* bogs, which were all greatly degraded in the past, due to peat cutting and large-scale drainage for the purpose of forestry. From 1988 onwards, these bogs were rewetted, but the developmental success varied significantly between bogs;

some bogs developed well, whereas others did not. It is hypothesized that in these hydrologically degraded bog remnants the restoration of *Sphagnum* growth is limited by the availability of CO_2. We hypothesize that the bogs that are developing well in this area are being fed by lateral inflow of carbon-rich groundwater. Groundwater with high concentrations of inorganic carbon that enter a bog will release high amounts of CO_2 when it comes into contact with the more acidic water around the *Sphagnum* mass. We expect, therefore, that this increase in the availability of CO_2 will stimulate the growth of aquatic *Sphagnum* mosses and subsequent bog development.

Materials and methods

Study area

Study area is the "Dwingelderveld", one of Europe's largest areas of wet heathland (about 3500 hectares), situated in the northern part of the Netherlands (52°49'6.71"N, 6°27'28.48"E). The landscape consists of pine forest, wet and dry heathland and many small peat bogs (0.5–5.0 ha.) scattered throughout the area (Fig. 1). The presence of boulder clay underneath the reserve is responsible for the generally wet character of the area. Wind erosion resulted in differences of up to 5 m in the depth of the cover of Pleistocene sand. During the second half of the last century most of the wet heathland and bogs dried out due to drainage activities both in the reserve (for the benefit of pine plantations) and surrounding brook valleys (for the benefit of agriculture). Many small bogs were also subjected to small-scale peat cutting by farmers. These activities ended around 1975.

Between 1985 and 1988 large scale rewetting measures, i.e. the drainage ditches in the surrounding forests and in the bogs were closed. Around the bogs many trees were also cut to reduce their shading effect on the bogs. These activities led to a considerable increase in the water levels in the bogs, but the regrowth of floating *Sphagnum* carpets in the different bogs varied considerably. The mean depth of the water in the bogs after restoration was 80–100 cm (Verschoor et al. 2003). In some parts of the bogs the water was deeper (Zandveen; 150 cm and Diepveen > 4 m). Interestingly, Grootjans et al. (2003) observed that bogs with abundant growths of *Sphagnum* were located in old erosion gullies, while those without *Sphagnum*-dominated succession were not in or at the edge of gullies. In these erosion gullies, impermeable podsolic layers stretch out beyond the border of the bogs. The groundwater levels in the sandy hills are generally higher than in the gullies (Verschoor et al. 2003). Since the vertical conductance of these podsolic layers is very low, a horizontal subsurface flow of groundwater towards the bogs is facilitated, prolonging the residence time of water in the soil, which possibly results in the groundwater becoming enriched with inorganic carbon (Grootjans et al. 2003, Fig. 2).

Classification of the peat bogs

At 10 different bogs 20 sampling sites were selected (Fig. 1; Table 1). Aerial photographs of the area taken in1982 and 2006 were used to determine the developmental success of the bogs at each of the sampling sites. We evaluated the success of bog development by measuring the increase in surface area covered by floating mats of *Sphagnum* mosses; nota bene not in terms of infilling of the bog systems by peat.

Fig. 1. – Aerial photograph of the research area in the "Dwingelderveld". All bogs in this part of the nature reserve are outlined by a black line. The bogs used in this field study are indicated by a number corresponding to the numbers used in Table 1. The numbers of the poorly developed bogs are underlined. The locations of the sampling sites are indicated by black circles. The white spot on the Diepveen (6) photograph is open water, which was confirmed by field observations.

Using image analysis software (ImageJ, version 1.41o, National Institute of Health, USA) the area of open water at each site in both 1982 and 2006 was calculated based on differences in the grey scale between vegetation and open water. The developmental success was determined by calculating the relative decrease in the surface area of open water between 1982 and 2006. The following formula was used: $(\%OW_{1982} - \%OW_{2006}) / \%OW_{1982}$, where %OW is the percentage of the surface of the bog occupied by open water in 1982 or 2006. In this analysis of the aerial photographs the vegetation was assumed to be bog vegetation dominated by *Sphagnum* mosses. This was validated by

Table 1. – Names, coordinates, the percentage of open water in 1982 and 2006, the decrease in open water and the developmental success of the bogs investigated at "Dwingelderveld". The developmental success of the bogs was determined by calculating the relative decrease in the area of open water in 2006 compared to that recorded in 1982; + indicates a well-developed bog, – indicates a poorly developed bog. For three bogs the developmental success was not determined using aerial photographs and this is indicated by *. See the Materials and methods section for a more detailed explanation. The numbers in the first column correspond with those in Fig. 1.

No.	Name	Coordinates	Surface open water %		Decrease in open water (%)	Developmental success
			1982	2006		
1	Barkmans Veen	N52°49.423" E6°26.283"	29	6	78	+
2	Groote Veen	N52°49.178" E6°25.991"	51	0	100	+
3	Reigersplas	N52°50.019" E6°26.946"	62	0	100	+
4	Adderveen	N52°49.885" E6°27.058"	74	43	42	–
5	Cootjes Veen	N52°49.000" E6°26.244"	0	0	*	–
6	Diepveen	N52°49.140" E6°26.404"	52	56	–8	–
2	Groote Veen East	N52°49.171" E6°26.243"	71	0	*	–
7	Kliploo	N52°50.082" E6°26.380"	100	98	2	–
8	Schurenberg	N52°49.551" E6°25.951"	100	83	17	–
9	Veerles Veen	N52°49.003" E6°25.992"	61	0	*	–
10	Zandveen	N52°49.694" E6°26.471"	85	69	19	–

