# Università degli Studi di Ferrara

## DOTTORATO DI RICERCA IN
## BIOLOGIA EVOLUZIONISTICA E AMBIENTALE

CICLO XXIII

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# Effects of Global Change on Peatland Ecosystems

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# General Summary

## 1. Introduction

Peatlands are wetland ecosystems in which the rate of accumulation of organic matter called "peat" is greater than the rate of decomposition. This feature has important implications for carbon cycling. In effect, peatlands store one third of terrestrial carbon (Gorham 1991): despite covering only 3% of the Earth's land surface, boreal and subarctic peatlands store about 15–30% of the world's soil carbon as peat (200–400 $10^{15}$g C; Turunen et al 2002).

Peatland formation is the results of different factors. First of all water enable peat accumulation. The large heat capacity of water and the large energy demand for vaporization induce lower than ambient temperatures, whereas the limited diffusion rate of gases in water leads to a low availability of oxygen (Ball 2000, Denny 1993). The resulting relatively cold and anaerobic conditions inhibit the activities of decomposing organisms (Moore 1993, Freeman et al 2001). Second, the presence of *Sphagnum* spp, mosses belonging to Sphagnaceae family. A lack of water-conducting organs enables peat formation by mosses only where water loss by evapotranspiration is restricted. In these areas, where most peatlands are concentrated, peatland science came into being. Therefore moss growth is the central model of peatland development. In addition, *Sphagnum* litter is recalcitrant to decomposition because of chemical protection of cell wall polysaccharide, mainly by the polyphenolic network polymers20, but also by lipid surface coating (containing C14-C2~ hydroxy acids, C20-C24 dicarboxylic acids, fatty alcohols and fatty acids). Third, the climate. Climate determines the amount of water available in the landscape via the amount of net precipitation, while temperature affects both the production and decay of organic material. Accumulation and maintenance of peat is only possible when the balance between production and decay is positive. Peatlands are therefore especially abundant in cold (i.e. boreal and sub-arctic) and wet (i.e. oceanic and humid tropical) regions. In areas where the precipitation/evaporation balance is less favourable for accumulation, peatlands are only found where landscape features enable water to collect. Approximately 4 million $km^2$ of the Earth (some 3% of the land area) is covered with peatland (with >30 cm of peat). Peatlands are found in almost every country of the world. The general inventory status of peatlands is (largely) inadequate. For some regions almost nothing is known about peatlands. This is the case, for example, for large parts of Africa and South America and for the mountain areas of central Asia. In Italy peatlands cover approximately 100-120.000 ha (Immirzi et al 1992) and they are located mainly in Alps and in northern Appennines.

On the basis of acidity (base saturation) and nutrient availability (trophic conditions) different "ecological peatland types" are distinguished. A classical distinction is between *bogs* – which lay higher than their surroundings and are only fed by precipitation – and *fens* in landscape depressions – which are also fed by water that has been in contact with mineral soil or bedrock.

In bogs pH is low, below 4.5. The topography is heterogeneous and we can distinguish different microhabitat. In order to simplify, we can recognize hummocks and hollows. Hummocks are dominated by *Sphagnum* sp. and only few specialized vascular plants can survive: *Andromeda polifolia*, *Drosera rotundifolia*, *Vaccinium microcarpum* and *Eriophorum vaginatum*. These species possess particular adaptations in order to cope with the lack of nutrients. Hollows are dominated by graminoids such as *Rhynchospora alba* and *Carex limosa*.

In fens pH is higher and they are characterized by a lawn microtopography dominated by mosses. The parts characterized by depressions fed by water are occupied by *Carex* spp. in particular *Carex rostrata* together with *Menyanthes trifoliata* and *Eriophorum latifolium*.

Bogs and can see as a continuum in which variables concerning vegetation, chemistry and water derivation differ along this gradient.

## 1.1 Global Change and peatlands

With the term global change we refer to the variation at a global scale. In the past the causes of this change were natural and they have been solar output, volcanism, meteorite impact etc. Nowadays, the main cause of global change is the growing of human population that increases the demand for energy. Global change involves influences in atmospheric chemistry, climate and land use. The main cause of global change is the increasing in atmospheric $CO_2$ concentration in the coming decades that led to a cascade of effect.

The problem in studying the effects of global change on the ecosystems is due to the interactions between variables. For example, temperature affects all biological processes and the net response to the combined effects of warming and $CO_2$ are not simply described (Norby and Luo 2004). In addition, ecosystem responses to $CO_2$ and temperature are likely to be modified by other environmental factors, in particular availability of water and nitrogen, which in turn are modified by $CO_2$ and temperature (Medlyn et al 2000, McGuire et al 2001).

Changes in plant communities have occurred during the last 50 years that may be related to recent climate change. Many natural peatlands appear timeless and unchanging, but recently it has been shown that even on pristine peatlands, there have been changes in plant communities over the last 50 years recorded by directly by plant ecologists. There are only a few places in the world where direct comparisons of plant inventories over long periods of time are possible. In Sweden, some species disappeared and others colonised one site where comparative data were available from 1954 and 1997 (Gunnarsson 2002). In northern Britain species changes have also been recorded since the 1950s (Chapman 1991).

Peatlands have an important role in climate regulation. Over the past 10,000 years peatlands have absorbed an estimated 1.2 trillion tonnes of carbon dioxide, having a net cooling effect on the earth. Peatlands are now the world's largest terrestrial long-term sink of atmospheric carbon storing twice as much carbon as the biomass of the world's forests. However in the last 100 years, clearance, drainage and degradation of peatlands have turned them from a net store to a source of carbon emissions. This, combined with large-scale emissions from use of fossil fuels and forest clearance, has contributed to significant global increases in the

concentration of carbon dioxide and other greenhouse gases – the root cause of global climate change.

The main changes in climate are highlighted in the Summary for Policymakers of the IPCC Fourth Assessment Report (IPCC 2007).

Different studies reported the visible effects of global change. Otherwise, a lot of effects are still to be studied.

*Precipitation.* Global changes in precipitation over the last 100 years are harder to detect but there is strong evidence to suggest changes in total precipitation, seasonality and extremes in some regions where peatlands are found. Concerns have been raised that frequent drought could reduce the capacity of wetlands to function as sinks for global C, or eventually turn them into sources of atmospheric C. Substantial C losses have been already reported from boreal and sub-arctic bogs and fens due to lower water levels during warm and dry summers (Schreader et al 1998, Alm et al 1999, Moore et al 2002). In addition, persistent droughts (longer than years) can be expected to induce significant changes in vegetation community structure (Weltzin et al 2000, Weltzin et al 2003), which leads to shifts in microbial communities by altering litter quality and physicochemical soil environments (e.g. nutrient status, acidity and soil structure; Tilman and Downing, 1994, Jaatinen et al 2007). Change in precipitation and water table have an important effect on the microenvironment in which Sphagnum mosses grow, and may affect the competition between co-occurring species. Decreased water tables and increased temperatures are known to have different effects on different *Sphagnum* mosses (Robroek et al 2007a). Precipitation directly affects capitulum water content (Robroek et al 2007b), where most of the $CO_2$ uptake takes place.

*Global warming.* temperatures have risen by approximately 0.74°C since the early 20th century, with the increases occurring mostly during the first half of the 20th century and since around 1970 (Trenberth et al 2007). These changes can only be explained by invoking both natural climate forcings (solar and volcanic) and the effects of increasing greenhouse gas concentrations in the atmosphere (principally carbon dioxide, $CO_2$, and methane, $CH_4$) (Mitchell et al 2001). Although results are still controversial to some extent, a number of studies have shown that it is likely that the 1990s were the warmest decade for at least the last 600 years and probably the last 1000 years (Mann et al 1999, Moberg et al 2005). The high latitudes occupied by peatlands are expected to see the greatest amount of climatic warming in the next several decades (Pastor et al 2003). Whether the huge amounts of C in peatlands will response positively or negatively to global warming depends not only on the temperature sensitivity of net primary productivity but also the temperature sensitivity of soil organic carbon decomposition rate. If the C stored in northern peatlands is transferred to the atmosphere by a warming- induced acceleration of its decomposition, a positive feedback to climate change would occur. However, the real issue about release of carbon from soils to the atmosphere is how temperature, soil water content and other factors interact to influence decomposition of soil organic matter (Davidson et al 2000). annual variation of temperature sensitivity of soil carbon decomposition in north peatlands was influenced not only by the type of peat but also by temperature and hydraulic condition, which are the main factors controlling the thermal response of soil car- bon decomposition. It has been suggested that

soil organic carbon in cold regions may be highly sensitive to above-average current and predicted climate warming at northern high latitudes (Kattsov et al 2005) because of the higher temperature sensitivity of soil respiration at low temperatures (Goulden et al 1998, Kirschbaum et al 1995). The extensive reservoirs of organic C in northern peatlands are thus highly sensitive to climate warming. Dorrepaal et al (2009) estimate that a mild growing-season temperature increase of about 1 °C during the coming decades may induce a global increase in heterotrophic respiration from northern peatlands of 38–100 megatonnes of C per year (1 megatonne = $10^{12}$ g).

*Nitrogen deposition.* A threat to the C sequestration of ombrotrophic bogs in northwestern Europe is the high levels of airborne anthropogenic nitrogen deposition. High levels of nitrogen deposition ($>1 \, g \, m^{-2} \, yr^{-1}$) will reduce *Sphagnum* growth rates (Gunnarsson and Rydin, 2000, Nordbakken et al 2003, Vitt et al 2003), enhance litter decomposition (Bragazza et al 2006) and may change the plant community composition after long time exposure (Bubier et al 2007, Gunnarsson and Flodin 2007, Wiedermann et al 2007). One of the main causes of the low C input rates is the high level of nitrogen deposition, which enhances decomposition and changes the vegetation from peat-forming *Sphagnum*-dominance to dominance by dwarf shrubs and graminoids.

*Extreme events.* During summer 2003 Europe was affected by an extreme climate anomaly. Temperature in July were 6°C above long-term means and annual precipitations deficits up to 300 mm yr-1, 50% below the average (Ciais et al 2005). In Europe, Ciais et al (2005) estimated a reduction in gross primary productivity of 30% which resulted in a net source of carbon dioxide (0.5 Pg C yr-1). In the southern Alps (Gerdol et al 2008) the heatwave influenced the bog ecosystem to a much greater extent than our experimental manipulation of nutrient inputs.

*Land use change.* About 14 – 20 % of peatlands in the world are currently used for agriculture and the great majority of them are used as meadows and pastures. For agricultural use, fens and raised bogs have to be drained in order to regulate the air and water conditions in the soil to meet the requirements of cultivated or pasture plants. In many European countries, GHG emissions from agricultural peatlands dominate national emissions of GHGs from peat sources. The utilization of peatlands for forestry is concentrated in Nordic countries (Norway, Sweden, and Finland) and Russia, where over 10 million ha of peatlands have been drained for this purpose. Peat has been used for domestic energy purposes by local communities in many parts of the world for centuries. Electricity generation, using peat as a fuel, developed in the 20th Century in some European countries and the Soviet Union. Today, Finland, Ireland, Russian Federation, Belarus and Sweden account for almost 90% of the world's production and consumption of energy peat. In terms of greenhouse gas emissions peat combustion which in Finland accounts for 7% of primary energy, is there responsible for 14% of $CO_2$ emissions from combustion of fossil fuels. Peat is also used in horticulture, as a growing medium, but the volume used annually is only about half that of fuel peat. Germany and Canada account for over half of horticultural peat extraction.

## 2. Aims of this thesis

The general aim of my thesis was to study various aspect of functional ecology of peatlands in relation to global change. The thesis consists of five original studies:

I) Variations in the foliar nutrient content of mire plants: effects of growth-form based grouping and habitat.

   Bombonato L, Gerdol R, Siffi C (2010) *Plant Ecology* 211:235-251

II) Aboveground production and nutrient status of the vegetation of different mire types in the South-eastern Alps (Italy)

   Gerdol R, Siffi C, Bombonato L (2010) *Botanica Helvetica* 2:85-93

III) Hydrologic controls on water chemistry, vegetation and ecological patterns in two mires in the South-Eastern Alps (Italy)

   Gerdol R, Pontin A, Tomaselli M, Bombonato L, Brancaleoni L, Gualmini M, Petraglia A, Siffi C, Gargini A (2011) *Catena* (accepted)

IV) Manipulating snow cover in an alpine bog: effects on soil micro-organisms and plants

   Bombonato L, Gerdol R (2011) *Climatic Change* (submitted)

V) Effect of tree on *Sphagnum* spp. and feathermosses evapotranspiration rates (draft)

   Bombonato L, Waddington M (draft)

The first study is focused on the use of Plant Functional Types (PFTs) in order to investigate the foliar nutrient concentrations in mire ecosystems. The PFT approach is based on the assumption that a suite of inter-related plant traits are useful for predicting, on one hand, how species groups respond to environmental factors and, on the other hand, how species groups influence ecosystem processes (Gitay and Noble 1997). Therefore, the PFT approach can help us understand how environmental changes associated with climate warming will affect terrestrial ecosystems either through direct effects on ecosystem functioning or through indirect effects mediated by compositional changes in vegetation (Wahren et al 2005, Voigt et al 2007, Welp et al 2007).

The aim of the second was to determine the aboveground net primary production (ANPP) of different mire types in the Southern Alps of Italy. Our final objective was to detect whether

ANPP patterns along the poor-rich gradient could be related to the limiting effects of one or several nutrients for biomass production.

The third study investigated relationships among peatland hydrology, vegetation and ecological patterns in this region. As the ecological features and, eventually, the very existence of peatlands closely depend on amount and quality of water input, it is important to understand how hydrology controls vegetation composition and ecosystem functioning in these habitats. The latter point is, in turn, a fundamental basis for any policy of peatland conservation and/or restoration. The objective of this paper was to analyze relationships between hydrology, on one hand, and vegetation composition and ecological processes, on the other hand, in peatlands on the South-Eastern Alps.

The fourth study is an experiment on the effects of snow cover on peatlands. Snow cover is an important environmental factor that influences ecosystem functioning. During last years, otherwise, studies observed decreasing snow cover precipitations in alpine region (Dye 2002, Groisman et al 1994, Lopez-Moreno 2005) often correlated with an increment of air temperatures (Marty 2008). Few studies on the effect of snow cover manipulation in peatland are available and they were made in sub-arctic peatlands in order to investigate the effects of a deeper snow cover together with an increasing of air temperatures both in summer (Aerts et al 2009) and in spring (Dorrepaal et al 2009). The aim of this study is the evaluation of the effects of snow cover on ecosystem respiration (ER) and on nutrient cycling in microbial biomass and in plants.

The fifth work has been carried out in Canadian peatlands in collaboration with the Prof. Waddington from the School of Geography and Earth Science of McMaster University (Ontario) and it has been inserted in a wider project named Peatfire. Fire in Canada is a critical problem and it is strictly associated with climate change. In effect climate change has strong impact on weather: less precipitations and higher temperatures will increase the number of wildfire. In this study we studied how the trees influence the evapotranspiration (ET) in *Sphagnum* sp. and in feathermosses.

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Effects of Global Change on a bog located at Lupicino. We can observe several damaged hummocks with desiccated peat mosses due to the 2003 heatwave.

**Variations in the foliar nutrient content of mire plants: effects of growth-form based grouping and habitat**

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**Abstract**

We determined concentrations of major nutrients in the vegetation of six habitat types (hummock, scrub, lawn, fen meadow, hollow and marginal stream), spanning a broad range of environmental conditions as regards water-table depth and water chemistry, in five mires on the southern Alps of Italy. Our study was based on chemical analyses of living tissues of plant species, grouped into growth-form based plant functional types (PFTs). We aimed at assessing to what extent the observed differences in tissue nutrient content were accounted for by community composition (both in terms of species and PFTs) and by habitat. Nutrient concentrations were overall lowest in *Sphagnum* mosses and highest in forbs, although the latter showed large variations presumably due to heterogeneity in mechanisms and adaptations for acquiring nutrients among species within this PFT. Nutrient content patterns in the other three PFTs varied greatly in relation to individual nutrients, with evergreen shrubs showing low nitrogen (N) concentrations, graminoids showing high N concentrations but low potassium (K) and magnesium (Mg) concentrations and deciduous shrubs showing rather high phosphorus (P) concentrations. Habitat accounted for a modest fraction of variation in tissue concentration of all nutrients except P. We concluded that the nutrient status of mire vegetation is primarily controlled by community composition and structure although habitat does exert a direct control on P concentration in the vegetation, presumably through P availability for plant uptake.

# 1. Introduction

Grouping plant species in plant functional types (PFTs) is a common practice in modern ecology, especially for broad scale surveys (Xia and Wan 2008). The PFT approach is based on the assumption that a suite of inter-related plant traits are useful for predicting, on one hand, how species groups respond to environmental factors and, on the other hand, how species groups influence ecosystem processes (Gitay and Noble 1997). Therefore, the PFT approach can help us understand how environmental changes associated with climate warming will affect terrestrial ecosystems either through direct effects on ecosystem functioning or through indirect effects mediated by compositional changes in vegetation (Voigt et al 2007, Wahren et al 2005, Welp et al 2007). PFTs can be defined on the basis of many kinds of traits, ranging from plant morphology, to phenology, growth strategy, leaf chemistry and others (Eviner and Chapin 2003), although recent studies have questioned the concept that those traits always co-vary consistently. For example, Eviner (2004) reported great variation in terms of growth rates among herbaceous species with similar litter chemistry, and Lavorel and Garnier (2002) observed poor match between plant traits associated with responses to fire and plant traits associated with flammability.

In northern, cold territories plant ecologists usually employ PFTs based on growth form. These groupings have been utilized widely in experimental research at arctic sites (see Dorrepaal 2007, for review) and, although to a lesser extent, at alpine sites (Brancaleoni et al 2007). Growth-form based PFTs have the advantage to be easily recognizable by means of 'soft' traits (sensu Hodgson et al 1999) concerning whole-plant morphology and are, furthermore, suitable to be employed across large territories. Growth-form based PFTs have also been used by mire ecologists, especially when the objective was to compare ecological patterns among different regions and/or mire types. However, it is still questioned if and to what extent growth-form based PFTs represent reliable predictors of ecosystem processes in mires. Humphreys et al (2006) reported similar mid-summer $CO_2$ and water vapour fluxes in peatlands dramatically differing from each other as regards growth-form composition. On the other hand, Dorrepaal et al (2005) observed that litter chemistry of different growth forms varied consistently in peatlands across a latitudinal gradient in Europe, but growth forms were better to predict leaf litter decomposition in warm-temperate peatlands than in subarctic peatlands.

Foliar nutrient content has since long been recognized as a major factor controlling ecosystem processes (Melillo et al 1982, Enriquez et al 1993, Grime et al 1997, Hobbie 2008). Foliar nutrient, especially nitrogen (N), concentration is positively related to photosynthetic capacity and dark respiration rates (Evans 1989, Reich et al 1998). Foliar nutrient content controls relative growth rate (Cornelissen et al 1997) and nutrient-use efficiency (NUE) of living plants (Aerts and Chapin 2000) and also exerts a long-term effect, after leaf senescence, since nutrient-rich litter usually breaks down faster, thus accelerating nutrient cycling in the ecosystem (Cornelissen and Thompson 1997). Foliar nutrient content in mire plants may vary greatly due both to variations in tissue chemistry among plant species and to variations influenced by soil nutrient availability. In particular, N and

phosphorus (P) concentrations as well as the N : P ratio in plant tissues can be used for detecting which nutrient limits biomass production in wetland ecosystems (Güsewell and Koerselman 2002).

The objective of this paper was to investigate relationships between growth-form based plant classification and foliar nutrient concentrations in mire ecosystems. We especially aimed to assess if and to what extent intrinsic differences in the nutrient content of leaves from different plant species can be synthesized by grouping species into growth-form based PFTs. We also examined if the resulting patterns vary across a range of mire habitats.

## 2. Material and methods

### 2.1 Study sites

The study was carried out during the summers 2005 and 2006 at five mires located in two different areas in the southern Alps of Italy: Coltrondo, Carnic Alps (46° 39' N, 12° 26' E; 1800-1900 m) and Marcesina, Venetian Prealps (45° 57' N, 11°36' E; 1350 m). The mires were described in detail elsewhere (Gerdol et al unpublished). In synthesis, three of the mires investigated lie at Coltrondo and the other two at Marcesina.

The three Coltrondo mires are: Coltrondo N, a poor fen covered by open vegetation with a ground layer rich in peat mosses; Coltrondo W, a bog with large *Pinus mugo* scrubs on a carpet of peat mosses; Coltrondo S, an intermediate fen mostly covered by fen meadows with interspersed peat-moss hummocks. The two Marcesina mires are: Palù San Lorenzo, a rich fen covered by fen meadows almost totally lacking peat mosses in the ground layer, and Palù di Sotto, a poor fen with a mosaic of hummocks and hollows and small *Pinus mugo* patches.

### 2.2 Environment and vegetation

In early June 2005 a number of 1-m$^2$ plots (131 in total: 19 Coltrondo N, 26 Coltrondo W, 41 Palù San Lorenzo and 27 Palù di Sotto) were positioned at the five mires. The plots were located along transects in order to account for the whole range of habitat variation occurring at each mire. Within each plot a 1-m long perforated polyvinylchloride pipe (internal diameter 14 mm, wall thickness 2 mm) was inserted into the peat, with the top at the mire ground. Water-table depth (WTD) was measured weekly from June to November 2005 and 2006 in every pipe. The cover of all species (vascular plants, bryophytes and lichens) occurring at each of the 131 plots was estimated visually at the peak (end July – early August, when the aboveground biomass had reached maximum cover) of the growing seasons 2005 and 2006.

In August 2006 pH and electrical conductivity (EC) were measured in the field by portable instruments at all plots. Subsequently, a water sample was collected from every pipe, stored in polythene bottles and deep frozen until laboratory analysis. The values of EC were corrected for H$^+$ (Sjörs 1952). Concentrations of major cations (Na$^+$, K$^+$, Ca$^{2+}$ and Mg$^{2+}$)

were determined by atomic absorption spectrophotometry after adding lanthanum to reduce anionic interference.

Each plot was assigned one of six habitat types: hummock, scrub, lawn, fen meadow, hollow and marginal stream, based both on visual field observation of surface morphology and vegetation structure.

## 2.3 Sampling and chemical analysis of plant material

Samples of plant tissues were collected at 43 selected plots. Fully developed, sound current-year leaves of all vascular plants and the top 1-cm (the so-called 'capitulum') of all *Sphagnum* species occurring in the plots were harvested at the peak of the growing season 2006 (end July – early August).

The plant material was sorted by species, cleaned, oven-dried at 60°C for 24 h, ground through a 1-mm mesh titanium mill and then digested according to the Kjeldahl procedure. Nitrogen and P concentrations were determined colorimetrically by a flow-injection autoanalyser (FlowSys, Systea, Roma, Italy). Magnesium (Mg) and potassium (K) concentrations were determined by atomic-absorption spectrophotometry (SOLAAR 969, UNICAM, Cambridge, UK). To ensure accuracy within 5%, standard reference material of known N, P, K and Mg concentrations (NIST *Citrus* leaves 1572, National Bureau of Standards, Washington, DC, USA) was analyzed together with the samples.

The species were then grouped into the following growth-form based PFTs: *Sphagnum* mosses, evergreen shrubs, deciduous shrubs, graminoids, forbs. Non-*Sphagnum* mosses, lichens and pteridophytes were not considered because they occurred very rarely in the sampling plots. In summary, we processed 357 samples of 39 species in total.

## 2.4 Statistical analyses

Relationships among nutrient content in plants, PFT grouping, habitat type and environmental features of habitat were explored by redundancy analysis (RDA). In this analysis, the 'environment' dataset consisted in: median WTD, pH, EC and cation concentrations in pore water. On the other hand, the 'species' dataset consisted in nutrient concentrations and N : P ratio in all plant samples. Since preliminary Shapiro-Wilk tests did not reveal normal distributions of nutrient concentrations in plant samples, these data were log-transformed prior the analysis. We used dummy 0/1 variables for relating the plant species to PFT and habitat type.

Partial RDAs (Borcard et al 1992) were applied to assess the fraction of variation in foliar nutrient concentration that was explained by species {Sp}, PFTs {PFT} and habitat {H}. In the partial RDAs we used the same datasets of the previous RDA, with appropriate adjustments. We run three partial RDAs to detect the variation due to species and habitat and three partial RDAs to detect the variation due to PFTs and habitat. Total variation was quantified as the total inertia (Ti; sum of all unconstrained eigenvalues). The fraction of variation explained by the variables together (species and habitat, Sp∪H; PFT and habitat,

PFT∪H) corresponded to the sum of all canonical eigenvalues of the three partial RDAs run to detect the variation explained by species and habitat and the sum of the three partial RDAs run to detect the variation explained by species and PFTs, respectively. The fraction of variation explained by {Sp}, not shared by {H} (Sp|H), was found by partial RDA using the variables in {H} as covariables and the variables in {Sp} as constraining variables and in the same way for PFTs and habitat. The fraction of variation explained by {H}, not shared by {Sp} (H|Sp), was found by partial RDA using the variables in {Sp} as covariables and the variables in {H} as constraining variables and in the same way for habitat and PFTs. The variance shared by species and habitat (Sp∩H; variation explained by the redundant portion of both) was calculated by subtracting from Sp∪H both Sp|H and H|Sp. In the same way, we calculated PFT∩H. The unexplained variation was calculated by subtracting from total inertia (Ti) both Sp∪H and PFT∪H.

Variations in nutrient concentrations were assessed by calculating coefficients of variation (CV). The latter were obtained by dividing standard deviation by mean, after adjusting for sample size, as described below.

The overall CV was calculated according to formula (1)

$$CV_{\text{overall}} = \frac{SD}{\overline{X}} \times 100 \tag{1}$$

Where:

$SD$ = overall standard deviation (across all samples)

$\overline{X}$ = overall mean (across all samples)

The interspecific CV, the interPFT CV and the interhabitat CV were calculated according to formulas (2-4).

$$CV_{\text{interspecific}} = \frac{\sqrt{\dfrac{\sum\limits_{i=1}^{n_{\text{sp}}} \left[ \left( \overline{x}_{\text{SP}i} - \overline{X} \right)^2 \times n_{\text{SP}i} \right]}{N-1}}}{\overline{X}} \times 100 \tag{2}$$

$$CV_{\text{interPFT}} = \frac{\sqrt{\dfrac{\sum\limits_{i=1}^{n_{\text{pft}}} \left[ \left( \overline{x}_{\text{PFT}i} - \overline{X} \right)^2 \times n_{\text{PFT}i} \right]}{N-1}}}{\overline{X}} \times 100 \tag{3}$$

$$CV_{\text{interhabitat}} = \frac{\sqrt{\dfrac{\sum\limits_{i=1}^{n_{\text{hab}}}\left[\left(\overline{x}_{\text{HAB}i} - \overline{X}\right)^2 \times n_{\text{HAB}i}\right]}{N - 1}}}{\overline{X}} \times 100 \qquad (4)$$

Where:

$n_{\text{sp}}$ = total number of species (39)

$n_{\text{pft}}$ = total number of PFTs (5)

$n_{\text{hab}}$ = total number of habitats (6)

$\overline{x}_{\text{SP}i}$ = mean of the i-th species

$\overline{x}_{\text{PFT}i}$ = mean of the i-th PFT

$\overline{x}_{\text{HAB}i}$ = mean of the i-th habitat

$\overline{X}$ = overall mean (as in formula (1))

$n_{\text{SP}i}$ = number of samples for the i-th species

$n_{\text{PFT}i}$ = number of samples for the i-th PFT

$n_{\text{HAB}i}$ = number of samples for the i-th habitat

$N$ = total number of samples (357)

For each of the five PFTs, the within-PFT CV was calculated according to formula (5).

$$CV_{\text{within-PFT}} = \frac{\sqrt{\dfrac{\sum\limits_{i=1}^{n_{\text{SPpft}}}\left[\left(\overline{x}_{\text{sp}i} - \overline{x}_{\text{PFT}}\right)^2 \times n_{\text{sp}i}\right]}{N_{\text{PFT}} - 1}}}{\overline{x}_{\text{PFT}}} \times 100 \qquad (5)$$

Where:

$n_{\text{SPpft}}$ = number of species in the corresponding PFT

$\overline{x}_{\text{sp}i}$ = mean of the i-th species

$\overline{x}_{\text{PFT}}$ = mean of all species means in the corresponding PFT

$n_{\text{sp}i}$ = number of samples of the i-th species

$N_{\text{PFT}}$ = number of samples in the corresponding PFT

Mixed-models ANOVAs were employed to assess the components of variation due to PFT, habitat and their interaction, for each nutrient and for the N : P ratio. PFTs were used as fixed factors, while habitat and PFT × habitat interactions were used as random factors.

We used the software CANOCO version 4.02 for Windows (Ter Braak and Smilauer, 2002) for multivariate analyses and the the package STATISTICA (Release 6; StatSoft Inc., Tulsa; USA) for univariate statistics.

