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The elemental and biochemical composition of bryophytes from the maritime Antarctic

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Abstract: The elemental and biochemical composition of eight moss species from the maritime Antarctic were determined fornightly (summer) or monthly (winter) from December 1992 to November 1994. Short-duration summer carbohydrate maxima in *Calliergon sarmentosum* were seen in both years, but no other seasonal patterns were observed. The absence of seasonality in carbon, nitrogen and phosphorus concentrations or their atomic ratios suggest that the mosses were nutrient-sufficient throughout the year, and that nutrient availability was not important in determining moss productivity. Mosses from hydric habitats had lower carbohydrate and higher protein, nitrogen and phosphorus contents than those from drier habitats, possibly as a consequence of higher productivity and continual flushing with nutrients in wet habitats. The results are consistent with the importance of water and the primacy of physical factors in the ecology of Antarctic mosses.

Key words: carbohydrate, moss, nitrogen, phosphorus, protein, seasonality, water availability

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Introduction

Most studies on the limitation of growth of Antarctic plants have concentrated on physical factors (Longton 1988). Recent work on the productivity of Antarctic mosses has demonstrated that growth may be limited by low temperature, low irradiance or low water availability (Davey 1997a, 1997b, Davey & Rothery 1996, 1997). However, it is essential to understand the role of nutrient limitation to complement these studies.

This paper aims to describe the cellular composition of selected Antarctic moss species in response to seasonal and spatial changes in environmental factors and to determine the extent of nutrient limitation of growth.

Materials and methods

Eight moss species were collected on Signy Island, South Orkney Islands, covering a range of maritime Antarctic terrestrial habitats and growth forms (Smith 1984, Davey & Rothery 1997): *Calliergon sarmentosum* (Wahlenb.) Kindb., *Brachythecium austro-salebrosum* (C. Muell.) Kindb., *Drepanocladus uncinatus* (Hedw.) Warnst., *Chorisodontium aciphyllum* (Hook. f. et Wils.) Broth., *Polytrichum alpestre* Hoppe, *P. alpinum* Hedw., *Andreaea depressinervis* Card. and *A. gainii* Card. Five samples of each moss were collected at two-weekly intervals from November to March and at monthly intervals from April to October between December 1992 and November 1994, returned to the laboratory within 15 min of collection and trimmed to a thickness of 5 or 10 mm, the depth of photosynthetic tissue. Samples were stored at -80°C and then freeze-dried, which led to a *c.* 1% overestimate of dry weight compared to oven drying at 105°C, a negligible error relative to the observed inter-replicate variation.

Sub-samples of 1–5 mg dry weight were taken for biochemical analyses. Protein was determined using the Folin-Ciocalteu reagent (Herbert *et al.* 1971) against bovine serum albumin standards following digestion in 0.5 N sodium hydroxide for 30 min at 100°C. Carbohydrate was determined using the phenol method (Dubois *et al.* 1956), as modified by Clarke *et al.* (1992), against glucose standards following digestion in 10% trichloroacetic acid solution for 30 min at 100°C. The remainder of each sample was oven-dried overnight at 105°C and ground. Ash content and ash-free dry weight were calculated from sub-samples of 1–2 g ashed at 550°C overnight. Phosphorus was determined by the molybdate method (Eisenreich *et al.* 1975) on sub-samples of 1–10 mg following digestion using 0.17% sulphuric acid and 0.04 M potassium persulphate for 30 min at 120°C. Carbon and nitrogen were determined using a Fisons Instruments EA1108 CHN elemental analyser against sulphanilamide standards on sub-samples of 2–3 mg. All analyses were corrected for sample ash content and results expressed in terms of ash-free dry weight.

Results

Peaks in carbohydrate content of *C. sarmentosum* were observed in December of both years, but there were no discernible patterns to the results from any of the other analyses or species. The results for each species were amalgamated (Table I) and re-examined for trends based on water availability using Kendall's rank correlation coefficient (T). A positive correlation for protein ($T = +0.64$, $P = 0.001$), a negative correlation for carbohydrate ($T = -0.64$, $P = 0.001$) and a negative correlation for carbohydrate:protein ratio

Table I. Chemical and biochemical analyses based on amalgamated data for each moss species. Mosses are listed in order from the most hydric to the most xeric. Figures given are the min (mean) max results (mg g^{-1} ash-free dry weight) obtained for each analysis over the sampling period.