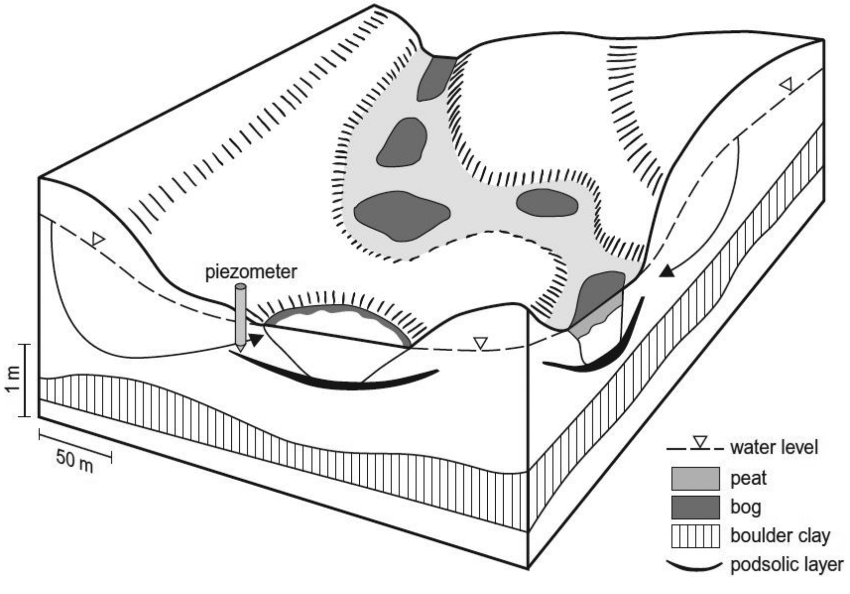

Fig. 2. – A cross section of a part of the study area in the "Dwingelderveld". The small bogs are situated in gullies, which are surrounded by a Pleistocene sand deposits. A layer of boulder clay is present underneath the whole area, resulting in wet conditions throughout the area. The bogs are characterized by the presence of podsolic layers, responsible for the wet conditions and bog development. Note the lack of peat development in the bog in the forefront, which lies outside the gully. Groundwater samples were taken adjacent to the border of the bogs, using piezometers.

field observations. Most of the *Sphagnum* cover was either *S. cuspidatum* or *S. fallax*, although in 2006 terrestrial *Sphagnum* species, such as *S. magellanicum* and *S. papillosum,* were also present in the more advanced developmental stages of the floating mats. In some cases, Cootjes Veen, Groote Veen East and Veerles Veen, the analysis of the aerial photographs had to be adjusted. Here the vegetation did not consist of *Sphagnum*, but almost entirely of vascular plants (e.g. *Molinia caerulea*). Consequently, these bogs were classified as poorly developed bogs.

Sampling and analysis of water

At all the sites both the groundwater and surface water were sampled in February and April 2007, August and October 2008 and September 2009. Groundwater samples were collected using piezometers (∅ 32 mm PVC tubes with nylon filters) and a peristaltic pump. The piezometers were placed just outside but within 10 m of the bogs and on the slopes of the gully, always with the filters above the impervious layer. The placement of the piezometers on the concave shaped impermeable layers ensures the samples are of inflowing water. The exact positioning of the piezometers was based on the results of a previous hydrological study of the area (Verschoor et al. 2003). Before sampling the water present in the piezometers was flushed out with fresh groundwater. Surface water samples were collected from the bog close to the piezometers by filling a 30 mL airtight bottle by gently submersing it in the surface water. Water samples were transported to the laboratory in a cool box, where the pH and TIC were measured immediately. The remaining samples were stored frozen until analyzed. Precipitation data for the "Dwingelderveld" were obtained from the Royal Netherlands Meteorological Institute (www.knmi.nl, station number 327 "Dwingeloo").

The concentration of total inorganic carbon (TIC) in the water samples was determined by measuring the CO_2, released after acidifying the samples to a $pH < 3$, using an Infra-Red Gas Analyzer (IRGA, ABB Advance Optima). The pH of the water samples was determined using a combined pH electrode with an Ag/AgCl internal reference (Cole Parmer Instrument Company, USA) and a PHM 64 pH meter (Radiometer, Copenhagen). The concentrations of CO_2 and bicarbonate in the water samples were calculated based on the pH and the TIC concentration. Concentrations of nitrate (NO_3), ammonium (NH_4) and chloride (Cl) were measured colorimetrically according to Geurts et al. (2008) and potassium (K) by flame photometry using an Auto Analyzer 3 system (Bran+Luebbe, Germany). Aluminium (Al), calcium (Ca), iron (Fe), magnesium (Mg), manganese (Mn), sodium (Na), total phosphorus (P), sulphur (S), silicon (Si) and zinc (Zn) were measured using an ICP Spectrometer (IRIS Intrepid II, Thermo Electron Corporation, USA).

Statistical analysis

Data were tested for normality using a Kolmogorov-Smirnov test and equality of variance using Levene's test. The assumption of homogeneity of variance was not always met, not even after transformation of the data. According to Heath (1995), the analysis of variance appears not to be greatly affected by heterogeneity in variance if sample sizes are more or less equal. Therefore, we decided to continue our analysis using non-transformed data. A multivariate analysis of variance (Manova) was used to test for differences in inorganic carbon, pH and nutrient concentrations in groundwater and surface water and between well and poorly developed bogs (bog development as fixed factor) for groundwater and surface water, respectively.

