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# Factors causing the limitation of growth of terrestrial algae in maritime Antarctica during late summer

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**Summary.** The factors causing the cessation of growth and decline of microalgal communities on Antarctic fellfield soils during late summer were investigated. Physical and chemical amendments were applied within small enclosures and the size and taxonomic composition of the communities assessed. Most treatments had no effect on the microalgal communities or individual taxa. The addition of calcium nitrate to the soil either singly or as part of a complete growth medium promoted growth of all taxa studied on most sites. As the cation was naturally present in excess in the soil it is concluded that growth of the microalgal communities during late summer was nitrogen-limited.

## Introduction

Cryptogamic fellfields are the most widespread and common terrestrial ecosystems of the ice-free areas of the maritime Antarctic (Aleksandrova 1980). They are characterized by a flora consisting largely of mosses and lichens interspersed with areas of seemingly bare soil (Gimmingham and Smith 1970).

Substrata are exposed by the recession of ice-fields (Smith 1990) and soils are formed by frost-shattering of rocks followed by frost-sorting of particles into polygons of soil fines surrounded by larger stones and rocks (Chambers 1966, 1967; Holdgate et al. 1967). It is these soil fines that provide suitable substrata for primary colonization by bacteria, cyanobacteria and algae (Wynn-Williams 1990). The cyanobacteria and algae (hereafter referred to jointly as microalgae) are of particular importance, often being filamentous in nature and may act to bind together soil particles, stabilize the soil and promote secondary colonization (Wynn-Williams 1990).

The development of the fellfield community during the early stages of colonization is dependent upon the rate of growth of the microalgal populations. The potential growth season is limited by low temperatures (Davey et al., 1992). Comparisons of microalgal growth rates in culture (Davey 1991a) with measurements of temperatures in fellfield soils (Davey 1991b) have suggested that the period conducive to growth is restricted to a short time during spring and summer (November to March). However, studies on the periodicity of microalgal populations have shown that the actual growth season is much shorter than that predicted from such comparisons. Growth of soil microalgae during early summer produces a population maximum at the beginning of February which is followed by a decline in all taxa until the soil freezes in April (Davey 1991b). This reduction in the growth season by about 40% may slow community development by a similar amount, and identification of the limiting factor is important in understanding the dynamics of these ecosystems.

The most likely causes of the decline in microalgal populations in late summer are either desiccation or nutrient limitation. The British Antarctic Survey Fellfield Ecology Research Programme (FERP) has hypothesized that growth in these ecosystems is limited by water availability rather that the direct effects of temperature (British Antarctic Survey 1981). Desiccation of the soil may occur during the latter half of the summer (Northover and Grimshaw 1967) and cause a reduction in photosynthesis (Davey 1989) and a decrease in viability (Davey 1991a) of the microalgae. The placing of clear plastic cloches over the soil has led to an increase in microalgal populations (Wynn-Williams 1990), although this increase may have been caused by either increased humidity or increased temperature in the cloches. Alternatively, the microalgae may be limited by the availability of nutrients. Fellfield soils generally have low concentrations of all plant nutrients (Allen and Northover 1967; Allen et al. 1967). A survey of soil polygons (M.C. Davey and P. Rothery, unpublished data) has suggested that nitrogen concentrations and N:P ratios in the soils are low, but has not confirmed that growth is nitrogen-limited.

This paper describes the results of a series of amendments to soil polygons during the period from before the summer population maximum to near the end of the

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microalgal decline. Results reflect the interpolygon variability that occurs in these ecosystems, but suggest that water is not an important factor and that growth is probably nitrogen-limited.

## Materials and methods

All experiments were carried out at the FERP site at Jane Col, Signy Island, South Orkney Islands (British Antarctic Survey 1982). This site consists of an immature fellfield, ca. 150 m altitude, that has been exposed by a receding ice-field during the last 30 years. Soil fines occur as more than 100 soil polygons up to 2.5 m maximum linear dimension colonized by entirely microbial communities surrounded by stones which support small clumps of mosses (mainly *Ceratodon purpureus* (Hedw.) Brid.).