## 3. Results

### 3.1 Habitat and vegetation

The six habitats differed significantly from each other based on all variables related to hydrology and water chemistry (Table 1). Median WTD was greatest in hummocks and scrubs, lowest in hollows and marginal streams and intermediate in lawns and fen meadows. The pore water in hummocks, scrubs and lawns had lower pH and EC, as well as lower $Ca^{2+}$ and $Mg^{2+}$ concentrations compared to fen meadows, hollows and marginal streams. Conversely, pore-water concentrations of $Na^+$ and $K^+$ were higher in acidic habitats, especially scrubs and lawns (Table 1). Those patterns were clearly mirrored in the RDA biplot of environment scores where WTD was separated from $K^+$ and, to a lesser extent, $Na^+$ at the opposite ends of the first axis while pH, EC, $Ca^{2+}$ and $Mg^{2+}$ were all bulked in the lower half of the second axis (Fig 1a).

|  | Hummocks | Scrubs | Lawns | Fen meadows | Hollows | Marginal streams | *P* |
|---|---|---|---|---|---|---|---|
| WTD (cm) | - 28 ± 2 [c] | - 24 ± 4 [c] | - 6 ± 2 [b] | - 6 ± 1 [b] | 2 ± 1 [a] | 1 ± 3 [a] | *0.000* |
| pH | 5.05 ± 0.13 [b] | 4.84 ± 0.35 [b] | 4.96 ± 0.12 [b] | 6.33 ± 0.11 [a] | 6.08 ± 0.23 [a] | 6.02 ± 0.19 [a] | *0.000* |
| EC (µS cm⁻¹) | 41 ± 6 [b] | 69 ± 28 [ab] | 23 ± 2 [b] | 161 ± 30 [a] | 193 ± 42 [a] | 174 ± 63 [a] | *0.000* |
| Na⁺ (mg l⁻¹) | 0.90 ± 0.10 [bc] | 1.37 ± 0.44 [ab] | 1.73 ± 0.38 [a] | 0.67 ± 0.10 [c] | 0.76 ± 0.13 [bc] | 0.86 ± 0.15 [bc] | *0.001* |
| K⁺ (mg l⁻¹) | 0.51 ± 0.07 [abc] | 0.77 ± 0.16 [a] | 0.64 ± 0.19 [ab] | 0.35±0.05 [cd] | 0.28±0.03 [d] | 0.36 ± 0.06 [bcd] | *0.009* |
| Ca²⁺ (mg l⁻¹) | 3.15 ± 0.57 [b] | 4.06 ± 1.31 [b] | 3.28 ± 0.58 [b] | 14.58±2.16 [a] | 14.62±2.86 [a] | 11.95 ± 2.78 [a] | *0.000* |
| Mg²⁺ (mg l⁻¹) | 0.49 ± 0.12 [c] | 0.32 ± 0.04 [c] | 0.43 ± 0.06 [c] | 1.11 ± 0.19 [ab] | 0.75 ± 0.14 [bc] | 1.63 ± 0.34 [a] | *0.000* |

Table 1. Mean (± 1 SE) values of median water-table depth (WTD), pH, electrical conductivity (EC) and cation concentrations in the six habitats. The last column contains the *P* values of one-way ANOVAs with habitat as the fixed factor.
Within each row, the means followed by the same letter do not differ significantly (*P* = 0.05) based on Fisher's LSD post-hoc tests
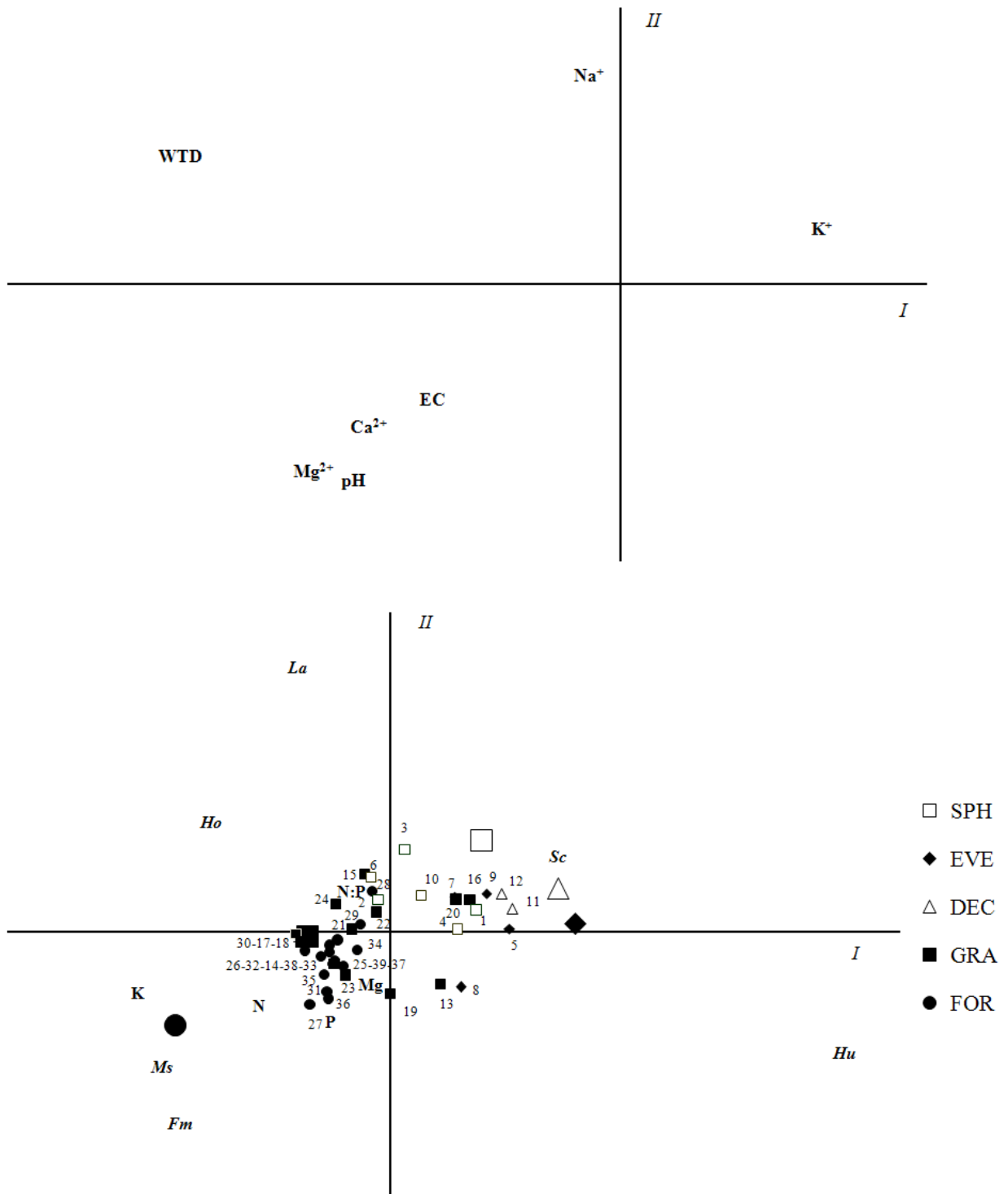
Fig. 1. Biplot scores of 'environment' variables (panel a) and 'species' variables (panel b) along the first two RDA axes.

Abbreviations in panel a: WTD = median water-table depth; EC = electrical conductivity.

In panel b each small symbol corresponds to one species (numbered as in the Appendix). The species were grouped into the following PFTs (abbreviations: SPH = *Sphagnum* mosses; EVE = evergreen shrubs, DEC = deciduous shrubs, GRA = graminoids, FOR = forbs.). The large symbols are the centroids of the five PFTs.

Abbreviations for habitats in panel b: *Hu* = hummocks; *Sc* = scrubs; *La* = lawns; *Fm* = fen meadows; *Ho* = hollows; *Ms* = marginal streams

The centroid of *Sphagnum* mosses was located in the right half of the diagram (Fig. 1b) since this PFT was principally associated with hummocks and scrubs, where *S. capillifolium* and *S. magellanicum* represented overall abundant species and *S. fuscum* occurred only in hummocks. On the other hand, *S. compactum* was typical of lawns and *S. subsecundum* was found only in hollows (Appendix). Evergreen shrubs and deciduous shrubs also were most abundant in scrubs and hummocks so that their centroids were located in the right half of the diagram, close to that of *Sphagnum* mosses (Fig. 1b). Shrubs were fairly frequent in lawns as well, with only *Andromeda polifolia* and partly *Calluna vulgaris* being found in fen meadows and hollows as well (Appendix). Forbs were associated with marginal streams, fen meadows and, to a lesser extent hollows, in the left half of the diagram (Fig. 1b). Indeed, among forbs only *Drosera rotundifolia* and *Potentilla erecta* were found in acidic dry habitats (Appendix). The graminoid centroid was located in the central part of the diagram (Fig. 1b) since this PFT was well represented in all habitats, although most graminoid species had maximum frequencies in wet habitats (lawns to marginal streams: *Carex fusca*, *C. lepidocarpa*, *C. rostrata*, *C. stellulata*, *Eriophorum angustifolium*, *Luzula sudetica*, *Trichophorum alpinum* and *T. caespitosum*). Conversely, *Carex pauciflora* and *Eriophorum vaginatum* were more abundant in acidic, dry habitats. *Carex limosa* occurred only in hollows, while *Molinia coerulea* had high frequencies in all habitats, except marginal streams (Appendix).

*3.2 Variations in nutrient content*

The fraction of variation in nutrient contents accounted for by species (Sp|H) was much greater than that accounted for by habitat (H|Sp). Similarly, the fraction of variation accounted for by PFT (PFT|H) was greater than that accounted for by habitat (H|PFT), although the difference was smaller than for species (Table 2). The fraction of variation explained by species and habitat together (Sp∪H), the fraction of variation explained only by species (Sp|H) and the fraction shared by species and habitat (Sp∩H) were all greater than the corresponding fractions of variance involving PFTs and habitat (PFT∪H, PFT|H and PFT∩H, respectively; Table 2). On the other hand, the fraction of variation explained by habitat, not shared by PFT (H|PFT) was greater than that explained by habitat, not shared by species (H|Sp; Table 2).

| Ti | Sp∪H | Sp|H | H|Sp | Sp∩H |
|------|------|------|------|------|
| 1.00 | 0.73 | 0.53 | 0.03 | 0.17 |

| Ti | PFT∪H | PFT|H | H|PFT | PFT∩H |
|------|------|------|------|------|
| 1.00 | 0.55 | 0.35 | 0.09 | 0.11 |

Table 2. Results of partial RDAs for species (upper row) and PFTs (lower row): Ti = total inertia (total variation); H = habitat; Sp = species; PFT = Plant functional type; ∪ = fraction of variation explained by the groups together; | = variance shared only by one group; ∩ = variance shared by groups (variation explained by the redundant portion of groups)

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The overall mean concentrations of the four nutrients in plant tissues were ranked as follows: N > K > Mg > P. Across all samples, N and P concentrations presented narrower ranges of variation (5× for N and 9× for P) compared to K concentration (18×) and Mg concentration (30×). All four nutrients presented highest concentrations in forbs and lowest concentrations in *Sphagnum* mosses (Table 3). However, the concentration patterns of the four nutrients varied differently in the other three PFTs. In graminoids, N concentration was as high as that in forbs, but concentrations of P, Mg and K were lower than in forbs (Table 3). Graminoids showed lower P and Mg concentrations, but higher K concentration compared to evergreen and deciduous shrubs. Deciduous shrubs had higher N concentration than evergreen shrubs. On the other hand, P, Mg and K concentrations were similar in these two PFTs (Table 3). The N : P ratio was highest in *Sphagnum* mosses and, among the vascular PFTs, it was higher in graminoids than in forbs and evergreen shrubs. The N : P ratio in deciduous shrubs was intermediate (Table 3).

| | N (mg g$^{-1}$) | P (mg g$^{-1}$) | N : P | Mg (mg g$^{-1}$) | K (mg g$^{-1}$) |
|---|---|---|---|---|---|
| Sphagnum mosses (43) | 10.0 ± 0.3 [c] | 0.46 ± 0.2 [d] | 23.73 ± 1.24 [a] | 1.12 ± 0.05 [c] | 4.55 ± 0.17 [d] |
| Evergreen shrubs (55) | 13.1 ± 0.2 [b] | 0.98±0.3 [bc] | 14.06 ± 0.49 [d] | 1.66 ± 0.07 [b] | 5.61 ± 0.17 [c] |
| Deciduous shrubs (22) | 17.8 ± 0.5 [a] | 1.11 ± 0.04 [ab] | 16.24 ± 0.54 [c] | 1.72 ± 0.08 [b] | 6.66 ± 0.37 [c] |
| Graminoids (154) | 17.2 ± 0.3 [a] | 0.95 ± 0.03 [c] | 19.68 ± 0.47 [b] | 1.28 ± 0.04 [c] | 8.56 ± 0.23 [b] |
| Forbs (83) | 18.2 ± 0.5 [a] | 1.33 ± 0.05 [ab] | 14.70 ± 0.53 [cd] | 3.5 ± 0.21 [a] | 15.7 ± 1.21 [a] |
| Overall (357) | 16.0 ± 0.2 | 1.00 ± 0.02 | 17.93 ± 6.38 | 1.86 ± 0.07 | 9.16 ± 0.36 |
| **P** | **0.000** | **0.000** | **0.000** | **0.000** | **0.000** |

Table 3. Mean (± 1 SE) values of nutrient concentrations and N : P ratio in the five PFTs and overall means (sample numbers in parentheses). The last row contains the *P* values of one-way ANOVAs with habitat as the fixed factor. The values are expressed in mg g$^{-1}$.
Within each column, the means followed by the same letter do not differ significantly ($P = 0.05$) based on Fisher's LSD post-hoc tests

clearly related to the broad range of variation in nutrient concentrations observed in forb species. In particular, most of the forb species occurring with highest frequency in, or even being confined to, marginal streams exhibited higher nutrient (especially N and, even to a greater extent K) concentrations compared to others (for example: *Caltha palustris*, *Cirsium palustre*, *Menyanthes trifoliata*, *Myosotis palustris* and *Viola palustris*; Appendix). Shrubs had low within-PFT CV, with deciduous shrubs presenting the lowest within-PFT CV for P, Mg and N : P ratio, and evergreen shrubs the lowest within-PFT CV for N (Fig. 2). The within-PFT CV in *Sphagnum* mosses was highest for N (Fig. 2), essentially because of higher N concentration in *S. subsecundum* compared to other *Sphagnum* species (Appendix). On the other hand, the within-PFT CV in graminoids was overall intermediate, with no clear differences related to individual nutrients (Fig. 2).

PFT explained a greater part of variance, compared with habitat, for N, Mg and N : P ratio, although habitat accounted for a significant fraction of variation in the N : P ratio as well (Fig. 3). In contrast, habitat accounted for a larger part of variation in P concentration (Fig.

3). Indeed, several species of different PFTs presented highest P concentration and lowest N : P ratio in scrubs, among acidic drier habitats (hummocks, scrubs and lawns) and in marginal streams, among less acidic wet habitats (fen meadows, hollows and marginal streams), respectively. This was the case, for example, of: *S. capillifolium* and *S. magellanicum* for *Sphagnum* mosses; *Calluna vulgaris* and *Vaccinium microcarpum* for evergreen shrubs; *Carex fusca*, *C. pauciflora*, *C. rostrata*, *C. stellulata* and *E. vaginatum* for graminoids; *Menyanthes trifoliate*, *Cirsium palustre*, *Swertia perennis* and *Valeriana dioica* for forbs (Appendix). Habitat also explained an important fraction, barely less than PFT, of variance in K concentration. However, the effect of habitat on K concentration did not vary consistently among PFTs as shown by the significant PFT habitat interaction (Fig. 3), the latter being in turn related to the large coefficient of variation in K concentrations across the samples.
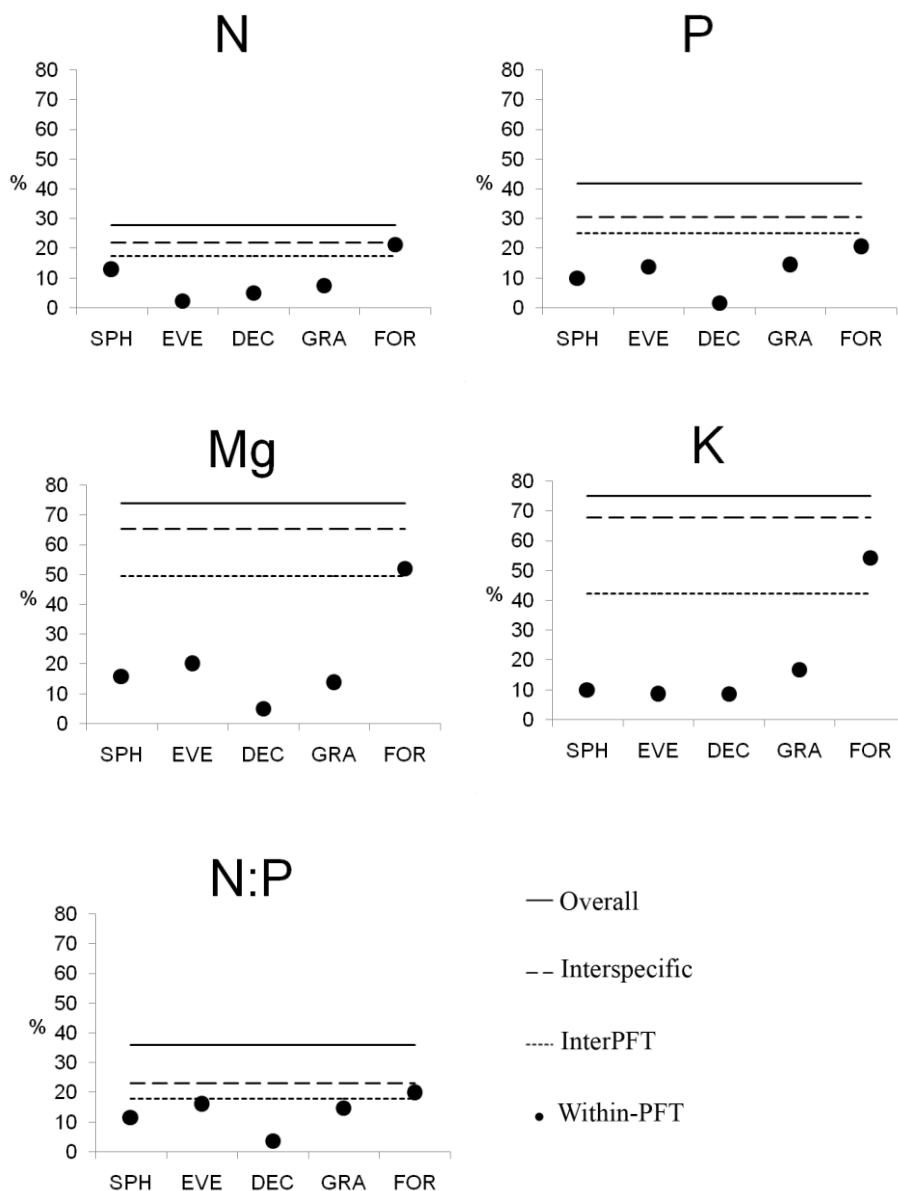


Fig. 2. Overall CV, interspecific CV, interPFT CV and within-PFT CV for nutrient concentrations and N:P ratio. Abbreviations for PFTs as in Fig. 1.
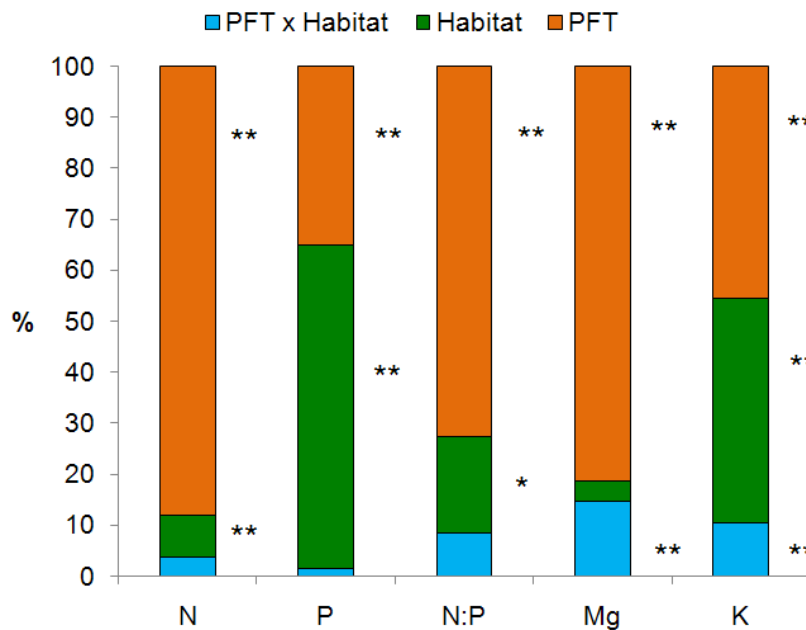
— Overall

–– Interspecific

···· InterPFT

• Within-PFT

Fig. 3. Percentage F-values for PFT, habitat and their interaction obtained by mixed-model ANOVAs of nutrient concentrations and N:P ratio. * = $P < 0.05$; ** = $P < 0.01$

## 4. Discussion

### 4.1 Habitat and vegetation

The habitats investigated in our study spanned broad ranges along two gradients, namely the WTD gradient and the acidity-alkalinity gradient, representing important directions of variation in mire vegetation in boreal high-latitude regions (Økland 1990, Vitt and Chee 1990), in mid-latitude mountainous areas (Bragazza and Gerdol 1999, Johnson and Steingraeber 2003, Marini et al 2008) and even in the southern hemisphere (Dickinson et al 2002, Kleinebecker et al 2008). The WTD gradient played the primary role in controlling the distributional patterns of species in the five mires, as frequently observed in temperate peatlands (see, e.g., Bubier et al 2006, Pellerin et al 2009). The WTD gradient can be regarded as a complex gradient, resulting from multiple responses of species along simple gradients, the latter showing direct relationships with individual ecological factors, especially dissolved oxygen concentration and, hence, redox potential (de Mars and Wassen 1999), but also soil temperature and soil moisture (Nakayama 2008, Nekola 2004). The vascular PFTs presented a sharp segregation along the WTD gradient. In particular, both evergreen and deciduous shrubs, all belonging to the ericaceous family, were almost totally restricted to well-aerated habitats because the associated mycorrhizal partners do not tolerate anoxia in the rooting layer (Wallén 1987). Conversely, forbs were overall more abundant in wet habitats with some species such as *Caltha palustris* and *Menyanthes trifoliata* even tolerating prolonged waterlogging. On the other hand, graminoids were less tightly associated to any type of habitat presumably because graminoid species possess differing adaptations to position and seasonal fluctuations of the water table, mostly related to rooting depth (Økland 1989).

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The acidity-alkalinity gradient closely depends upon the nature of water supply to the peat body. The pore water in mire habitats receiving high levels of mineral water input usually has slightly acidic to subneutral pH and relatively high EC and cation concentrations. In contrast, mire habitats fed solely by precipitation have acidic pore water with low concentrations of dissolved cations and correspondingly low EC values (Proctor et al 2009). *Sphagnum* mosses presented a much sharper segregation along the acidity-alkalinity gradient compared with the WTD gradient. Indeed, *Sphagnum* mosses were typical of acidic habitats, especially hummocks, shrubs and, to a lesser extent, lawns and hollows. In contrast, individual species within the *Sphagnum* PFT exhibited narrow niches along the WTD gradient, as observed by Bragazza and Gerdol (1996). *S. fuscum* was confined to the driest habitats, *S. subsecundum* occurred only in wet hollows, while *S. capillifolium*, *S. magellanicum* and *S. fallax* were more abundant at intermediate water levels.

*4.2 Effects of species and PFT*

We used partitioning of variance and CV as criteria for testing to what extent species, PFT and habitat could be regarded as predictors of nutrient concentrations in mire vegetation. Differing concentrations of major nutrients at the species level accounted for the largest part of the observed variations across the mire habitats investigated. Indeed, species accounted for more than half of the total variance not shared with habitat and, furthermore, interspecific CV was high for all nutrients and for the N : P ratio. Nonetheless, PFTs revealed as good predictors of nutrient concentrations in mire vegetation because interPFT CV was overall greater than within-PFT CV (Fig. 2). PFTs have also been found to explain a large part of variability in plant nutrient concentrations across wet habitats ranging from flowing water to bog (Demars and Edwards 2008). *Sphagnum* mosses presented lowest concentrations of all nutrients as observed, e.g., by Aerts and Chapin (2000) for N and P and by Ohlson (1988) for K and Mg.

Nutrient concentration patterns in vascular PFTs were rather complex because the among-PFT differences varied considerably in relation to individual nutrients. The four vascular PFTs differed from each other as regards within-PFT CV (Fig. 2). Deciduous shrubs revealed as the PFT most predictive of intermediate concentrations of all nutrients, while evergreen shrubs were good predictors of low N and K concentrations. Several studies reported consistently lower N concentrations and, to a lesser extent, K concentrations in evergreen shrubs, compared with deciduous shrubs, in acidic mires and heaths (Eckstein and Karlsson 1997, Gerdol 2000, Small 1972). Low foliar N concentrations, along with long leaf-lifespans, allow evergreens to achieve a higher N use-efficiency in habitats experiencing low N availability (Aerts 1995). Graminoids predicted relatively high N concentration and N : P ratio, on one hand, as well as lowest P and Mg concentrations, on the other hand. Such a general pattern, however, conceiled a rather high variation in nutrient content among species within this PFT. Similar variations in nutrient concentrations among co-existing graminoid species have been observed, for example, in mires of South Sweden (Malmer and Wallén 2005) and Japan (Nakamura et al 2002). The causes accounting for the observed variations in nutrient content among graminoids still are obscure. Root morphology, which provides key

information on the ability of plants to exploit soil resources (Berntson 1997), and/or differential responses of root uptake capacity to pH and redox potential in the soil (Hinsinger et al 2009) may play a role with this respect.

Forbs, although overall indicating high concentrations of all nutrients and low N : P ratio were by far the least predictive PFT with respect to foliar nutrient content. High within-PFT CV for all nutrients in forbs were probably related to heterogeneity in mechanisms and adaptations for acquiring nutrients among species within this PFT. Deep-rooted forbs, e.g., *Menyanthes trifoliata* and *Caltha palustris* presented higher concentrations of N, P and K compared to shallow-rooted forbs, with the only exception of the biennial forb *Cirsium palustre* (Falinska 1997). A possible explanation resides in higher nutrient uptake rates for deep-rooted forbs compared with shallow-rooted forbs (Pokorny et al 2005). In addition, *Menyanthes trifoliata* possesses long green rhizomes which store large amounts of nutrients (Hewett 1964). The capacity of storing reserves has great adaptive significance, especially in cold ecosystems characterized by short growing season and strong seasonal fluctuations in soil nutrient availability (Jaeger and Monson 1992, Kleijn et al 2005). Other mechanisms can account for additional heterogeneity in nutrient concentrations among shallow-rooted forbs. For example, species frequently containing arbuscular mycorrhiza (AM) in their roots, such as *Potentilla erecta* (Titus and Leps 2000) and *Ranunculus acris* (Kytoviita and Ruotsalainen 2000) had higher nutrient, especially P, concentrations compared with species lacking AM, such as *Swertia perennis* (Cripps and Eddington 2005). Indeed, the mycorrhizal partner assists the host plant in soil nutrient, mainly P, uptake (George et al 1995). On the other hand, *Bartsia alpina* had higher foliar N concentration than all others shallow-rooted forbs because of its hemiparasite behaviour (Quested et al 2003). Rather suprisingly, the carnivorous forbs *Drosera rotundifolia* and *Pinguicula vulgaris* had overall lowest N concentrations among forbs, even if carnivorous plants can obtain half of their N requirement from insect preys (Millet et al 2003).

*4.3 Effects of habitat*

Previous studies showed mean concentrations of all major nutrients to be overall highest in marginal streams and lowest in hummocks (Gerdol et al unpublished). This pattern was clearly related to plant community composition in terms of both species and PFTs, since marginal streams presented highest frequency of nutrient-rich forbs and hummocks highest frequency of nutrient-poor *Sphagnum* mosses. We conclude that habitat type, through environmental filters, such as WTD and pore-water chemistry, has a direct influence on vegetation structure and composition. The latter, in turn, indirectly control the nutrient status of the vegetation because of intrinsic differences in nutrient concentrations at the species and/or PFT level (Aerts et al 2009). Nonetheless, this study provided evidence that habitat does influence directly P concentration in plant tissues. Indeed, foliar P concentration is closely related to P availability in the soil (Hidaka and Kitayama 2009). Interestingly, soil P availability has been found to play a major role in controlling plant growth rate in an alpine ecosystem in N America (Litaor et al 2005). On the other hand, recent studies in tundra ecosystems showed that foliar N content does not vary consistently with soil N availability

(Welker et al 2005), while foliar Mg and K even presents differing among-habitat differences in species belonging to differing PFTs (Hobbie and Gough 2002).

The overall mean N : P ratio in the vegetation across all habitats in the five mires was close to 18, which suggests biomass production to be P-limited (Koerselman and Meuleman 1996). Previous studies found aboveground net primary production (ANPP) to be positively correlated with P concentration, and negatively correlated with N : P ratio, in the vegetation while concentrations of other nutrients in the vegetation were unrelated with ANPP (Gerdol et al unpublished). Therefore, P appears as the nutrient primarily limiting biomass production at our study sites. Differences in plant community composition, but also a direct influence of habitat on P availability for plant uptake, play a role with this respect. Soil P availability seems to be mainly depending on soil pH, which brings about P deficieny both in acidic habitats, such as hummocks, and in subneutral to alkaline habitats such as fen meadows and hollows. Recent research has reported several examples of P limitation in mire habitats, ranging from acidic bog or extremely poor fen (Clarkson et al 2005) to alkaline spring fens (Rozbrojova and Hajek 2008). In conclusion, P limitation in mires closely depends on habitat conditions, although it can be further affected by atmospheric N deposition, especially by exacerbating P limitation of bryophyte production (Phuyal et al 2008).

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**Aboveground production and nutrient status in the vegetation of different mire types in the South-eastern Alps (Italy)**

**Abstract**

We determined aboveground net primary production (ANPP) in five mires in the South-eastern Alps of Italy. The mires differed considerably from each other with regard to pore-water chemistry, ranging from bog to rich fen. In different habitat types (hummock, scrub, lawn, fen meadow, hollow and marginal stream) within each mire type we assessed nutrient status based on measurements of nutrient concentrations and nutrient ratios in the plant biomass. Our final objective was to detect if ANPP patterns along the poor-rich gradient could be related to the limiting effects of one or several nutrients for biomass production. Vegetation composition varied considerably both among mire sites and among habitat types in terms of individual species and plant functional types (PFTs). Nonetheless, mean ANPP was similar in the five mires. However, ANPP showed a positive correlation with total P concentration and negative correlations with the N : P ratio and with the K : P ratio of the vegetation. We conclude that plant biomass production is limited by P, rather than by other nutrients, across a broad range of mire types in this region.