Additionally, the data were analyzed by carrying out principal component analyses (PCA) using Aabel (version 3.0.3; Gigawiz Ltd. Co., USA). All data were normalized.

Results

Classification of the peat bogs

The area of open surface water decreased at all sites between 1982 and 2006, except for Diepveen, where the area increased slightly by 8%. Based on the aerial photographs and field observations, the success in redeveloping the bogs selected was classified into two categories; well-developed bogs, with a decrease in the area of open water of at least 78% and poorly developed bogs with a decrease in the area of open water of less than 42% (Table 1). For most sites the field observations confirmed the classification based on the analysis of the aerial photographs: there was a luxurious and dominant growth of *Sphagnum* spp. without or with only a small area of open water in the well-developed bogs, whereas there was only a marginal increase in the growth of *Sphagnum* spp. and large patches of open water and/or the presence of vascular plants, which are not typical of well established bogs, in the poorly developed bogs. In most cases the decrease in the area of open water in the poorly developed bogs was less than 20%.

Water chemistry

The groundwater was relatively acid and CO_2 was the main inorganic carbon species (Table 2). The chemical composition of groundwater and surface water differed significantly ($P < 0.05$) in concentrations of TIC, bicarbonate, Al, Ca, Fe, Mg, Na, S, Si and Zn, with higher values in the groundwater, and K, P with higher values in the surface water (Table 2).

The average groundwater TIC concentration near the well-developed bogs was 4984±802 $\mu mol \cdot L^{-1}$ and ranged from 2620 to 6215 $\mu mol \cdot L^{-1}$ (Fig. 3) The poorly developed bogs, with an average TIC concentration of 2766±1427 $\mu mol \cdot L^{-1}$, showed a much wider range in TIC concentration both between measurements at individual locations and between locations. A significant main effect of bog development on groundwater TIC concentrations was recorded ($F_{1,12} = 20.246$, $P = 0.001$). For the well-developed bogs the average CO_2 concentration in the surface water was 1215±730 $\mu mol \cdot L^{-1}$ and for poorly developed bogs 743±626 $\mu mol \cdot L^{-1}$ (Table 2). In addition, the surface water of well-developed and poorly developed bogs also differed significantly with respect to CO_2 concentration, $F_{1,13} = 6.063$, $P = 0.029$.

The difference in composition of groundwater from well-developed and poorly developed bogs is further illustrated by the results of PCA (Fig. 4). The groundwater samples from well and poorly developed bogs appear as clusters along the first principal component axis, which is dominated by high TIC, iron (Fe) and silica (Si), indicating that good development of *Sphagnum* is associated with groundwater that is relatively rich in iron and silica and rich in inorganic carbon. The second axis is associated with nutrients, which are not differentially associated with the well-developed and poorly developed sites.

Table 2. –Analysis of the ground- and surface water of well- and poorly-developed bogs; Data are presented as mean ± SD. Ion concentrations are given in μmol·L^{-1}. Significant differences between well- and poorly-developed bogs, as well as between ground- and surface water (middle column), are indicated by an asterisk ($P < 0.05$), n.s – not significant.

	Surface water			P	Groundwater		
	Well (n = 35)	Poor (n = 59)	P		Well (n = 35)	Poor (n = 53)	P
TIC	1230±737	768±638	*	*	4984±802	2766±1427	*
HCO_3^-	15±18	25±51	n.s.	*	153±103	64±72	*
CO_2	1215±730	743±626	*	*	4831±756	2701±1390	*
pH	4.3±0.3	4.6±1	*	n.s.	4.8±0.3	4.5±1	*
NH_4	77±70	72±80	n.s.	n.s.	95±55	84±79	n.s.
NO_3	8.5±14	9.2±15	n.s.	n.s.	7.6±15	8.2±13	n.s.
K	26±19	34±28	n.s.	*	14±11	26±24	*
P	4.3±8	4.2±7	n.s.	*	2.6±4	1.7±2	n.s.
Al	10±8	7.5±9	n.s.	*	42±31	36±33	n.s.
Ca	31±35	34±32	n.s.	*	62±60	52±32	n.s.
Cl	256±80	290±152	n.s.	n.s.	246±58	341±182	*
Fe	42±107	12±14	*	*	61±24	25±18	*
Mg	26±14	30±13	n.s.	*	67±21	42±27	*
Mn	0.6±0.3	1.2±2	*	n.s.	0.5±0.2	1.0±1	*
Na	192±48	227±95	*	*	231±38	285±130	*
S	22±16	28±22	n.s.	*	39±18	54±56	n.s.
Si	36±22	19±22	*	*	263±106	121±84	*
Zn	1.0±1	0.8±1	n.s.	*	8.1±14	5.7±5	n.s.

