

# The seasonal growth pattern of *Sphagnum magellanicum* Brid. in different microhabitats on a mire in the southern Alps (Italy)

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**Abstract.** On a nutrient-poor mire in the southern Alps of Italy *Sphagnum magellanicum* achieved a total linear elongation of 28-31 mm and a dry matter increment of 12-13 mg per plant during the growing season 1994. *Sphagnum magellanicum* grew actively whenever night temperature was above zero, but during this period growth was primarily controlled by water availability. The growth rates were very much the same in open sites compared to areas covered by *Pinus mugo* scrubs. However, plants growing in the two habitats showed different adaptations to environment. This implied a different pattern of physiological control on the growth rates of *Sphagnum magellanicum* in the two habitats. Provided the moisture content of the capitula was not limiting, the growth rates in shaded habitats were greatest when the concentrations of chlorophyll *b* as well as the ratio of chlorophyll to carotenoids were highest. Conversely, the growth rates in the open were negatively correlated with the ratio chlorophyll *a* to *b*, probably because chlorophyll *a* was degraded more rapidly than chlorophyll *b* in conditions of environmental stress. Red wall pigments (sphagnorubin s.l.) were more concentrated in the open, especially at the end of the growing season, the synthesis of such pigments being enhanced by high irradiance coupled with night chilling. However, the concentrations of sphagnorubin did not show the expected negative correlations with chlorophyll concentration and growth rate, presumably because of a different timing of the metabolic pathways of sphagnorubin synthesis and chlorophyll degradation.

**Keywords:** environmental factors, mire ecology, open vs. shaded habitats, photosynthetic pigments, production, seasonal growth rates.

## Introduction

Light conditions exert a profound influence on the growth response of bryophytes (Hoddinott and Bain 1979; Rincón 1993). In *Sphagnum* mosses the rates of growth in weight increase with irradiance, at least within a certain range of photon flux density, whereas growth in length is usually greater under

low light, thus determining etiolation when the plants are shaded (Clymo 1973). However, high irradiance may limit *Sphagnum* growth as a probable effect of photoinhibition of photosynthesis (Harley *et al.* 1989; Murray, Tenhunen and Nowak 1993). This general trend may be further complicated when light level interacts with water table (Li, Glime and Liao 1992), temperature (Koskimies-Soininen and Nyberg 1987; Kurets *et al.* 1993) and photoperiod (Li and Glime 1991; Gerdol 1995).

*Sphagnum* mosses cover vast areas, especially in the boreal and north-temperate regions, some species often forming the bulk of living and dead biomass in nutrient-poor peatlands. *Sphagna* also represent an important component of mire vegetation in the mountainous territories at mid-latitudes. *Sphagnum* species may be exposed to varying light regimes, ranging from full ambient irradiance to moderately deep shade. As variations in the rates of *Sphagnum* production may affect the carbon and nutrient cycling (van Breemen 1995), as well as the composition of the vascular vegetation (Malmer, Svensson and Wallén 1994), it is of great ecological interest to analyse the causal relationships between environmental factors and the adaptive responses of *Sphagnum* mosses to environment.

In this paper we sought to determine to which extent the growth pattern of *Sphagnum magellanicum* is influenced by light regime in a montane mire on the Alps.

## Materials and methods

### Description of the study site

The study was carried out in a small mire at Forcella Lavardet, lying on the borderline between the provinces of Belluno and Udine (46°, 12°38' E), at 1,530 m above sea level, in the Carnian Alps (North-eastern Italy). The geological substrate consists of Permian sandstones. The regional climate is cool-suboceanic, with a mean annual temperature of 6 °C at 1,200 m. Annual precipitation averages 1,500 mm and is rather evenly distributed in the period May-November, with a minimum in winter (Fliri 1975).