	Ash	Protein	Carbohydrate	Carbon	Nitrogen	Phosphorus
C. sarmentosum	37 (188) 395	301 (365) 455	168 (228) 369	446 (480) 537	15.7 (24.9) 41.5	0.9 (3.4) 6.5
B. austro-salebrosum	61 (181) 404	240 (332) 409	191 (268) 343	430 (474) 574	6.7 (25.1) 41.6	1.6 (4.3) 6.3
D.uncinatus	27 (172) 313	260 (336) 405	168 (239) 316	450 (479) 522	12.2 (18.5) 25.2	1.0 (2.2) 5.2
C. aciphyllum	13 (30) 49	105 (155) 203	144 (208) 260	444 (463) 484	4.3 (5.7) 8.2	0.3 (0.8) 1.8
P. alpestre	12 (27) 49	163 (277) 379	214 (273) 260	457 (479) 501	7.8 (12.9) 19.8	0.4 (1.2) 1.7
P. alpinum	24 (84) 265	153 (205) 313	234 (314) 440	459 (482) 535	10.2 (14.6) 20.1	1.0 (1.7) 3.1
A. depressinervis	43 (84) 188	78 (118) 158	197 (281) 376	444 (475) 510	7.7 (14.8) 23.5	0.4 (0.9) 2.3
A. gainii	49 (263) 660	132 (183) 261	241 (324) 453	404 (463) 512	7.8 (14.7) 34.5	0.6 (1.5) 3.4

($T = -0.71$, $P = 0.001$) with increasingly hydric habitat were observed. There were no significant trends in any of the elemental contents or their atomic ratios.

To identify further trends, the results were further amalgamated into three groups: hydric, mesic and xeric; these were compared using simple *t*-tests to reveal any differences in the group means (Table II). The ash content of the mesic species were lower than the hydric or xeric species, probably as a result of the peat-forming habit of two of the mesic species which reduced the incorporation of the underlying substratum (xeric species) or deposition from overlying water flow (hydric species). Carbon content was similar throughout, but nitrogen and phosphorus were higher in hydric than xeric or mesic species, and equivalent differences were observed in their atomic ratios.

Discussion

The only observed seasonal pattern was the short-duration December maxima of carbohydrate in the hydric moss *Calliergon sarmentosum*, for which there was no obvious single cause. Continental Antarctic mosses also show little seasonal change in biochemical composition (Melick & Seppelt 1994), although some related Arctic species have exhibited seasonality (Sveinbjörnsson & Oechel 1991). However, there may be variation in the biochemical composition of the mosses masked by the constant total concentrations; Tearle (1987) reported that the polyol concentrations of Antarctic mosses varied seasonally by an order of magnitude despite there being no detectable variation in the total carbohydrate content.

Table II. Results of *t*-tests on elemental composition results. Where differences are indicated $P < 0.001$.

Ash	Hydric	=	Xeric	>	Mesic
Carbon	Hydric	=	Mesic	=	Xeric
Nitrogen	Hydric	>	Xeric	>	Mesic
Phosphorus	Hydric	>	Mesic	=	Xeric
C:N	Hydric	<	Xeric	<	Mesic
C:P	Hydric	<	Mesic	=	Xeric
N:P	Hydric	<	Mesic	<	Xeric

There were no seasonal patterns in the carbon, nitrogen or phosphorus contents or their atomic ratios in any of the species studied, and no correlations with the seasonal changes in water contents, temperatures and incident irradiance previously reported (Davey 1997a, 1997b, Davey & Rothery 1996, 1997). As their nutrient status was constant, the mosses must have been either nutrient sufficient or consistently nutrient deficient throughout the study. Given existing data on nutrient availability the latter seems highly unlikely, but could be tested in future by controlled fertilisation experiments. It seems more likely that the growth of these mosses was not nitrogen or phosphorus limited at any time. No previous data on the seasonality of the elemental composition of Antarctic mosses have been reported, nor do there appear to be such data for temperate species. The present study corroborates the view that nutrient limitation is unusual in slow-growing plants in physically harsh environments.

There were clear spatial differences in the biochemical and elemental composition of the mosses correlated with the availability of water. Hydric mosses showed higher protein, nitrogen and (especially) phosphorus and lower carbohydrate contents than mesic or xeric mosses. This is consistent with earlier studies on Antarctic (Christie 1987) and subantarctic (Smith 1984) mosses. Such results are to be expected from plants growing in habitats flushed with nutrients and where higher rates of photosynthesis occur (Davey & Rothery 1996, 1997). It is clear that the availability of water within a habitat is an important factor in determining the cellular composition of Antarctic mosses.

The mosses investigated were apparently not nutrient limited and interspecific differences in cellular composition were correlated with water availability. These conclusions support the importance of water (Kennedy 1993) and the primacy of physical rather than chemical factors (Longton 1988) in the ecology of these ecosystems. However, the paucity of this type of data makes it impossible to extrapolate to mosses from other regions.

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