Changes in the size of the microalgal community were monitored during summer 1990 from the time when the polygons became free of snow and ice to the end of the experiments using the concentration of chlorophyll in the soil as an indicator of microalgal biomass. Four 14 mm diameter cores were collected from near the centre of each of two soil polygons using cut-off syringes as corers. Microscopic examination confirmed that the cores did not contain moss particles or propagules. The cores were returned to the laboratory within 1 h and frozen overnight to maximise extraction efficiency (Hansson 1988). Pigment was extracted from the upper 5 mm of the core, being the zone containing most of the microalgal community (Davey and Clarke 1991), using hot 90% methanol and absorbance measured at 665 and 750 nm before and after acidification to $10^{-3}$ M HCl. Total chlorophyll *a* concentration and the undegraded and degraded fractions were then calculated using the equations of Talling et al. (1978) and Marker et al. (1980).

### *Description of sites*

Five soil polygons were chosen for soil amendment experiments. The polygons were spread over the study site and included the polygon containing a large *Nostoc* sp. population described by Davey and Clarke (1991). The polygons were visually similar, a photograph of a typical fellfield polygon is given by Wynn-Williams (1990).

The prevailing physical and chemical conditions on the polygons were determined on 13 February and 25 February 1990. On each date 12 cores of 16 mm diameter were collected to a depth of 5 mm. Three cores were placed in preweighed crucibles, weighed, dried overnight at 105°C, reweighed, ashed overnight at 550°C and reweighed to determine soil water content and loss on ignition. The ashed soil from all replicates was bulked and used for soil particle size analysis by sieving and sedimentation methods (Holme and McIntyre 1971). Eight cores were left to extract overnight into 50 ml distilled water per core, centrifuged and the supernatant used for chemical analyses: two each for soluble reactive phosphorus (SRP), soluble reactive silica (SRSi), ammonium nitrogen ($NH_4$–N) and nitrate nitrogen ($NO_3$–N) using the methods of Mackereth et al. (1978). One core was used for the determination of soil pH following the addition of sufficient distilled water to just 'puddle' the soil. The maximum and minimum linear dimensions, the percentage of stones immediately around the polygon covered by moss and the date that the polygons were first clear of snow and ice were also noted.

At the start of the experiments six 16 mm diameter cores were collected from each polygon for initial ($t_0$) description of the microalgal flora. Three were used for the determination of soil chlorophyll as described above and three for direct counts of the microalgal community. Cores for direct counts were placed in a Petri dish, wetted with distilled water if necessary, a coverslip placed on the soil surface and incubated overnight at an irradiance of 40 $\mu$mol $m^{-2} s^{-1}$ at 5°C. The coverslip was then removed along with the attached algae (Broady 1979). The unicellular algae were counted directly and the populations of filamentous taxa estimated by measurement of total lengths of filaments using the grid intercept method (Olson 1950). The top of the core was also examined by epifluorescence microscopy, and counts of any algae remaining on the core added to those from the coverslip. Previous studies have indicated that this combination of methods allows almost all the soil microalgae to be counted (Davey 1991b; Davey and Clarke 1991).