**Key words** Bog, Fen, Nutrient limitation, Peatland, Plant functional type, Poor-rich gradient

## 1. Introduction

Mire ecologists have since long recognized the importance of the poor-rich gradient in northern peatlands. In fact, the seminal classification systems of mire vegetation set up by Fennoscandian authors are mainly based on variations of species composition along this gradient (Du Rietz 1949 Sjörs 1948). The ecological basis of the poor-rich gradient in mires is principally related to the level of inflow of mineral water, which results in increasing values of pH, electrical conductivity and concentrations of cations, especially $Ca^{2+}$ and $Mg^{2+}$, in pore water from bog to poor fen, intermediate fen and rich fen (Comeau and Bellamy 1986, Gerdol 1995, Proctor et al 2009, Sjörs 1952). The poor-rich gradient, therefore, corresponds to a gradient in richness of mineral elements in the pore water. However, the poor-rich gradient as defined by the mineral content in pore water has often been associated with nutrient status in the environment, with bogs being regarded as extremely poor in nutrients and fens as richer in nutrients especially at less acidic habitats (Gore 1983).

Several studies have questioned that the poor-rich gradient coincides with a nutrient gradient in mires. On one hand, concentrations of nutrient ions (especially $NO_3^-$, $NO_4^+$ and $PO_3^{3-}$) usually do not parallel increasing concentrations of mineral ions from bog to fen pore water (Vitt and Chee 1990, Wheeler and Proctor 2000). On the other hand, although total concentrations of most elements in the peat do increase along the poor-rich gradient (Bragazza and Gerdol 2002), chemical analyses of peat extracts can hardly assess nutrient availability in mire habitats, due to two main reasons. First, nutrient concentrations in the soil solutions vary strongly with time as a result of complex interactions between microbial activity and plant uptake (Miller et al 2009). Second, total soil concentrations of major nutrients such as nitrogen (N) and phosphorus (P) do not discriminate the different chemical forms of nutrients that the plants actually take up from organic soils (Graham et al 2005, McKane et al 2002). The anecdotic assumption that productivity in mire ecosystems increases along the poor-rich gradient has also been scrutinized by measurements of aboveground net primary production (ANPP) in various mire types from different climatic regions. In boreal mires, Thormann and Bayley (1997) did not observe any difference between ANPP of bogs and fens in southern Alberta, although ANPP was significantly higher in marshes compared to both bogs and fens. Similarly, Golovatskaya and Dyukarev (2009) did not find appreciable differences between ANPP of *Sphagnum* bog and sedge fen in western Siberia. Szumigalski and Bayley (1996) observed a hump-shaped pattern of ANPP along the poor-rich gradient, with ANPP increasing from bogs to moderate-rich fens and decreasing again in extreme-rich fens in central Alberta. In temperate mires of Central Europe and Minnesota, respectively, Francez (1992) and Chapin et al (2004) found even somewhat higher ANPP in bogs than in fens.

The objective of this paper was to determine ANPP in different mire types, ranging from bog to rich fen, in the southern Alps of Italy, a region where no data of ANPP in mire ecosystems have been published so far. We also aimed to investigate relationships between ANPP and nutrient status in the different habitat types within each mire type. In order to avoid flaws arising from estimates of nutrient availability by chemical analyses of peat, as discussed above, we assessed nutrient status based on measurements of nutrient concentrations and

nutrient ratios in the plant biomass. Our final objective was to detect if ANPP patterns along the poor-rich gradient could be related to the limiting effects of one or several nutrients for biomass production.

## 2. Materials and Methods

### 2.1 Study sites

The study was carried out at five mires located in two different areas in the southern Alps (North Italy). Although the two areas are rather far from each other, we chose those mires as study sites because they represent excellent examples of pristine mires covering a broad range of water chemical features, from ombrotrophic acidic to strongly minerotrophic alkaline habitats. The first area (Coltrondo) lies in the Carnic Alps, province of Belluno (46° 39' N, 12° 26' E). The climate in this area is cool montane with mean annual temperature of ca 4 °C and mean total annual precipitation of ca 1200 mm. Three mires were chosen for investigations in this area: Coltrondo W, Coltrondo N and Coltrondo S. The second area (Marcesina) lies in the Venetian Prealps, province of Vicenza (45° 57' N, 11°36' E). The climate is cool prealpine, with mean annual temperature of ca 4 °C and mean total annual precipitation of ca 1500 mm. We chose for investigations the only two mires, Palù di Sotto and Palù San Lorenzo, occurring in this area, both developing on glacial loam.

Water chemistry and vegetation composition of the five mires were recorded in the years 2005 and 2006. The results of the vegetation analysis in relation to topography, hydrology and water chemistry will be presented elsewhere. For the purpose of this study, vegetation composition and water chemistry served as the bases for classification of the mires. At a finer scale, hydrotopographic features of the mires were categorized into six habitat types: hummock, scrub, lawn, fen meadow, hollow and marginal stream. A brief description of the vegetation of the five mires is given in the following, further details are in Appendix 1.

Coltrondo W, a bog covered by *Pinus mugo* scrub patches, interspersed with *Sphagnum fuscum* and *S. capillifolium* hummocks and few hollows in the central part, while the peripheral sector is mostly covered by *S. compactum* lawns.

Coltrondo N, a poor fen covered by open vegetation rich in *Sphagnum* mosses, mostly *S. capillifolium* in hummocks, *S. magellanicum* and *S. compactum* in lawns, besides some scattered *Pinus mugo* scrub patches.

Coltrondo, S an intermediate fen mostly covered by fen meadows and, to a lesser extent, *S. compactum* lawns. *Sphagnum* hummocks and *Pinus mugo* scrubs are present but overall less abundant compared to the bog and the poor fen. Hollows are rare, and a marginal stream is well developed especially at two of the mire edges.

Palù di Sotto, a poor fen, mostly covered by *S. fuscum* and *S. capillifolium* hummocks and, to a lesser extent, by a mosaic of *S. magellanicum* lawns and *S. subsecundum* hollows.

Palù San Lorenzo, a rich fen, almost totally covered by fen meadows and hollows with only two small isolated patches of *Pinus mugo*. A marginal stream can be recognized at the two long edges of the mire.

*2.2 ANPP*

A total of 40 plots (2 m × 2 m in size) were set up for determining ANPP and for subsequent sampling of plant material. The choice of the sampling plots was made using vegetation maps (M. Tomaselli et al., unpublished), in order to recognize areas of homogeneous vegetation cover that were representative for each habitat type in the five mires.

At the beginning of the growing season 2006 (early June), four cranked wires were inserted into the *Sphagnum* mat. At the peak of the growing season 2006 (end July – early August), the whole aboveground biomass of graminoids and forbs, as well as the current-year (leaf and shoot) tissues of evergreen and deciduous shrubs were harvested from half of the area of each plot. At the end of the growing season 2006 (mid September), the elongation of *Sphagnum* plants with reference to the cranked wires (Clymo 1970) and the bulk density of the 2 cm section of the *Sphagnum* plants below the uppermost 1 cm segment (the so-called capitulum) were determined in three 100 cm$^2$ sub-quadrats per plot.

We determined ANPP as follows:

- For *Sphagnum* plants, we multiplied the mean linear elongation measured at the four cranked wires by the mean bulk density measured in the three sub-quadrats.

- For evergreen and deciduous shrubs, we considered the total mass of current-year tissues as an estimate of ANPP. In that way, we probably underestimated the aboveground production of deciduous shrubs where stem secondary growth may account for up to 20% of annual aboveground production (Gerdol 2005). However, we feel confident that this simplification did not cast too much bias onto our estimates of ANPP because the cover of deciduous shrubs was overall modest.

- For graminoids and forbs, we assumed that the whole aboveground mass had been produced during current growing season. While this is certainly true for the latter, ANPP of graminoids may have been somewhat overestimated since the yellow basal part of the leaves may correspond to overwintering senescing tissues.

Since non-*Sphagnum* mosses and lichens occurred only in a small fraction of the plots, always with modest biomass, they were not considered in the calculations.

*2.3 Sampling and chemical analysis of plant material*

Samples of plant tissues were collected at all 40 selected plots, from the area not used for biomass harvest. Fully developed, intact current-year leaves of all vascular plants and the capitulum of all *Sphagnum* species occurring in the plots were harvested at the peak of the growing season 2006 (end July – early August).

The plant material was sorted by species, cleaned, oven-dried at 60°C for 24 h, ground through a 1-mm mesh titanium mill and then digested according to the Kjeldahl procedure. Nitrogen and P concentrations were determined colorimetrically by a flow-injection autoanalyser (FlowSys, Systea, Roma, Italy). Potassium (K) concentration was determined by atomic-absorption spectrophotometry (SOLAAR 969, UNICAM, Cambridge, UK). To ensure accuracy within 5%, standard reference material of known N, P and K concentration (NIST

Citrus leaves 1572, National Bureau of Standards, Washington, DC, USA) was analyzed together with samples.

The species were then grouped into the following growth-form-based plant functional types (PFTs): *Sphagnum* mosses, evergreen shrubs, deciduous shrubs, graminoids, forbs. Non-*Sphagnum* mosses, lichens and pteridophytes were not considered in the analyses because they occurred very rarely in the sampling plots. In total, we processed 368 samples from 39 species.

*2.4 Statistics*

Significance of differences among sites and habitat types in terms of ANPP, nutrient concentrations and nutrient ratios in the whole vegetation was assessed by mixed-models ANOVAs, with site as fixed factor, habitat as random factor and interaction as fixed factor. Significance of differences among habitats in nutrient concentrations and nutrient ratios within each of the five PFTs was assessed by one-way ANOVAs. Whenever appropriate, Fisher's LSD tests were employed to assess post-hoc differences. Relationships between ANPP, on one side, and nutrient concentrations and nutrient ratios on the other side, were assessed by calculating Pearson's product-moment correlation coefficients. The statistical computations were made using the package STATISTICA (Release 6; StatSoft Inc., Tulsa; USA).

## 3. Results

*3.1 ANPP*

The ANPP values recorded at the 40 plots varied by one order of magnitude, from 40 to 640 g dry matter $m^{-2}$ $yr^{-1}$. Mean ANPP did not differ among sites but did differ among habitat types, with a significant site × habitat type interaction (Table 1; Fig. 1). Scrubs and marginal streams were more productive than hummocks, lawns and fen meadows, while mean ANPP in hollows was intermediate (Fig. 1B). The ANPP of fen meadows was somewhat higher in the richest fens compared to the bog (Table 2). The ANPP of hummocks was highest in one of the poor fens (Coltrondo N), while those of scrubs and marginal streams were highest in the rich fen (Table 2). The ANPP of lawns was somewhat higher in the poor sites (bog and one of the poor fens). The ANPP of hollows presented the greatest range of between-site variation (Table 2).

The partitioning of total ANPP among PFTs varied considerably both among sites and among habitat types (Fig. 1). Graminoids accounted for a considerable part of total ANPP in all sites, but the corresponding fraction was much higher in the intermediate fen and especially in the rich fen (Fig. 1A). In contrast, the ANPP of *Sphagnum* mosses varied strongly, from almost zero in the rich fen to about half of total ANPP in poor fens and somewhat lower values in the bog (Fig. 1A). The ANPPs of evergreen shrubs and deciduous shrubs were overall modest, with the exception of the bog. The ANPP of forbs generally was negligible. Only in the rich fen did forbs account for a perceivable, although low, fraction of total ANPP (Fig.

1A). Graminoids represented the dominant PFT in lawns, fen meadows, hollows and marginal streams, but were rather frequent in hummocks and scrubs as well (Fig. 1B). *Sphagnum* mosses were most abundant in hummocks and scrubs and, to a lesser extent, in lawns and hollows. Evergreen shrubs accounted for a considerable fraction of total ANPP in scrubs but were absent in all other habitat types except hummocks (Fig. 1B). Deciduous shrubs and forbs had overall low frequencies, except for deciduous shrubs in scrubs and forbs in marginal streams, respectively (Fig. 1B).

| | Site (4) | Habitat type (5) | Interaction (12) |
|---|---|---|---|
| ANPP | 0.26 | **0.001** | **0.007** |
| N | 0.66 | **0.03** | 0.71 |
| P | 0.36 | **0.001** | 0.75 |
| K | 0.27 | **0.001** | 0.07 |
| N : P | 0.22 | **0.004** | 0.99 |
| N : K | 0.08 | **0.01** | 0.08 |
| K : P | 0.52 | **0.001** | 0.26 |

**Table 1** *P* values resulting from mixed-model ANOVAs of ANPP, and nutrient concentrations and nutrient ratios in the vegetation, with site as fixed factor, habitat type and interaction site × habitat type as random factors (d.o.f. in parentheses). Significant ($P < 0.05$) values are in boldface

| | Coltrondo W BOG | Coltrondo N POOR FEN | Palù di Sotto POOR FEN | Coltrondo S INTERM. FEN | Palù San Lorenzo RICH FEN |
|---|---|---|---|---|---|
| Hummock | 179 ± 15 | 300 ± 42 | 160 ± 26 | 162 ± 10 | - |
| Scrub | 342 ± 13 | 434 | 355 | 345 | 626 |
| Lawn | 229 ± 45 | 238 ± 115 | 133 | 124 | - |
| Fen meadow | 179 | - | - | 252 ± 74 | 212 ± 26 |
| Hollow | 218 ± 22 | 238 | 640 | 39 | 235 ± 118 |
| Marginal stream | 339 ± 39 | - | - | 323 | 594 |

**Table 2** Mean (± SE) ANPP (as g m$^{-2}$ yr$^{-1}$) in the six habitat types at the five mires
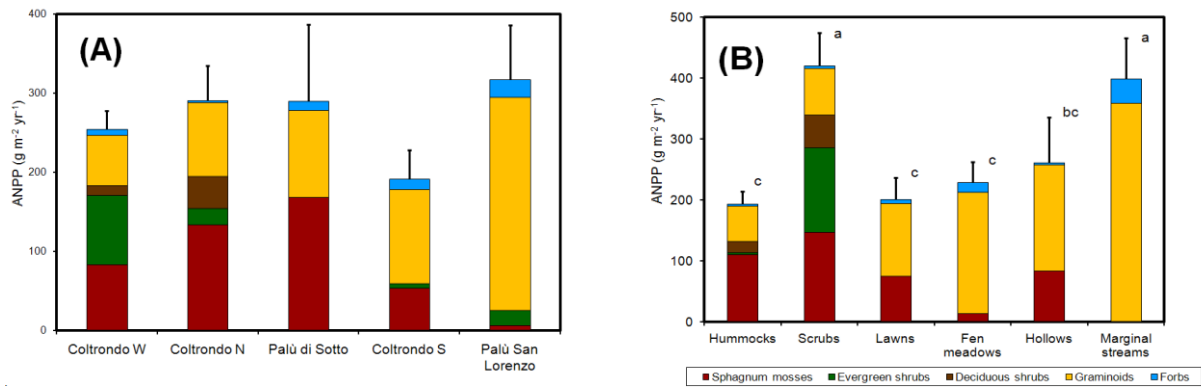
**Fig. 1** Mean (+ 1 SE) ANPP, subdivided according to PFTs, in the five mires (upper panel) and in the six habitat types (lower panel). In the lower panel, the means followed by different letters differ significantly (*P* < 0.05) from each other. The mire sites are ordered, from bog to rich fen, according to increasing mean pH of pore water

## 3.2 Nutrients

Nutrient concentrations, as well as nutrient ratios, in the vegetation differed significantly among habitat types, but not among sites. Neither were there any significant site × habitat type interactions (Table 1). Mean N concentration in the vegetation was close to 1.5% in four of the five mires, with somewhat lower values in one of the poor fens (Coltrondo N; Table 3). Mean P concentration in the vegetation was comprised between 0.8 and 1.0% in four mires and was, again, somewhat lower in one of the poor fens (Palù di Sotto; Table 3). Mean K concentration in the vegetation varied more, although still not significantly, among sites, with highest value in the intermediate fen and lowest value in the rich fen. The three nutrient ratios varied approximately to the same extent among the sites (20-26%), always with highest values in one of the poor fens (Palù di Sotto; Table 3).

The concentrations of all three major nutrients in the vegetation were highest in marginal streams and lowest in hummocks (Table 4). Nutrient concentrations in the vegetation of the four other habitats also varied considerably but with differing among habitat patterns. Indeed, N and K concentrations in the vegetation of fen meadows and hollows were somewhat higher than in scrubs, while P concentration in the vegetation of scrubs was significantly higher than in the vegetation of lawns and, especially, in that of hollows (Table 4). The mean N : P ratio in the vegetation of scrubs and marginal streams was around 14 or lower, i.e., much smaller than in all other habitat types, where the mean N : P ratio was > 18. The mean N : K ratio was highest in the vegetation of hummocks and lowest in that of marginal streams. Conversely, the mean K : P ratio was highest in the vegetation of hollows and lowest in that of scrubs (Table 4).

|  | Coltrondo W BOG | Coltrondo N POOR FEN | Palù di Sotto POOR FEN | Coltrondo S INTERM. FEN | Palù San Lorenzo RICH FEN |
|---|---|---|---|---|---|
| N (%) | 1.55 ± 0.09 | 1.32 ± 0.06 | 1.48 ± 0.11 | 1.47 ± 0.13 | 1.53 ± 0.10 |
| P (‰) | 1.01 ± 0.12 | 0.81 ± 0.09 | 0.64 ± 0.04 | 0.83 ± 0.13 | 0.83 ± 0.07 |
| K (%) | 0.49 ± 0.04 | 0.33 ± 0.04 | 0.44 ± 0.08 | 0.55 ± 0.22 | 0.25 ± 0.03 |
| N : P | 17.0 ± 1.5 | 17.0 ± 1.5 | 23.1 ± 1.5 | 19.1 ± 1.6 | 19.0 ± 1.3 |
| N : K | 1.87 ± 0.10 | 2.33 ± 0.26 | 2.47 ± 0.21 | 2.01 ± 0.17 | 2.16 ± 0.15 |
| K : P | 9.1 ± 0.5 | 7.8 ± 1.1 | 9.7 ± 1.2 | 9.7 ± 0.6 | 9.1 ± 0.8 |

**Table 3** Mean (± SE) nutrient concentrations and nutrient ratios in the vegetation of the five mires. No means did differ significantly among sites

|  | Hummocks | Scrubs | Lawns | Fen meadows | Hollows | Marginal streams |
|---|---|---|---|---|---|---|
| N (%) | 1.31 ± 0.08 c | 1.34 ± 0.07 bc | 1.43 ± 0.08 bc | 1.59 ± 0.10 b | 1.55 ± 0.12 bc | 1.92 ± 0.11 a |
| P (‰) | 0.67 ± 0.05 d | 1.02 ± 0.13 b | 0.77 ± 0.09 cd | 0.88 ± 0.07 bc | 0.67 ± 0.04 d | 1.55 ± 0.12 a |
| K (%) | 0.55 ± 0.03 d | 0.60 ± 0.13 cd | 0.75 ± 0.06 bc | 0.83 ± 0.06 b | 0.74 ± 0.06 bc | 1.41 ± 0.23 a |
| N : P | 19.9 ± 1.0 ab | 14.0 ± 1.7 c | 19.3 ± 1.5 ab | 18.5 ± 1.5 b | 23.0 ± 1.2 a | 12.8 ± 1.8 c |
| N : K | 2.43 ± 0.15 a | 2.30 ± 0.14 ab | 1.94 ± 0.12 bc | 1.95 ± 0.13 bc | 2.11 ± 0.12 abc | 1.56 ± 0.43 c |
| K : P | 8.4 ± 0.5 b | 6.1 ± 0.6 c | 10.0 ± 0.8 ab | 9.6 ± 0.6 ab | 11.0 ± 0.5 a | 8.9 ± 0.9 ab |

**Table 4** Mean (± SE) nutrient concentrations and nutrient ratios in the vegetation of the six habitat types. Within each row, the means followed by different letters differ significantly ($P < 0.05$) from each other

Relationships between nutrient concentrations and nutrient ratios, on one hand, and vegetation composition in terms of PFTs were rather complex. In particular, the vegetation of marginal streams was dominated by graminoids (Fig. 1B), a PFT showing overall intermediate nutrient concentrations and nutrient ratios. In graminoids, nutrient concentrations were significantly higher, and N : P and N : K ratios significantly lower in marginal streams than in all other habitat types (Appendix 2). Forbs, although having overall highest nutrient concentrations and overall lowest nutrient ratios, also presented higher P and K concentrations, and lower N : K ratio, in marginal streams compared to all other habitats (Appendix 2). *Sphagnum* mosses, exhibiting the overall lowest nutrient concentrations as well as the overall highest nutrient ratios, were rather abundant in four habitat types (hummocks, scrubs, lawns and hollows), nonetheless considerably differing from each other as regards mean nutrient concentrations and mean nutrient ratios in the vegetation. This was at least partly related to significantly higher nutrient, especially P, concentrations and

significantly lower N : P ratio in *Sphagnum* mosses of scrubs compared to the other three habitats (Appendix 2).

Across all plots, ANPP was unrelated to N concentration ($r$ = 0.23; $P$ = 0.16; $N$ = 40), K concentration ($r$ = 0.08; $P$ = 0.60; $N$ = 40) and N : K ratio ($r$ = 0.14; $P$ = 0.40; $N$ = 40) in the vegetation. In contrast, ANPP showed a significant positive correlation with P concentration ($r$ = 0.37; $P$ = 0.02; $N$ = 40), and significant negative correlations with the N : P ratio ($r$ = - 0.31; $P$ = 0.05; $N$ = 40) and with the K : P ratio ($r$ = - 0.44; $P$ = 0.005; $N$ = 40) in the vegetation.

## 4. Discussion

### 4.1 ANPP patterns

The mean ANPPs in our mires in the Southern Alps were very similar to those recorded in several mires of the boreo-nemoral regions of North America and Northern Eurasia, generally ranging from 200 to 300 g m$^{-2}$ yr$^{-1}$ (see Rydin and Jeglum 2006 and references therein). Few data are so far available for comparing our data with estimates of ANPP in mires of mountainous regions. For example, Francez (1992) reported mean ANPPs of ca. 300 g m$^{-2}$ yr$^{-1}$ for mires in the Massif central. Conversely, mean ANPPs in mires of the (sub)arctic regions are somewhat lower (ca. 200 g m$^{-2}$ yr$^{-1}$ or less, Camill et al 2001), while those in oceanic regions of western Europe usually are considerably higher (> 500 g m$^{-2}$ yr$^{-1}$; Forrest and Smith 1975). In summary, patterns of ANPP in mires at a broad geographic scale seems to be primarily controlled by climate, particularly by length of the growing season. At a smaller scale, namely at the site level, our data supported evidence from recent studies, all reporting poor if any variation in ANPP from bogs to fens. Indeed, ANPP did not show any consistent variation pattern when the sites were ordered from bog to rich fen. Neither did ANPP differ significantly among the sites, although mean ANPP was somewhat lower in the transitional fen than in the other sites. At an even smaller scale, ANPP varied much more. We found significant differences in ANPP among habitat types, with scrubs and marginal streams being significantly more productive than all other habitats. We also observed considerable differences in ANPP within the same habitat type at different sites. The resulting, rather complex pattern could be interpreted on the basis of nutrient concentrations and nutrient ratios in the vegetation.

### 4.2 Relationships between ANPP and nutrients in the vegetation

The overall positive correlation of ANPP with P concentration in the vegetation and the overall negative correlations of ANPP with the N : P ratio and with the K : P ratio in the vegetation suggest that ANPP in our mires was primarily limited by P availability. Phosphorus limitation occurred in different habitat types, however without any consistent patterns along the bog-fen gradient. Indeed, mean ANPP was lowest in habitats differing greatly from each other as regards water-table-depth, pore-water chemistry and vegetation composition, i.e. hummocks, lawns, fen meadows and, to a lesser extent, hollows. In all of

these habitat types, mean P concentration in the vegetation was < 1‰ and, even more important, the mean N : P ratio in the vegetation was > 18, a threshold indicating P limitation (Koerselman and Meuleman 1996). Although our study was not designed for providing mechanistic explanations of P availability in mire ecosystems, recent studies reported a tight coupling between soil P content and P concentration in plants (Han et al 2005, Hedin 2004). The observed between-habitat differences in P status may reside in the wide variety of P fractions occurring in organic soils (Schlichting et al 2002). These P forms undergo various types of biogeochemical controls, in close relation to soil pH, that ultimately regulates their availability for plant uptake (Bridgham et al 2001).

Labile organic P forms usually dominate in acidic soils, like those of hummocks and lawns. The behaviour of the microbial pool has major implications for controlling P availability in acidic organic soils (Kellogg and Bridgham 2003), as microbial P represents up to 70% of total P in this type of soils (Williams and Silcock 2001). Contrary to acidic habitat types, geochemical control is active in subneutral fens because of P fixation by Fe- and Al-hydroxides or calcareous components (Boeye et al 1995). Hollows exhibited the overall poorest P status, as indicated by the lowest P concentration and the highest N : P and K : P ratios in the vegetation (Table 4). However, this was not mirrored in similarly lowest mean ANPP in hollows. Indeed, ANPP varied greatly, even by one order of magnitude, within hollows, probably in relation to soil aeration, in turn depending of water level. Anoxic or intermittently anoxic conditions may decrease microbial activity, thus slowing decomposition and P immobilization. For example, Johnson and Damman (1991) measured slower rates of mass low from *Sphagnum cuspidatum* litter in anoxic layers than in the oxic layers of a raised bog.

On the other hand, we found highest mean ANPP in scrubs and marginal streams although the environmental conditions in these two habitats were quite different. Nonetheless, P did not appear to be limiting in either of the two habitats, as mirrored by relatively high P concentration (> 1‰) and low N : P ratios (< 14) in the vegetation. Higher P availability in scrubs may be related to accumulation of needle litter and subsequent nutrient dynamics during litter breakdown. Rutigliano et al (1998) observed rapid losses of P, both by leaching and mineralization, from decomposing needle litter independent of the initial P content in the litter itself. In addition, P is leached from pine roots as well (Comerford and Smethurst 1993). As a consequence, P leached from living and/or senescing pine tissues accumulates as soluble reactive P in the pore water of scrubs (R Gerdol et al, unpublished), thus improving P availability for plant uptake in this habitat type. Marginal stream was the by far most productive habitat type, which matched with the highest nutrient status. In fact, concentrations of all nutrients in the vegetation of marginal streams were much higher than in all other habitat types, even if nutrient concentrations in the pore water were not (R. Gerdol et al., unpublished). This seemingly contradictory pattern is probably due to high water flow rates implying improved nutrition in marginal streams independent of the chemical features and the origin of the water (Økland 1989).

*4.3 Relationships between ANPP, nutrient status and vegetation composition*

Habitat types defined on a hydrotopographic basis accounted for much of the variation in terms of both ANPP and nutrient status of the vegetation. However, the observed variation patterns were largely independent of the poor-rich gradient, as currently defined by hydrochemical criteria. The significant correlations between ANPP and P concentration in the vegetation, besides the related nutrient ratios, provide indirect evidence that P content in plants represents a good proxy of P availability for plant uptake. Between-habitat differences in the overall plant P contents could arise from: (i) differing composition in terms of species and/or PFTs having intrinsically different nutrient contents, (ii) differing nutrient concentrations in plant species or PTFs in relation to habitat, or (iii) a combination of these two causes. The third cause appeared to hold in our case, as the coverage of PFTs varied considerably among habitat types and the PFTs presented overall significant differences as regards nutrient concentrations and nutrient ratios. However, P concentrations, N : P ratios and K : P ratios within PFTs differed considerably among habitats. Previous studies also reported significant effects of habitat on foliar P content in wetland vascular species (Güsewell and Koerselman 2002), bog vascular species (Aerts et al 1999, Eckstein & Karlsson 1997) and *Sphagnum* mosses (Wojtuń 1994).

It seems rather surprising that ANPP did not differ among mire sites in spite of significant differences in the mean ANPPs of habitat types. Possible explanations could reside in the different coverage of habitat types at the five mires and/or in the between-site variations of ANPP for certain habitat types. We are aware that our estimates of ANPP at the site level may be somewhat biased because our sampling design implied a low number of replicate plots among sites for most habitat types. A higher number of replicate plots would have been unmanageable because of the big work required for determining ANPP and, especially, nutrient content in the plant biomass. However, estimates of ANPP based on the coverage of habitat types drawn from vegetation maps (M. Tomaselli et al, unpublished), did not differ appreciably from those obtained in our study.

**5. Conclusion**

This study provided evidence that biomass production in a set of mires on the South-eastern Alps was mostly limited by P deficiency, but P limitation was largely unrelated to environmental conditions underlying the poor-rich gradient in mire vegetation. Our findings support, at a local scale, the results of broad-scale surveys suggesting that P limitation in mire ecosystems is more frequent than previously recognized. In ombrotrophic habitats P (and perhaps K) deficiency affects ANPP by limiting growth of *Sphagnum* mosses if atmospheric N deposition exceeds a threshold implying N saturation in the moss layer (Bragazza et al 2004). On the other hand, low productive fens often are P-limited although ANPP in rich fens can be controlled by N availability when P in pore water is enriched by man's impact (Olde Venterink and Vittoz 2008, Wassen et al 2005).