The site can be typified as a transitional mire. The vegetation mainly consists of an open carpet of *Sphagnum magellanicum*, *S. compactum* and *S. russowii* having *Trichophorum caespitosum* as the dominant species in the field layer (association: *Eriophoro-Trichophoretum caespitosi*), and of scrubs

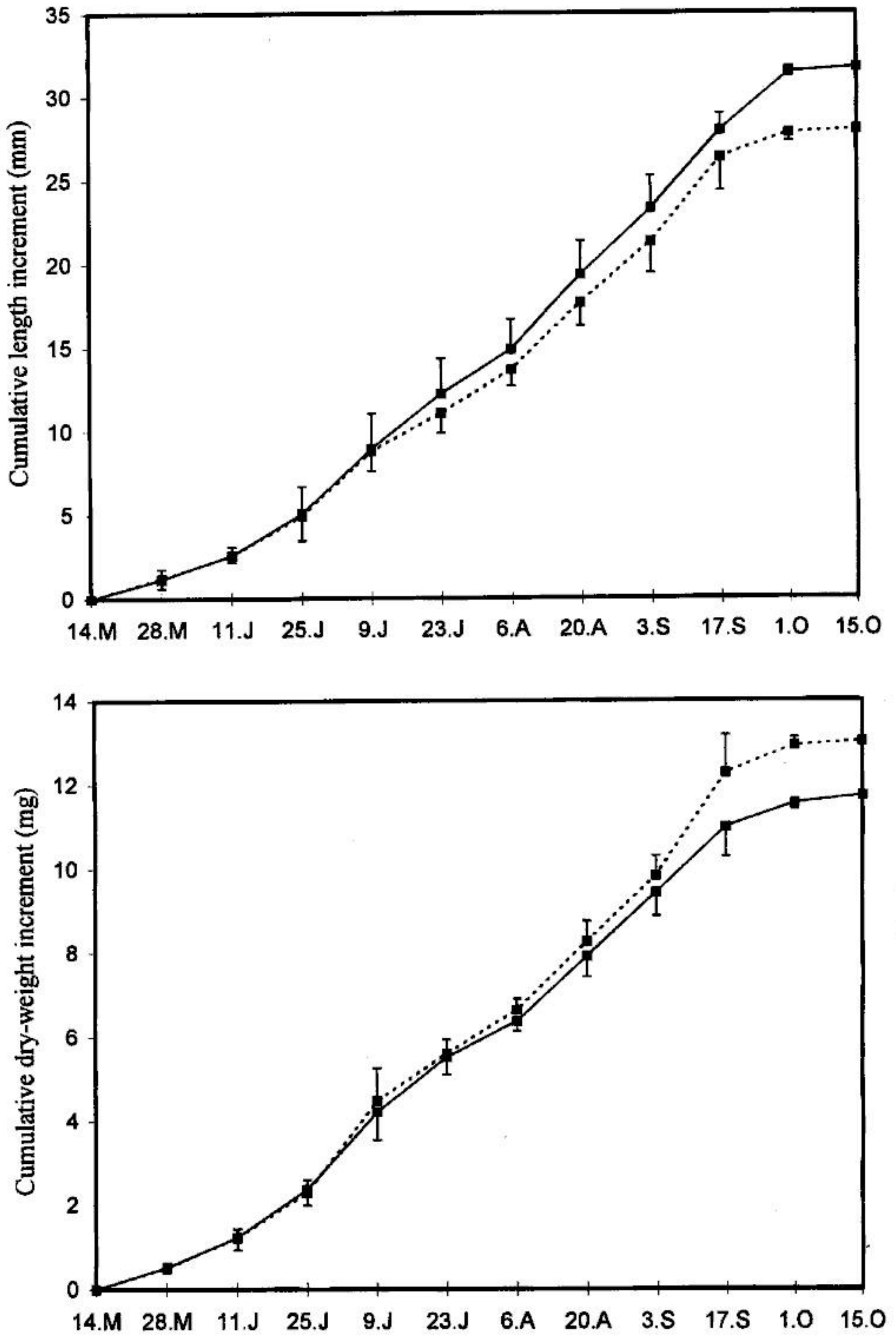


Fig. 1. Seasonal patterns of growth in length (above) and growth in weight (below) of *Sphagnum magellanicum* in open habitats (dashed lines) and under *Pinus mugo* cover (full lines). The symbols represent mean values with one S.E.

of prostrate pine (*Pinus mugo*) rich in ericaceous shrubs (*Vaccinium myrtillus*, *V. vitis-idaea* and *Andromeda polifolia*), having *Sphagnum magellanicum* as the dominant species in the bottom layer (asso-

ciation: *Pino mugo-Sphagnetum magellanicum*). A narrow belt in the central part of the mire is covered by a community of *Cardamine amara* developing on gently sloping mineral ground (Gerdol 1994). Peat