### *In situ Amendment experiments*

Sixty-six extruded polypropylene tubes 30 mm long and 16 mm internal diameter were placed into each polygon to a depth of 20 mm. Six of these enclosures selected at random in each polygon were used for each of eleven amendments. Replication was limited by the availability of suitable sites within each polygon. Chemical amendments consisted of 2 ml of the appropriate solution and were applied on alternate days using an automatic pipette, all other amendments were continuous. Amendments were as follows (i) control, (ii) distilled water, (iii) growth medium (Table 1), (iv) $Ca(NO_3)_2 \cdot 4H_2O$, (v) $KH_2PO_4$, (vi) $Na_2SiO_3$, (vii) $NaHCO_3$, (viii) glucose, (ix) proline, (x) transparent lid placed on enclosure and 1 mm diameter air holes drilled in the side to form a minicloche, (xi) enclosure covered with black netting to reduce irradiance by 50%. The volume of water added with the amendments (5 mm · $day^{-1}$) was much greater than that from precipitation on Signy Island in February (average 1 mm · $day^{-1}$; Davis 1986). The amount of growth medium applied was known to be sufficient to support a much higher biomass of microalgae in culture for four weeks. Inorganic amendments were applied at the same concentrations as in the growth medium; organic amendments were applied at the same concentrations of carbon as in the growth medium, i.e. 5.7 mg · $l^{-1}$ glucose or 4.4 mg · $l^{-1}$ proline.

Amendments were started on 28 January and continued until 1 March 1990, a total of 32 days. At the end of the experimental period the enclosures and their cores were collected and used for analysis of the microalgal community by chlorophyll analysis and direct counts as described for the $t_0$ samples above.

### *Environmental monitoring*

Throughout the experiments environmental factors were monitored using a Grant Squirrel data logger (Smith 1988; Davey et al. 1992). Microthermistors (3 mm diameter, resolution ±0.3°C) at the soil surface and Vaisala relative humidity probes (sensor 5 × 5 mm, resolution ±0.5%) 5 mm above the soil surface were placed both within the minicloches and outside the enclosures. Data were recorded at intervals of 10 min.

**Table 1.** Composition of the growth medium used in amendment experiments

| Constituent | Concentration (mg · $l^{-1}$) |
|---|---|
| $Ca(NO_3)_2 \cdot 4H_2O$ | 20 |
| $KH_2PO_4$ | 6.2 |
| $MgSO_4 \cdot 7H_2O$ | 25 |
| $NaHCO_3$ | 15.9 |
| $Na_2SiO_3$ | 25 |
| EDTA · Fe · Na | 2.27 |
| $H_3BO_3$ | 2.48 |
| $MnCl \cdot 4H_2O$ | 1.39 |
| $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$ | 1.00 |
| Cyanocobalamin | 0.002 |
| Thiamine | 0.002 |
| Biotin | 0.002 |
| pH adjusted to 6.0 by addition of 1M HCl | |

Measurements of incident ultraviolet light using a Macam UV103 radiometer indicated that the minicloches reduced the amount of UV light reaching the soil surface by 25–30%. The reduction in photosynthetically active radiation (PAR, 400–700 nm) by the minicloches as measured with a Skye Instruments quantum sensor was <10%.

## Results

Changes in the soil chlorophyll concentration during the ice free period of summer 1990 are shown in Fig. 1. Results from the two polygons studied were not significantly different and have been amalgamated. The pattern was very similar to that previously reported from these sites (Davey 1991b); an initial decline in biomass following the disappearance of ice from the site was followed by an increase to a community maximum in early February and subsequent decline for the remainder of the summer. The period covered by the amendment experiments is also shown in Fig. 1. These results demonstrate that the experiments were carried out during the period relevant to consideration of the factors affecting the limitation of microalgal growth and decline of the community.

The results of physical and chemical measurements of the experimental polygons are given in Table 2. These