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**Appendix 1** Summary of environmental features and pore-water chemistry in the five mire sites. EC = electrical conductivity

| | Coltrondo W | Coltrondo N | Coltrondo S | Palù di Sotto | Palù San Lorenzo |
|---|---|---|---|---|---|
| Mire type | Bog | Poor fen | Intermediate fen | Poor fen | Rich fen |
| Elevation (m) | 1830 | 1910 | 1790 | 1330 | 1360 |
| Area (ha) | 1.2 | 1.7 | 2.1 | 1.7 | 6.7 |
| Mean pH | 4.30 | 4.91 | 6.01 | 5.39 | 6.60 |
| Mean EC ($\mu$S cm$^{-1}$) | 20 | 33 | 58 | 75 | 247 |
| Mean Ca$^{2+}$ conc. (mg l$^{-1}$) | 2.0 | 2.5 | 7.9 | 5.9 | 18.5 |

**Appendix 2** Mean (± SE) nutrient concentrations and nutrient ratios in the five PFTs at the six habitat types and *P* values obtained by one-way ANOVAs. Whenever the among-habitat differences are significant at *P* < 0.05 (figures in boldface), the means followed by the same letter do not differ at *P* < 0.05 based on Fisher's post-hoc LSD test.
(D.o.f.: *Sphagnum* mosses 3,39; evergreen shrubs 4,50; deciduous shrubs 2,19; graminoids 5,148; forbs 5,77)

| | | Hummocks | Scrubs | Lawns | Fen meadows | Hollows | Marginal streams | *P* |
|---|---|---|---|---|---|---|---|---|
| *Sphagnum* mosses | N (%) | 0.97 ± 0.06 | 0.97 ± 0.03 | 0.99 ± 0.05 | - | 1.21 ± 0.27 | - | *0.34* |
| | P (‰) | 0.38 ± 0.03 b | 0.55 ± 0.03 a | 0.44 ± 0.05 ab | - | 0.49 ± 0.08 ab | - | ***0.02*** |
| | K (%) | 0.41 ± 0.02 | 0.49 ± 0.03 | 0.47 ± 0.03 | - | 0.49 ± 0.07 | - | *0.23* |
| | N : P | 27.5 ± 2.7 a | 18.0 ± 0.8 c | 24.5 ± 1.9 ab | | 24.0 ± 1.6 abc | | ***0.02*** |
| | N : K | 2.41 ± 0.11 | 2.05 ± 0.11 | 2.20 ± 0.14 | | 2.43 ± 0.21 | | *0.18* |
| | K : P | 11.3 ± 0.8 | 9.1 ± 0.6 | 11.5 ± 1.0 | | 10.0 ± 0.6 | | *0.16* |
| Evergreen shrubs | N (%) | 1.25 ± 0.04 | 1.34 ± 0.06 | 1.37 ± 0.04 | 1.31 ± 0.06 | 1.52 | - | *0.52* |
| | P (‰) | 0.99 ± 0.05 | 1.08 ± 0.07 | 0.98 ± 0.06 | 0.70 ± 0.04 | 0.81 | - | *0.13* |
| | K (%) | 0.57 ± 0.03 | 0.56 ± 0.04 | 0.55 ± 0.03 | 0.47 ± 0.03 | 0.72 | | *0.49* |
| | N : P | 13.3 ± 0.7 | 12.2 ± 0.6 | 14.5 ± 1.1 | 18.9 ± 0.7 | 18.6 | | *0.06* |
| | N : K | 2.30 ± 0.10 | 2.35 ± 0.10 | 2.52 ± 0.14 | 2.80 ± 0.16 | 2.09 | | *0.32* |
| | K : P | 5.9 ± 0.3 | 5.3 ± 0.3 | 5.7 ± 0.3 | 6.8 ± 0.2 | 8.9 | | *0.07* |
| Deciduous shrubs | N (%) | 1.68 ± 0.06 | 1.85 ± 0.08 | 1.93 ± 0.08 | - | - | - | *0.10* |
| | P (‰) | 1.02 ± 0.04 b | 1.19 ± 0.06 a | 1.25 ± 0.01 a | - | - | - | ***0.04*** |
| | K (%) | 0.62 ± 0.07 | 0.71 ± 0.04 | 0.70 ± 0.05 | - | - | - | *0.56* |
| | N : P | 16.6 ± 0.8 | 15.8 ± 0.9 | 15.8 ± 1.9 | | | | *0.78* |
| | N : K | 3.09 ± 0.42 | 2.68 ± 0.16 | 2.77 ± 0.27 | | | | *0.68* |
| | K : P | 6.4 ± 0.8 | 6.1 ± 0.6 | 5.7 ± 0.3 | | | | *0.90* |
| Graminoids | N (%) | 1.80 ± 0.05 ab | 2.02 ± 0.14 a | 1.71 ± 0.06 bc | 1.67 ± 0.06 bc | 1.57 ± 0.06 bc | 1.95 ± 0.07 ab | ***0.005*** |
| | P (‰) | 0.93 ± 0.04 b | 1.28 ± 0.16 a | 0.99 ± 0.06 b | 0.92 ± 0.05 b | 0.73 ± 0.04 c | 1.56 ± 0.10 a | ***0.001*** |
| | K | 0.75 ± 0.05 | 0.92 ± 0.08 b | 0.91 ± 0.05 b | 0.82 ± 0.04 | 0.83 ± 0.04 | 1.37 ± 0.14 a | ***0.001*** |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | (%) | c | | | bc | bc | | |
| | N : P | 20.2 ± 0.9 ab | 16.8 ± 1.2 bc | 19.3 ± 1.1 b | 19.4 ± 0.9 b | 22.3 ± 1.1 a | 12.7 ± 0.6 c | *0.002* |
| | N : K | 2.66 ± 0.15 a | 2.30 ± 0.23 ab | 2.06 ± 0.13 bc | 2.18 ± 0.12 b | 1.96 ± 0.09 bc | 1.52 ± 0.17 c | *0.001* |
| | K : P | 8.5 ± 0.6 b | 8.0 ± 1.1 b | 9.9 ± 0.5 b | 9.5 ± 0.6 b | 11.8 ± 0.6 a | 8.7 ± 0.7 b | *0.002* |
| Forbs | N (%) | 1.64 ± 0.07 | 2.12 ± 0.06 | 1.67 ± 0.10 | 1.76 ± 0.09 | 1.80 ± 0.18 | 2.07 ± 0.09 | *0.06* |
| | P (‰) | 1.21 ± 0.01 b | 1.17 ± 0.03 b | 1.22 ± 0.01 b | 1.18 ± 0.06 b | 1.08 ± 0.06 b | 1.78 ± 0.10 a | *0.001* |
| | K (%) | 0.88 ± 0.08 b | 0.99 ± 0.10 b | 1.46 ± 0.22 b | 1.22 ± 0.16 b | 0.89 ± 0.01 b | 2.73 ± 0.26 a | *0.001* |
| | N : P | 14.4 ± 1.5 | 18.0 ± 1.0 | 14.5 ± 1.1 | 15.8 ± 1.1 | 17.1 ± 1.8 | 12.2 ± 0.7 | *0.07* |
| | N : K | 1.93 ± 0.11 ab | 2.15 ± 0.16 ab | 1.50 ± 0.19 b | 1.76 ± 0.14 ab | 2.14 ± 0.23 a | 0.93 ± 0.11 c | *0.001* |
| | K : P | 7.7 ± 0.9 b | 8.5 ± 1.1 b | 12.9 ± 2.4 ab | 11.0 ± 1.5 ab | 8.3 ± 0.9 b | 16.6 ± 2.0 a | *0.02* |

# Hydrologic controls on water chemistry, vegetation and ecological patterns in two mires in the South-Eastern Alps (Italy)

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## ABSTRACT

We examined how hydrology influenced water chemistry, vegetation, nutrient status, aboveground net primary production (ANPP) and litter decomposition rates in two mires on the South-Eastern Alps of Italy. One of the mires had a modest hydraulic gradient and prevalently acted as a recharge system, although there were short phases of vertical flow reversal during dry periods. This peatland was, therefore, prevalently fed by rainwater and was covered by bog-like vegetation, mainly hummocks and scrubs with a ground layer rich in *Sphagnum* mosses. The other peatland presented a steeper hydraulic gradient, with the surface being fed by mineral water either by surface runoff and by vertical, upwards directed ground-water flow. Compared to the bog-dominated peatland, the pore water was less acidic and richer in telluric cations. This mire was covered by fen-like vegetation, prevalently fen meadows. Nitrogen (N) content in the vegetation was very similar in the two peatlands, while phosphorus (P) content was lower in the fen-dominated site. Contrary to our expectations, ANPP did not differ significantly between the two sites while litter decomposition rates were significantly lower in the fen-dominated peatland, presumably because of P limitation of decomposers. This suggests that the development of ombrogenous peatlands in this region need not be due to increased accumulation of peat during succession from mineralwater-fed to rainwater-fed conditions.

Key words: Bog; Decomposition; Fen; Map; Nutrient; Production.

# 1. Introduction

Peatlands are widespread in high-latitude territories of the northern hemisphere, especially boreal and subarctic regions, where they cover vast areas (Mitsch and Gosselink 2000) and store about one-third of the total soil carbon (C) pool (Gorham 1991). In spite of their abundance, peatlands represent vulnerable ecosystems, strongly depending on delicate equilibria among water input, nutrient loading, climate and major ecological processes, especially plant production and organic-matter decomposition (Rydin and Jeglum, 2006). Palaeoecological records of peat deposits have documented repeated changes in the vegetation of northern peatlands during the Holocene. Most of these changes were triggered by climatic variations, in turn implying modifications in peatland hydrology (Hughes and Barber 2003, Charman 2007). In the last few decades, peatlands underwent environmental changes at an unprecedented rapid pace as an effect of human activities (Mauquoy and Yeloff 2008). Water-table drawdown and/or increased evapotranspiration under warmer climatic conditions result in drying of the peatland surface (Strack et al 2006, Gerdol et al 2008). This will probably interact with increased nutrient, particularly nitrogen (N), input in affecting processes and patterns in peatland ecosystems. In particular, dryness and/or eutrophication are expected to reduce net C sequestration by accelerating C losses either as dissolved organic C (Strack et al 2008) or as gaseous $CO_2$ emissions (Lund et al 2007). The latter will presumably exert a positive feedback effect on atmospheric $CO_2$ concentration (Moore 2002). Peatlands also occur in mid-latitude territories, especially on mountains. In mountainous northern regions, especially the Alps, peatlands usually are situated in rather densely populated areas where, in spite of depopulation and modifications in the traditional land-use practice (Tappeiner et al 2008), anthropic pressure generally is stronger than in high-latitude remote territories. Future changes in the structure and functioning of these ecosystems will decrease soil C stocks (Leifeld et al 2005) and will, furthermore, imply a decline of the landscape value (Gret-Regamey et al 2008) in terms of scenic beauty, recreation services and biodiversity. In the Southern Alps of Italy peatlands cover a modest fraction of the territory, well below 1% of the total area. Nonetheless, they possess a particularly high scientific and conservation importance because this region represents the southernmost outpost in Europe for several endangered species and priority habitat types of community interest (Gerdol and Tomaselli 1997).

Peatland ecosystems are primarily characterized by their hydrology, with origin of water input representing the main basis for peatland typification (Mitsch and Gosselink 2000). In particular, a major distinction has been made for several decades between minerogenous peatlands (fens), receiving water from the mineral soil, and ombrogenous peatlands (bogs), receiving water from precipitation (Sjörs 1948, Du Rietz 1954). Peatland ecology in the South-Eastern Alps has been the object of several papers, mostly based on plant community composition and occasional analyses of pore-water chemistry (see Gerdol and Tomaselli, 1997 and references therein). However, no study has so far investigated relationships among peatland hydrology, vegetation and ecological patterns in this region. As the ecological features and, eventually, the very existence of peatlands closely depend on amount and quality of water input, it is important to understand how hydrology controls vegetation

composition and ecosystem functioning in these habitats. The latter point is, in turn, a fundamental basis for any policy of peatland conservation and/or restoration.

The objective of this paper was to analyze relationships between hydrology, on one hand, and vegetation composition and ecological processes, on the other hand, in peatlands on the South-Eastern Alps. To this purpose, we chose two pristine peatlands strongly differing from each other as regards both water chemistry and vegetation cover, with one of the two sites being prevalently covered by bog-like vegetation and the other by fen-like vegetation. We hypothesized that the bog-dominated mire was mostly fed by rain water while the fen-dominated mire was prevalently fed by ground water, surface runoff or both. We also hypothesized that rates of organic-matter production and decomposition were slower in the bog-dominated mire than in the fen-dominated mire (Moore and Bellamy 1974, Gore 1983).

## 2. Material and methods

### 2.1 Study sites

The study was carried out during the years 2005 and 2006 at two mires in the Carnic Alps, municipality of Comelico superiore, province of Belluno (46°39'N, 12°26'E). The two mires lie 700 m apart at ca 1800 m on a geologic substrate consisting of phyllites and sandstones of late Palaeozoic age. Phyllites are metamorphic rocks composed by recrystallized phyllosilicates with lenses and nodules of quartz, quartzite, graphite and gneiss. Sandstones are sedimentary rocks rich in quartz and phyllosilicates. The mineral composition of both units is typically acidic and low in calcium. As a consequence, groundwater flowing inside these units (and potentially recharging peat pore-water) has low concentrations of dissolved electrolytes and low Ca/Mg ratio. The climate is cool with mean annual temperature of ca 4 °C and mean total annual precipitation of ca 1200 mm.

The first mire (Coltrondo W; elevation 1830 m, area 1.2 ha) is located on a saddle and has a peat thickness barely exceeding 2.5 m and is mostly covered by bog-like vegetation, so that it will be henceforth named 'bog site'. The second mire (Coltrondo S; elevation 1790 m, area 2.1 ha) is located in a structural elongated depression, with a small perennial creek draining the mire. The thickness of the peat body attains 7 m in the central part of the mire. Coltrondo S is mostly covered by fen-like vegetation, so that it will be henceforth named 'fen site'.

### 2.2 Hydrology and water chemistry

In early June 2005 a number of 1-m$^2$ plots were set up at the two mires (26 in the bog site and 18 at the fen site). The plots were located along transects in order to account for the whole range of habitat variation. Within each plot a 1-m long perforated PVC pipe (internal diameter 14 mm, wall thickness 2 mm) was inserted into the peat, with the top at the level of the mire surface. In each of these pipes (henceforth called phreatimeters) water-table depth was measured manually, at weekly intervals, from June to November 2005 and 2006. The

measurements of water-table depth were referred to the ground level, with positive values indicating water table above ground and negative values water table below ground.

Furthermore, 24 open-stand PVC piezometers (inside diameter 52 mm, wall thickness 4 mm) were set up in early October 2005. The piezometers, consisting in 0.5-1 m long modules with threaded joint and a 10-cm long slotted portion, were arranged in eight clusters of three piezometers each (3 at the bog site and 5 at the fen site). At each piezometer cluster the modules were assembled by positioning the slotted part at different depths in order to determine vertical profiles of head. The vertical profiles sampled at the two mires did not match, as regards depth of sampling, since the thickness of the peat body differed substantially between mires. The depths were chosen in relation to the peat stratigraphy recorded at each cluster site and grouped into three intervals (1) from ground surface down to 0.5 m depth; (2) in the middle portion of the peat body; (3) in the lower portion of the peat body.

The piezometers were drilled by an Eijkelkamp probe (Eijkelkamp, Van Essen Instruments, Schlumberger), attaining a maximum depth of 7 m below ground level. Collapsing of the peat mass around the pipes prevented hydraulic short-circuiting along the annulus between bore-hole and casing. Measurements of water-level inside the upper piezometers and phreatimeters, referred to a fixed external benchmark, were taken manually in order to obtain a detailed picture of water-table morphology. Indeed, the water levels recorded in the upper piezometers and phreatimeters correspond to the unconfined groundwater hosted in the upper part of the peat body (acrotelm). Conversely, the water level recorded in the middle and lower piezometers represent the hydraulic head of peat water in correspondence of the slotted portion of the piezometers.

In early June 2006 two of the piezometer clusters (one at each mire) were instrumented with DIVER type probes (Eijkelkamp, Van Essen Instruments, Schlumberger) for continuous monitoring of head during June-September 2006. Each probe consisted of a totally submerged, 12.5-cm long stainless steel mini pressure transducer, equipped with a sealed data-logger recording, at hourly intervals, absolute fluid pressure (water pressure + atmospheric pressure). The raw data were barometrically compensated through a BaroDIVER atmospheric pressure probes installed close to the piezometer clusters. The head data were compared with hourly records of precipitation obtained at a meteorologic station (Passo Monte Croce Comelico) ca 2 km apart. Barometric compensation was needed because submerged transducers measure total fluid pressure above the probe, so that daily and seasonal barometric variations can significantly affect long-time monitoring of head data.

In August 2006 a water sample was collected from all phreatimeters and piezometers. The pH was measured in the field by a portable instrument (CRISON PH 25, Crison Instruments, Alella). Subsequently, the water samples were stored in polyethylene bottles and deep frozen within a day until laboratory analyses. Concentrations of major telluric cations ($Ca^{2+}$ and $Mg^{2+}$) were determined by atomic absorption spectrophotometry (Solaar 969, Unicam, Cambridge) after adding lanthanum to reduce anionic interference.

*2.3 Vegetation*

The vegetation of the two mires was surveyed during Summer 2005. Six main vegetation types were identified based on a combination of vegetation structure and ground morphology, the latter implying major differences as regards depth to the water table.

1) Hummocks: raised areas  with a ground layer (namely the lower vegetation layer formed of non-vascular plant species) rich *Sphagnum* mosses and a field layer (namely the taller vegetation layer formed of vascular plant species) consisting in a mixture of dwarf shrubs and graminoids.

2) Scrubs: raised to undulating areas covered by a thick *Pinus mugo* canopy overlying a field layer of dwarf shrubs and a ground layer rich in *Sphagnum* mosses.

3) Lawns: flat areas  with a ground layer usually including a mixture of *Sphagnum* mosses, brown mosses and hepatics and a field layer rich in graminoids.

4) Fen meadows: flat areas with a ground layer mostly formed of brown mosses and a field layer consisting in a mixture of graminoids and forbs.

5) Hollows: wet areas  with a rather sparse vascular cover settled on a ground layer of brown mosses and/or *Sphagnum* mosses, or directly on the bare peat.

6) Marginal streams: wet areas  with water slowly flowing on the peaty ground, except in the driest periods. The vegetation mostly consists in graminoids and forbs with a poorly developed ground layer.

Vegetation composition was studied in the 44 plots used for hydrological surveys besides a number of additional 1-m$^2$ plots. The partitioning of these plots according to the six main vegetation types was approximately proportional to the coverage of the vegetation types in the two mires. Presence/absence of all species (vascular plants and bryophytes) was recorded in all plots at the top (end July – early August) of the growing season 2006.

*2.4 Topography and mapping*

The topography of the two mires was surveyed in August 2005 by GPS, using two Leica SR 530 double frequency receivers working in real time kinematics (RTK) modality. This procedure allowed for a large set of high accuracy data in reasonable time. Reference benchmarks for RTK surveys were preliminarily set up by static relative positioning and subsequent post-processing the data with those collected at the closest permanent station (Bolzano, Bozen; BZRG). About 1000 topographic points were georeferenced at each mire, with an average accuracy of 0.6 cm, 0.8 cm and 1.6 cm, for latitude, longitude and elevation, respectively. Detailed contourings (10-cm spacing) and digital elevation models (DEMs) were obtained for both mires using the Program Surfer 8 (Golden Software Inc.).

The morphology of the water table was mapped, using the median values of both head and water-table depth for the period June-October 2006. Contourings were obtained, for both mires, by kriging interpolation with default linear variogram using Program Surfer 8.

The distribution of the six main vegetation types in the two mires was mapped in Summer 2006 at 1:500 scale, using the topographic maps as a basis. Vegetation mapping was

performed with two GPS instruments (Trimble Pathfinder Pro XRS and Trimble GeoXT) and subsequent GIS elaboration of the data by Program ArcGIS 9.1.

*2.5 Production, nutrient content and decomposition*

Aboveground net primary production (ANPP) in the vegetation was recorded at a sub-sample of plots (12 at the bog site and 9 at the fen site). The method used for determining ANPP was described thoroughly elsewhere (Gerdol et al., 2010). In summary, for *Sphagnum* plants we multiplied the mean linear elongation by the mean bulk density. For evergreen and deciduous shrubs, we considered the total mass of current-year tissues as an estimate of ANPP. For graminoids and forbs, we assumed that the whole aboveground mass had been produced during current growing season. Non-*Sphagnum* mosses, lichens and ferns were neglected because they always presented modest cover (< 2% of the area).

The plant material harvested for determining ANPP was sorted by species, that were subsequently partitioned into groups, largely corresponding to functional types commonly used in studies dealing with mire vegetation. These groups (henceforth called plant functional types, PFTs) were: shrubs (no distinction was made between deciduous shrubs and evergreen shrubs), graminoids, forbs, hummock *Sphagna* and lawn *Sphagna*. Since our objective was to compare nutrient content in the vegetation of the two mires, we chose within each PFT, whenever possible, abundant species growing at both mires for determining concentrations of major nutrients in plant tissues. The species sampled were: for shrubs, *Calluna vulgaris* at both sites; for graminoids, *Carex rostrata* and *Eriophorum vaginatum* at both sites; for forbs, *Potentilla erecta* at both sites; for hummock *Sphagna*, *S. fuscum* at the bog site and *S. capillifolium* at the fen site; for lawn *Sphagna*, *S. magellanicum* at the bog site and *S. compactum* at the fen site. There were five replicate samples per each species at either sites. The plant material was cleaned, oven-dried at 60°C for 24 h and analyzed for N and phosphorus (P) concentrations by a flow-injection autoanalyser (FlowSys, Systea, Roma).

Short-term (1 yr) decomposition rates were assessed on plant litter of the same species selected for determining nutrient content in the vegetation. At the end of September 2005, we collected brown shoots with attached leaves from the shrub, freshly senesced leaves from graminoids and forbs, and the stem section located 2-4 cm below the capitulum from *Sphagnum* mosses. The litter material was cleaned, air dried and stored in the laboratory at room temperature. Litter bags were prepared using about 1.5 g of air-dried material. Litter bags were made of polyethylene fabric with a 0.5-mm mesh. For each plant species, three sub-samples of litter were oven-dried for 48 h at 40°C for determining oven-dry weight of each litter bag before burial. At the beginning of October 2005, six litter bags of each species were remoistened and placed horizontally just beneath the bog surface, with 72 bags in total. At both sites all of the litter bags were buried in a 15 m × 5 m area surrounding a phreatimeter. The two areas, totally comprised within lawns, had flat ground so that the median water-table depth recorded in the phreatimeter was representative of hydrologic conditions in the whole area. Percentage cover of PFTs was assessed visually in both areas. The litter bags were retrieved after 1 year, cleaned from debris before drying at 40°C for 48 h. Each bag was then weighed to the nearest 0.001 g to determine the remaining litter mass.

*2.6 Data elaborations and statistics*

The data of water-table depth, pH, $Ca^{2+}$ concentration and $Mg^{2+}$ concentration in pore water (sampled in the phreatimeters) were statistically analyzed by two-way factorial ANOVAs with mire site, vegetation type and their interaction as fixed factors. Similarly, the data of nutrient content in the vegetation were analyzed by two-way factorial ANOVAs with mire site, PFT and their interaction as fixed factors. At each mire, significance of differences in the mean values of each variable was assessed by Fisher's LSD post-hoc tests.

Estimates of ANPP were integrated to the whole mire area. To this aim, a weighted mean was calculated for each of the two mires by multiplying the average ANPP in each vegetation type by the percentage coverage of that vegetation type and then dividing the sum by 100. Decomposition rates were expressed as percentage of mass loss as follows:

$$DR\ (\%) = ((W_b - W_a) / W_b) \times 100) \qquad (1)$$

where DR is the decomposition rate, $W_b$ is the weight of plant litter in the bag before burial and $W_a$ the weight of the same material after 1 year.

More than half of the bags containing *Sphagnum* litter exhibited some gain in mass, possibly due to algal growth and/or colloid absorption onto the spongy surface of *Sphagnum* tissues. They, therefore, had negative decomposition rates according to formula (1). We normalized the decomposition rates of *Sphagnum* litter separately for each of the two *Sphagnum* species in the two peatlands. In each of the four groups of six litter samples, we set to zero the lowest DR and re-calibrated the DRs as follows:

$$DR_{norm} = DR - DR_{min} \qquad (2)$$

Where $DR_{norm}$ is the normalized decomposition rate, DR the decomposition rate calculated according to formula (1) and $DR_{min}$ the minimum DR (always negative) within each group of six litter samples.

We could not find out any method for assessing if, and to what extent, normalizing to minimum actually recovered true decomposition rates of *Sphagnum* litter. Therefore, we tried to perform an indirect check by comparing the decomposition rates recorded at our bog site (Coltrondo W; present study) with the one recorded at a peatland (Wölfl Moor; Bragazza et al., 2007) presenting much similar features as regards both vegetation composition and water chemistry, although lying about 80 km apart. In this comparison, we used untransformed 1-yr decay rates for all PFTs at Wölfl Moor, where no gain in mass was observed in any of the litter bags. On the other hand, we used untransformed 1-yr decay rates for vascular PFTs (i.e., shrubs, graminoids and forbs) and normalized 1-yr decay rates for both hummock *Sphagna* and hollow *Sphagna* at our bog site. The comparison was made by calculating, for all PFTs, Pearson's product moment correlation coefficients between 1-yr decay rates at Wölfl Moor and our bog site.

The data of decomposition rates were analyzed by two-way factorial ANOVA, with mire site, PFT and their interaction as fixed factors, as for water-table depth and water-chemistry variables. All computations were performed using the package STATISTICA (Release 6; StatSoft Inc., Tulsa).

## 3. Results

### 3.1 Hydrology

The bog site had a horseshoe shape with the ground gently sloping radially from South to West and North-East. Water flowed radially from the bulging central part of the mire, with an irregular undulating water-table morphology (Fig. 1). The fen site had an elliptic elongated shape. This mire exhibited a well-structured groundwater flow with a steep hydraulic gradient from NW to SE, in turn depending on a pronounced topographic gradient and to the existence of creeks draining water from the mire. (Fig. 1).
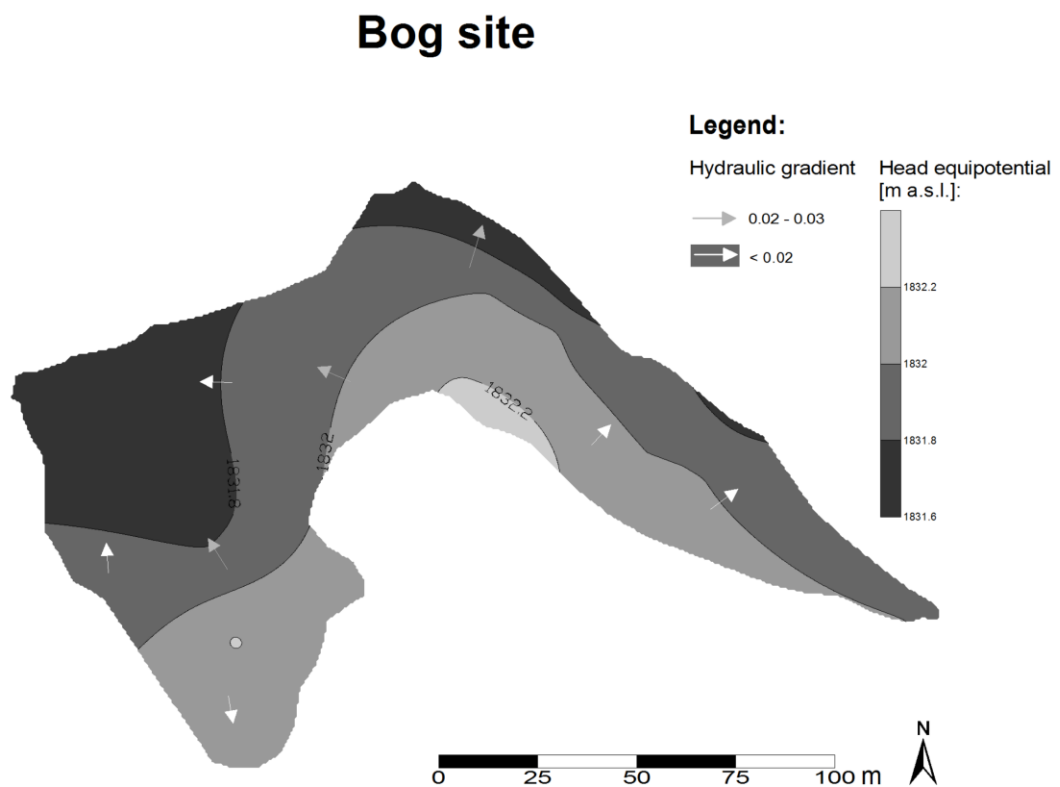
# Fen site
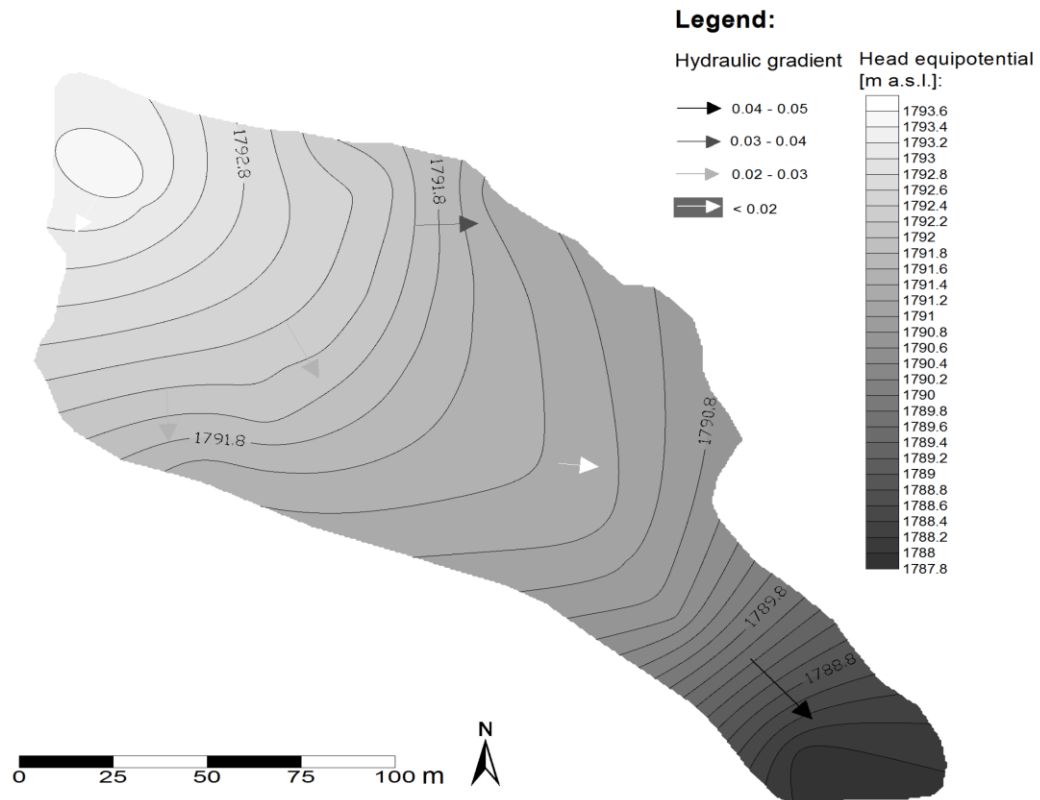


**Fig. 1.** Topographic maps of the bog site (Coltrondo W; upper panel) and fen site (Coltrondo S; lower panel). Hydraulic head is shown as differently shaded areas in the maps, hydraulic gradient is shown by arrows (note the different scale in the two maps).