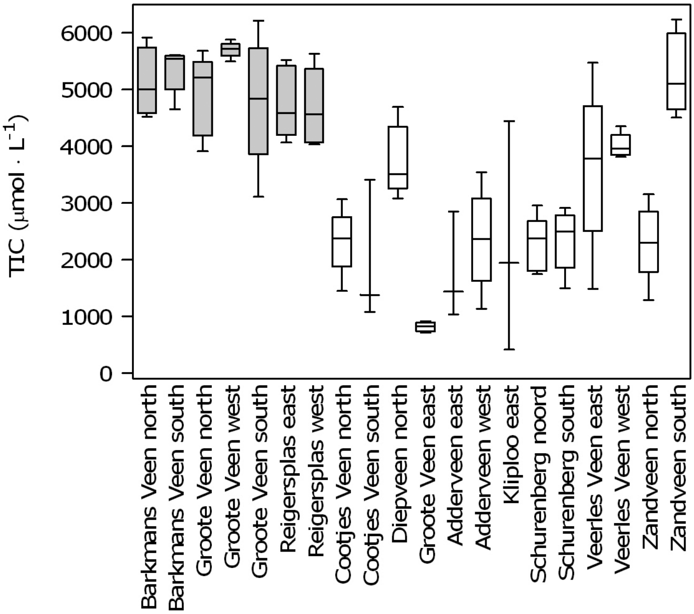

Fig. 3. – Box plot showing the total inorganic carbon (TIC) concentration in the groundwater in μmol·L^{-1} per location at both well (grey boxes) and poorly (white boxes) developed bogs. Box plots indicate the minimum, maximum, 25%, 75% quartiles and median values. Where used, north, south, east and west indicate sampling sites at one bog.

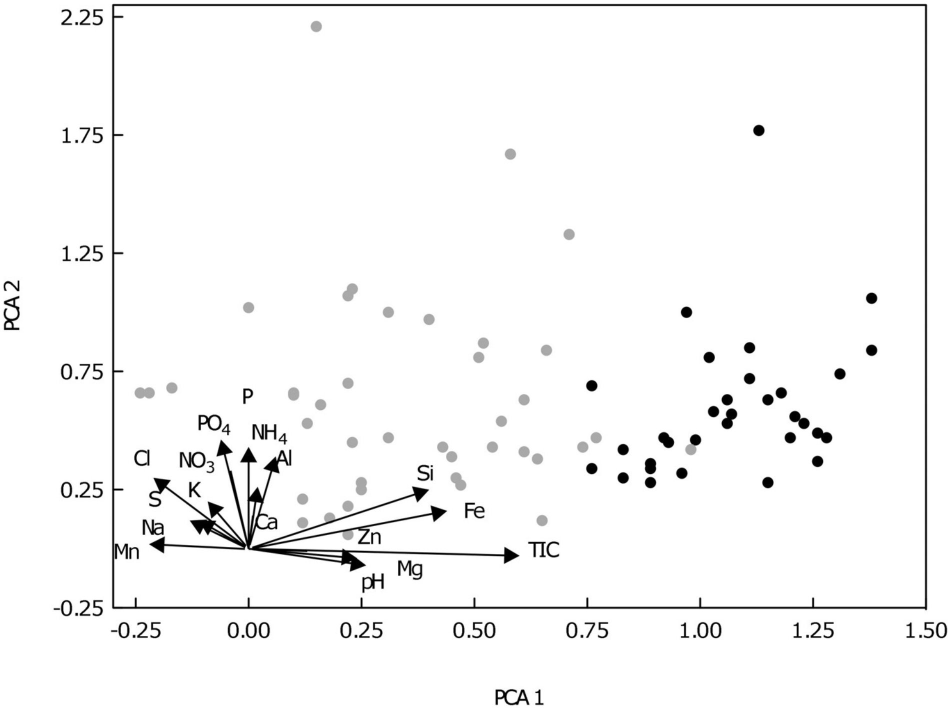

Fig. 4. – Principal component analysis (PCA) biplot of the results for all the groundwater samples and selected environmental variables. Each symbol represents a location sampled on one of the sampling dates. Black circles are well-developed bogs and grey circles poorly developed bogs. The first axis explained 27% of the variation and the second 20% of the variation.

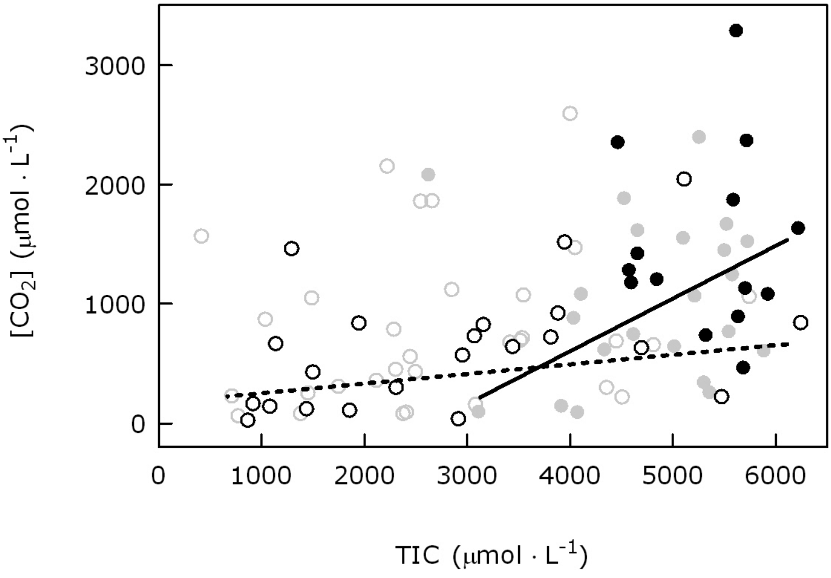

Fig. 5 – The relation between the total inorganic carbon (TIC) concentration in the groundwater and the CO_2 concentration in the surface water for well (filled circles) and poorly (open circles) developed bogs. Water samples collected in April and August are in black, others in grey. Lines are regression lines for well (solid line, $r^2 = 0.272$) and poorly (dashed line, $r^2 = 0.082$) developed bogs. For clarity of presentation non-transformed data are shown.