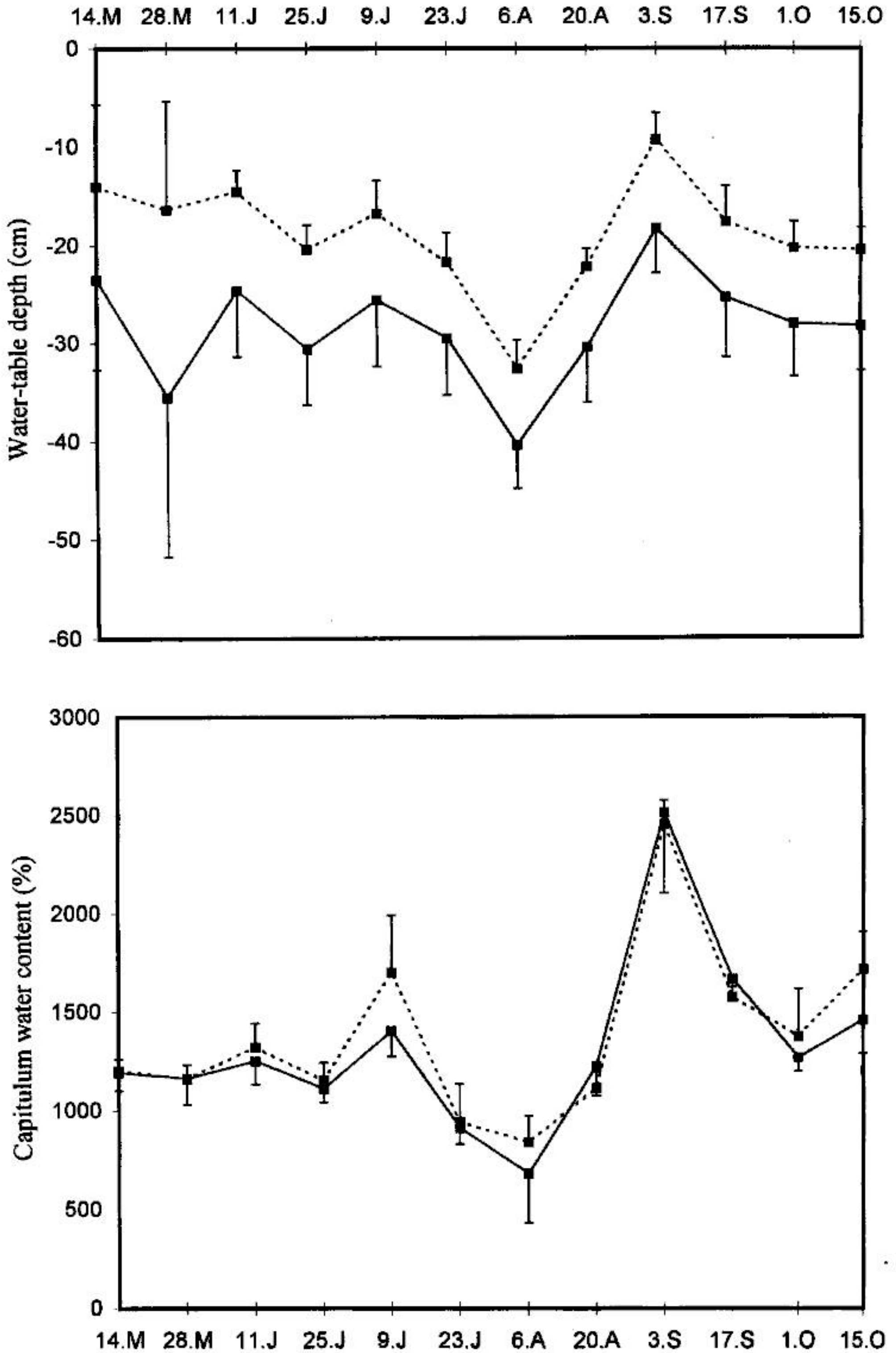


Fig. 2 . Seasonal patterns of water-table depth (above) and water content in the capitula of *Sphagnum magellanicum* (below) in open habitats (dashed lines) and under *Pinus mugo* cover (full lines). The symbols represent mean values with one S.E.

water is acid (pH: 4.2 - 4.8) and poor in electrolytes ( $\text{Ca}^{2+}$ : 1.2 - 2.8 mg L<sup>-1</sup>), whereas the water flowing on mineral ground is slightly alkaline (pH: 7.5) and much richer in electrolytes ( $\text{Ca}^{2+}$ : 25 mg L<sup>-1</sup>).