The vertical profiles of head within the peat body differed substantially between the two mires. Across all piezometer clusters, the vertical component of the hydraulic gradient from the upper to the mid peat layers at the bog site usually was positive, i.e., directed downwards (Fig. 2; Table 1). Conversely, that component was negative, i.e., directed upwards in about half of the samplings at the fen site (Fig. 2; Table 1). The vertical component of hydraulic gradient from the mid to the lower peat layers was always negative at the bog site, while it was positive in about a quarter of the samplings at the fen site (Fig. 2; Table 1).
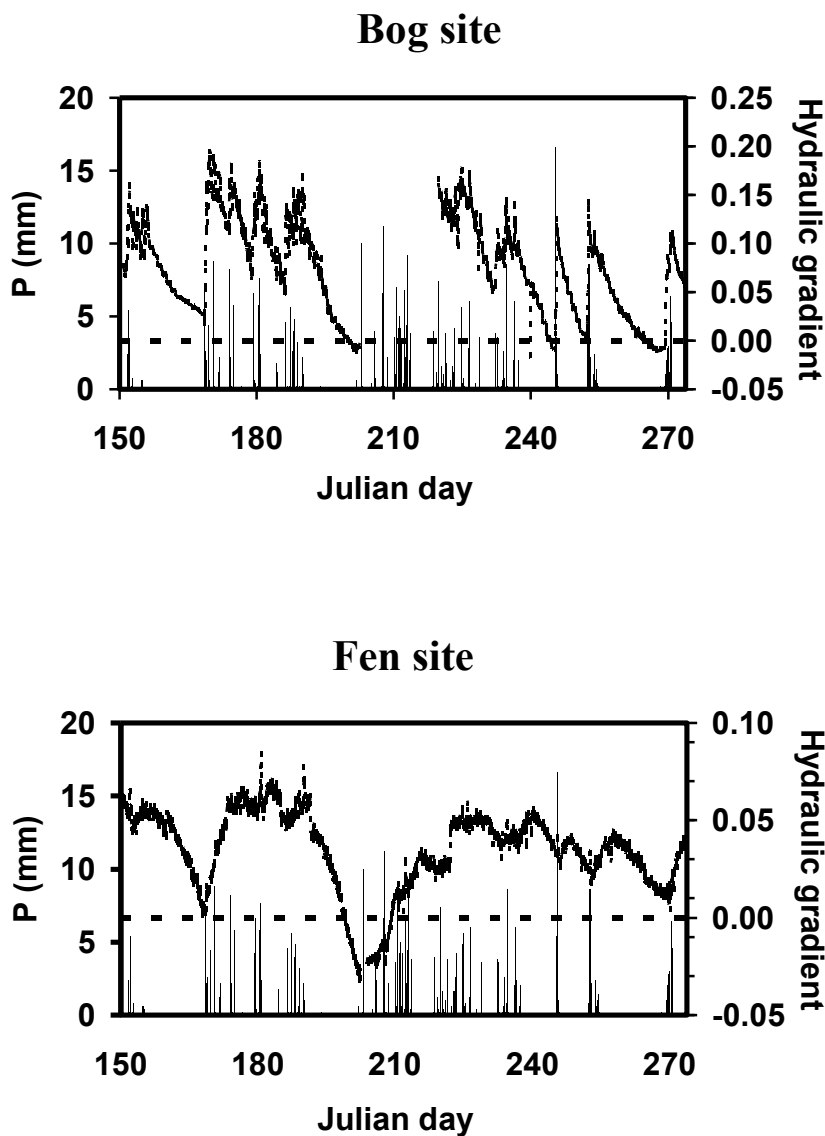
|  | Bog site | | Fen site | |
|---|---|---|---|---|
|  | Downwards | Upwards | Downwards | Upwards |
| Upper/mid peat layer | 76 | 24 | 52 | 48 |
| Mid/lower peat layer | 100 | 0 | 83 | 17 |

**Table 1.** Direction of the vertical component of hydraulic head between upper/mid layers and mid/lower peat layers at the two mire sites. The values are percentages calculated on weekly samplings from 3 piezometer clusters at the bog site (Coltrondo W) and 5 piezometer clusters at the fen site (Coltrondo S), respectively.
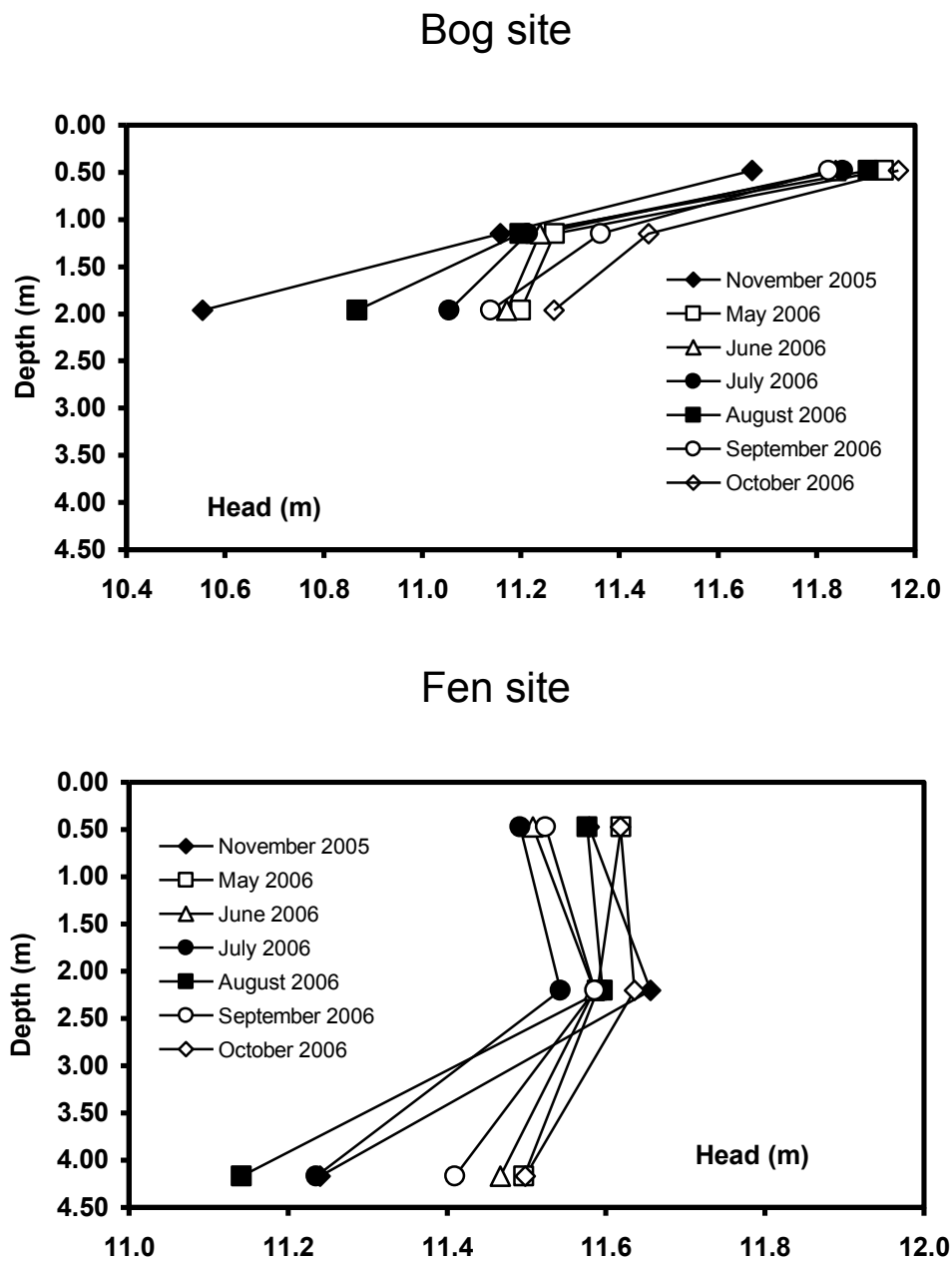
# Bog site



# Fen site



**Fig. 2.** Vertical profiles of hydraulic head in a representative piezometer cluster at the bog site (Coltrondo W; upper panel) and the fen site (Coltrondo S; lower panel).

Continuous monitoring of the vertical component of hydraulic gradient in the two selected piezometer clusters also showed considerable differences between the two mires. At the fen site the vertical component of the hydraulic gradient was positive, i.e., directed downwards, in wet periods (Fig. 3). At this mire, however, there were frequent phases of vertical flow inversion, since the vertical component of hydraulic gradient always became negative during dry periods. At the bog site, the vertical component of the hydraulic gradient was positive throughout the observation period, although three short episodes of weak flow inversion took place at the end of the longest dry periods (end July, early September and early October; Fig. 3).

## Bog site



## Fen site



**Fig. 3.** Continuous monitoring of the vertical component of hydraulic head at Coltrondo the bog site (Coltrondo W; upper panel) and the fen site (Coltrondo S; lower panel). The columns indicate daily precipitation recorded at a nearby meteorological station.

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The two mires differed greatly from each other as regards distributional pattern and coverage of the six main vegetation types. About half of the area at the bog site was covered with dense *Pinus mugo* scrubs, especially in the western sector of the mire (Fig. 4). Conversely, scrubs were much less abundant at the fen site, where some *Pinus mugo* patches occurred only at the south-eastern end of the mire (Fig. 4). Hummocks were well represented, covering almost 30% of the area at both mires, although with a somewhat differing distribution pattern. At the bog site, hummocks were mostly arranged as strips in the marginal part of the mire while at the fen site they were smaller and scattered especially in the central part of the mire (Fig. 4). Lawns never attended important coverage. Overall, lawns were more abundant at the bog site, where a continuous strip of lawns was present along the long axis of the eastern mire sector (Fig. 4). Fen meadows represented the by far most abundant vegetation type at the fen site, with a coverage of nearly 50% (Fig. 4), while they had modest abundance at the bog site. Hollows presented almost equally low coverage at both mires (Fig. 4). A marginal stream could be easily recognized at the northern border of the bog site. In contrast, marginal streams were virtually absent at the fen site (Fig. 4).

Vegetation composition presented important overall differences between the two mires. This depended both on different coverage of the six main vegetation types and on remarkable between-mire compositional differences for some vegetation types. The vegetation of hummocks and scrubs had evergreen and deciduous shrubs as the most frequent species in the field layer, although some graminoids (especially *Carex pauciflora* and *Eriophorum vaginatum*) were abundant as well (Table 2), while *Sphagnum* mosses were dominant in the ground layer. Vegetation composition of hummocks and scrubs was overall similar in the two mires but, nonetheless, some differences could be observed as regards occurrence and frequency of individual species. Hummocks at the fen site were richer in vascular species, because *Carex nigra* and *Potentilla erecta* did not occur at the bog site (Table 2). Hummocks had *Sphagnum capillifolium* as the dominant species in the ground layer at the fen site, while *S. fuscum* and *S. magellanicum* were dominant in the ground layer at the bog site (Table 2). On the other hand, *S. fallax* was abundant in the ground layer at the bog site but did not occur at the fen site.

The field layer of lawns was mostly formed of graminoids, with *Trichophorum caespitosum* representing the dominant species at both mires (Table 2). The ground layer also had the dominant species (*Sphagnum compactum*) in common. Nonetheless, the ground layer of the two mires did differ to a certain extent since some *Sphagnum* species (*S. capillifolium* and *S. magellanicum*) occurred at the bog site only, whereas *Campylium stellatum* and *Gymnocolea inflata* were more frequent at the fen site (Table 2). Conversely, the vegetation of fens was overall similar at the two mires, with *Trichophorum caespitosum*, *Bartsia alpina* and *Campylium stellatum* always representing the dominant species among graminoids, forbs and mosses, respectively (Table 2). The field layer of hollows had two graminoids (*Carex limosa* and *C. rostrata*) as the dominant species.

There were profound compositional differences in the ground layer of hollows, with *Sphagnum subsecundum* dominating at the bog site, and non-*Sphagnum* mosses (especially *Pseudocalliergon trifarium* and *Scorpidium cossonii*) dominating at the fen site (Table 2). Conversely, the vegetation of marginal streams was much similar. At both sites, *Carex nigra*

dominated among graminoids and *Caltha palustris* among forbs (Table 2). Marginal streams at the bog site were richer in species probably because this vegetation type covered a larger area in that mire (Fig. 4).

| | Hummock | | Scrub | | Lawn | | Fen meadow | | Hollow | | Marginal stream | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | B | F | B | F | B | F | B | F | B | F | B | F |
| **EVERGREEN SHRUBS** | | | | | | | | | | | | |
| *Andromeda polifolia* L. | X | XX | X | X | X | + | + | + | | + | | |
| *Calluna vulgaris* (L.) Hull | + | XX | | XX | | | | | | | | |
| *Pinus mugo* Turra | X | | XX | XX | | | | | | | | |
| *Vaccinium microcarpum* (Rupr.) Schmalh. | XX | X | X | XX | + | | | + | + | | | |
| *Vaccinium vitis-idaea* L. | XX | | XX | X | + | | | | | | | |
| **DECIDUOUS SHRUBS** | | | | | | | | | | | | |
| *Vaccinium myrtillus* L. | XX | X | XX | XX | | | | | | | | |
| *Vaccinium uliginosum* L. | XX | X | XX | XX | + | | | | | | | |
| **GRAMINOIDS** | | | | | | | | | | | | |
| *Carex canescens* L. | | | | | | | | | + | | XX | |
| *Carex echinata* Murray | | | | | X | | | + | | + | X | X |
| *Carex limosa* L. | | | | | | | | + | XX | XX | | |
| *Carex nigra* (L.) Reichard | | | | X | X | + | X | + | | + | XX | XX |
| *Carex pauciflora* Lightf. | X | XX | X | XX | X | + | | | | | | |
| *Carex rostrata* Stokes | | | | | X | XX | X | XX | XX | XX | X | XX |
| *Deschampsia cespitosa* (L.) P. Beauv. | | | | | | | | | | | X | X |
| *Eriophorum latifolium* Hoppe | | | | | | | | XX | | + | | |
| *Eriophorum vaginatum* L. | XX | X | XX | XX | XX | X | | | | | | |
| *Juncus filiformis* L. | | | | | | | | | X | | X | |
| *Molinia coerulea* (L.) Moench | + | X | X | | XX | | X | XX | | + | | |
| *Trichophorum alpinum* (L.) Pers. | | | | | | XX | | X | | + | | |
| *Trichophorum caespitosum* (L.) Hartm. | | | | | XX | XX | XX | XX | + | + | | |
| **FORBS** | | | | | | | | | | | | |
| *Bartsia alpina* L. | | | | | X | | XX | XX | | | | |
| *Caltha palustris* L. | | | | | | | | | | | XX | XX |
| *Drosera rotundifolia* L. | | | | X | X | | | | | | | |
| *Drosera anglica* Huds. | | | | | | | XX | X | X | | | |
| *Melampyrum pratense* L. | + | | | XX | | | | | | | | |
| *Menyanthes trifoliata* L. | | | | | | | X | + | X | XX | X | |
| *Potentilla erecta* (L.) Räuschel | | X | | | XX | | X | XX | | + | X | X |
| *Potentilla palustris* (L.) Scop. | | | | | | | | | | | XX | |
| *Valeriana dioica* L. | | | | | | | | | | | XX | XX |
| *Viola palustris* L. | | | | | X | | | | | | XX | + |
| *Willemetia stipitata* (Jacq.) Dalla Torre | | | | | X | | + | + | | | X | |
| **SPHAGNUM MOSSES** | | | | | | | | | | | | |
| *Sphagnum capillifolium* | X | XX | XX | X | XX | | | + | + | | | |
| *Sphagnum compactum* Lam. & DC. | | | | | XX | XX | | | | + | | |

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| *Sphagnum fuscum* (Schimp.) H.Klinggr. | XX | | | | | | | |
| *Sphagnum magellanicum* Brid. | XX | X | XX | X | | + | | |
| *Sphagnum fallax* (H.Klinggr.) H.Klinggr. | | XX | | | + | + | | + |
| *Sphagnum subsecundum* Nees | | | | | | | XX | + |
| **OTHER BRYOPHYTES** | | | | | | | | |
| *Campylium stellatum* (Hedw.) C.E.O. Jensen | | | | + | XX | XX | XX | X |
| *Dicranum bonjeanii* De Not. | | X | | XX | | | | |
| *Gymnocolea inflata* (Huds.) Dumort. | | | | X | XX | | + | + |
| *Pleurozium schreberi* (Willd. ex Brid.) Mitt. | + | XX | X | | | | | |
| *Pseudocalliergon trifarium* (Weber & D. Mohr) Loeske | | | | | | + | | XX |
| *Scorpidium cossonii* (Schimp.) Hedenäs | | | | | X | X | | XX |

**Table 2.** Synthesis of species frequencies in the six vegetation types at the two mire sites (B = Bog site, Coltrondo W; F = Fen site, Coltrondo S).
XX frequency > 50%; X frequency 25-50%; + frequency < 25%. Only the species reaching 25%-frequency in at least one of the vegetation types are included.
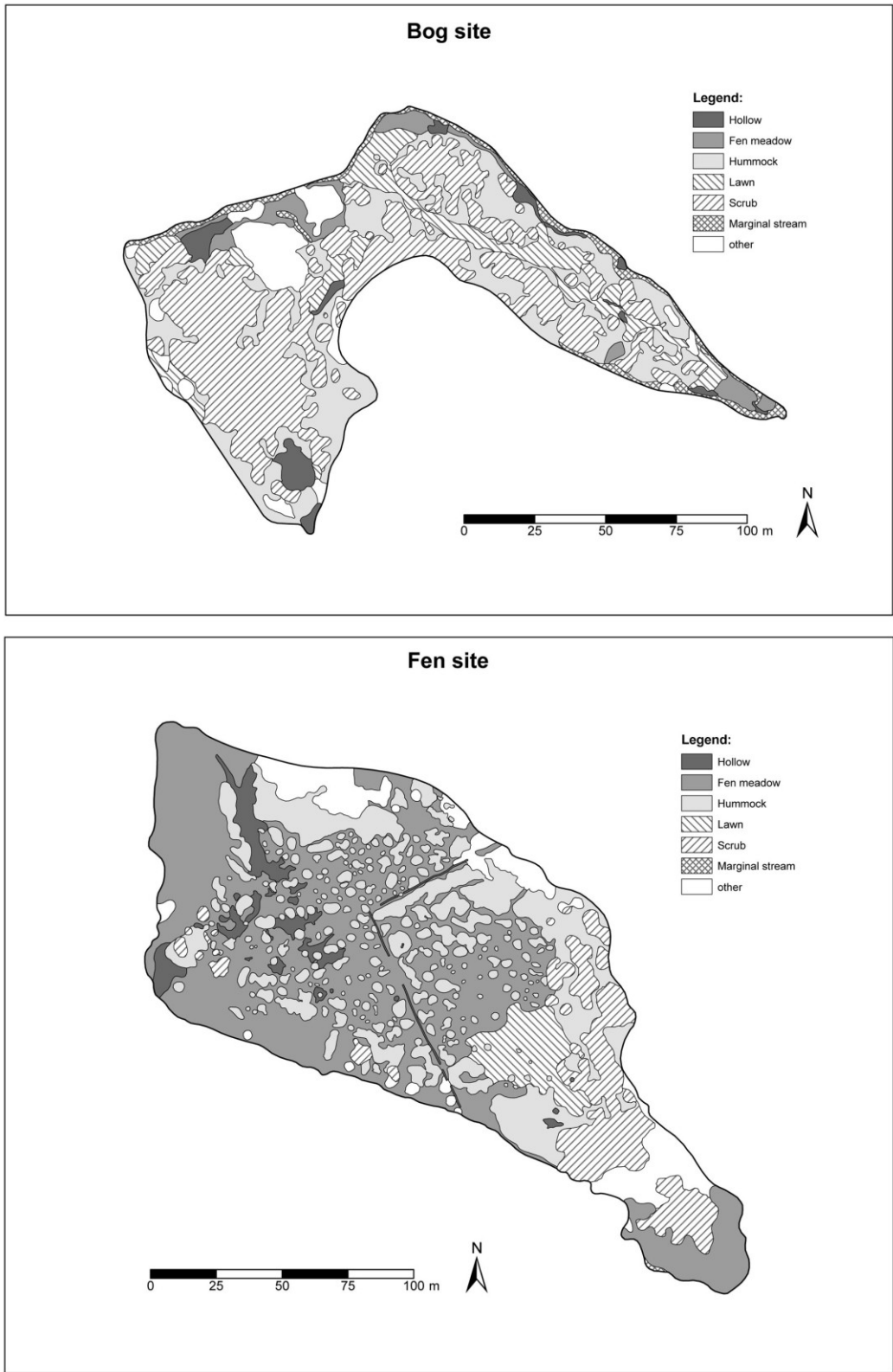
**Fig. 4.** Vegetation maps of the bog site (Coltrondo W; upper panel) and the fen site (Coltrondo S; lower panel).

*3.3 Environmental conditions, production and nutrient status*

Water-table depth and pore-water chemistry varied greatly both between mires and among vegetation types. Patterns of differences among the vegetation types were similar at the two mires, as shown by the very weak site × vegetation type interactions (Table 3). At both mires, water table was deepest, i.e., median water-table depth was most negative, in scrubs and hummocks (Fig. 5). Conversely, positive median water-table depth indicated wettest conditions in marginal streams where the water table usually lay above the ground. Median water-table depth was intermediate in lawns, fen meadows and hollows, with this latter vegetation type being somewhat wetter than the others, although the differences were not significant (Fig. 5). Median water-table depth did not differ significantly between the two mires (Table 3). However, the overall range of water-table depth was smaller at the bog site because median water table at this mire was less negative in dry habitats (hummocks and scrubs) and more negative in wetter habitats (especially fen meadows and marginal streams) compared to the fen site (Fig. 5).

Pore-water pH was significantly higher at the fen site ($6.03 \pm 0.12$) than at the bog site ($4.69 \pm 0.12$). Pore-water pH also differed significantly among vegetation types (Table 3), with overall higher values in fen meadows and marginal streams than in the other four vegetation types (Fig. 5). However, significant among-habitat differences occurred only at the bog site, while at the fen site pore-water pH in the six vegetation types was much more similar (Fig. 5). This resulted in a weakly ($P = 0.09$; Table 3) significant site × vegetation type interaction. Pore-water $Ca^{2+}$ and $Mg^{2+}$ concentrations were significantly higher at the fen site ($Ca^{2+}$: $7.90 \pm 1.56$ mg $l^{-1}$; $Mg^{2+}$: $1.74 \pm 0.26$ mg $l^{-1}$) than at the bog site ($Ca^{2+}$: $2.76 \pm 0.55$ mg $l^{-1}$; $Mg^{2+}$: $0.61 \pm 0.14$ mg $l^{-1}$). Concentrations of these two cations also varied significantly among habitats (Table 3), with overall higher values in fen meadows and marginal streams than in the other four vegetation types (Fig. 5). While such among-habitat difference did occur for $Mg^{2+}$ concentration at both mires, it was not observed for $Ca^{2+}$ concentration at the fen site, where $Ca^{2+}$ concentration did not differ significantly among habitats (Fig. 5). Therefore, a weakly ($P = 0.08$; Table 3) significant site × vegetation type interaction was detected for $Ca^{2+}$ concentration, similar to that for pH (Table 3).

|  | Site | Vegetation type | Site × Vegetation type |
|---|---|---|---|
| Water-table depth | 0.13 | **0.001** | 0.23 |
| pH | **0.001** | **0.001** | 0.09 |
| $Ca^{2+}$ concentration | **0.01** | **0.04** | 0.08 |
| $Mg^{2+}$ concentration | **0.004** | **0.005** | 0.94 |

**Table 3.** P values of two-way factorial ANOVAs of water-table depth, pH, $Ca^{2+}$ and $Mg^{2+}$ concentrations in pore water in the six vegetation types at the two mire sites. Degrees of freedom are 1 for site, 5 for vegetation type, 5 for interaction and 31 for error, respectively. Significant ($P < 0.05$) values are in boldface.
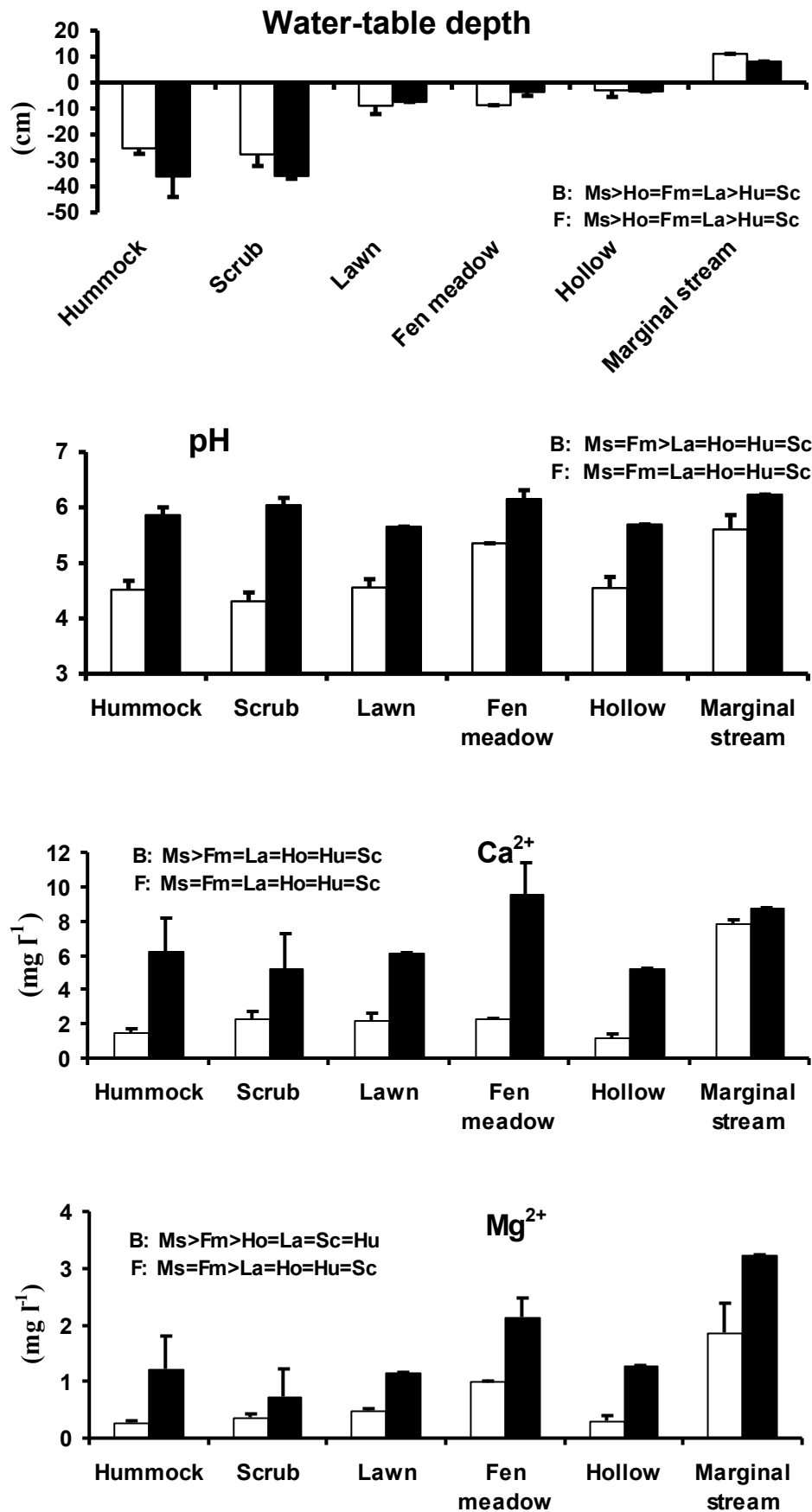
**Fig. 5.** Mean (+ 1 SE) values of water-table depth, pH, $Ca^{2+}$ and $Mg^{2+}$ concentrations in pore water in the six vegetation types at the bog site (Coltrondo W; white columns) and the fen site (Coltrondo S; black columns). Significance of differences (P < 0.05), as detected by Fisher's post-hoc tests, is shown separately in each panel for the two mires (B; bog site, Coltrondo W; F; fen site, Coltrondo S; Hu, hummocks; Sc, scrubs; La, lawns; Fm, fen meadows; Ho, hollows; Ms, marginal streams).

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The vertical profiles of water chemistry in the piezometer water samples differed considerably between the two mires (Table 4). Water chemistry at a depth of 0.50 m below ground was quite similar to that of surface pore-water at both mires. However, while pH, $Ca^{2+}$ concentration and $Mg^{2+}$ concentration increased steeply with depth at the bog site, the vertical gradients of pH and cation concentrations were much smoother at the fen site (Table 4).

| | pH | | $Ca^{2+}$ concentration (mg l$^{-1}$) | | $Mg^{2+}$ concentration (mg l$^{-1}$) | |
|---|---|---|---|---|---|---|
| | B | F | B | F | B | F |
| Upper layer | 4.84 ± 0.07 | 5.64 ± 0.30 | 3.14 ± 0.05 | 7.12 ± 0.38 | 0.74 ± 0.01 | 1.25 ± 0.07 |
| Mid layer | 5.64 ± 0.44 | 5.69 ± 0.34 | 5.55 ± 0.43 | 7.24 ± 0.43 | 1.40 ± 0.11 | 1.32 ± 0.08 |
| Lower layer | 5.78 ± 0.43 | 6.09 ± 0.28 | 5.95 ± 0.44 | 8.27 ± 0.38 | 1.51 ± 0.11 | 1.91 ± 0.09 |

**Table 4**. Mean (± 1 SE) pH, $Ca^{2+}$ concentration and $Mg^{2+}$ concentration in water samples from different depths at the two mire sites (B = Bog site, Coltrondo W; F = Fen site, Coltrondo S).