The logarithm of the TIC concentration in the groundwater was positively and significantly correlated with the logarithm of the CO_2 concentration in the surface water. However, this correlation was stronger for the well-developed bogs (Pearson's $r = 0.521$; $P < 0.01$) than for the poorly developed bogs ($r = 0.286$; $P < 0.05$) (Fig. 5).

Discussion

Restoration success

The situation at "Dwingelderveld" is that at this location there are a number of small *Sphagnum* bogs, which were subjected to identical restoration measures, but differ in groundwater quality and developmental success. This provided us with the opportunity to study the importance of groundwater quality on the development of groundwater-fed *Sphagnum* bogs in a field situation.

The analysis of aerial photographs revealed distinct differences in restoration success. The results were based on a quantitative approach; the general occurrence of a high cover of *Sphagnum* species. The success of the restoration was also evaluated by Everts et al. (2002) using total species composition. Their results are in accordance with our results obtained from an analysis of aerial photographs.

Evidence for influence of local groundwater flows

The PCA analysis based on all of the chemical data for groundwater clearly separated the well-developed and poorly developed bogs (Fig. 4) and indicates that differences in total inorganic carbon (TIC) are largely responsible for the separation; the groundwater collected close to well-developed bogs contained a significantly higher TIC concentration than that collected close to poorly developed bogs. Differences in nutrient concentrations are not associated with differences in the well- and poorly developed bogs.

We also found that the concentrations of CO_2 in the surface water of well-developed bogs were significantly higher than in the poorly developed bogs. Higher groundwater levels in the surrounding sandy areas resulted in a flow of local groundwater towards the bogs. The concave shaped impermeable layer, essential for bog formation, resulted in a unidirectional flow of local groundwater towards the bogs.

The chemical signature of the groundwater indicates that it originated from outside the bog. This was particularly indicated by the silica values, which are generally much higher in water that has been in contact with mineral sediments for a long period (Engelen & Jones 1986). These results are in agreement with the hypothesis that the well-developed bogs in our study are fed by a lateral inflow of carbon-rich groundwater.

The input of carbon rich groundwater from outside the bog will generate some positive feedbacks in the bog system. First of all, it will result in an enhancement of the growth of submerged *Sphagnum* (Fig. 6). The resulting accumulation of organic matter will enhance the internal generation of CO_2 from decomposition processes. Furthermore, it will result in a decrease in the depth of the water, which will increase light availability. It is unknown whether elements such as Si can affect *Sphagnum* growth in a direct way.

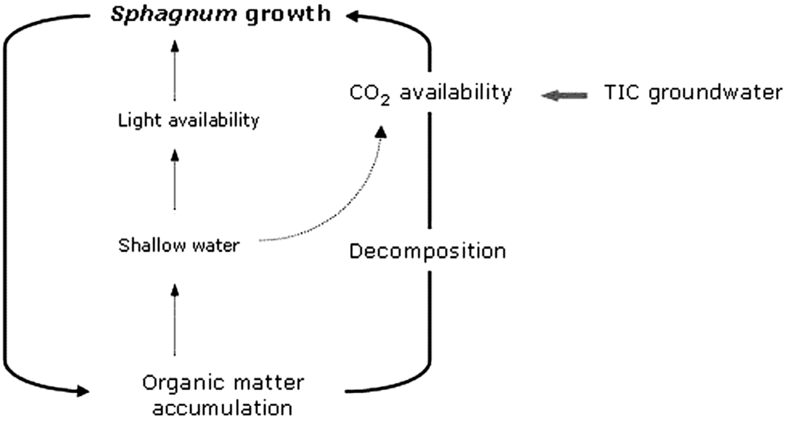

Fig. 6. – Schematic view of the positive feedbacks in CO_2 availability in a *Sphagnum* dominated bog resulting from the input of carbon-rich groundwater. In a well-developed bog the decomposition of accumulated organic matter results in a high availability of CO_2 stimulating *Sphagnum* growth, which in turn increases the accumulation of organic matter. During the initial stages of bog development organic matter is absent and the inflow of carbon-rich groundwater can substitute for the organic matter as a source of CO_2, stimulating *Sphagnum* growth and thereby inducing the internal positive feedback mechanism concerning CO_2 availability. In addition, the accumulation of organic matter decreases water depth, which increases light and CO_2 availability, which further stimulate the growth of *Sphagnum.*

Seasonality in the input of groundwater

During the wet period from October to March water tables rise in the surrounding elevated areas of the bogs due to reduced evapotranspiration and increased precipitation. The surface water levels in the bogs also increase, but less than in the higher ground where infiltration to deeper layers is restricted by layers of boulder clay (Verschoor et al. 2003). This results in an increase in the hydrological gradient and inflow of groundwater into the bogs, in particular in early spring when the water levels in the surroundings are highest. Interestingly, the period from April to August is the growing season of *Sphagnum* mosses (Clymo 1970) and the period when their consumption of CO_2 is highest.

Why do submerged Sphagnum species require high CO_2 concentrations?

Smolders et al (2003) reported that when inundated *Sphagnum* species grow very slowly on strongly humified ‘black’ peat, CO_2 concentrations in the water layer remained very low (< 20 µmol·L^{-1}). The same species, however, developed very well on weakly humified ‘white’ peat. In short, it is likely that low carbon availability in combination with low diffusion rates of CO_2 in water severely reduces CO_2 availability and limits *Sphagnum* growth.