#### Field work

The growth of *Sphagnum magellanicum* was measured during the 1994 growing season at 8 sample

plots, of which 4 were located in open areas and 4 under *Pinus mugo* cover. The experiment started as soon as the snow had melted away from the mire surface, on 14 May 1994. At each of the 8 plots a water gauge was inserted into the peat for measuring depth to the water table, and 15 individuals of *Sphagnum magellanicum* were cut to a standard length of 30 mm from the apex and placed again into the *Sphagnum* carpet at natural density. The cut plants were harvested after 14 days and remeasured to determine growth in length. Growth in weight was calculated by subtracting the initial capitulum weight (Clymo 1970) from the final mean dry weight, after oven-drying for 24 hr at 100 °C.

An additional sample of 4-7 capitula (50-100 mg dry-weight) was taken at each plot, stored in a portable freezer and carried to the laboratory within 24 hr for pigment extraction.

This procedure was repeated at 14-day intervals until 15 October 1994.

#### Pigment extraction and determination

The fresh capitula were immediately treated, on arrival in the laboratory, as described in Gerdol *et al.* (1996). The concentrations of photosynthetic pigments (chlorophyll *a* and *b* and total carotenoids) were determined spectrophotometrically using the extinction coefficients of Lichtenthaler (1987). In addition, the extinction at a wavelength of 526 nm was employed for estimating the concentration of red wall pigments (sphagnorubin s.l.; Rudolph, Kabsch and Schmidt-Stohn 1977).

#### Statistical analyses

The periodic growth increments (both growth in length and growth in weight) were related to environmental data by multiple regression analysis, using the following independent variables: 1) biweekly means of minimum temperature, mean temperature, maximum temperature and precipitation, obtained from 3 recording stations located within a radius of 10 km from the mire (details available on request); 2) biweekly means of photoperiod length; 3) water-table depth measured in the water gauges.

Comparisons between growth rates and pigment concentrations were made by correlation analysis and univariate ANOVA. As standard errors were not independent of means, all growth data were log-transformed before analysis.

Statistical computations were made using the package SPSS (Norusis, 1994).

## Results

#### Seasonal growth pattern and its relationship with environmental factors

The seasonal rates of growth in length and growth in weight were highly correlated with each other both in the open and under pine cover ( $r = 0.95$ ;  $P < 0.001$ ). The growth rates were low at the beginning of the season, gradually increasing until mid July, and declining again in mid summer. Growth was maxi-

mal from mid August to mid September, and decreased abruptly at the end of summer, virtually ceasing by mid October (Fig. 1).

The environmental variable most directly controlling the growth dynamics of *Sphagnum magellanicum* was minimum temperature, as it entered at  $P < 0.01$  both the multiple regression based on growth data in the open and that based on growth data under pine cover (Table 1). Precipitation only affected growth in the open, whereas mean temperature, maximum temperature, water-table depth and photoperiod played a minor role, if any, in controlling growth of *Sphagnum magellanicum*. None of the latter four variables entered the multiple regression runs (Table 1).

Habitat	Regression
Open	$\log(\text{Gr}) = 2.03 + 0.09T_{\text{min}} + 0.06P$ ( $R^2 = 0.90$ , $df = 2,8$ , $F = 35.6$ , $P < 0.001$ )
Pine-covered	$\log(\text{Gr}) = 2.36 + 0.08T_{\text{min}}$ ( $R^2 = 0.73$ , $df = 2,8$ , $F = 24.9$ , $P < 0.001$ )