Mean ANPP was somewhat higher at the bog site, but the error bars showed a considerable overlap between the two sites (Fig. 6). Nitrogen concentrations were overall similar ($F_{1,40}$ = 0.08; P = 0.78) at the two mire sites, while P concentrations were significantly ($F_{1,40}$ = 10.29; P = 0.003) higher, and N : P ratios significantly ($F_{1,40}$ = 18.02; P = 0.000) lower, at the bog site (Fig. 7). There were profound differences among PFTs as regards N concentration ($F_{4,40}$ = 46.04; P = 0.000), P concentration ($F_{4,40}$ = 14.98; P = 0.000) and N : P ratio ($F_{4,40}$ = 6.55; P = 0.001). Concentrations of both nutrients were higher in graminoids and, especially, forbs, intermediate in shrubs and lowest in *Sphagnum* mosses, with no significant differences between hummock and lawn *Sphagna* (Fig. 7). Conversely, the N : P ratio was highest in both groups of *Sphagnum* mosses compared with all three vascular PFTs (Fig. 7). The among-PFT differences in nutrient concentrations and N : P ratio were consistent at the two mires, so that no significant interaction Site × PFT interaction was detected.

ANPP (g m$^{-2}$)
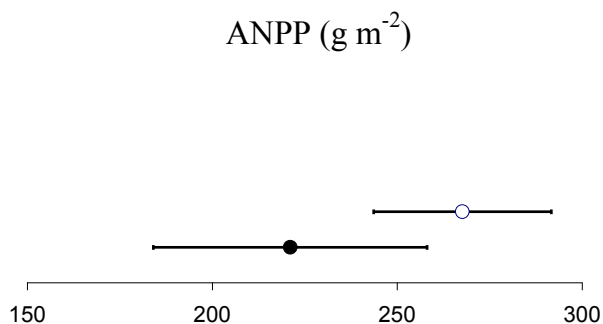
**Fig. 6.** Mean (± 1 SE) values of ANPP at the bog site (Coltrondo W; white symbol) and the fen site (Coltrondo S; black symbol).
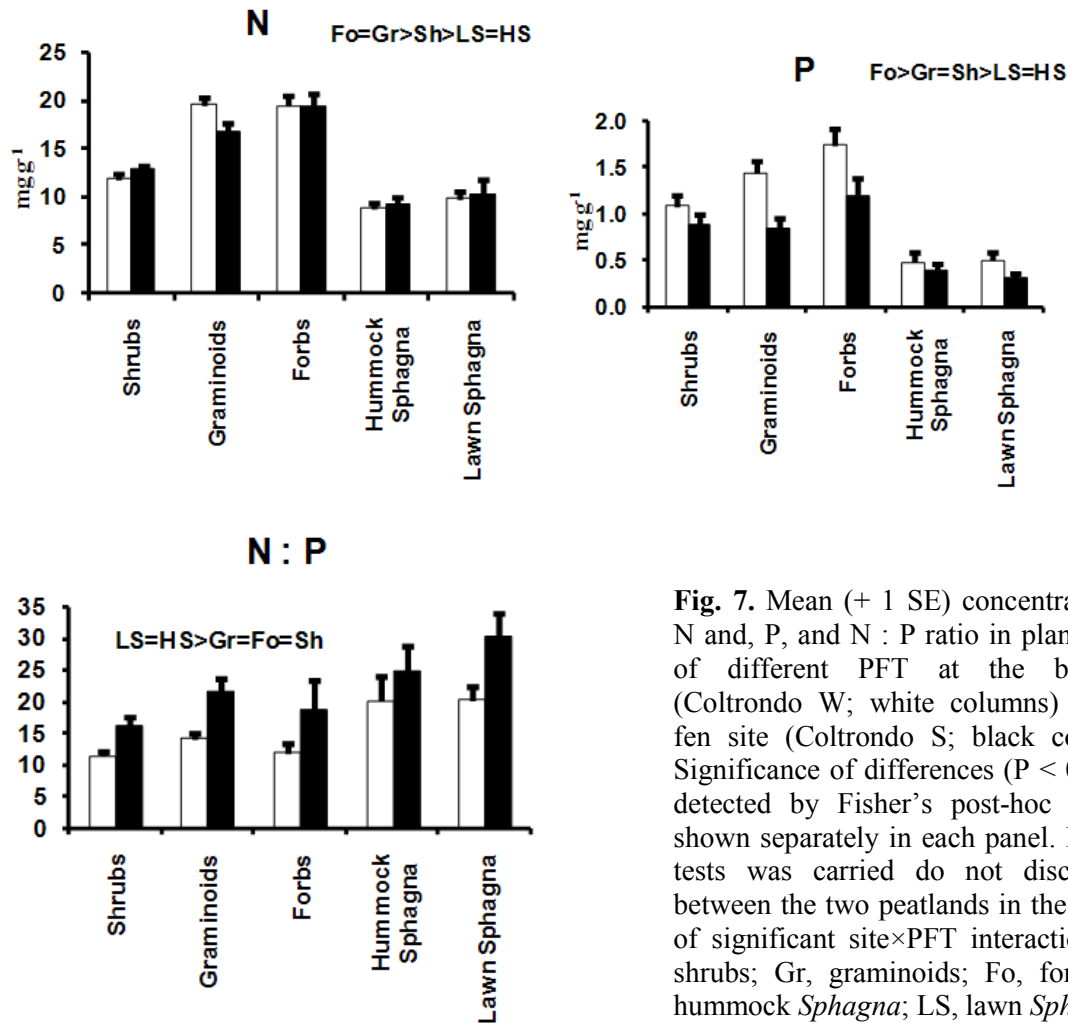
**Fig. 7.** Mean (+ 1 SE) concentrations of N and, P, and N : P ratio in plant tissues of different PFT at the bog site (Coltrondo W; white columns) and the fen site (Coltrondo S; black columns). Significance of differences (P < 0.05), as detected by Fisher's post-hoc tests, is shown separately in each panel. Post-hoc tests was carried do not discriminate between the two peatlands in the absence of significant site×PFT interactions (Sh, shrubs; Gr, graminoids; Fo, forbs; HS, hummock *Sphagna*; LS, lawn *Sphagna*).

*3.4 Decomposition*

Across all PFTs, 1-yr decomposition rates at the bog site were by 23.6% lower than at Wölfl Moor, which was related to lower mean annual temperature at the bog site compared with Wölfl Moor (ca 4 °C and 6 °C, respectively). Decomposition rates differed significantly among PFTs, that were ranked in the same order (forbs > shrubs = graminoids > lawn *Sphagna* = hummock *Sphagna*) at the two sites. In addition, there was a significant positive correlation between mean decomposition rates of all PFTs at the two sites (r = 0.98; P = 0.002; N = 5). Therefore, the normalized data can be regarded as a good proxy of true decomposition rates for *Sphagnum* mosses, although the latter may be somewhat underestimated compared with vascular PFTs (Appendix A).

The areas chosen for assessing decomposition rates at the bog site and the fen site had similar water-table depth while pH, $Ca^{2+}$ concentration and $Mg^{2+}$ concentration in pore water were all higher at the fen site (Appendix B). The cover of vascular plants was similar in the two areas, although shrubs were more abundant at the bog site and graminoids at the fen site (Appendix B). Forbs had modest cover in both areas. Conversely, *Sphagnum* cover differed greatly between the two areas, since *Sphagnum* mosses cover almost 30 % of the area at the bog site and only 3% of the area at the fen site (Appendix B).

Decomposition rates varied significantly both between sites, with greater mass loss at the bog site, and among PFTs. However, the fraction of variance explained by PFTs was much greater compared with that explained by site (Fig. 8). The percentage mass loss from litter of different PFTs was ranked as follows: forbs > shrubs = graminoids > lawn *Sphagna* = hummock *Sphagna* (Fig. 9). No significant site × PFT interaction was detected (Fig. 8), which suggested similar among-PFT differences in decomposition patterns at the two sites. However, mass loss from lawn *Sphagna* was somewhat (P = 0.03) greater than that from hummock *Sphagna* at the fen site, but not at the bog site (Fig. 9).
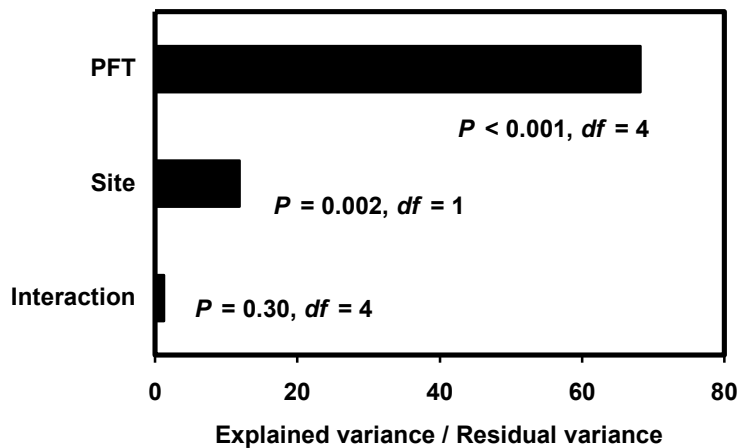


**Fig. 8.** Results of two-way factorial ANOVA of percentage mass loss from litter of different PFTs after 1 yr of incubation at the two sites (bog site, Coltrondo W and fen site Coltrondo S). Explained variance / residual variance corresponds to the F values of the ANOVA. Error df = 62.

**Fig. 9.** Mean (+ 1 SE) values of percentage mass loss from litter of different PFTs after 1 yr of incubation at the bog site (Coltrondo W) and fen site (Coltrondo S). For each site, the means followed by the same letter do not differ at P < 0.05 based on Fisher's post-hoc tests (lower-case letters for the bog site, white columns; upper-case letters for the fen site, black columns).
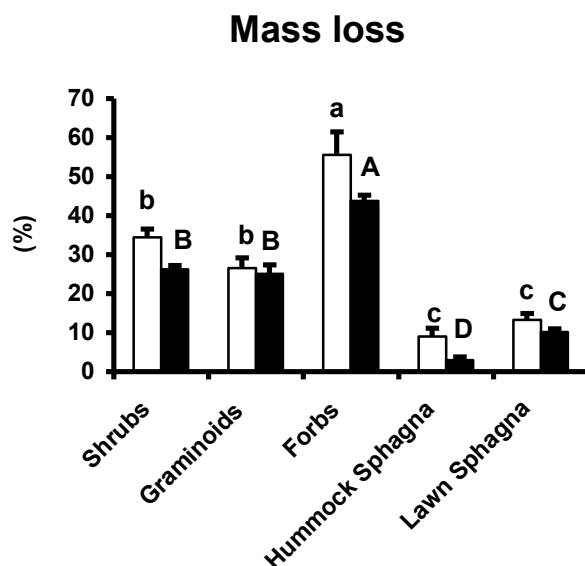


## 4. Discussion

*4.1 Hydrology, water chemistry and vegetation*

Both peatlands presented a sloping ground. The slope was very gentle at the bog site, while it was steeper at the fen site, which accounted for the higher hydraulic gradient in the latter site. At the fen site, the pore water was in contact with the mineral ground throughout the peatland surface. As regards vertical flow, the fen site acted as a discharge of groundwater from the mid to the upper peat layer during half of the sampling time. This implied frequent mixing of water through the vertical profile which resulted in weak gradients of pH and telluric cation concentrations in relation to depth. Whatever the source, i.e., surface runoff of mineral water, upward flux of ground water or both, contact with mineral water significantly raised $Ca^{2+}$ and $Mg^{2+}$ concentrations in the pore-water, although concentrations of telluric elements in the bedrock was quite low. Contact with mineral water in turn resulted in higher pH values compared to the bog water since calcium and magnesium, besides bicarbonate ions, exert a powerful buffering action towards the acidity generated by high concentrations of organic acid in peat pore-water (Siegel et al 2006, Whitfield et al 2010). At the bog site, the pore water had poor if any contact with the mineral ground, except for the northern margin of the peatland. As a consequence, pore water was acidic and telluric cation concentrations were rather low over most of the mire surface. The bog site prevalently acted as a recharge system, with water mostly flowing downwards through the peat profile. The vertical gradients in pH, $Ca^{2+}$ concentrations and $Mg^{2+}$ concentrations were, therefore, much stronger at the bog site compared with the fen site. Similarly, McNamara et al (1992) found much steeper vertical gradients of pH and dissolved cations at solute-poor sites than at solute-rich sites in a temperate peatland complex in North America. However, we observed flow reversal, i.e., upward evapotranspiration-controlled flux during prolonged dry periods even at the bog site. This supports the results of hydrological studies in North American peatlands where reversing flow from recharge to discharge conditions has been reported when evapotranspiration exceeded precipitation for some weeks (De Vito et al 1997, Fraser et al 2001).

Site hydrology was crucial to determine potential pathways of nutrient loading at the two peatlands. In particular, groundwater flow and vertical dispersive mixing represented major sources of solute transport (Glaser et al 1981, Reeve et al 2001). Hydrological features also had a profound influence on vegetation patterns as observed, for example, in a temperate peatland in New York (Drexler and Bedford 2002). Almost three quarters of the area at the bog site was covered by hummocks, hollows and, especially, scrubs. Vegetation composition in this area closely resembled that of European raised bogs, with dominant species both in the field layer and in the ground layer mostly indicating ombrogenous, viz. rain-fed, nutrient-poor conditions. Nonetheless, water chemistry in these vegetation types differed to a certain extent from that usually recorded in raised bogs. In particular, mean pH and $Ca^{2+}$ concentrations in pore water generally were ca 4.5 and ca 2 mg $l^{-1}$, respectively, both higher than in North European bogs (Rydin and Jeglum 2006). A possible explanation of these differences consists either in precipitation chemistry, with generally higher levels of dry deposition of carbonate dust particles in the Southern Alps compared with other European regions (Gerdol 1990), or in some influx of telluric water particularly through vertical flow.

Based on ground morphology, water-flow patterns, water chemistry and vegetation composition, the bog site can therefore be regarded as an ombrosoligenous bog (Gerdol et al 1994) rather than a raised bog.

The fen site was mostly covered by fen meadows. Hydrology, water chemistry and vegetation composition clearly indicated minerogenous conditions. However, part of this peatland was covered by vegetation types closely resembling those at the bog site, especially hummocks and scrubs, although water chemistry did differ considerably between the two sites, with significantly higher pH, $Ca^{2+}$ concentrations and $Mg^{2+}$ concentrations in hummock and scrub pore-water at the fen site. Nonetheless, some species commonly regarded as indicators of minerotrophic conditions, such as *Carex nigra*, did occur at the fen site but not at the bog site, probably because of the raised morphology of hummocks and scrubs which creates ombrotrophic conditions in the very surface layer, even if the water table was affected by mineral water input (Bellamy and Rieley 1967). The fen site can, therefore, be regarded as a moderate-rich fen, although the portion covered with *Sphagnum* hummocks had the features of a 'transitional mire' (Ellenberg 1988).

*4.2 Production and decomposition*

Despite considerable differences in water chemistry, ANPP did not differ substantially between the two sites with only weakly higher ANPP at the bog-dominated peatland compared to the fen-dominated peatland. This result may appear surprising since fens have often been regarded as more productive compared to bogs because total nutrient content in the peat usually parallels increasing pore-water ion concentrations from bogs to fens (Bragazza and Gerdol 2002). However, other studies reported similar values of ANPP along gradients ranging from bog to rich fen (Thormann and Bayley 1997, Golovatskaya and Dyukarev 2009) or even somewhat higher mean ANPP in bogs (Chapin et al 2004). A possible explanation resides in the fact that total soil concentrations of major nutrients may not actually assess nutrient availability for plant uptake (Bridgham et al., 2001). On the other hand, nutrient concentrations in the vegetation probably represents a better indicator of nutrient availability than soil nutrient content (Güsewell and Koerselman 2002). Interestingly, we found higher P concentration and lower N : P ratio at the bog site, which suggests that P deficiency limits plant production in the fen more than in the bog.

Vegetation structure and composition, in terms of PFTs rather than in terms of individual species, was the main factor accounting for the observed variations in litter decomposition rates. Cornwell et al (2008) also reported functional differentiation associated with the traits of green leaves to exert the strongest effect on decomposition rate across a wide range of biomes. Growth-form based PFTs have been found to explain the largest amount of variation in litter decomposition rates in cold boreal and arctic regions (Hobbie 1996), although relationships between PFTs and patterns of litter decomposability in peatlands may vary in relation to climate or other factors such as rates of atmospheric N deposition (Dorrepaal et al 2005). Litter decomposition rates also varied significantly with site. While we expected litter of all PFTs to break down faster in the fen compared with the bog (Moore et al 2007, Vitt et al 2009), the reverse was true. The reasons for such an unexpected finding are difficult to

explain since litter decomposition is controlled by several factors besides vegetation composition and structure.

Three factors could play a role with this respect: (i) water-table depth; (ii) soil temperature; (iii) litter chemistry and/or soil nutrient availability. The position of the water table is a well known factor controlling litter decomposition rates in peatlands (Ise et al 2008, Moore et al 2008). However, water-table depth was much the same in the areas chosen for the litter-bag experiment, so that position of the water table was unlikely to account for differences in decomposition rates between the two mires. On the other hand, vegetation structure did differ in the two litter bag areas, especially as regards the ground layer where the cover of *Sphagnum* mosses was one order of magnitude higher at the bog site. As a well developed *Sphagnum* layer exerts an insulating effect on the underlying peat layer (Vitt et al 1994), this may result in lower soil temperatures at the bog site compared to the fen site. If this actually happens and if temperature actually matters in accounting for differences in litter decomposition rates between the two mires, this will imply slower decomposition at the bog site while decomposition rates at the bog site were higher than at the fen site. Litter chemistry very probably also differed in the two peatlands, as an effect of differences in the chemistry of living tissues with higher P concentration and lower N : P ratio at the bog site. Several studies have reported significant effects of foliar chemistry on litter decomposition rates although the chemical traits really affecting decomposition and the underlying mechanisms still are rather unclear. Nutrient concentrations and nutrient ratios in plant tissues seem to play an important role in controlling decomposition rates of vascular litter. Güsewell and Freeman (2005) observed a correspondence between P limitation of production and P limitation of litter decomposition in vascular wetland plants, as a possible consequence of P limitation of decomposers under low P concentrations and high N : P ratios in the litter. Similar to our findings, Hobbie and Gough (2004) found higher decomposition rates at a moist acidic tundra site compared with a non-acidic tundra site in Alaska, but this difference was related to higher N availability in the moist acidic tundra soil. Conversely, decomposition of bryophyte litter is probably affected by more complex aspects of plant tissue chemistry than concentrations of major nutrients. For example, the molecular structure of primary and secondary compounds in plant tissues has revealed as a reliable predictor of decomposition rates across several subarctic bryophyte and lichen species (Lang et al 2009). On the other hand, resource partitioning between metabolic and structural carbohydrates has been found to predict decomposition rates of boreal *Sphagnum* mosses (Turetsky et al 2008).

## 5. Conclusion

In support to our first hypothesis, differences in site hydrology played a major role in affecting water chemistry and vegetation composition at the two peatlands investigated. Both surface runoff and vertical, upwards directed flow, represented important sources of mineral water inflow into the fen-dominated peatland. However, the bog-dominated peatland also received some mineral-water input due to flow reversal after prolonged dry periods. Contrary to our second hypothesis, ANPP did not differ significantly between the two sites while litter decomposition rates were even slower in the fen-dominated peatland, presumably because of

P limitation of decomposers, which resulted in greater peat thickness at the fen-dominated site. This suggests that the development of ombrogenous peatlands in this region need not be due to increased accumulation of peat during succession from mineralwater-fed to rainwater-fed conditions.

**Acknowledgements**

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**Appendix A**

Appendix A1. 1-yr Decomposition Rates (DR) at Coltrondo W and Wölfl Moor. Data are means ± 1 SE.

| DR | Coltrondo W | Wölfl Moor | Percentage difference (*) |
|---|---|---|---|
| | | | |
| Shrubs | 34.4 ± 2.1 | 38.2 ± 0.6 | 10 |
| Graminoids | 26.5 ± 2.7 | 34.3 ± 3.6 | 23 |
| Forbs | 55.5 ± 6.0 | 71.3 ± 1.1 | 22 |
| Hummock *Sphagna* | <span style="color:red">9.0 ± 2.2</span> | 14.3 ± 1.2 | 37 |
| Lawn *Sphagna* | <span style="color:red">13.2 ± 1.8</span> | 23.8 ± 1.6 | 44 |
| OVERALL | <span style="color:green">27.5 ± 2.9</span> | 36.0 ± 3.5 | 24 |

\* (Mean DR Wölfl Moor – Mean DR Coltrondo W) / Mean DR Wölfl Moor)) × 100

Black: untransformed data; <span style="color:red">red = normalized data</span>; <span style="color:green">green = mixture</span> (untransformed data for vascular PFTs, normalized data for *Sphagna*).

Appendix A2. Summary of 2-way factorial ANOVA of 1-yr DR at Coltrondo W and Wölfl Moor.

|  | Sum of squares | df | F | P |
|---|---|---|---|---|
| PFT | 17531 | 4 | 67.35 | ***0.001*** |
| Site | 1134 | 1 | 17.42 | ***0.001*** |
| PFT × Site | 248 | 4 | 0.95 | *0.44* |
| Error | 3644 | 56 |  |  |

**Appendix B.**

Appendix B1. Median water-table depth, pH and concentration of major cations in the pore water in the areas selected for the litter bag experiment at Coltrondo W and Coltrondo S.

|  | Coltrondo W | Coltrondo S |
| --- | --- | --- |
| Median water-table depth (cm) | - 12.6 | - 9.5 |
| pH | 4.59 | 5.73 |
| $Ca^{2+}$ concentration (mg $l^{-1}$) | 2.0 | 7.1 |
| $Mg^{2+}$ concentration (mg $l^{-1}$) | 0.4 | 1.4 |

Appendix B2. Percentage covers of the different PFTs in the areas selected for the litter bag experiment at Coltrondo W and Coltrondo S.

|  | Coltrondo W | Coltrondo S |
| --- | --- | --- |
| Shrubs | 32.5 | 18.7 |
| Graminoids | 39.8 | 49.3 |
| Forbs | 3.6 | 4.0 |
| Hummock *Sphagna* | 27.5 | - |
| Lawn *Sphagna* | 3.1 | 3.6 |

**Manipulating snow cover in an alpine bog: effects on soil micro-organisms and plants**

Abstract

Duration of snow cover in alpine regions is expected to decline as an effect of climate warming. We investigated effects of varying snow cover in an alpine bog by manipulating snow depth in experimental plots, with the following protocol: snow removal at the end of winter; snow removal in spring; snow addition in spring; removal of all aboveground plant tissues with no snow manipulation; no manipulation at all. The following response variables were measured, at different dates from late spring to early autumn: ecosystem respiration (ER), concentrations of carbon (C), nitrogen (N) and phosphorus (P) in the soil and in micro-organisms. Nutrient content in plants was determined in mid summer. We hypothesized that delayed snowmelt will lead to higher ER rates associated with increased microbial biomass and decreased soil nutrient availability. Contrary to our first hypothesis, ER and microbial C content were unaffected by the snow cover manipulations, probably because ER was decoupled from microbial biomass especially in summer, when $CO_2$ efflux was dominated by autotrophic respiration. Our second hypothesis also was partially contradicted because nutrient content in the soil and in plants did not vary in relation to snow cover. However, we observed unexpected effects of snow cover manipulations on the N : P ratio in the microbial biomass, which decreased after increasing snow cover. This probably depended on stimulation of microbial activity, which enhanced absorption of P, rather than N, by microbes. This may eventually reduce P availability for plant uptake.

Keywords: *Ecosystem respiration; Microbial biomass; Nutrient; Peatland; Snow; Vegetation*

# 1. Introduction

Snow cover is a major factor controlling important ecosystem processes in cold regions. First, the physical structure of the snow insulates the soil so that 40-50 cm of snow brings about uncoupling of soil and air temperatures, which dampens soil temperature fluctuations and constrains minimum soil temperatures at levels suitable for microbial metabolism even in winter (Brooks et al 1997, Sommerfeld et al 1993). $CO_2$ efflux from the snow pack has generally been regarded as an indication of microbial activity in winter (Clein and Schimel 1995, Grogan and Jonasson 2005, Zimov et al 1996), although Nobrega and Grogan (2007) observed that ecosystem respiration (ER) below snow cover is also associated to plants. Second, snow cover affects soil water content. Snowmelt timing controls soil moisture availability which in turn influences plant growth rates especially at the beginning of the growing season (Loffler 2007, Rammig et al 2010, Sutinen et al 2009). Third, long-lasting snow cover can result in higher soil nutrient availability because most of the nutrient load in the snowpack is released at high concentrations during snowmelt, thus determining a nutrient flush in a period of high nutrient demand by plants (Schöb et al 2010, Woolgrove and Woodin 1996). Fourth, the snow pack protects plants from harsh climatic factors, such as strong wind and, especially, spring frost. Recent studies have shown that anticipated snow melt does not raise plant production in late snowmelt sites because of increased risks to plants from spring frost events (Baptist et al 2010, Wipf and Rixen 2010). On the other hand, early snow melt can have detrimental effects both on plants and on the soil microbial component. The latter applies especially if early snowmelt is associated with freeze-thaw cycles. Indeed, repeated freeze-thaw events stress the microbial component, eventually causing microbe mortality (Schimel and Clein 1996). This, in turn, determines rapid nutrient mobilization followed by nutrient loss (Fitzhugh et al 2001).

In the last two decades, several studies have documented decreasing snow precipitation in alpine regions (Dye 2002, Groisman et al 1994, Lopez-Moreno 2005), especially at low to moderate altitudes (Valt and Ciafarra 2010). Reduced snow falls, and correspondingly lower duration of snow cover, generally are correlated with an increment in air temperatures (Marty 2008). Projections based on models predict further reduction in snow precipitation for the next future (Trivedi et al 2007) although, at least initially, snow falls could even increase at high elevation, e.g., above 2000 m in the Alps.

Few studies have so far investigated responses of peatland ecosystems to varying duration and depth of snow cover. Experimental manipulation of snow cover in winter and subsequent manipulation of air temperature in spring and summer resulted in increased production of *Sphagnum fuscum* in sub-arctic peatlands as a consequence of deeper snow pack and higher temperatures in the growing season (Dorrepaal et al 2004). Otherwise, Aerts et al (2009) in a subarctic bog observed that with a deeper snow depth the variation of plant nutrient content due to species was higher in respect to the variation due to snow depth manipulation. On the other hand, very little is known about possible effects of snow distribution on the activity of soil micro-organisms in peatlands. Should variations in the snow cover significantly affect microbial activity in peaty soils, this would have consequences on important ecological

processes, such as ER and nutrient cycling (Van der Heijden et al 2008). This will probably in turn influence nutrient availability for plant uptake and rates of carbon (C) accumulation in the peat body (Haugwitz et al 2011, Wardle et al 2004).

The aim of this study was to assess the effects of snow cover on ER and on nutrient cycling in an alpine peatland. We hypothesized that delayed snow melt will lead to: i) higher ER rates associated with increased microbial biomass ii) decreased availability of major nutrients for plant uptake because of nutrient immobilization by micro-organisms.

## 2. Methodology

### 2.1 Study site and experimental design

The study was conducted in a bog located close to Passo San Pellegrino, Province of Trento, Northern Italy (46°21′ N, 11°44′ E; 1800 m above sea level). The moss layer is dominated by *Sphagnum* species belonging to the sections Acutifolia (*S. russowii, S. fuscum, S. rubellum*) and Sphagnum (*S. magellanicum*). The field layer includes vascular species of different plant functional types (PFTs): deciduous shrubs (*Vaccinium myrtillus*), evergreen shrubs (*Calluna vulgaris, Vaccinium vitis-idaea, Empetrum hermaphroditum*), graminoids (mostly *Eriophorum vaginatum*) and forbs (*Potentilla erecta* and *Homogyne alpina*). The regional climate is cool-temperate and moderately humid, with mean annual temperature of c. 3°C and mean total annual precipitation of c. 1000 mm (of which c. 500 mm falling during the growing season) at 2000 m.

Fifteen 1.5 m$^2$ plots were set up in August 2008 and randomly assigned to the following treatments, with three replicates per treatment:

-SW, the snow cover was removed at the end of winter, in order to anticipate snowmelt by *ca.* 20 days compared to the non-treated plots;

-SS, the snow cover was removed in early spring, in order to anticipate snowmelt by *ca.* 10 days compared to the non-treated plots;

+SS, snow was added and an aluminum cloth was positioned on the snowpack in early spring, in order to delay snowmelt by *ca.* 10 days compared to the non-treated plots;

-V, all aboveground plant tissues, including both vascular plant parts and the top 1-cm photosynthesizing segment of *Sphagnum* mosses, were removed in September 2008 and any regrowth cut several times during the 2009 growing season;

C, snow was let melt naturally with no other manipulations.

The snow was removed with a plastic shovel in order to reduce as much as possible mechanical disturbance to the vegetation. On 6 November 2008, five temperature loggers (HOBO Pendant, Onset Computer Corporation) were inserted in the soil, 10 cm below ground, in one plot per treatment. Temperature was logged every hour from 6 November 2008 to 29 September 2009.

*2.2 Chamber CO$_2$ fluxes measurements*

Closed chamber CO$_2$ flux measurements were done at bi-weekly intervals during spring thaw (April-May) in each plot. From June to September, the CO$_2$ flux measurements were done every month. When the plot was snow-covered, the chamber was positioned on the snow and sealed with the snow itself. We did not remove the snow because altering the pressure of the snow would affect CO$_2$ pressure in the peat, thus making the measurement unstable. CO$_2$ concentrations in a plexiglas chamber (basal area 900 cm$^2$), equipped with a circulation fan and a pressure equilibration tube, were measured with a Li-Cor 800 infrared gas analyser (Li-Cor Instruments, Lincoln, NE, USA), attached by hoses to the chamber wall and connected with a 0.6 cm plastic pipe to the chamber itself in a closed circuit.