Under natural conditions the stagnant bog water will result in thick boundary layers and long diffusion path lengths, which strongly reduces the availability of CO_2 for inundated plant species. For this reason, *Sphagnum* species that grow in water require a relatively high CO_2 availability, like most aquatic plants lacking a mechanism for concentrating carbon (Raven et al. 1998). Submerged *Sphagnum* species (*S. cuspidatum, S. fallax)* have

CO_2 compensation values (this is the CO_2 concentration at which CO_2 fixation by photosynthesis balances the CO_2 loss by respiration), which are much higher than the CO_2 concentrations in air-equilibrated water (10–20 $\mu mol \cdot L^{-1}$ at 10–25 °C; Patberg 2011*)*. Therefore, submerged *Sphagnum* species are unable to grow without an additional source of carbon dioxide (Paffen & Roelofs 1991, Smolders et al. 2003).

In the acidic environment of bogs, where there is no reservoir of bicarbonate to replace the CO_2 that is taken up, carbon dioxide is largely derived from the decomposition of peat. Baker & Boatman (1990) report that *S. cuspidatum* is able to adapt to conditions of low CO_2 availability by forming smaller and thinner leaves, which reduces the boundary layer resistance and facilitates CO_2 uptake. Nevertheless, Paffen & Roelofs (1991) conclude that a dissolved CO_2 concentration of at least 750 $\mu mol \cdot L^{-1}$ is necessary for the optimal growth of *S. cuspidatum* and the subsequent formation of floating vegetation. In the poorly developing bogs at Schurenberg North, Cootjes Veen, South and Groote Veen East the average CO_2 concentrations in the surface water was 233, 287 and 122 $\mu mol \cdot L^{-1}$, respectively, which is likely to severely hamper the growth of *Sphagnum* at all these sites.

For the successful reestablishment of aquatic *Sphagnum* species in small isolated bog systems it is crucial that there is an additional source of carbon. Rain water in equilibrium with aerial CO_2 concentrations does not contain more than 20 $\mu mol \cdot L^{-1}$ CO_2. A simple calculation of the CO_2 concentrations in bogs solely fed by rain water shows that it will add about 200 mmol CO_2 per year per m^2 (assuming a rainfall of 1000 mm per year). Assuming a rate of seepage of 1 mm/day, this will add 365 × 5000 = 18,250 mmol CO_2 per year even if only 10% of the surface of the bog receives groundwater; this is almost 10 times more than the input via rain. The concentrations measured in the surface water already indicate that input via rain is of minor importance as CO_2 concentrations are about 60 times greater than those in air-equilibrated water.

This field study suggests that the inflow of carbon-rich groundwater can substitute for the peat layer as a source of CO_2 during the initial stages of bog development.

Other explanations for the restricted growth of Sphagnum in peat ponds

Many factors affect the reestablishment of *Sphagnum* and subsequent development of a bog (Money et al. 2009). The lack of recolonization by *Sphagnum* mosses and hampered growth of those already established are often ascribed to high levels of deposition of atmospheric nitrogen (Twenhoven 1992, Money & Wheeler 1999, Lamers et al. 2000). The ammonium availability in the surface water at all the sites sampled (Table 2) reflects the currently high nitrogen loads in the north of the Netherlands, which on average are 28 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Limpens et al. 2003, Beijk et al. 2009). However, since there are no significant differences in nitrogen availability in the well and poorly developed bogs (Table 2) the current level of nitrogen deposition does not seem to determine the rate of development of these bogs. Moreover, Tomassen et al. (2004), suggest that bog vitality is much less affected by high nitrogen deposition if other environmental factors, such as water table and availability of other nutrients, or CO_2, are optimal.

In the majority of the bogs studied, the growth of *Sphagnum* appears to be limited by the availability of CO_2. However, there are several interesting exceptions. This is illustrated by the high CO_2 availability in some of the poorly developed bogs (Fig. 3). Nutrient and light limitation might be responsible for poor *Sphagnum* recolonization (e.g. Money

& Wheeler 1999, Smolders *et al* 2003). A shortage of nutrients is likely to prevent an increase in production at enhanced CO_2 concentrations in natural ecosystems (Kramer 1981). The Diepveen and the Zandveen are two bogs where the recolonization by *Sphagnum* is poor even though there is apparently sufficient inorganic carbon there (Fig. 3). Smolders et al. (2003) conclude that the availability of both light and CO_2 have to be sufficient to enable submerged *Sphagnum* to attain high photosynthetic and growth rates. These factors might indeed affect the development of *Sphagnum* in both Diepveen and Zandveen-South, where the depth of the water is generally several meters in the center of the bog and on average > 50 cm at the edges, which reduces the light available for the growth of *Sphagnum*. In addition, physical constraints like wind and wave action possibly hamper the growth of *Sphagnum* in large open water bodies (Money et al. 2009), which even in natural mires can remain open for many centuries (Couwenberg & Joosten 2005).

Thresholds in the restoration of bogs

The present study demonstrates that *Sphagnum* bogs in the “Dwingelderveld” are part of the total landscape hydrology instead of being hydrologically distinct entities. This might also be the case for many other damaged *Sphagnum* bogs and it indicates that a landscape approach is needed for successful bog restoration. The current findings suggest that at least in the early phases of bog regeneration, a high CO_2 availability is a prerequisite for the successful reestablishment of *Sphagnum* mosses. Hydrological measures in the surrounding landscape could in many cases assist in improving the results of bog restoration in areas where other constraints, like high atmospheric N-deposition are still affecting the bogs.