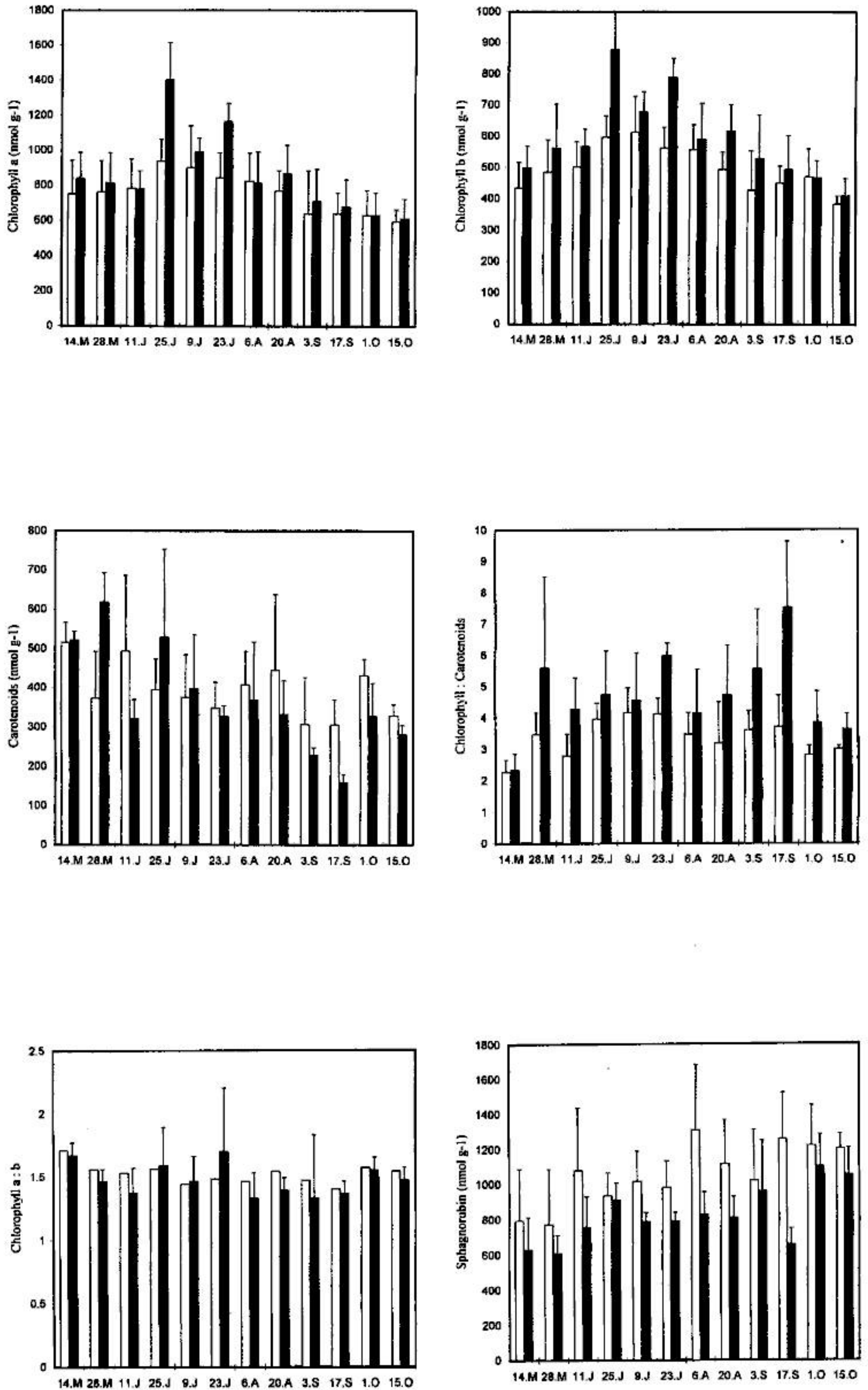
**Table 1.** Statistics of stepwise multiple regressions of growth in weight (Gr) for *Sphagnum magellanicum* in two habitats. The independent variables included in the analyses are: minimum temperature ( $T_{\text{min}}$ ), mean temperature, maximum temperature, precipitation (P), depth to the water table and photoperiod. Only the variables which entered the runs at  $P < 0.01$  were retained in the final equation.

There were profound differences between open and pine-covered habitats as far as both hydrology and light levels are concerned. Depth to the water table was considerably greater under pine cover than in the open during the whole season (Fig. 2). Irradiance under pine cover was reduced by ca. 50% compared to full ambient levels. In spite of such remarkable differences, *Sphagnum magellanicum* grew at much the same rate in the two habitats. The mean cumulative length increment was slightly greater under pine cover than in the open (31.89 vs. 27.98 mm plant<sup>-1</sup>, respectively). Conversely, the mean cumulative dry-weight gain was somewhat greater in the open (13.03 mg plant<sup>-1</sup> vs. 11.71 mg plant<sup>-1</sup> under pine cover). Both differences were not statistically significant.