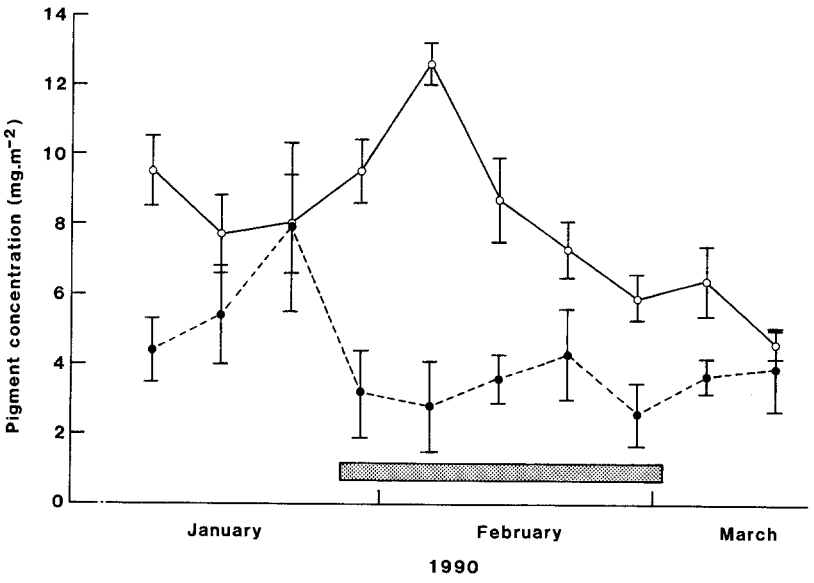


**Fig. 1.** Changes in plant pigment concentrations within soil polygons during summer 1990. ○ = undegraded chlorophyll, ● = degraded chlorophyll, ▨ = period of amendment experiments. *Error bars* indicate standard errors ($n = 8$)

**Table 2.** Physical and chemical characteristics of soil polygons used in amendment experiments. Measurements of variable factors were made on 2 separate occasions, means for each date are given ($n = 2$ for chemical factors, $n = 3$ for physical factors). Conservative factors were measured once ($n = 1$).

| Factor | Date | Polygon no. | | | | |
|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 |
| Water content | 3/II | 0.91 | 0.211 | 0.165 | 0.190 | 0.168 |
| ($g \cdot g^{-1}$ dry wt) | 25/II | 0.192 | 0.181 | 0.164 | 0.198 | 0.169 |
| Loss on ignition | 3/II | 0.93 | 1.46 | 0.89 | 0.82 | 1.29 |
| (%) | 25/II | 1.05 | 1.64 | 0.99 | 1.25 | 2.05 |
| [SRP] | 3/II | 2.8 | 4.5 | 6.3 | 3.8 | 17.1 |
| ($mg \cdot m^{-2}$) | 25/II | 10.5 | 12.6 | 12.7 | 18.4 | 66.8 |
| [SRSi] | 3/II | 30.3 | 23.0 | 15.8 | 17.6 | 61.7 |
| ($mg^{-2}$) | 25/II | 21.4 | 35.6 | 13.1 | 11.0 | 82.4 |
| [$NH_4$–N] | 3/II | 2.4 | 2.2 | 2.5 | 3.6 | 2.6 |
| ($mg \cdot m^{-2}$) | 25/II | 2.3 | 2.1 | 2.9 | 6.8 | 2.7 |
| [$NO_3$–N] | 3/II | 0.00 | 0.18 | 0.54 | 1.53 | 2.61 |
| ($mg \cdot m^{-2}$) | 25/II | 0.18 | 0.92 | 0.36 | 1.40 | 2.61 |
| pH | 3/II | 6.1 | 6.1 | 6.1 | 6.1 | 5.9 |
| | 25/II | 6.1 | 6.0 | 6.2 | 6.1 | 6.0 |
| Median particle size ($\mu$m) | | 84 | 89 | 121 | 85 | 173 |
| Modal particle size ($\mu$m) | | 54 | 69 | 65 | 86 | 96 |
| % clay | | 1.2 | 1.2 | 0.3 | 1.0 | 2.4 |
| % silt | | 41.7 | 41.1 | 36.2 | 39.9 | 29.6 |
| % sand | | 43.8 | 47.2 | 44.9 | 46.1 | 54.3 |
| % other | | 13.3 | 10.5 | 18.6 | 13.0 | 13.7 |
| Maximum linear dim. (m) | | 0.6 | 0.8 | 0.7 | 1.0 | 1.3 |
| Minimum linear dim. (m) | | 0.5 | 0.4 | 0.5 | 0.5 | 0.4 |
| % moss surround | | 30 | 70 | 20 | 40 | 0 |
| Date clear of snow/ice | | 21/XII | 21/XII | 4/I | 2/I | 18/I |

