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

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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 in order to test whether 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.

Keywords Bog · Fen · Nutrient limitation · Peatland · Plant functional type · Poor-rich gradient

Produzione primaria e status nutritizio nella vegetazione di torbiera nelle Alpi sud-orientali italiane

Riassunto In questo lavoro viene analizzata la produzione primaria netta in cinque torbiere delle Alpi sudorientali. Queste torbiere presentano notevoli differenze nel chimismo dell'acqua di falda e la loro tipologia varia da torbiere alte ombrotrofiche a torbiere basse fortemente minerotrofiche. La vegetazione di queste torbiere differisce inoltre considerevolmente sia in termini di composizione specifica che di frequenza dei tipi funzionali. Nonostante tali differenze, la produzione primaria nelle cinque torbiere non presenta differenze significative tra le cinque torbiere. La produzione primaria risulta invece positivamente correlata con la concentrazione totale di fosforo nella vegetazione e negativamente correlata con il rapporto N:P e con il rapporto K:P nella vegetazione. In conclusione, la produzione primaria nei siti esaminati è principalmente limitata da carenze di fosforo. Tale limitazione si esercita in un ampio ambito di tipi di torbiera.

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 values of pH, electrical conductivity and concentrations of cations (especially Ca^{2+} and Mg^{2+}) in pore water increasing 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.

The poor-rich gradient as defined by the mineral content in pore water has often been associated with nutrient status

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in the environment, with bogs being regarded as extremely poor in nutrients and fens as richer in nutrients, especially in less acidic habitats (Gore 1983). However, several studies have questioned whether the poor-rich gradient coincides with a nutrient gradient in mires. On one hand, concentrations of nutrient ions (especially NO_3^-, NH_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 of which no data on ANPP of mire ecosystems have been published so far. We also aimed at investigating 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 whether ANPP patterns along the poor-rich gradient could be related to the limiting effects of one or several nutrients for biomass production.

Materials and methods

Study sites

The study was carried out at five mires located in two different areas in the southern Italian Alps (Northern 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 a mean annual temperature of *c* 4°C and a mean total annual precipitation of *c* 1,200 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 *c* 4°C and mean total annual precipitation of *c* 1,500 mm. The only two mires occurring in this area, Palù di Sotto and Palù San Lorenzo (both developing on glacial loam) were investigated for our study.

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 basis 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 is a bog covered by *Pinus mugo* scrub patches, interspersed with *Sphagnum fuscum* and *Sphagnum capillifolium* hummocks and few hollows in the central part, while the peripheral sector is mostly covered by *Sphagnum compactum* lawns. Coltrondo N, a poor fen, is covered by open vegetation rich in *Sphagnum* mosses, mostly *S. capillifolium* in hummocks, *Sphagnum magellanicum* and *S. compactum* in lawns, besides some scattered *P. mugo* scrub patches. Coltrondo S, an intermediate fen, is mostly covered by fen meadows and, to a lesser extent, *S. compactum* lawns. *Sphagnum* hummocks and *P. mugo* scrubs are present but less abundant compared to the previous sites. Hollows are rare, and a marginal stream is well developed especially at two of the mire edges. Palù di Sotto, a poor fen, is 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, is almost totally covered by fen meadows and hollows with only two small isolated patches of *P. mugo*. A marginal stream runs along the two long edges of the mire.

ANPP

A total of 40 plots (2 m × 2 m in size) were set up to determine ANPP and subsequently sample plant material. The choice of the sampling plots was made with the help of detailed vegetation maps (M. Tomaselli et al., unpublished), in order to detect areas of homogeneous vegetation cover representative for each habitat type in the five mires.

At the peak of the growing season 2006 (end July–early August), the whole aboveground biomass of graminoids and forbs and the current-year tissues (leaves and shoots) 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 four cranked wires (Clymo 1970) inserted at the beginning of the growing season (early June), 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/plot.

We determined ANPP as follows: (1) 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. The estimates were upscaled to the plot size by visually assessing *Sphagnum* cover in the 2 m × 2 m plots. Non-*Sphagnum* mosses and lichens occurred only in a small fraction of the plots and always with low biomass, thus they were not considered in the ANPP calculations. (2) For evergreen and deciduous shrubs, we considered the total mass of current-year tissues as an estimate of ANPP. This probably underestimated the aboveground production of deciduous shrubs, as stem secondary growth may account for up to 20% of their annual aboveground production (Gerdol 2005). However, the cover of deciduous shrubs was overall modest. (3) 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.