#### Relationships between growth and physiological status of the *Sphagnum* plants

Depth to the water table exerted a primary influence on the water content of the *Sphagnum magellanicum* capitula, both following almost the same seasonal pattern (Fig. 2). Although depth to the water table was considerably greater under pine cover than in the open, the plants growing in the two habitats did not exhibit appreciable differences as far as capitulum water content is concerned ( $F_{1,20} = 1.84$ ;  $P = 0.18$ ).

The concentrations of both chlorophyll *a* and chlorophyll *b* in the capitula were low at the beginning of the growing season, abruptly peaking at the end of June and gradually decreasing during the rest of the season (Fig. 3). Only chlorophyll *b* did show significantly higher concentrations in the capitula of



**Fig. 3.** Seasonal patterns of pigment concentrations and pigment ratios in the capitula of *Sphagnum magellanicum* in open habitats (open columns) and under *Pinus mugo* cover (full columns). The columns represent mean values with one S.E.

plants from pine-covered habitats ( $F_{1,20} = 4.10$ ;  $P < 0.05$ ). In contrast, carotenoids were most concentrated at the beginning of the season and declined more irregularly during summer and early autumn (Fig. 3). The concentrations of carotenoids did not differ significantly between the two habitats ( $F_{1,20} = 0.46$ ;  $P = 0.50$ ).

The ratio chlorophyll *a* to *b* was slightly higher in the open than under pine cover but the difference was not significant ( $F_{1,20} = 1.54$ ;  $P = 0.23$ ). The ratio of chlorophyll to carotenoids was significantly higher under pine cover ( $F_{1,20} = 16.04$ ;  $P < 0.01$ ) and reached its highest values in late summer. Conversely, sphagnorubin was more concentrated in the open ( $F_{1,20} = 13.35$ ;  $P < 0.01$ ), peaking at the end of the growing season (Fig. 3).

The growth rates of *Sphagnum magellanicum* were uncorrelated with the capitulum water content (Table 2), presumably because *Sphagnum* growth is mainly controlled by minimum temperature both at the beginning and at the end of the season. Nonetheless, the hydric status of the plants did affect growth in warmer periods, as clearly shown by a marked reduction in growth during the dry period from mid July to mid August (Fig. 1).

The growth rates of *Sphagnum magellanicum* in the open were independent of the concentrations of photosynthetic pigments but exhibited a highly significant negative correlation with the ratio chlorophyll *a* to *b*. In contrast, growth in weight under pine cover was positively correlated with the concentration of chlorophyll *b*. Furthermore, both growth in length and growth in weight under pine cover were positively correlated with the ratio chlorophyll to carotenoids (Table 2).

The concentration of sphagnorubin did not show any significant correlation with growth in any of the two habitats (Table 2).

	Gr. in length\Gr. in weight	
	Open	Pine-covered
Capitulum water cont.	0.23\0.28	0.27\0.31
Chlorophyll <i>a</i>	0.37\0.39	0.34\0.47
Chlorophyll <i>b</i>	0.50\0.53	0.41\0.58*
Chlorophyll ( <i>a</i> + <i>b</i> )	0.35\0.37	0.32\0.52
Carotenoids	0\0	-0.21\0.16
Chlorophyll <i>a</i> : <i>b</i>	-0.71**\0.76**	-0.21\0.30
Chlorophyll:Carot.	0.31\0.40	0.62\0.64*
Sphagnorubin	-0.14\0.13	0\0.05

**Table 2.** Correlation coefficients between growth rates of *Sphagnum magellanicum* (growth in length and growth in weight) and physiological variables in two habitats. \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

## Discussion

The growth pattern of *Sphagnum magellanicum* resulting from this study was very similar to those outlined for other *Sphagnum* species from different regions in Europe (Backéus 1988; Lindholm 1990; Francez 1992), thus suggesting that the growth dynamics of *Sphagnum* mosses obey much the same general law: peat mosses grow actively in the period

during which night temperature is above zero provided sufficient moisture is available for hydrating the capitula.

The individuals of *Sphagnum magellanicum* growing under differing light regimes, i.e. open vs. pine-covered habitats, exhibited a set of adaptive traits presumably directed to increase resource acquisition (Grime, Rincón and Wickerson 1990). These mainly consist of pigment acclimation. Bryophytes show a general tendency to exhibit significantly greater amounts of total chlorophyll as the irradiance increases (Martin and Churchill 1982; Kershaw and Webber 1986). This was not exactly the case in the present study, only chlorophyll *b* being more concentrated in the plants growing under pine cover. However, such an adaptation is ecologically meaningful since higher concentrations of chlorophyll *b* allow a greater photon capture in shaded habitats, chlorophyll *b* being more directly involved in light harvesting than chlorophyll *a* (Björkman 1981). This is further supported by the positive correlation between chlorophyll *b* concentration and dry weight increment under pine cover (Table 2). Also Martin (1980) found a higher chlorophyll *b* content in shade-adapted bryophytes.