The CO$_2$ fluxes were calculated on the basis of changes in headspace CO$_2$ concentrations with time and expressed as mass of CO$_2$ exchange per square meter and hour, using the ideal gas law. Change in headspace CO$_2$ concentration was measured every 15 s until stabilization. The CO$_2$ exchange was the measured under darkness, obtained by covering the chamber with a thick, black plastic sheet.

*2.3 Soil collection and analyses*

In each plot a 10 x 10 cm soil sample was sawed out of the peat to a depth of 10 cm after the CO$_2$ measurements in June, July and September. The soil samples were enclosed in plastic bags, kept cool, and sorted within 48 h. As many roots as possible were removed by hand sorting during a standardized time of 30 min and the soil was divided into three subsamples. A subsample of 2 g was used for determination of water content by drying for 24 h at 101°C. A second subsample of 20 g was immediately extracted in 200 mL of 0.5 M K$_2$SO$_4$ to recover dissolved organic C (DOC), dissolved total nitrogen (DTN) and dissolved total phosphorus (DTP). After the K$_2$SO$_4$ addition, the samples were shaken, filtered through a Whatman GF-D filter, and kept frozen until analysis. The third subsample of 20 g was fumigated for 24 h in chloroform (CH$_3$Cl) vapor ethanol-free to release nutrients from the microbial biomass, after which the samples were extracted and handled in the same way as the unfumigated samples.

The extracts were analyzed on a Shimadzu TOC-5000A total organic C analyzer for DOC and extractable microbial C, estimated as the difference between the DOC content in fumigated and unfumigated samples. The value was divided by 0.45 (Sparling et al 1990).

The DTN content was determined by the blue-indophenol method and DTP by the molybdovanadate method (Allen, 1989) after UV-digestion using a continuous flow autoanalyser (FlowSys; Systea, Anagni, Italy).

Microbial biomass nitrogen (MBN) and microbial biomass phosphorus (MBP) were determined by subtracting the concentration in the nonfumigated, digested sample from the concentration in the fumigated, digested sample. The values was divided by 0.54 for MBN and by 0.40 for MBP (Brookes 2001).

*2.4 Plant biomass and plant N and P concentration*

At the peak of the growing season (end July), we collected aboveground vascular plant tissues and living moss tissues. The plant material was sorted by PFT: hummock *Sphagna* (*Sphagnum* species forming raised microhabitats, all belonging to the section Acutifolia); lawn *Sphagna* (*Sphagnum* species forming flat microhabitats, prevalently *S. magellanicum*); non-*Sphagnum* mosses; evergreen shrubs; graminoids; forbs.

About 50 mg of plant material, previously oven-dried for 48 h at 40°C and powdered with a mill, was digested in 3 ml of $H_2SO_4$ at 420°C for determination of total N concentrations by the blue-indophenol method, and total P concentration by the molybdovanadate method, using in both cases a continuous flow autoanalyser (FlowSys; Systea, Anagni, Italy).

In order to obtain area-based nutrient contents, the values of N and P concentrations were multiplied by the biomass and expressed as g m$^{-2}$.

*2.5 Statistical analyses*

Statistical analyses were conducted using STATISTICA (Release 6; StatSoft Inc., Tulsa, OK, USA). In order to evaluate the effects of treatments on $CO_2$ fluxes, dissolved C and nutrients in the soil, C and nutrient concentrations in the microbial biomass, we applied two-way factorials ANOVAs with treatment, sampling date and their interaction as fixed factors. Whenever appropriate, significance of post-hoc differences was assessed by LSD tests. In data sets where the distribution of resulting residuals was not normal (as assessed by the Kolmogorov-Smirnov test), the data were log-transformed and reanalysed.

## 3. Results

*3.1 Snow cover and soil temperature*

Snow cover in winter 2008-2009 was much greater than in the winters 2002-2008 (ca 144 cm vs. ca 60 cm), for which data are available at a nearby station. The soil temperatures started to stabilize after the first snow falls (end November 2008) and remained constant at *ca.* 0.3°C until thaw (Fig 1), on 30 April in the -SW treatment, on 9 May in the -SS treatment, on 21 May in the C and the -V treatments and on 28 May in the +SS treatment (Fig. 1). After the snow manipulation the temperature didn't dropped below 0°. On 18 July there was a drop in soil temperature by ca. 8°C in all the treatments. In September the soil temperature started to decrease until *ca.* of 8°C on 22 September at the end of the recording period (Fig. 1).
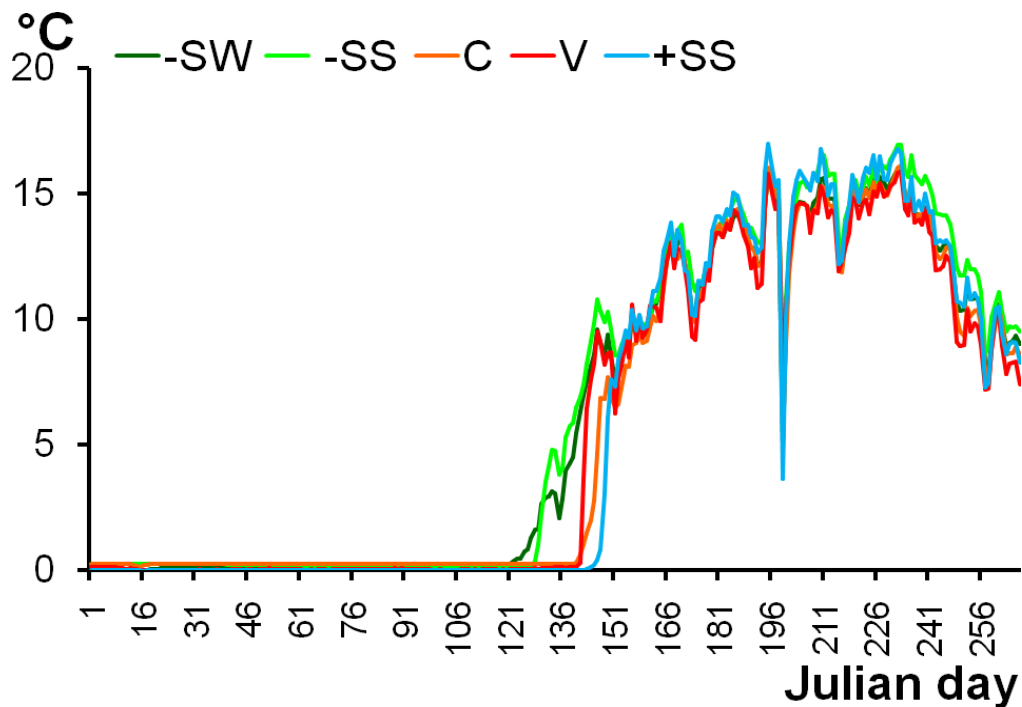
Fig 1 Hourly mean soil temperatures in the year 2009 at 10 cm depth.
Abbreviations for the treatments: -SW, snow removal in early spring; -SS, + SS, snow addition in spring; -V, removal of all aboveground plant tissues with no snow manipulation; C, no manipulation.

*3.2 ER*

The ER rates differed significantly per sampling date and per treatment (Table 1). ER showed a seasonal pattern in which the highest rates were observed during July and June (Fig. 2). The -V treatment had much lower ER rates that all other treatments in the summer, but not in spring and early autumn. ER did not differ significantly among the other treatments, with the only exception of -SW presenting somewhat higher ER in September (Fig. 2)
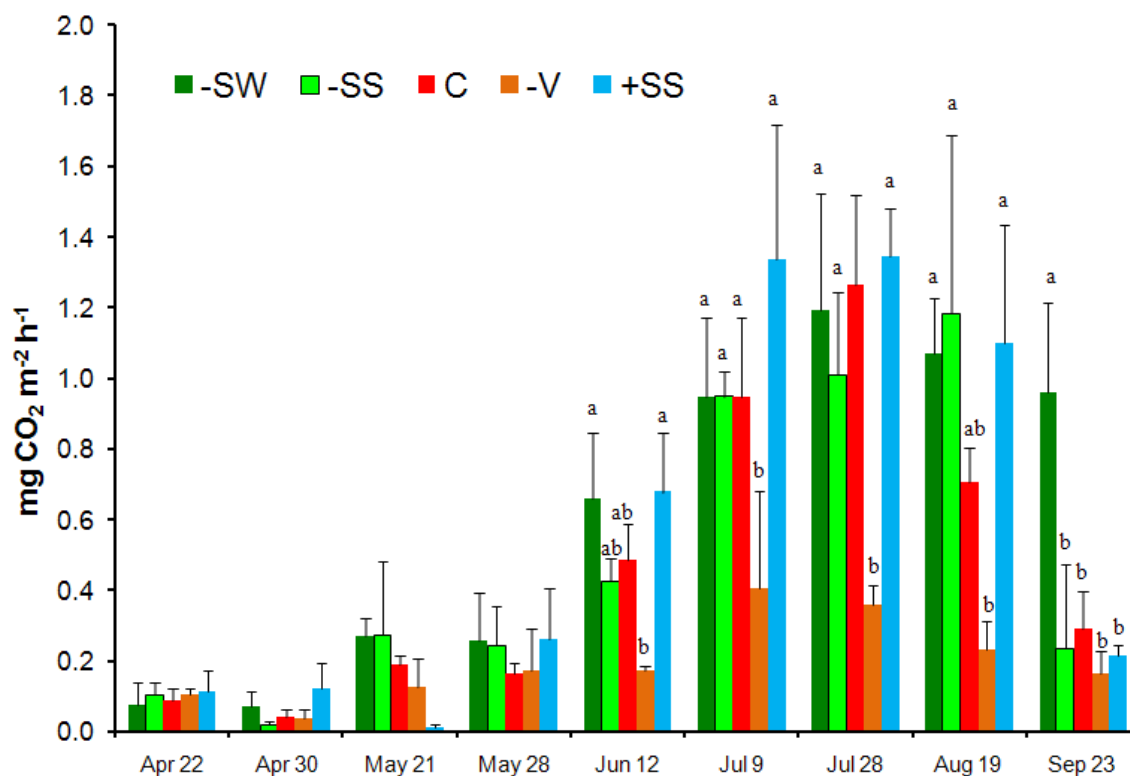
Fig 2 Mean (± SE) rates of ecosystem respiration (ER). On each sampling date, different letters indicate significant (P < 0.05) differences between treatments. Abbreviations for the treatments as in Fig. 1.

|  | Sampling date | Treatment | Sampling date × Treatment |
|---|---|---|---|
| ER | 23.98 (8) *** | 8.06 (4) *** | 1.49 (32) |
| DOC | 6.89 (2) ** | 1.56 (4) | 0.16 (8) |
| DTN | 1.15 (2) | 1.10 (4) | 0.19 (8) |
| DTP | 2.65 (2) † | 1.38 (4) | 0.33 (8) |
| Soil N : P | 0.19 (2) | 1.33 (4) | 0.23 (8) |
| MBC | 2.80 (2) † | 1.25 (4) | 0.24 (8) |
| MBN | 3.37 (2) * | 0.90 (4) | 0.60 (8) |
| MBP | 4.32 (2) * | 0.58 (4) | 0.09 (8) |
| Microbial N : P | 3.91 (2) * | 6.29 (4) *** | 1.54 (8) |

Table 1 F values (df in parenthesis) obtained by two-way factorials ANOVAs of ER, C, N, P concentrations, and N : P ratio in the soil and in the microbial biomass. Symbols indicate significant values: † P < 0.10;* P < 0.05; ** P < 0.01;*** P < 0.001

*3.3 Peat and microbial pools of C, N, P and N:P ratio*

DOC in the peat showed significant differences per sampling date but not per treatment (Table 1), with higher values than July and September (Fig. 3). DTP showed weakly

significant differences per sampling date but not per treatment (Table 1), with somewhat higher values in July than in September. DTN and the N : P ratio did not present significant differences either per sampling date or per treatment Table 1; Fig. 3).

MBC, MBN and MBP showed significant differences per sampling date but not per treatment (Table 1), always with highest values in June (Fig. 4). Conversely, the N : P ratio in the microbial biomass showed significant differences both per date and per treatment, with no significant interactions between these two factors (Table 1). The N : P ratio in the microbial biomass was significantly higher values in July than in September. The microbial N : P ratio in the +SS was significantly lower than in the -SS, and somewhat lower than in the –SW treatment, in July and September (Fig. 4).
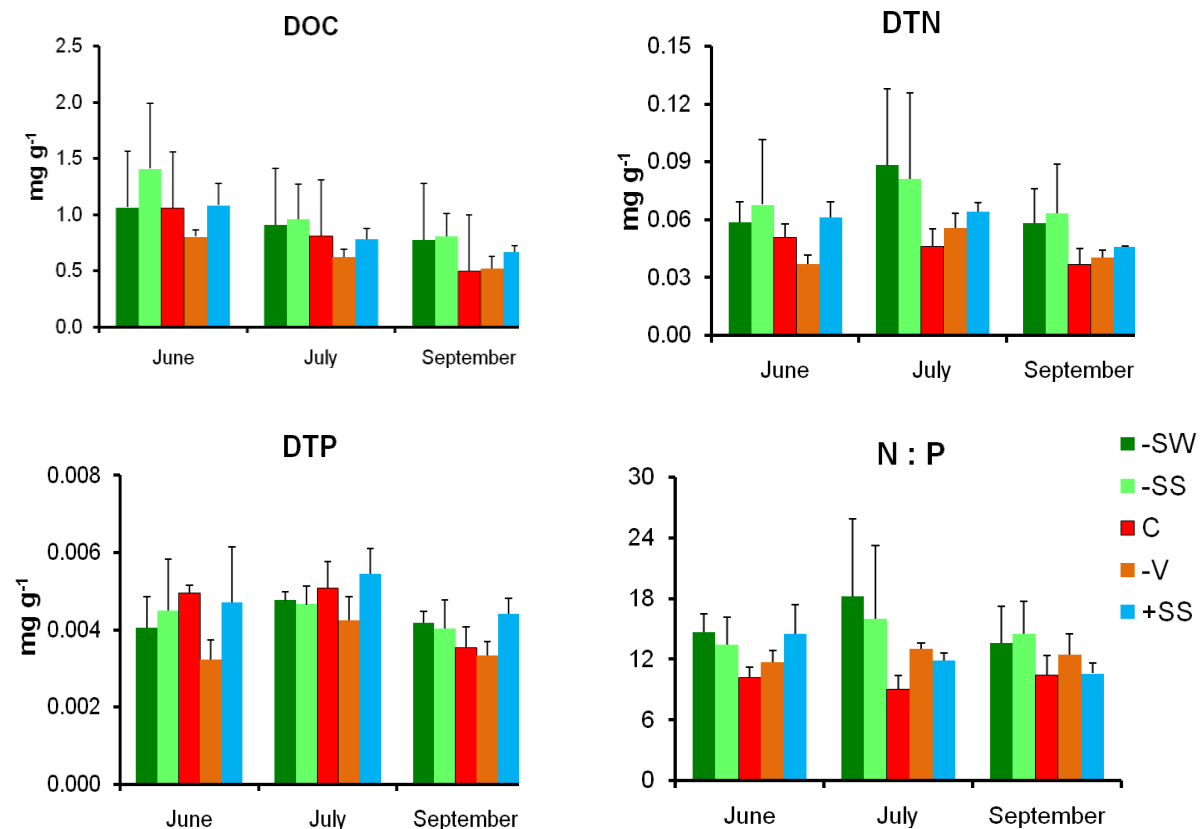


Fig 3 Mean (± SE) values of DOC, DTN, DTP and N : P ratio in the soil. No means do differ significantly (P < 0.05) between treatments on any sampling dates. Abbreviations for the treatments as in Fig. 1.
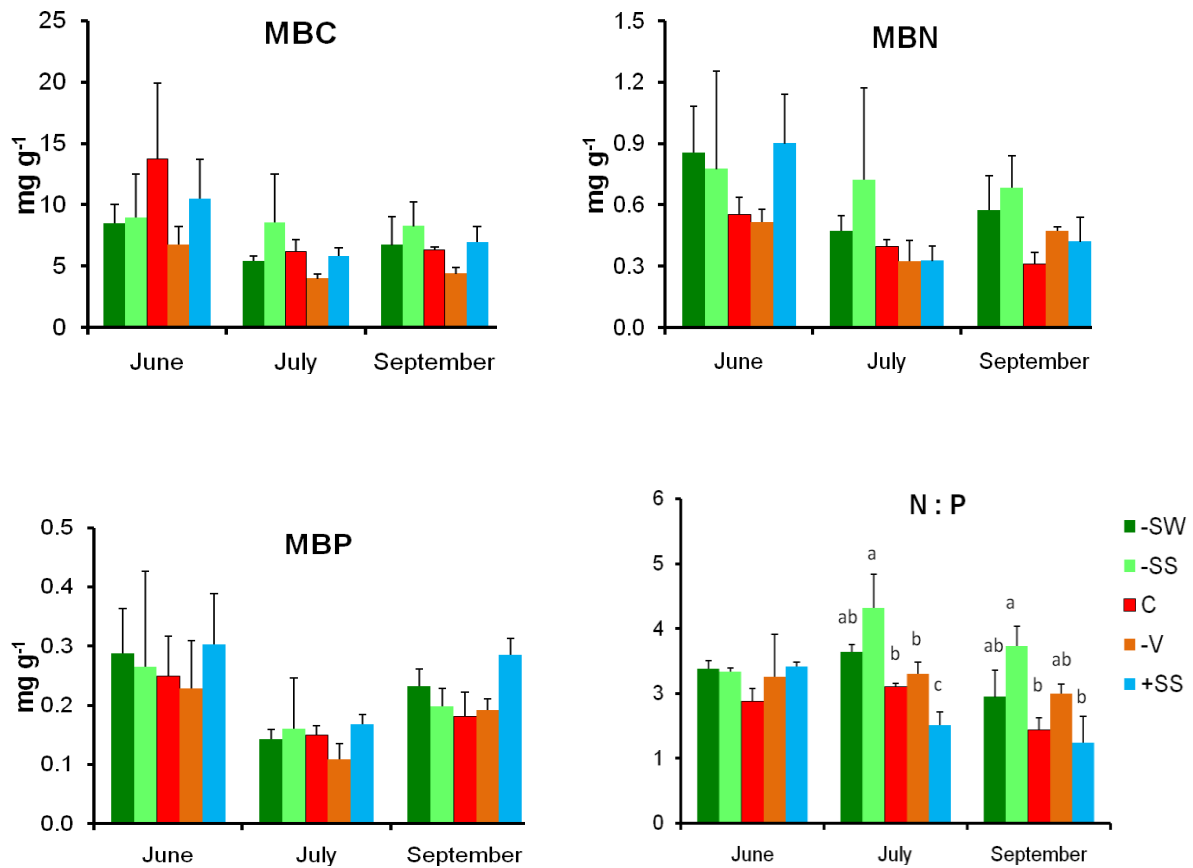
Fig 4 Mean (± SE) values of MBC, MBN, MBP and N : P ratio in the microbial biomass. The mean values of MBC, MBN and MBP do not differ significantly (P < 0.05) between treatments on any sampling dates. Different letters indicate significant (P < 0.05) differences between treatments for the mean N : P values in July and September. Abbreviations for the treatments as in Fig. 1.

### 3.4 Plant nutrient content of N, P and N:P ratio

N content differed significantly per PFT (F = 5.04, dof = 5, P = 0.001), but not per treatment (F = 0.16, dof = 3, P = 0.92). P content also differed significantly per PFT (F = 4.04, dof = 5, P = 0.005) but not per treatment (F = 0.57, dof = 3, P = 0.60). Hummock *Sphagna*, evergreen shrubs and graminoids had the highest nutrient N and P contents, followed by lawn *Sphagna*, non-*Sphagnum* mosses and forbs (Table 2).

|  |  | -SW | -SS | C | +SS |
|---|---|---|---|---|---|
| **N** | **Hummock *Sphagna*** | 1.68 ± 0.77 | 0.97 ± 0.56 | 1.87 ± 0.38 | 0.46 ± 0.45 |
|  | **Lawn *Sphagna*** | 0.52 ± 0.50 | 0.96 ± 0.49 | 0.33 ± 0.22 | 1.16 ± 0.46 |
|  | **other mosses** | 0.17 ± 0.09 | 0.17 ± 0.07 | 0.23 ± 0.08 | 0.21 ± 0.1 |
|  | **Evergreen shrubs** | 1.38 ± 0.68 | 0.95 ± 0.35 | 1.29 ± 0.45 | 0.93 ± 0.14 |
|  | **Graminoids** | 0.82 ± 0.08 | 0.75 ± 0.10 | 0.90 ± 0.15 | 1.15 ± 0.31 |
|  | **Forbs** | 0.01 | 0.05 ± 0.05 | 0.01 | 0.03 |
|  | **Total** | 5.66 ± 0.14 | 5.71 ± 0.51 | 5.37 ± 0.50 | 5.19 ± 0.87 |
| **P** | **Hummock *Sphagna*** | 0.11 ± 0.06 | 0.047 ± 0.03 | 0.14 ± 0.03 | 0.03 ± 0.02 |
|  | **Lawn *Sphagna*** | 0.03 ± 0.03 | 0.06 ± 0.04 | 0.02 ± 0.01 | 0.07 ± 0.03 |
|  | **other mosses** | 0.02 ± 0.01 | 0.02 ± 0.01 | 0.02 ± 0.01 | 0.02 ± 0.01 |
|  | **Evergreen shrubs** | 0.12 ± 0.07 | 0.06 ± 0.02 | 0.10 ± 0.04 | 0.07 ± 0.01 |
|  | **Graminoids** | 0.06 ± 0.01 | 0.04 ± 0.01 | 0.08 ± 0.02 | 0.09 ± 0.03 |
|  | **Forbs** | 0.001 | 0.005 ± 0.001 | 0.001 | 0.005 |
|  | **Total** | 0.41 ± 0.04 | 0.36 ± 0.017 | 0.44 ± 0.07 | 0.45 ± 0.14 |

Table 2 Mean (± SE) N and P contents (as g m$^{-2}$) in the different PFTs and in the total plant biomass.

## 4. Discussion

### 4.1 Ecosystem respiration and microbial biomass

Our manipulation of snow cover altered considerably the timing of snowmelt in the experimental plots, so that snow in the +SS plots melted away almost one month later than in the -SW plots. During spring thaw (end April to end May), ER rates in the plots from which aboveground plant tissues had been removed were comparable to those in all other treatments. This means that heterotrophic respiration accounted for the largest fraction of ER in this period. Conversely, autotrophic respiration dominated during the growing season, when vegetation removal implied strong reduction of ER rates. Similarly, in a Canadian temperate bog heterotrophic respiration contributed mostly to overall $CO_2$ efflux during autumn, winter and spring, while autotrophic respiration dominated during the growing season (Lafleur et al. 2003). Johnson et al (2000) also found largest contribution of autotrophic respiration to ER. Conversely, heterotrophic respiration has been found to account for a similar (Ward et al 2009) or even higher (Dorrepaal et al 2009) portion of ER compared with autotrophic respiration in (sub)arctic peatlands. We recorded ER at higher temporal resolution during spring since we expected to observe larger effects of our snow depth manipulations due to differential microbial mortality during the spring thaw period (Schmidt and Lipson 2004). However, contrary to our first hypothesis, experimentally increased snow depth did not influence ER during spring thaw. This supports the results of a recent study reporting no effects of snow cover manipulation on spring ER rates in subarctic heath and beach forest (Larsen et al 2007).

We could not perform repeated collections of soils samples during the spring thaw period because this would have caused excess damage to the experimental plots. Therefore, we do not regrettably know if and to what extent the observed patterns of ER rates were matched by

consistent variations in microbial pool size. The latter can indeed undergo short-time fluctuations as an effect of freeze-thaw events (Edwards et al 2006, Larsen et al. 2007). Since microbial activity, as assessed by ER rates, did not vary in relation to the the snow cover manipulations, two explanations are possible. First, MBC values did fluctuate during spring thaw, although we did not record them, even in the absence of any difference in ER rates in relation to the treatments. If so, $CO_2$ efflux must be regarded as a poor indicator of microbial activity. Support to this explanation may be drawn from literature data reporting microbial respiration, so-called 'overflow metabolism', even when C in not incorporated into microbial biomass (Schimel and Weintraub 2003). Second, overall similar ER rates across the experimental plots were accompanied by consistently similar MBC values, although the latter obviously are unknown. Support to this explanation may be found in our own data that did not record soil freezing during the spring thaw period (Fig. 1). Air temperatures also were considerably above the mean during spring 2009 (Saibanti and Barbiero 2009).

Whatever the reasons accounting for the lack of responses of the microbial population to the snow cover manipulations, summer ER rates also were substantially unaffected by increased snow depth. This further contradicted our first hypothesis, with ER being even somewhat stimulated at the end of summer by anticipating snow melt, possibly due to a carry-over effect of longer growing season in the –SW plots (Fig. 2). Our finding also contrasts with results of recent studies reporting higher ER rates in summer after deepening snow cover in winter in a mixed-grass prairie in North America (Chimner et al 2010, Chimner and Welker 2005). A possible explanation of the lack of consistent responses of summer ER and MBC to the snow cover manipulations may consist in a decoupling of microbial biomass from ER in summer, when $CO_2$ efflux is dominated by autotrophic respiration (Wardle 1992, Michelsen et al 2004).

*4.2 Nutrient pools in microorganisms, soils and plants*

The MBN and MBP values in our bog were comparable to those reported for heath (Nielsen et al 2009), tundra (Jonasson et al 1996) and peatland (Francez et al 2000) soils, and were overall highest at the beginning of the growing season (Fig. 4). Such seasonal pattern of microbial nutrient content is in apparent contrast with that observed in alpine soils, where nutrient pools in micro-organisms decline to a minimum at the end of spring thaw. In this season, the nutrients initially immobilized in the microbial biomass are transferred to vegetation and their concentrations remain low until autumn (Brooks et al 1998). On the other hand, microbial nutrient content has not been found to fluctuate so much in temperate heath or peatland, with overall similar values throughout the snow-free period (Nielsen et al 2009), or even highest values at the beginning of the growing season (Baum et al 2003), as observed in our study. Since this transfer of nutrients from micro-organisms to plants seems to be triggered by freeze/thaw events determining lysis of microbial cells (Brooks et al 1998), the observed lack of soil freezing during spring thaw may be a cause explaining the high nutrient content in microbes at the beginning of the growing season. This also suggests that competition for nutrients between plants and micro-organisms is weaker in temperate peatlands than in alpine and arctic soils.

Our second hypothesis was partly contradicted by the results of this study because soil nutrient availability (Fig. 3) was unaffected by the snow cover manipulations. Larsen et al (2007) also observed no effects of snow addition on concentrations of major nutrients in sub-arctic soils. Our manipulations did, however, exert some effect on the microbial nutrient status, although in a rather unexpected way. Indeed, MBP was somewhat higher and especially the N : P in the microbial biomass was significantly lower as an effect of increased snow cover (Fig. 4). This means that longer snow cover has stimulated nutrient absorption by microbes. Because of the peculiar nutrient stoichiometry of the microbial biomass, consisting in a much lower N : P ratio compared to plant tissues, any change in microbial activity affects P more that N (Jonasson et al 1996). As an effect, stimulated microbial activity enhanced P immobilization in the microbial biomass. Buckeridge and Grogan (2008) also observed that deeper snow cover not only increased nutrient pools but also changed the physiological functioning of microbial communities in tundra. This may eventually reduce P availability for plant uptake (Amador and Jones 1993). Indeed, P in peaty soils is present most in organic forms (Williams 1994) and the microbial biomass accounts for as much as 30% of the total P (Brake et al 1999), vs. *ca* 3% on average in mineral soils (Brookes et al 1994). This could have strong implications in peatland in which P has a strong environmental influence in vegetation (Bombonato et al 2010). In particular, P limitation could inhibit microbial biomass in peatland influencing rate of decomposition of organic matter (Gerdol et al, unpublished).

In conclusion, our short-term experiment of snow cover manipulation had slight effects on a bog ecosystem. Although increased snow cover promoted P immobilization in the microbial biomass, concentrations of major nutrient in the soil was unaffected. Neither did plant nutrient content vary significantly. Therefore, a year may be not enough for detecting significant effects of varying snow cover. For example, the microbial component of a sub-arctic heath was significantly affected by climatic change only after 10 years, when the ecosystem had experienced variations in plant biomass and community composition (Rinnan et al 2007).

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**Influence of trees on evapotranspiration in *Sphagnum* sp. and feathermosses**

Bombonato L, Waddington M *(draft)*

# 1. Introduction

Wildfire is an important process affecting peatlands in Canada (Turetsky et al 2002) and it affects the carbon released from peat. Wildfires might increase on peatlands under future climate change as temperatures increase and rainfall patterns change (Li et al 2007). The fires themselves release carbon into the atmosphere through the burning process and are likely to result in short to longer-term changes, at least, to hydrology caused by decreased albedo and changes in near-surface peat properties. Additionally there is diminished net primary productivity in the aftermath of the fire that may last for about 20 years (Wieder et al 2007). In order to understand which factors lead the spreading of fire it is necessary to understand the ecology of peatlands and how the energy is distributed through this ecosystem. The study of the evapotranspiration (ET) is an important component of the water (and thus energy) balance (Price and Maloney 1994, Fraser et al 2001) in peatlands. In a recent study in a minerotrophic fen Sonnentag et al (2009) found that ET is explained mainly by radiation (67%) and the contribution of water table depth (33%) was a minor factor. Otherwise, the ET depends also on the physiological features of vegetation. For example, hummock *Sphagnum* species possess high water holding capacity (Hájek and Beckett 2008) and have higher spatial density of capitula (Gunnarsson and Rydin 2000) in respect with hollow *Sphagnum* sp. The last feature is an important component to understand the behaviour of fire in a peatland because of the heterogeneous microtopography (Benscoter and Wieder 2003). Brown et al (2010) measured ET in microhabitat dominated by *Sphagnum* sp., lichenes or feathermosses. *Sphagnum* species showed the highest ET followed by lichenes and feathermosses. In that study they hypothesized that the low rate of ET was due to the shading conditions in which feathermosses grow. In effect, in peatlands it has been observed the increasing occurrence of *P. schreberi* with increased tree canopy formation (Gunnarsson et al., 2002) and the presence of feathermosses at last stage of a bog succession after fire (Benscoter and Vitt, 2008). We know thus that feathermosses growth better than *Sphagnum* species near the trees, but we don't know in which measure trees affect the water balance of *Sphagnum* species and feathermosses and which are the particular mechanism in which one species outcompetes the other. This study is also important because we don't have data based on microtopography in Alberta peatlands, in an ecosystem very important for the energy.