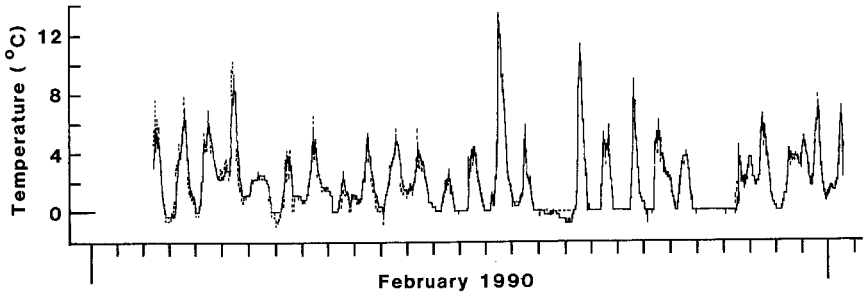


**Fig. 2.** Soil surface temperatures oustide (———) and inside (– – –) minicloches during amendment experiments

results are similar to those from a wider survey of soil polygons on the site (M.C. Davey and P. Rothery, unpublished data) indicating that the polygons chosen were representative. Interpolygon variation in most factors was small, although there were differences in the concentrations of $NO_3$–N and SRP in the soil, the amount of moss around the polygons and the data at which the polygons were clear of snow and ice. The latter two factors were obvious at the time of polygon selection and the range deliberately maximised. Interdate variation in non-conservative factors was also small, although concentrations of SRP in all polygons and $NO_3$–N in some polygons increased as the microalgal communities declined.

*Environmental data*

Soil surface temperature (Fig. 2) varied in a similar manner to previous observations in these ecosystems that included the period of microalgal growth (Davey 1991b; Davey et al. 1992). Temperatures fell to around 0°C at night, although there were few sub-zero temperatures, and rose during the day to 2°–14°C with much interday variation. There was little variation between temperatures within and without the experimental enclosures. This is in contrast to larger cloches where a marked temperature increase (average 3.2°C) has been observed (Wynn-Williams 1990), and is probably an indication that the minicloches were too small to overcome the cooling effects of the surrounding soil.

Data on above soil humidities were continually interrupted during the experiments due to equipment failure and only a representative portion is given (Fig. 3). This demonstrates that the within cloche humidities were consistently higher than those outside. However, neither probe recorded very harsh drying conditions and humidities did not fall to values likely to cause increased mortality in the microalgae during the periods when the probes were operational (Davey 1991a).

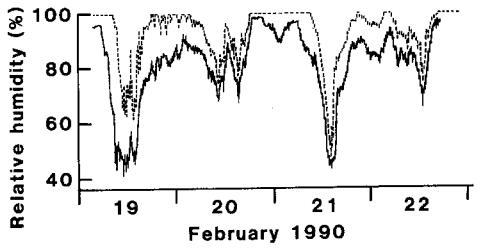


**Fig. 3.** Above soil relative humidities outside (——) and inside (– – –) minicloches on selected dates during amendment experiments

*Microalgal data*

As in previous studies (Davey 1991b; Davey and Clarke 1991) the polygons were dominated by a very small number of taxa (Table 3). The most notable difference between polygons was the large populations of the cyanobacteria *Nostoc* spp. found on polygon 1, but absent from all other polygons. The other taxa found in sufficient quantities to take part in the statistical analyses were the cyanobacteria *Phormidium autumnale* (Agardh) Gomont, *Pseudanabaena catenata* Lauterborn and *Oscillatoria* sp.