Higher concentrations of chlorophyll *b* in bryophytes growing under a closed canopy need not necessarily imply a proportional increase in the concentration of chlorophyll *b* with respect to chlorophyll *a*. As a consequence, shade plants did not always exhibit lower ratios chlorophyll *a* to *b* than sun plants (Vapaavuori and Nurmi 1982; Martin *et al.* 1985). The ratios chlorophyll *a* to *b* in *Sphagnum magellanicum* were low both under pine cover and in the open, without any significant difference between the two habitats. However, the seasonal pattern of the ratio chlorophyll *a* to *b* differed to a certain extent between habitats, thus pointing to different mechanisms regulating the proportional concentrations of the two chlorophylls in open vs. shaded habitats. The pattern of chlorophyll *a* concentrations followed, although not proportionately, that of chlorophyll *b* in shaded habitats. In contrast, chlorophyll *a* declined more abruptly in open habitats at the end of the season (Fig. 3). Consequently, the ratio chlorophyll *a* to *b* showed a negative correlation with growth in the open habitats but was uncorrelated with growth rates in the open (Table 2). This presumably was an effect of a rapid degradation of chlorophyll *a*, which is lost at a faster speed than chlorophyll *b* especially in exposed habitats (Gerdol, Bonora and Poli 1994).

The high concentrations of carotenoids at the beginning of the growing season were a consequence of their stability. In contrast, both chlorophylls are degraded to a greater extent during the resting period, so that the ratio of chlorophyll to carotenoids did not increase any longer during the remainder of the growing season either in the open or under pine cover (Fig. 3). Carotenoids were relatively enriched in exposed habitats, especially in periods of active growth. This resulted in a highly significant correlation between the ratio of chlorophyll to carotenoids and growth under pine cover. The relative enrichment of carotenoids in open habitats may be due to an accumulation of pigments exerting a photoprotective action in sun plants

(Demming-Adams 1990). Individuals of *Sphagnum magellanicum* from exposed habitats were found to have higher concentrations of pigments of the xanthophyll cycle (viz. antheraxanthin, violaxanthin and zeaxanthin) than individuals from shaded habitats (Schmidt-Stohn 1977).

The significantly higher concentrations of sphagnorubin in open habitats compared to pine-covered habitats, as well as their general increase towards the end of the growing season can be explained considering that the synthesis of sphagnorubin is enhanced by high irradiance coupled with cold-stress (Rudolph 1964; Tutschek 1982). When *Sphagnum magellanicum* was cultivated under controlled conditions, the accumulation of sphagnorubin was accompanied by decreasing concentrations of chlorophyll (Rudolph, Kabsch and Schmidt-Stohn 1977) as well as a dramatic decline in the rates of net photosynthesis (Rudolph 1968). This should obviously result in a negative correlation between sphagnorubin concentration on one side, and growth rate and chlorophyll concentration on the other side. We could, however, not observe any of the expected correlations, as a probable consequence of the different timing of the physiological processes involved. Whereas sphagnorubin synthesis requires several cold-night events to be triggered, the degradation of chlorophyll has a half time of a few days (Lichtenthaler and Grumbach 1974). When growth of *Sphagnum* is measured at relatively short intervals, as was our case, the growth rates need not show a direct relationship with the concentrations of chlorophyll. Gaberscik and Martincic (1987) did not even find any correlation between growth and net photosynthesis in *Sphagnum papillosum*. This indicates that *Sphagnum* mosses are able to compensate for reduced photosynthetic rates in the capitulum by translocating reserves from older senescing tissues (Skre, Oechel and Miller 1981; Rydin and Clymo 1989).

In conclusion, the growth of *Sphagnum magellanicum* in the field undergoes a complex environmental control. However, the mosses exhibit a high acclimation potential resulting in a well-defined set of adaptations. Consequently, populations of *Sphagnum magellanicum* may grow to much the same rate in different habitats.

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