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Souhrn

Opětovné uchycení rašeliníků je základem úspěšné obnovy vrchovišť. Ukazuje se, že pro růst rašeliníků je důležitá dobrá dostupnost oxidu uhličitého. Na dobře vyvinutých zachovalých vrchovištích je velké množství oxidu uhličitého produkováno dekompozicí organického materiálu v mocné rašelinné vrstvě, zatímco na vytěžených rašeliništích je tento zdroj uhlíku silně omezen. Tato studie ukazuje význam oxidu uhličitého ve vodním prostředí, kde rašeliníky po vytěžení rašeliny začaly tvořit nové plovoucí koberce. Autoři diskutují výsledky obnovných opatření v rozsáhlé rezervaci Dwingelderveld, kde se vyskytují malá kyselá rašeliniště (0,5-5 hektarů) v mozaice s borovými lesy, vřesovišti a jinými acidofilními keříčkovými společenstvy. Po opětovném zavodnění se některá vrchoviště vyvíjela nápadně dobře, zatímco jiná nikoliv. Autoři hodnotili úspěšnost obnovy pomocí leteckých snímků a analýz povrchové a podzemní vody. Analýza chemismu vody ukázala, že úspěšně se obnovující rašeliniště měla v povrchové i podzemní vodě vyšší koncentraci oxidu uhličitého (zjišťovanou pomocí stanovení celkové koncentrace anorganického uhlíku a pH) než špatně se obnovující rašeliniště. Z toho autoři vyvozují, že v raných fázích vzniku rašelinišť rostou rašeliníky lépe tam, kde je mokřad sycen uhlíkem bohatou podzemní vodou z okolí. Dosavadní zjištění naznačují, že dobrá dostupnost oxidu uhličitého je nutným předpokladem pro úspěšné uchycení rašeliníků při obnově vrchovišť a že uhlíkem bohatá podzemní voda se může stát zdrojem oxidu uhličitého, který nahradí odtěženou rašelinnou vrstvu.

References

Bain J. T. & Proctor M. C. F. (1980): The requirement of aquatic bryophytes for free CO_2 as an inorganic carbon source: some experimental evidence. – New Phytol. 86: 393–400.

Baker R. G. E. & Boatman D. J. (1990): Some effects of nitrogen, phosphorus, potassium and carbon-dioxide concentration on the morphology and vegetative reproduction of *Sphagnum cuspidatum* Ehrh. – New Phytol. 116: 605–611.

Beijk R., Mooibroek D. & Hoogerbrugge R. (2009): Jaarboek Luchtkwaliteit 2008 [Air quality yearbook 2008]. – Report RIVM 680704008/2009, Bilthoven.

Bridgham S. D. & Richardson C. J. (1992): Mechanisms controlling soil respiration (CO_2 and CH_4) in southern peatlands. – Soil Biol. Biochem. 24: 1089–1099.

Clymo R. S. (1970): Growth of *Sphagnum*: methods of measurement. – J. Ecol. 58: 13–49.

Couwenberg J. & Joosten H. (2005): Self-organization in raised bog patterning: the origin of microtope zonation and mesotope diversity. – J. Ecol. 93: 1238–1248.

Engelen G. B. & Jones G. P. (1986): Developments in the analyses of groundwater flow systems. – IAHS Publications 163, Wallingford.

Everts F. H., Baaijens G. J., Grootjans A. P., Verschoor A. J. & De Vries N. P. J. (2002): Hoogveenontwikkeling in veentjes en kleinschalige hoogveencomplexen op het Dwingelderveld [Bog development in small bogs in the Dwingelerveld; a landscape approach. Part 1: Landscape development and hydrology]. – Report University of Groningen & EGG Consultants Everts & de Vries, Groningen.

Geurts J. J. M., Smolders A. J. P., Verhoeven J. T. A., Roelofs J. G. M. & Lamers L. P. M. (2008): Sediment Fe: PO_4 ratio as a diagnostic and prognostic tool for the restoration of macrophyte biodiversity in fen waters. – Freshw. Biol. 53: 2101–2116.

Glatzel S., Basiliko N. & Moore T. (2004): Carbon dioxide and methane production potentials of peats from natural, harvested, and restored sites, eastern Quebec, Canada. – Wetlands 24: 261–267.

Grootjans A. P., Adema E., Baaijens G. J., Rappoldt C. & Verschoor A. J. (2003): Mechanisms behind restoration of small bog ecosystems in a cover sand landscape. – Arch. Nat. Schutz Landsch. Forsch. 3: 43–48.

Grootjans A. P., Van Diggelen R., Joosten H. & Smolders F. (2012): Restoration of mires. – In: van Andel J. & Aronson J. (eds), Restoration ecology: the new frontier. Ed. 2, p. 203–213, John Wiley & Sons, Chichester.

Heath D. (1995): An introduction to experimental design and statistics for biology. – UCL Press, London.

Jauhiainen J. & Silvola J. (1999): Photosynthesis of *Sphagnum fuscum* at long-term raised CO_2 concentrations. – Ann. Bot. Fenn. 36: 11–19.

Joosten H. & Clark D. (2002): Wise use of mires and peatlands: background and principles including a framework for decision-making. – International Mire Conservation Group and International Peat Society, Saarijarvi.

Kip N., van Winden J. F., Pan Y., Bodrossy L., Reichart G.-J., Smolders A. J. P., Jetten M. S. M., Damste J. S. S. & Op den Camp H. J. M. (2010): Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. – Nat. Geosci. 3: 617–621.

Kramer P. J. (1981): Carbon-dioxide concentration, photosynthesis, and dry-matter production. – BioScience 31: 29–33.