**Table 3.** Undegraded chlorophyll concentrations, total biovolumes and counts for major algal taxa for initial ($t_0$) samples from the soil polygons used in the amendment experiments. Results are given as means of three replicates (range of results). Biovolumes and counts are given as per 16 mm i.d. core. Key: [Chl] = chlorophyll concentration ($mg \cdot m^{-2}$), Biovo = biovolume ($10^6 \cdot \mu m^3$), *Phorm* = *Phormidium* (mm), *Pseud* = *Pseudanabaena* (mm), *Oscil* = *Oscillatoria* (mm), *Nost*A = *Nostoc* sp. A (mm), *Nost*B = *Nostoc* sp. B (mm), *Pinn* = *Pinnularia* (cells)

| Polygon no. | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| [Chl] | 13.4 (9.4–17.3) | 4.7(3.9–5.5) | 6.8(3.9–9.4) | 10.7(10.2–11.8) | 4.7(3.1–6.3) |
| Biovo | 7.6(5.1–9.9) | 4.3(1.7–7.7) | 2.6(0.5–6.6) | 7.3(6.1–9.2) | 1.4(0.2–3.1) |
| *Phorm* | 4.0(3.1–4.6) | 13.1(10.6–16.4) | 63.0(8.5–11.7) | 174(135–229) | 34.7(4.0–75.7) |
| *Pseud* | 59.2(18.7–103) | 278(129–450) | 17.1(6.8–29.9) | 79.5(48.3–126) | 8.3(3.7–11.4) |
| *Oscil* | 4.4(1.2–10.1) | 1.6(0.0–4.9) | 5.8(4.2–6.7) | 0.0 | 11.1(5.0–23.0) |
| *Nost*A | 564(336–748) | 0.0 | 0.0 | 0.0 | 0.0 |
| *Nost*B | 2.1(1.1–2.9) | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pinnu* | 0.7(0–2) | 466(18–1355) | 2.0(1–3) | 3.0(0–6) | 3.7(3–5) |

and the diatom *Pinnularia borealis* var. *rectangularis* Carlson.

To allow for the interpolygon variability in the microalgal communities results from each polygon were initially analysed separately. In addition to the counts of each individual taxon, all taxa were converted to biovolumes and summed to produce a estimate of the total biovolume in each enclosure. To overcome the problems associated with the large differences in counts between taxa and between polygons, results were converted to the ratio of the treatment count to the control count. As the standard deviation of the measurements increased in proportion to the mean, statistical analyses were carried out on log transformed data ($y = \log(x+1)$).

Means and standard errors of replicates ($n=3$) were calculated and each treatment compared to the control samples using a pooled estimate of the random variability based on a one-way analysis of variance and a t-test. As a large number of analyses (11 per variable per polygon) were carried out the chances of the data producing spurious significant differences were high. To overcome this problem Tukey's honestly significant difference method (Sokal and Rohlf 1981) was used to indicate significant differences between treatments.

Despite producing a large number of results, the individual polygon approach suffered from the low replication within polygons. Hence, in many cases, even where differences between treatment and control were consistent both within and between polygons, these were not always statistically significant. Therefore, the results from all polygons were combined to determine the overall significant factors in limiting microalgal growth. Ratios of each treatment value to the control value were calculated for each polygon and the mean ratios for the five polygons determined to compare each treatment with the control (Table 4). In most cases the treatment results were not significantly different from the controls. In particular, it should be noted that the addition of water to the soils did not promote growth or even arrest the decline in the microalgal communities. However, the addition of nitrate did have a significant beneficial effect on the microalgae whether added on its own or as part of a total growth medium. Even in the cases where the difference from the control was not statistically significant (eg. *Pseudanabaena*) an increase was observed. The results for the addition of nitrate alone were consistently more significant than those for the medium, but direct comparison of the two suggested that this difference was not itself significant.

