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Bryophyte-cyanobacteria associations on sub-Antarctic Marion Island: are they important in nitrogen fixation?

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Five Marion Island bryophyte species containing epiphytic cyanobacteria showed acetylene reduction in the laboratory at ca. *20 °C. Only* Ditrichum strictum *exhibited reduction* in situ *at low (around zero) temperatures. This species occurs as a spherical cushion or ball on cold, windswept, rocky plateaux and contains a band of cyanobacteria a few millimetres below the surface of the cushion. The absence of acetylene reduction* in situ *for mire bryophyte species containing epiphytic cyanobacteria is ascribed to low temperatures during the incubation and it is thought that during the warm summer months fixation by bryophyte-cyanobacteria associations may significantly contribute towards the nitrogen status of mire habitats.*

Vyf van Marioneiland se briofietspesies met epifitiese siaanbakterieë het in die laboratorium by ongeveer 20 °C asetileenreduksie getoon. Slegs Ditrichum strictum *het* in situ *reduksie by lae temperatuur (ongeveer nul grade) getoon. Hierdie spesie kom as sferiese kussings of balle op die koue, winderige, rotsagtige plato's voor en die siaanbakterieë kom as 'n band enkele millimeters onderkant die kussing se oppervlak voor. Die feit dat asetileenreduksie nie* in situ *by moerasbriofiete aangetoon kon word nie, word aan die lae temperatuur toegeskryf wat tydens die eksperimente geheers het. Daar word egter vermoed dat stikstoffiksering in die warm somermaande 'n belangrike bron van stikstofverbindings vir die moerasagtige gebiede moet uitmaak.*

Introduction

Moss-cyanobacteria associations have been found to be significant agents of nitrogen fixation in sub-Arctic bogs, Fennoscandia tundra and Arctic tundra (Granhall & Selander 1973, Granhall & Basilier 1973, Granhall & Lid-Torsvik 1975, Alexander, Billington & Schell 1978). This has also been noted for alpine tundra and humid, cool-temperate oceanic island ecosystems (Porter & Grable 1969, Alexander *et al.* 1978, Englund 1976, 1978).

Bryophytes are an important component of the vegetation of sub-Antarctic islands (Taylor 1955, Greene 1964, Hébrard 1970, Huntley 1971) and are often closely associated with cyanobacteria which occur epiphytically on (occasionally endophytically in) the leaves. To date, however, no assessment of the possible role of these associations in nitrogen fixation has been made for a sub-Antarctic site. Croome (1973) found

significant acetylene reduction by free-living cyanobacteria occurring in mixed algal populations in a jelly-like mat on the surface of some mire peats on Marion Island (54°45'S, 37°45'E). Lindeboom (1979) also noted acetylene reduction by soil cyanobacteria in two of the three mires he investigated on this island, but estimated that yearly fixation of nitrogen by these free-living organisms is insignificant as a source of reduced nitrogen to the island ecosystem, and speculated that fixation by moss-cyanobacteria associations is not much more important than free living fixation.

On Signy Island (maritime Antarctic), Heywood (1968) found high concentrations of nitrate-N in the inflow of streams of two lakes. These streams flow through moss stands and *Nostoc commune*-rich flushes. Horne (1972) demonstrated significant nitrogen fixation by cyanobacteria in these areas and postulated that the fixed nitrogen gives rise to ammonium-nitrogen in the soil and once this is nitrified, the nitrate moves quickly into the streams. However, both Horne (1972) and Fogg and Stewart (1968) present data which indicate that fixation at moss-dominated sites on Signy Island is very low and often absent.

This paper presents the results of laboratory and field demonstrations of nitrogen fixation by bryophyte-cyanobacteria associations on Marion Island using the acetylene-reduction technique.

Materials and methods

In September 1978 replicated samples of the bryophyte mat were collected from five sites on the island and placed in 250 cm³ incubation vessels fitted with silicone rubber stoppers. To four of the replicates from each site H_2SO_4-scrubbed acetylene was added to a concentration of 0,1 atmosphere. The incubations were carried out on a laboratory bench adjacent to a north-facing window. A fifth replicate from each site was incubated without acetylene to assess endogenous ethylene production. After 24 hours, 5 cm³ of incubation atmosphere was withdrawn through the rubber stopper using a double-ended needle and a re-evacuated 5 cm³ "venoject" tube. The five sites were occupied by well-developed "mire vegetation" *sensu* Gremmen (1981), but differed in their exposure to wind. The bryophyte material was not identified but all contained epiphytic cyanobacteria.