Lamers L. P. M., Bobbink R. & Roelofs J. G. M. (2000): Natural nitrogen filter fails in polluted raised bogs. – Glob. Change Biol. 6: 583–586.

Limpens J., Berendse F. & Klees H. (2003): N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. – New Phytol. 157: 339–347.

Maberly S. C. & Madsen T. V. (2002): Freshwater angiosperm carbon concentrating mechanisms: processes and patterns. – Funct. Plant Biol. 29: 393–405.

Money R. P. & Wheeler B. D. (1999): Some critical questions concerning the restorability of damaged raised bogs. – Appl. Veg. Sci. 2: 107–116.

Money R. P., Wheeler B. D., Baird A. J. & Heathwaite A. L. (2009): Replumbing wetlands: managing water for the restoration of bogs and fens. – In: Maltby E. & Barker T. (eds), The wetlands handbook, p. 755–779, Blackwell Publishing, Oxford.

Paffen B. G. P. & Roelofs J. G. M. (1991): Impact of carbon-dioxide and ammonium on the growth of submerged *Sphagnum cuspidatum*. – Aquat. Bot. 40: 61–71.

Patberg W. (2011): Solute transport in *Sphagnum* dominated bogs; the ecophysiological effects of mixing by convective flow. – PhD thesis, University of Groningen.

Raghoebarsing A. A., Smolders A. J. P., Schmid M. C., Rijpstra W. I. C., Wolters-Arts M., Derksen J., Jetten M. S. M., Schouten S., Damste J. S. S., Lamers L. P. M., Roelofs J. G. M., den Camp H. & Strous M. (2005): Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. – Nature 436: 1153–1156.

Raven J. A., Griffiths H., Smith E. C. & Vaughn K. C. (1998): New perspectives in the biophysics and physiology of bryophytes. – In: Bates J. W., Ashton N. W. & Duckett J. G. (eds), Bryology for the twenty-first century, p. 261–275, Maney Publishing and the British Bryological Society, Leeds.

Riis T. & Sand-Jensen K. (1997): Growth reconstruction and photosynthesis of aquatic mosses: influence of light, temperature and carbon dioxide at depth. – J Ecol. 85: 359–372.

Robroek B. J. M., Schouten M. G. C., Limpens J., Berendse F. & Poorter H. (2009): Interactive effects of water table and precipitation on net CO2 assimilation of three co-occurring *Sphagnum* mosses differing in distribution above the water table. – Glob. Change Biol. 15: 680–691.

Rochefort L. & Price J. (2003): Restoration of *Sphagnum* dominated peatlands. – Wetl. Ecol. Manage. 11: 1–2.

Silvola J. (1990): Combined effects of varying water-content and CO_2 concentration on photosynthesis in *Sphagnum fuscum*. – Holarctic Ecol. 13: 224–228.

Smolders A. J. P., Tomassen H. B. M., Pijnappel H. W., Lamers L. P. M. & Roelofs J. G. M. (2001): Substrate-derived CO_2 is important in the development of *Sphagnum* spp. – New Phytol. 152: 325–332.

Smolders A. J. P., Tomassen H. B. M., van Mullekom M., Lamers L. P. M. & Roelofs J. G. M. (2003): Mechanisms involved in the re-establishment of *Sphagnum*-dominated vegetation in rewetted bog remnants. – Wetl. Ecol. Manage. 11: 403–418.

Tomassen, H. B. M., Smolders A. J. P., Lamers L. P. M. & Roelofs J. G. M. (2004): Development of floating rafts after the rewetting of cut-over bogs: the importance of peat quality. Biogeochemistry 71: 69-87.

Tomassen H. B. M., Smolders A. J. P., Van der Schaaf S., Lamers L. P. M. & Roelofs J. G. M. (2010): Restoration of raised bogs: mechanisms and case studies from the Netherlands. – In: Eiseltová M. (ed.), Restoration of lakes, streams, floodplains and bogs in Europe: principles and case studies, p. 285–330, Springer, Dordrecht.

Twenhoven F. L. (1992): Competition between 2 *Sphagnum* species under different deposition levels. – J. Bryol. 17: 71–80.

Vermeer J. G. & Joosten J. H. J. (1992): Conservation and management of bog and fen reserves in the Netherlands. – In: Verhoeven J. T. A. (ed.), Fens and bogs in the Netherlands: vegetation, history, nutrient dynamics and conservation, p. 433–478, Kluwer Academic Publishers, Dordrecht.

Verschoor A. J., Baaijens G. J., Everts F. H., Grootjans A. P., Rooke W., Van der Schaaf S. & De Vries N. P. J. (2003): Hoogveenontwikkeling in veentjes en kleinschalige hoogveencomplexen op het Dwingelerveld; een landschaps-benadering. Deel 2: Landschapsontwikkeling en hydrologie [Bog development in small bogs in the Dwingelerveld; a landscape approach. Part 2: Landscape development and hydrology]. – Report Expert Centre Ministry of Agriculture, Nature Conservation and Fisheries, Ede.

Waddington J. M., Rotenberg P. A. & Warren F. J. (2001): Peat CO_2 production in a natural and cutover peatland: implications for restoration. – Biogeochemistry 54: 115–130.

Williams T. G. & Flanagan L. B. (1996): Effect of changes in water content on photosynthesis, transpiration and discrimination against (CO_2)-C-13 and (COO)-O-18-O-16 in *Pleurozium* and *Sphagnum*. – Oecologia 108: 38–46.

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