The apparently significant results for *Pinnularia* should be treated with extreme caution. Counts for this taxon were low (Table 3) increasing the probability of spurious results. Further, the medium and nitrate amendments tended to cause opposite effects (Fig. 4) suggesting that the results were not consistent.

Results for all polygons showing the effects of medium and nitrate amendments are given in Fig. 4. These illustrate the significant results from Table 4, and also demonstrate the range of results between polygons. The overall measures of biomass (chlorophyll and biovolume) show the most consistent effects and the taxa with low counts the most variability.

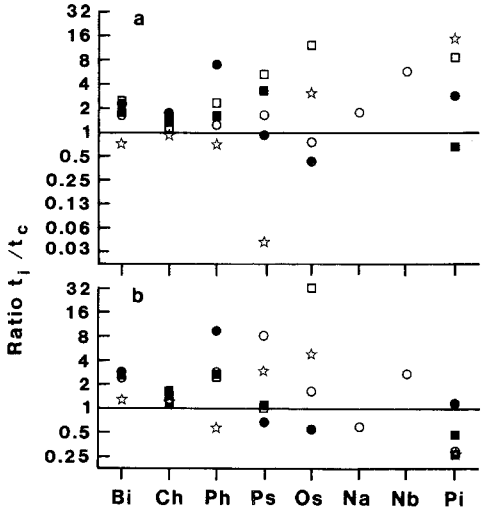


**Fig. 4.** Ratios of sizes of microalgal communities and populations in the enclosures treated with (**a**) and medium or (**b**) calcium nitrate ($t_i$) to those in the control enclosures ($t_c$) at the end of the amendment experiments. *Bi* = total microalgal biovolume, *Ch* = undegraded chlorophyll, *Ph* = *Phormidium*, *Ps* = *Pseudanabaena*, *Os* = *Oscillatoria*, *Na* = *Nostoc* sp. A, *Nb* = Nostoc, sp. B, *Pi* = *Pinnularia* ○ = polygon 1, ● = polygon 2, □ = polygon 3, ■ = polygon 4, ☆ = polygon 5

**Table 4.** Mean ratios of treatment:control enclosures from five soil polygons ($n=5$) for total biovolume, chlorophyll concentration and four taxa of microalgae (*Nostoc* spp. are not included as they occurred only on one polygon)

| Treatment | Biovolume | [Chl] | *Phorm* | *Pseud* | *Oscil* | *Pinn* |
|---|---|---|---|---|---|---|
| t=0 | 1.56 | 1.35 | 0.86 | 1.42 | 0.39** | 16.22 |
| Control | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Water | 1.22 | 1.07 | 1.44 | 1.08 | 2.49 | 0.79* |
| Medium | 1.80* | 1.35* | 2.53 | 2.22 | 3.43 | 5.47 |
| $Ca(NO_3)_2 \cdot 4H_2O$ | 2.27** | 1.36** | 3.55* | 2.65 | 8.15 | 0.43* |
| $KH_2PO_4$ | 1.00 | 1.36 | 1.14 | 1.21 | 1.06 | 0.50* |
| $Na_2SiO_3$ | 1.12 | 1.21 | 1.25 | 1.14 | 2.34 | 0.79 |
| $NaHCO_3$ | 0.84 | 1.03 | 0.86 | 1.99 | 2.37 | 0.18** |
| Glucose | 0.93 | 1.02 | 1.30 | 1.59 | 1.94 | 0.55 |
| Proline | 1.36 | 1.26 | 1.46 | 1.88 | 1.16 | 0.44* |
| Minicloche | 1.22 | 1.00 | 0.96 | 1.31 | 1.82 | 1.26 |
| Netting | 1.08 | 0.95 | 1.56 | 2.55 | 1.02 | 3.47* |

## Discussion

Despite the large interpolygon variation in the communities of soil microalgae this study has identified those factors responsible for the limitation of growth of the microalgae during late summer. Although the identification of the limiting factor is important, consideration of some of those factors that did not arrest the decline of the microalgae is also informative.