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 peak 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. N 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 the 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.

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-model ANOVAs, with site as a fixed factor, and habitat and the site × habitat interaction as random factors. 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).

Results

ANPP

The ANPP values recorded in the 40 plots varied by one order of magnitude, from 40 to 640 g dry matter m^{-2} $year^{-1}$. 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

Table 1 *P* values resulting from mixed-model ANOVAs of ANPP, nutrient concentrations and nutrient ratios in the vegetation, with site as fixed factor, habitat type and interaction site × habitat type as random factors (degrees of freedom in *parentheses*)

	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

Significant values ($P < 0.05$) are indicated in *bold*

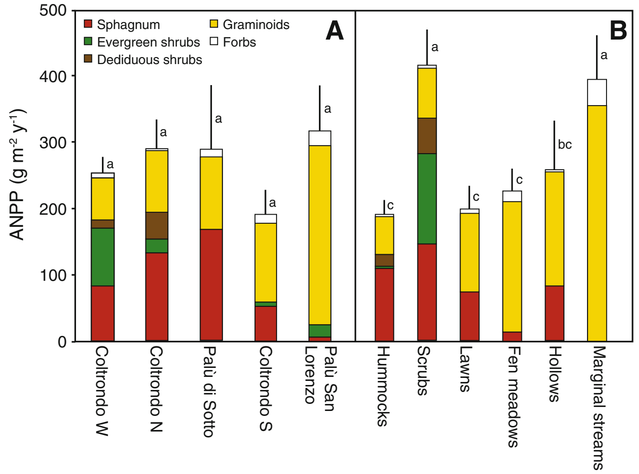

Fig. 1 Mean (+1 SE) ANPP, subdivided according to PFTs, of the five mires (panel **a**) and of the six habitat types (panel **b**). Means followed by *different letters* differ significantly ($P < 0.05$) from each other. The mire sites are ordered, from bog to rich fen, according to increasing mean pH of the pore water

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).

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 around 15 mg g^{-1} 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 between 0.8 and 1.0 mg g^{-1} in four mires and 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 values in the intermediate fen and lowest in the rich fen. The three nutrient ratios (N:P, N:K, K:P) varied approximately by the same extent among the sites (20–26%), always with highest values in one of the poor fens (Palù di Sotto; Table 3).

Table 2 Mean ANPP (g m^{-2} $year^{-1}$ ± SE) in the six habitat types at the five mires studied (for details see *text*)

	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 3 Mean (±SE) nutrient concentrations (mg g^{-1}) and nutrient ratios in the vegetation of the five mires

	Coltrondo W BOG	Coltrondo N POOR FEN	Palù di Sotto POOR FEN	Coltrondo S INTERM. FEN	Palù San Lorenzo RICH FEN
N	15.5 ± 0.9	13.2 ± 0.6	14.8 ± 1.1	14.7 ± 1.3	15.3 ± 1.0
P	1.01 ± 0.12	0.81 ± 0.09	0.64 ± 0.04	0.83 ± 0.13	0.83 ± 0.07
K	4.9 ± 0.4	3.3 ± 0.4	4.4 ± 0.8	5.5 ± 2.2	2.5 ± 0.3
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

Means did not differ significantly between sites

Table 4 Mean (±SE) nutrient concentrations (mg g^{-1}) and nutrient ratios in the vegetation of the six habitat types

	Hummocks	Scrubs	Lawns	Fen meadows	Hollows	Marginal streams
N	13.1 ± 0.8 c	13.4 ± 0.7 bc	13 ± 0.8 bc	15.9 ± 1.0 b	15.5 ± 1.2 bc	19.2 ± 1.1 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	5.5 ± 0.3 d	6.0 ± 1.3 cd	7.5 ± 0.6 bc	8.3 ± 0.6 b	7.4 ± 0.6 bc	14.1 ± 2.3 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

Within each *row*, the means followed by *different letters* differ significantly ($P < 0.05$) from each other

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 habitat types 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 lawns and especially in 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).

Relationships between nutrient concentrations and nutrient ratios, on one hand, and vegetation composition in terms of PFTs on the other hand 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.