In this study we wanted to study the effects of the trees, important component in peatfire models, on the evapotranspiration of *Sphagnum* and feathermosses, by cutting down the trees in the peatland. We hypothesize that in absence of trees there will be an increasing of ET in feathermosses and in *Sphagnum* sp. after cutting the trees.

# 2. Materials and methods

## 2.1 Site description

This study was conducted at Crow Lake bog (55°80'1"N 113°19'5"W) located ca. 150 km south of Fort McMurray, Alberta, Canada. The bog was burned in 1935. We selected this site because of the scattered presence of *Picea mariana*. At this stage of bog succession after fire

*S. fuscum* achieved dominance, forming a relatively stabile and spatially homogenous community that persists since approximately 25– 80 years post-fire. Feathermosses (particularly *Pleurozium schreberi*) may be photo-inhibited (Palviainen and others 2005) and compete poorly with *Sphagnum* mosses at high water table positions (Mulligan and Gignac 2001), therefore restricting feathermosses to higher hummocks with greater shading by the *Picea mariana* canopy.



Fig 1. Bog at Burned Crow. We can see *Picea mariana*. The bog is dominated by *Ledum groenlandcum* and *Sphagnum fuscum*. Near the trees growth feathermosses.

*2.2 Research design*

We set up 20 plots divided in 10 controls (C) and 10 treatments (T). Of these 20 plots, 10 plots are dominated by *Picea mariana* and feathermosses and 10 are dominated by *Picea mariana* and *S. fuscum*. For each kind of plot we have 5 replicates.

The division of the plot is the following:

- 5 controls: +trees+feathermosses (CF1, CF2, CF3, CF4, CF5)
- 5 controls: +trees+*S. fuscum* (CS1, CS2, CS3, CS4, CS5)
- 5 T1: -trees+feathermosses (TF1, TF2, TF3, TF4, TF5)
- 5 T2: -trees+*S. fuscum* (TS1, TS2, TS3, TS4, TS5)

To study the influence of the trees on *Sphagnum fuscum* and feathermosses, the trees has been cut on 17th June in the treatment plots in order to assess the situation before the cut.

*2.3 Environmental variables measurements*

Moisture and soil temperature were measured at each plot in association with each $CO_2$ and water vapour flux measurement.

The moisture content was measured with a HH2 moisture meter Delta-T Device (Cambridge-England).

The temperature of the peat was measured at 2, 5, 10, 15, 20, 25 and 30 cm with a thermocouple-thermometer OAKTON temp JKT (Acorn series).

The canopy information was taken with 185° fish-eye lenses. Hemispherical canopy photography is one indirect optical technique that has been widely used in studies of canopy structure and forest light transmission. Photographs taken skyward from the forest floor with a $180_o$ hemispherical (fisheye) lens produce circular images that record the size, shape, and location of gaps in the forest overstory. Image processing involves the transformation of image pixel positions into angular coordinates, the division of pixel intensities into sky and non-sky classes, and the computation of sky-brightness distributions. These data are subsequently combined to produce estimates of growing-season light transmission, as well as other measures more directly related to canopy structure, such as openness, leaf area, and sunfleck frequency (Chazdon and Field 1987, Becker et al. 1989, Rich 1990, ter Steege 1993, Canham 1995).

The photos were then imported and elaborated with the software GLA. The Gap Light Analyzer (GLA) is a Windows-based software application designed to import, display, and analyze digital hemispherical (fisheye) canopy photographs. GLA will compute canopy and site openness, effective leaf area index ($L_e$), sunfleck-frequency distribution and daily duration, and the amount of above- and below-canopy (transmitted) direct, diffuse, and total solar radiation incident on a horizontal or arbitrarily inclined receiving surface.

*2.4 Water vapour exchange measurements*

On $25^{th}$ May 2010 we placed one collar for each plot. The collars were positioned in correspondence of a homogeneous cover of *Sphagnum fuscum* (CS and TS) or feathermosses (CF and TF). The collars were put in the peat until they reached the ice layer in the ground. The roots were cut with care in order to minimize the damage.

Water vapour fluxes were measured inside a transparent chamber placed on top of the collar. The chamber was connected to a EGM-4 in a closed circuit. During 3 min water vapour fluxes were recorded. During measurements, air from inside the chamber was circulated through the $CO_2/H_2O$ analyser, placed next to the chamber, and then returned to the chamber. In combination with the short duration of the measurements (3 min) it is highly unlikely that significant pressure changes took place.

Water vapour fluxes were calculated from the linear change water vapour concentration during the first minute of measurement. The recording started almost immediately after deploying the chamber and the concentrations were averaged over intervals of 5 s. Though we recorded for two minutes, only the first minute was used for the calculations, because the increase in water vapour concentration levelled off considerably during the second minute. Measurements were obtained between 10:00 and 16:00 to minimize flux variations caused by the diurnal cycle (Laporte *et al* 2002) and to obtain fluxes operating at maximum levels to

ensure that the existing spatial variability is captured. The site has been measured once per week.

To calculate the instantaneous rate of evapotranpiration (ETin), the slope of vapour pressure (e) from within the chamber was plotted against time using the least squares method. This calculated slope value was then used within a modified equation (Stannard, 1998) to calculate ET inside the chamber over the 5-min measurement interval,

$$ETin=3.6(MVC/A)$$

Where ET in is the rate of evapotranspiration (mm/h), M is the slope of the vapour pressure over time measurement for each interval ($g/m^3/s$), V is the volume inside the chamber ($m^3$), C is the calibration factor to account for vapour absorption within the chamber (dimensionless) and A is the area of ground surface covered by the chamber ($m^2$). The conversion factor of 3.6 was used in order to convert a volume of water per unit area ($g\ H_20/m^2/s$) into an hourly flux rate (mm/h).
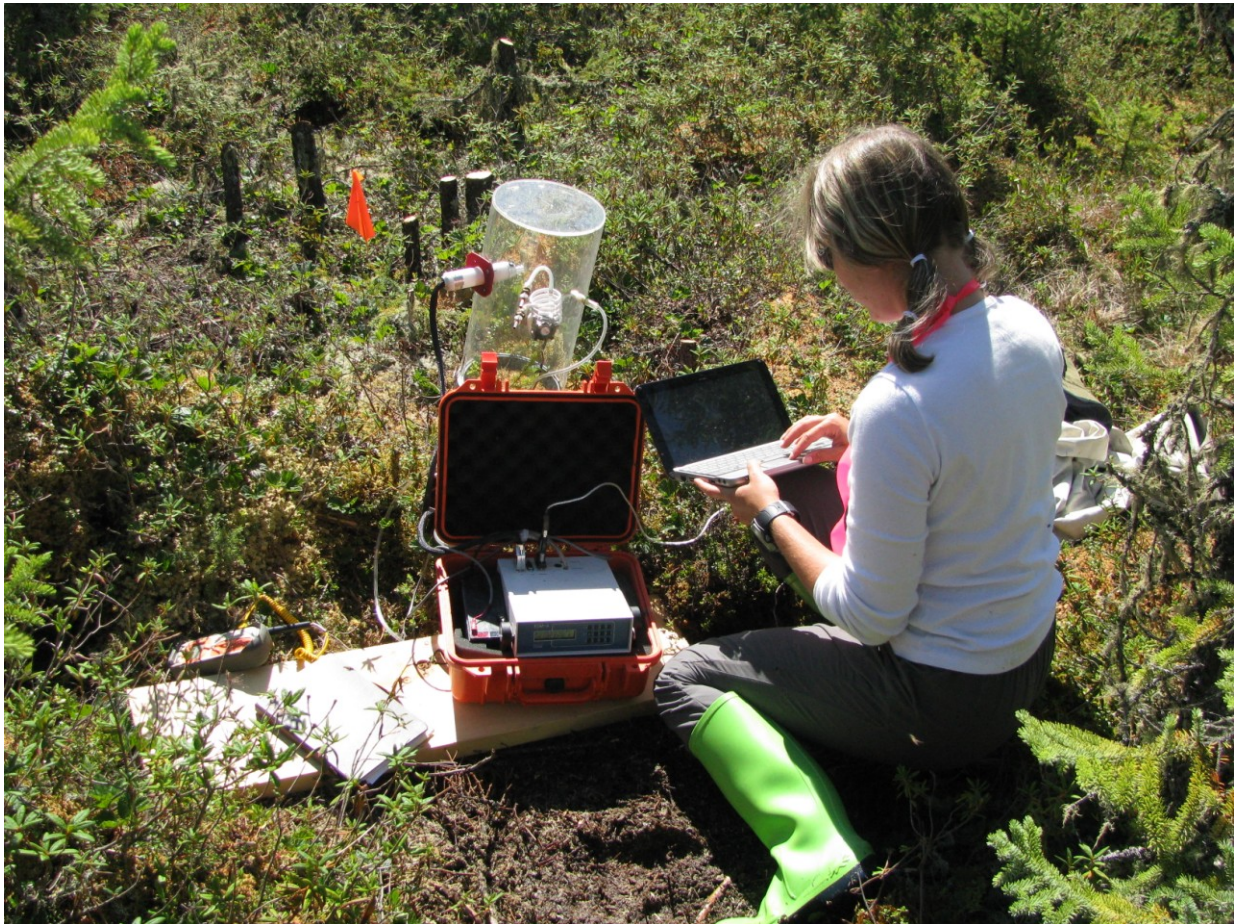


Fig. 2. Measuring water vapour fluxes and $CO_2$ fluxes at Burned Crow. In the photo we can see the EGM-4 connected with the chamber and with the laptop.

*2.5 Statistical analyses*

All the analysis were performed with the software STATISTICA (Release 6; StatSoft Inc., Tulsa, OK, USA). In order to evaluate the effects of treatments on ET, moisture and peat temperature we applied three-way factorials ANOVAs with species, treatment, sampling date and their interaction as fixed factors. Whenever appropriate, significance pf post-hoc differences was assessed by LSD tests. We didn't report species effect because it always differed between *Sphagnum* and feathermosses plot.

In order to evaluate the correlation between ET and environmental variables we applied Person's correlation.

## 3. Result

*3.1 Environmental variables*

*Canopy openness*

The percentage of canopy openness in the treatment plots before cutting down the trees was 45.53, in the treatment plots after cutting down the trees was 65.25, in the control plots was 43.90. The difference of canopy openness expressed in percentage between control plots and treatment plots was 21.35.

The LAI in the treatment plots before cutting down the trees was 0.67, in the treatment plots after cutting down the trees was 0.179, in the control plots was 0.73. The difference of canopy openness expressed in percentage between control plots and treatment plots was 0.55.

After the treatment, TF and TS had greater values of canopy openness in respect to the pre-treatment and in respect to the controls, and lower values of LAI in respect to the pre-treatment and in respect to the controls.

*Moisture content.* The moisture content differed significantly between the species: feathermosses had lower moisture content in respect to *Sphagnum* sp.

Moisture differed per treatment (dof=3, F=123.78, P=0.000) and per date (dof=15, F=4.58, P=0.000). We observed significant differences per date with a lower moisture content during the end of July and August.
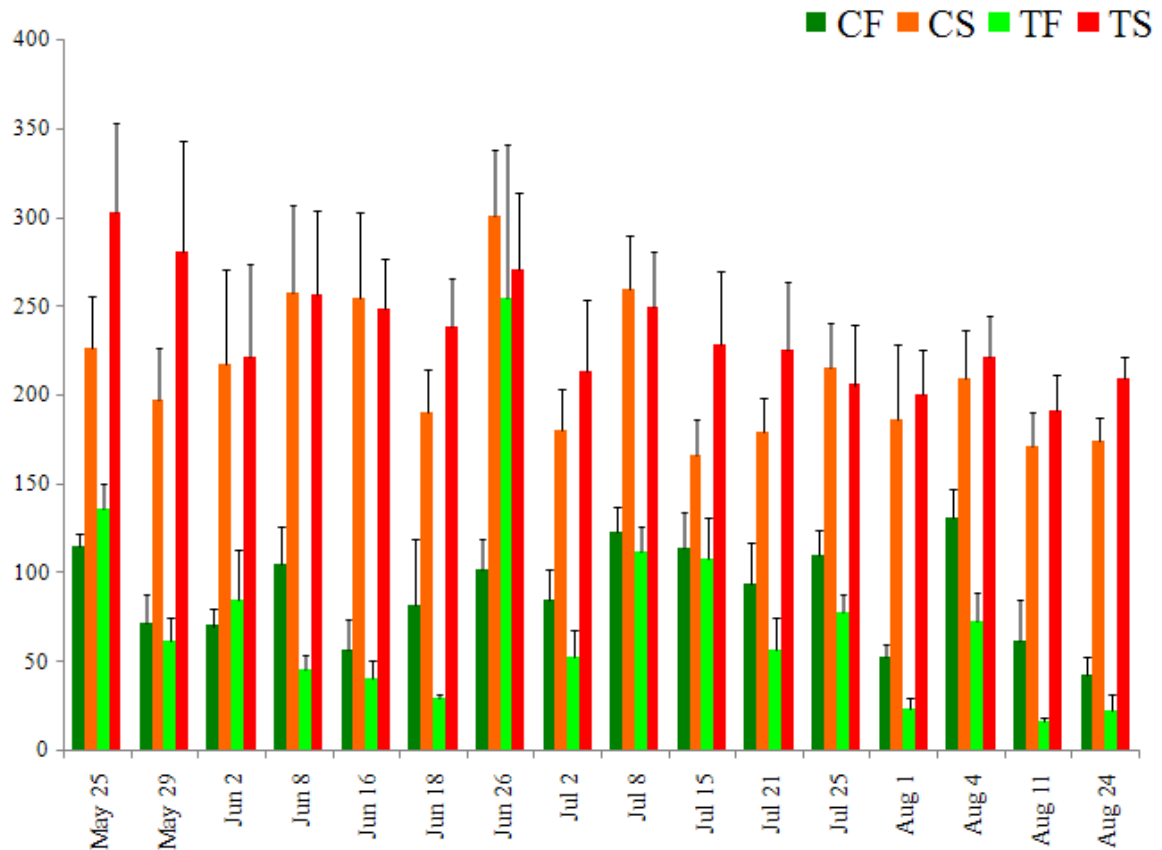
Fig. 3. Moisture content in the plots espressed in a dimensionless unit.

## 3.2 Evapotranspiration

ET differed per date (dof=14, F=20.49, P=0.000), per treatment (dof=3, F=65.9, P=0.000) and the interaction between date and treatment (dof=42, F=2.58, P=0.000). In particular, we can observe significant differences only after cutting down the trees (June 17). On 18$^{th}$ June, there are significant differences between CS and TS but not between CF and TF. On 18$^{th}$ June the weather was very sunny and all the treatment plots were well exposed to sunny conditions. Otherwise, on 26th June there weren't significant differences between the treatments but also between the feathermosses and the *Sphagnum* sp. On 26$^{th}$ of June the weather was overcast and the week before it was characterized by thunderstorms. On 2$^{nd}$ July we observed significant differences between feathermosses and *Sphagnum* sp. but we didn't observe significant differences between the controls and the treatments. The weather was overcast and so, the ET was lower in respect to the sunny days. On 8$^{th}$ July we observed differences between CF and TF and between CS and TS, with greater values of ET in the treatments, but there were not significant differences between CF and CS and between TF and TS. On 15$^{th}$ July TS had significant greater values in respect to CF, CS and TF. On 21$^{th}$ and on 25$^{th}$ July CS and TS had significant greater values in respect to CF and TF. The values of TS were greater in respect to the values of CS but low significantly greater (p=0.08) only on 21$^{th}$. On 1$^{st}$ August the weather was sunny and hot and on 4$^{th}$ August the weather was

foggy, cloudy during the morning and relative humidity was high (58% of relative humidity at 10:30 am). On 1st August we observed significantly differences between TS and CS, with a greater value of ET for TS. CF and TF differed from *Sphagnum* sp., both with lower values of ET in respect with *Sphagnum* sp., but we didn't observe significant differences between CF and TF. On the contrary, we didn't observe significant differences on 4th August. On 11th August we observed significant differences between *Sphagnum* sp. and feathermosses. We observed significant higher values of TS in respect to CS. We didn't observe significant differences between TF and CF. The weather was sunny with the presence of some cloud. On 24th August with didn't observe significant differences between *Sphagnum* sp. and feathermosses, and between the treatments and the controls. The weather was initially overcast and only at the end of the sampling it was sunny mostly with cloudy periods. In general, *Sphagnum* sp. had significant higher rate of evapotranspiration while feathermosses had lower values. During sunny days, *Sphagnum* treatments had significant higher ET values than *Sphagnum* controls. We didn't observe differences during cloudy days.
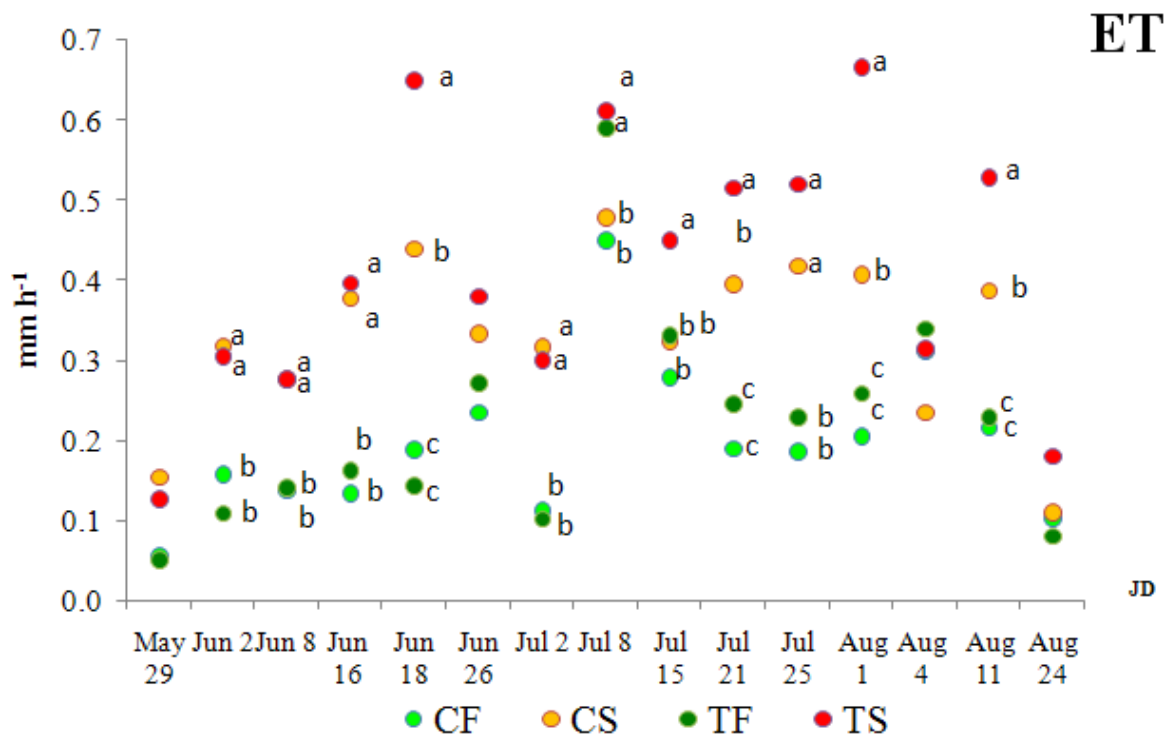


Fig.4. Evapotranspiration rates expressed in millimiters per hour (mm h$^{-1}$).

### 3.3 Correlations

ET showed significant correlations with PAR, %RH, Tair, T peat at 2cm and moistureWhen considered separately per treatment, correlations differed. ET in CF showed significant correlations with Tair and T2cm. ET in CS showed significant correlations with PAR, Tair and T peat at 2cm. ET in TF showed significant correlations with PAR, %RH, Tair and T

peat at 2cm. ET in TS showed significant correlations with PAR, %RH, Tair and T peat at 2cm.

| | ET | | | | |
|---|---|---|---|---|---|
| | Total | CF | CS | TF | TS |
| PAR | **0.48** | 0.21 | **0.56** | **0.52** | **0.60** |
| | p=0.000 | p=0.074 | p=0.000 | p=0.000 | p=0.000 |
| %RH | **0.21** | 0.20 | -0.08 | **0.26** | -0.17 |
| | p=0.000 | p=0.082 | p=0.534 | p=0.028 | p=0.166 |
| Tair | **0.55** | **0.55** | **0.65** | **0.60** | **0.79** |
| | p=0.00 | p=0.000 | p=0.000 | p=0.000 | p=0.000 |
| T2cm | **0.40** | **0.29** | **0.36** | **0.44** | **0.68** |
| | p=0.000 | p=0.013 | p=0.002 | p=0.000 | p=0.000 |
| Moisture | **0.37** | 0.15 | 0.16 | 0.19 | -0.11 |
| | p=0.000 | p=0.204 | p=0.183 | p=0.098 | p=0.367 |

Tab.1. Pearson's correlations between ET and environmental variables (PAR, relative humidity (%RH), air temperature (Tair), peat temperature at 2 cm (T2cm) and moisture).

## 4. Discussion

We observed that evapotranspiration is influenced first by weather and second by species. In effect, our results showed that *Sphagnum* sp. had significantly greater ET than feathermosses only when weather was sunny. In Bond-Lamberty et al (2011) field measurements of *E* averaged 0·37 mm day$^{-1}$ and ranged from 0·03 (*Pleurozium schreberii* in a 77-year-old dry stand) to 1·43 mm day$^{-1}$ (*Sphagnum riparium* in a 43-year-old bog).

The differences in ET rate between *Sphagnum* and feathermosses are due both to physiology and growth. *Sphagnum* sp lack specialized water conduction systems, water is transported by an external wick system and adsorption along the stem and leaf surfaces (Nichols and Brown 1980). The leaves are only one cell layer thick, so each cell is in direct contact with the mire water. *Sphagnum* sp have two kind of cells: chlorophyllous and hyaline cells. In chlorophyllous cells all biological processes take place. Hyaline cells, which cover the larger part of the leaf, are dead cells occupying most part of the tissues and they play a pivotal role in maintaining water availability for the photochemical reactions in chlorophyllose cells (Proctor 2000).

On the contrary, feathermosses lack hyaline cells or a mechanism that allow to maintain water. In addition, no mechanisms of water transport are known for feather mosses (Callaghan et al 1978).

About growth, *Sphagnum* stems growth very near one another and with the different capitula they create a strict hummock that allows to maintain particular conditions inside. Feathermoss growth with the cauloid prostrated and the branches are not protected from the

light. For these reasons the latters have the tendency to dry up very quickly and they growth in areas sheltered by trees and shrubs.

*Sphagnum* spp. and feathermoss, as shown in our study, showed a different water content, with the first having greater water content than the second. Heijmans et al (2004) showed that *Hylocomium splendens* was the only species studied that reacted strongly to water additions, but a high water level per se did not increase evaporation. This suggests that in addition to microclimate, precipitation frequency is an important factor for evaporation in this species. Monthly growth rates were strongly correlated to precipitation frequency (Busby et al 1978) and experimental water additions resulted in an increased cover of *Hylocomium* (Phoenix et al 2001).

Evapotranspiration rates were higher in respect to studies conducted in other ecosystems because ET depends not only to species but also to habitat openness (Heijmans et al 2004) and climate. In our study, ET was first of all positively correlated with air temperature and PAR. In Heijmans et al (2004) light conditions strongly influence water vapour fluxes (Heijmans et al 2004, Busby et al 1978) but wind has a strong influence on *Sphagnum* evaporation in bog vegetation (Heijmans et al 2001).

In Alberta, there has been an overall upward trend in the annual temperature and the north appears to be warming at a greater rate than the south. Calgary has warmed by about 0.6°C and Edmonton by about 1.3°C throughtout the 20th century. Fort Mcmurray has warmed by 3.5°C. The precipitation data shows a mixed trend over the 20th century across Alberta because there is a large range of variability in precipitation. However, there is evidence of a drier climate. Higher temperatures and less precipitations will increase the incidence of wildfires. But, first of all, the rate of water loss from these ecosystems will be great and the energy required to burn peatlands will be low.


## 5. Conclusions

Evapotranspiration is an important component in peatlands and wildfire has strong effects on ET by increasing soil evaporation and by lowering canopy evaporation and transpiration. The trees are an important component because they start the fires in the peatlands. The experiment here pointed out the importance of trees in conserving water in hummocks. Otherwise, in water fluxes, first weather conditions and second species, have a greater importance than trees.

In addition, the data collected in this experiment will help to improve the energy model in order to predict peatfires. In effect, water vapour fluxes are important in order to understand the activation energy required to start a fire. So the microtopographies in which feathermoss growth need a lower activation energy than the *Sphagnum* hummock in order to propagate fire in the peatland. The study presented here pointed out a further question: the weather is the driving factor for energy fluxes, but what will happen if the weather conditions will become too harsh and it will be losed more water from the hummocks?

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# CONCLUSIONS

## 1. General summary

This thesis includes different works devoted to the effects of global change on peatland ecosystems. Each of the studies reported in here is important in order to understand the different facies of the global change. The first work highlighted the importance of PFTs in peatlands. In effect, PFTs are categories investigated in ecology that allow to summarize ecosystem attributes. We observed that PFTs strongly differed in nutrient content and in nutrient variation one another and the classification in PFTs is more important (except for P) for nutrient content. Different studies showed how global change first act directly on PFTs or on species composition and indirectly on nutrient concentration. In our study we observed that habitat act both directly on PFTs and species composition and indirectly on nutrient concentration except for phosphorus.

The second work highlighted the relationship between ANPP of different peatland types and nutrient concentration. In particular, we observed a strong relationship between ANPP and phosphorus plant concentration. In ombrotrophic habitats P deficiency affects ANPP by limiting growth of *Sphagnum* mosses if atmospheric N deposition exceeds a threshold implying N saturation in the moss layer. On the other hand, low productive fens often are P-limited although ANPP in rich fens can be controlled by N availability when P in pore water is enriched by man's impact.

The third work highlighted the relation between hydrology, ANPP and decomposition in a bog-dominated peatland and in a fen-dominated peatland. The fen-dominate had a lower rate of decomposition in respect to bog-dominated peatland. We could attribute this to P limitation in peat and to highlight, one more time, the relevance of P in peatlands.

The fourth work highlighted two important things. First of all, one year snow cover manipulation could modify the N:P ratio in the peat through the microbial biomass. Second, we found a great contribution to ecosystem respiration from the vegetation, and this could be attributed to climate change.

The fifth work, still a draft, highlighted the importance of weather in evapotranspiration and the different contribution to water cycling by feathermosses and *Sphagnum* spp.

## 2. Perspectives

All the studies presented here raise further questions for future researches.

First of all the concept of Plant Functional Types is still to be investigated. Previous studies reported the importance of understanding how to apply these categories. In peatlands they are important because they control different ecosystem functions: patterns of carbon exchange (Ward et al 2009), decomposition (Hoorens et al 2010) and functional microbial diversity (Artz et al 2008). In the first paper presented in this thesis we demonstrated the relevance of PFTs in determining foliar nutrient concentration. Aerts et al (1999) observed that PFTs are more important in respect to mire type (fen vs bog) in determining nutrient use efficiency.

Otherwise this concept is sometimes limited (Dorrepaal et al 2005) and the great goal is to what extent we can apply this generalization.

Second, nutrient limitation in peatlands. Studies conducted in European peatlands observed N-limitation (Koersselman and Meuleman 1996) but in America it's still not clear which is the limitant nutrient in peatlands (Bedford et al 1999). In fens P is more limitant (Boyer and Wheeler 1989) because $H_2PO_4$ reacts with FeOH and precipitates (Zak et al 2004). But this is not an universal rule, and the mechanism controlling P cycling and his bioavailability is far to be understood in peatlands. The interesting thing is that 4 studies showed up the importance of phosphorus in alpine peatlands in presence of P deficiency. First of all the importance that the habitat (and so the features related to hydrology, hydrochemistry and topography) covers in plant phosphorus concentration. Second his importance in influencing ANPP and decomposition. And third the role of microbial biomass in P cycling in peatlands.

The role of nutrient limitation is strongly related to another important topic that has still to be investigated in peatlands: microbial biomass and biodiversity. The link between aboveground and belowground biota it's an important topic in all the ecosystems (Bardgett et al 2005) because microorganisms influence key functions like nutrient cycling, energy flow and biodiversity and it's unknown how changes in these functions are linked to variations in microbial community. In peatlands plants are adapted to harsh conditions such as oligotrophy, acidity, anaerobic conditions. In particular, plants adapted to oligotrophy have particular adaptations in order to cope with the lack of nutrients: organs for nutrient storage, carnivory, michorryzae, … In Andersen et al (2010) they showed how microbial community is related to vegetation cover and to the physicochemical environment. In addition, nutrient input in peatlands strongly influences microorganisms (Gilbert et al 1998). For this reason one important topic is the relative contribution of the microbes and plants to peatland functioning. In my thesis, we can observe this question in study IV, in relation to ecosystem respiration. In the study on snow cover manipulation we observed that, during summer, most of ecosystem respiration is autotrophic. This suggests that, in alpine peatland at that latitude, the $CO_2$ emission from plants is greater that the $CO_2$ emission from microorganisms so decomposition. We still don't know the reason, we can make hypothesis this is one of the greatest topic in peatland ecology.

About the last study conducted in Canada, we can apply the same protocol to do research in Italian alpine peatlands. It's true that Italian peatlands are not subjected to wildfire, but it's also true that water loss from *Sphagnum* spp could help us to explaining changes that we are observing in our ecosystems. In particular, we could investigated the relationship between water vapour loss and $CO_2$ loss from the peatland. In effects, the study on snow cover experiment underlined $CO_2$ losses from the vegetation and, only in a less extent, from the decomposition. Gerdol et al (2008) in other parts of the peatland located in Passo San Pellegrino, observed $CO_2$ losses through ecosystem respiration and they explained this loss because of the strong heatwave happened in 2003.

## 3. References

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