In September 1979 the nitrogen fixation capability of one moss and two liverwort species in association with cyanobacteria was investigated *in situ* using the acetylene reduction assay. The moss *Ditrichum strictum* (Hook F. & Wils.) Hamp. occurs as spherical balls up to 12 cm in diameter on wind-swept rocky ridges and plateaux occupied by *fjaeldmark* vegetation (Huntley 1971). A band of algae and cyanobacteria often occurs a few mm below the surface of the mossball. The liverwort *Jamesoniella grandiflora* (Lindenb. & Gottsche) Steph. is found on relatively well-drained peat (water content 300-1 500%) with the water table generally several centimetres below the peat surface. *Clasmatocolea humilis* (H.F. & T) Steph. is found on wetter peats (water content > 1 500 %) with the water table close to the surface. Both liverwort species exhibited epiphytic cyanobacteria.

Replicated samples of detached bryophyte mat or segment of the moss ball were placed in 250 cm³ wide-mouthed glass incubation vessels which were inserted into the bryophyte turf so that the level of vegetation in the vessel was the same as the surrounding vegetation. The vessels were left in position for 24 hours before fitting with silicone rubber stoppers and adding scrubbed acetylene to a concentration of 0,1 atmospheres. Incubations were carried out for 48 hours before sampling the incubation atmosphere using "venoject" tubes. A further sample of each bryophyte species was incubated without acetylene to assess endogenous ethylene production.

A 1 cm³ gas subsample from each evacuated tube was introduced into a Varian Aerograph gas chromatograph equipped with a 2 m × 2 mm Propak R column maintained at 60 °C. Ethylene contents in the gas samples were obtained by computing the area under the ethylene peak using a Hewlett-Packard 3352 B Data System linked to the chart recorder producing the chromatogram. The ethylene contents were corrected for background concentrations of ethylene in the acetylene and for endogenous ethylene production by the plants.

Table 1

Acetylene reduction by Bryophyte/cyanobacteria samples in the laboratory.

Collection site	Acetylene reduced* (μl/sample/hr)
Sheltered mire near meteorological station	4,1 — 9,1
Exposed mire near meteorological station	0,1 — 3,7
Sheltered slope at Albatross Lakes; very luxuriant bryophyte growth	17,2 — 27,4
Bog vegetation, edge of Albatross Lake, moderately exposed	11,4 — 31,8
Bog vegetation at northern edge of Albatross Lake, very exposed	14,1 — 26,3

* Range of 4 replicates, corrected for endogenous ethylene production and background ethylene concentration in the purified acetylene.

Table 2

Acetylene reduction by Bryophyte/cyanobacteria samples *in situ*.

Bryophyte Species		Sample dry weight (g)	C_2H_4 reduced* (μg/g/48 hrs)
Ditrichum strictum	(1)	1,92	1,17
	(2)	2,06	1,21
Clasmatocolea humilis	(1)	1,65	0
	(2)	0,87	0
Jamesoniella grandiflora	(1)	1,84	0
	(2)	0,96	0

* Values of two replicates corrected for endogenous ethylene production and background concentration of ethylene in purified acetylene.

Results and discussion

All the replicates of the bryophyte/cyanobacteria material exhibited marked acetylene reduction at laboratory temperatures (±20 °C; Table 1). The dry weights of incubated material were not measured, so meaningful intersite comparison of fixation rates is not possible.

Only *Ditrichum strictum* demonstrated acetylene reduction *in situ* (Table 2). Mean ambient temperature 25 mm above the moss surface during these incubations was −1,7 °C. *D. strictum* occupies a far colder habitat than the sheltered, low altitude mires in which the two hepatic species are found and possibly fixation by the epiphytic cyanobacteria on these species was suppressed by the low temperature during the incubation. Fogg and Stewart (1978) regarded temperature to be the most important factor governing cyanobacteria

nitrogen fixation rates in the maritime Antarctic and found that most fixation occurred during periods when the temperature of the microhabitat reached 10 °C or more. Huntley (1971) showed that temperatures in moss and algal mats on Marion Island are in excess of 10 °C for most of the day in summer and often reach up to 20 °C in the mid-afternoon. During summer months, therefore, nitrogen fixation by bryophyte-cyanobacteria associations may be a significant source of nitrogen for the island mire communities. The marked acetylene reduction exhibited by these associations in the laboratory supports this conjecture.

Nitrogen supply is suspected to limit primary production in the Marion Island mires (Smith 1976) and in this aspect N input through fixation may be highly significant. At many northern hemisphere tundra sites damp, moss-dominated environments are associated with populations of cyanobacteria which are very active in N fixation and experiments at some of these sites indicate that the newly-fixed N is transferred fairly rapidly to the mosses and to vascular plants (Sonesson 1973, Granhall & Lid-Torsvik 1975, Alexander *et al.* 1978).

At *fjaeldmark* habitats nitrogen fixation by cyanobacteria must significantly contribute towards the nitrogen status of *Ditrichum strictum*, since balls of this species are seldom intimately connected to the rawmark soil and rely more on reduced nitrogen in precipitation received directly by the moss surface than on nutrient uptake from the substrate.

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