It is clear that the addition of calcium nitrate, either singly or as part of a medium, greatly reduced the decline in microalgal populations and usually promoted growth above the $t_0$ samples. Therefore, it is tempting to conclude that growth in these ecosystems is nitrogen-limited during late summer. Such a conclusion is supported by the low concentrations of $NO_3$–N and $NH_4$–N and hence low N:P ratios in the soil. One polygon supported a large population of the nitrogen-fixing cyanobacterium *Nostoc*, a taxon that is often associated with nitrogen-limited systems, and this population did not decline during the experimental period or respond to the $NO_3$–N supplement, observations that are consistent with nitrogen limitation. Such a conclusion may be significant in wider considerations of immature fellfield ecosystems where microalgae constitute the largest component of the flora.

Although the concentrations of soil nitrogen did not decrease during the experiment, this does not preclude nitrogen-limitation of growth. $NO_3$–N concentrations were much lower than those during the December to January growth period (*c.* 11 $mg \cdot m^{-2}$ $NO_3$–N; R.J. Arnold, unpublished data) suggesting that microalgal growth had utilized a significant proportion of the soil nitrogen. Further, both sets of analyses reported here were conducted at or after the community maximum when the soil nitrogen may have already fallen to limiting concentrations.

The effects of calcium and nitrate additions were not tested separately, and the possibility that the cation was having a significant effect must be considered. Previous studies on these fellfield soils have shown that they contain up to 0.3 $mg \cdot g^{-1}$ extractable calcium (Allen and Northover 1967; Allen et al. 1967). This figure is approximately an order of magnitude greater than the total amount of calcium added to each enclosure suggesting that the added calcium would not have had any great effect on the soil algae. Therefore it is reasonable to conclude that the microalgae were nitrogen-limited.

The main hypothesis of the FERP considered the relative importance of water availability and temperature to the survival of organisms in fellfield habitats (British Antarctic Survey 1981). The results presented here demonstrate that the addition of water had no effect on the decline of the microalgae and that the microalgae were not limited by the availability of water. Environmental monitoring showed that temperatures during the summer were always above those likely to be fatal to microalgae and that daytime maxima were sufficient to sustain growth (Davey 1991a). Daytime irradiances also remained above saturation intensities for these taxa (Davey 1991a). This result may appear contradictory to that of Wynn-Williams (1990) who reported an increased biomass inside plastic cloches and attributed this to temperature or humidity effects. However, the cloches were in place for many years and may have been prompting microalgal growth at different times of the year than this study.

Also of note are the observations that the addition of organic carbon compounds had no effect on the microalgal decline. This result is the opposite of that from earlier experiments. Wynn-Williams (1990) applied a series of amendments to the soils to determine the factors limiting growth; these suggested that microalgal growth may be promoted by the addition of organic carbon and, to a lesser extent, by inorganic nitrogen. However, these experiments were carried out during the early part of summer (December to January) when microalgal growth occurs in unamended soil (Davey 1991b) and do not relate to the period of growth limitation. It is important to distinguish between those factors that increase microalgal populations by promoting an increase in growth rate during the growing season, such as the organic nutrients reported by Wynn-Williams (1990), and those factors that increase microalgal populations by extending the growing season by reducing the effects of limitation, such as the nitrogen additions described here. Comparison of these two studies demonstrate the marked seasonal changes in these ecosystems and stress the dangers of extrapolating short-term experiments to the ecosystem in general.

The lack of response to the addition of organic nitrogen to the soil may have been due to the low rate of breakdown of these compounds in the soil. Rates and causes of organic loss and breakdown in these soils requires further study.

The results reported here have shown that the microalgal populations are nitrogen-limited and that this leads to a decline in the community in late summer. In addition to the direct effects of the nutrient limitation it is possible that the stress imposed on the microalgae may predispose them to the detrimental effects of freezing during the autumn leading to further decline in the community.

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