Discussion

ANPP patterns

The mean ANPP in our mires in the Southern Alps were very similar to that recorded in several mires of the boreo-nemoral regions of North America and Northern Eurasia, generally ranging from 200 to 300 g m^{-2} $year^{-1}$ (see Rydin and Jeglum 2006 and references therein). Few data is available to compare our data to estimates of ANPP of mires in mountainous regions. For example, Francez (1992) reported mean ANPPs of ca. 300 g m^{-2} $year^{-1}$ for mires in the Massif central. Conversely, mean ANPPs in mires of the (sub)arctic regions are somewhat lower (ca. 200 g m^{-2} $year^{-1}$ or less; Camill et al. 2001), while those in oceanic regions of western Europe usually are considerably higher (>500 g m^{-2} $year^{-1}$; Forrest and Smith 1975). In summary, patterns of ANPP in mires at a broad geographic scale seem to be primarily controlled by climate, particularly by length of the growing season. At a smaller scale, namely at the site level, our data supports evidence from recent studies, all reporting poor if any variation in ANPP from bogs to fens. Indeed, neither did ANPP show any consistent pattern when the sites were ordered from bog to rich fen, nor did ANPP differ significantly among the sites in our study, 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.

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, low ANPP values were found in habitats differing greatly from each other with regard to 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 mg g^{-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 to provide 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 be caused by the wide variety of P fractions occurring in organic soils (Schlichting et al. 2002). These P fractions undergo various types of biogeochemical transformations, 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 fen meadows because of P fixation by Fe- and Al-hydroxides or calcareous components (Boeye et al. 1995). Hollows exhibited the overall poorest P status of all vegetation types, 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, which in turn depends on water levels. 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 loss 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 between these two habitats differ strongly. Nonetheless, P did not appear to be limiting in either of the two habitats, as mirrored by relatively high P concentrations (>1 mg g^{-1}) and low N:P ratios (<14) in the vegetation. Higher P availability in *P. mugo* 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 vegetation was the by far the most productive, 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).

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, provided 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: (1) differing composition in terms of species and/or PFTs having intrinsically different nutrient contents, (2) differing nutrient concentrations in plant species or PTFs in relation to habitat, or (3) a combination of these two causes. The third cause appeared to hold true in our case, as the proportion 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 and Karlsson 1997) and *Sphagnum* mosses (Wojtuń 1994).

It seems rather surprising that ANPP did not differ among sites in spite of significant differences in ANPP between habitat types. Possible explanations could lie in the different cover of habitat types within 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.

Conclusions

This study provides evidence that biomass production in a series of mires in the South-eastern Alps was mostly limited by P availability, 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 human 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

	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)	1,830	1,910	1,790	1,330	1,360
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

EC electrical conductivity

Appendix 2

Mean (±SE) nutrient concentrations (as mg g^{-1}) and nutrient ratios in the five PFTs at the six habitat types and *P* values obtained by one-way ANOVAs

	Hummocks	Scrubs	Lawns	Fen meadows	Hollows	Marginal streams	*P*
Sphagnum mosses							
N	9.7 ± 0.6	9.7 ± 0.3	9.9 ± 0.5	–	12.1 ± 2.7	–	*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	4.1 ± 0.2	4.9 ± 0.3	4.7 ± 0.3	–	4.9 ± 0.7	–	*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	12.5 ± 0.4	13.4 ± 0.6	13.7 ± 0.4	13.1 ± 0.6	15.2	–	*0.52*
P	0.99 ± 0.05	1.08 ± 0.07	0.98 ± 0.06	0.70 ± 0.04	0.81	–	*0.13*
K	5.7 ± 0.3	5.6 ± 0.4	5.5 ± 0.3	4.7 ± 0.3	7.2		*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	16.8 ± 0.6	18.5 ± 0.8	19.3 ± 0.8	–	–	–	*0.10*
P	1.02 ± 0.04 b	1.19 ± 0.06 a	1.25 ± 0.01 a	–	–	–	***0.04***
K	6.2 ± 0.7	7.1 ± 0.4	7.0 ± 0.5	–	–	–	*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	18.0 ± 0.5 ab	20.2 ± 1.4 a	17.1 ± 0.6 bc	16.7 ± 0.6 bc	15.7 ± 0.6 bc	19.5 ± 0.7 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	7.5 ± 0.5 c	9.2 ± 0.8 b	9.1 ± 0.5 b	8.2 ± 0.4 bc	8.3 ± 0.4 bc	13.7 ± 1.4 a	***0.001***
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	16.4 ± 0.7	21.2 ± 0.6	16.7 ± 1.0	17.6 ± 0.9	18.0 ± 1.8	20.7 ± 0.9	*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	8.8 ± 0.8 b	9.9 ± 1.0 b	14.6 ± 2.2 b	12.2 ± 1.6 b	8.9 ± 0.1 b	27.3 ± 2.6 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***

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

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