Folia Fac. Sci Nat. Univ. Masarykianae Brunensis, Geographia 25 (2001): 19-33

# PLANT COLONISATION RESPONSE TO CLIMATE CHANGE IN THE ANTARCTIC

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## ABSTRACT

Throughout the maritime Antarctic, and in some continental Antarctic areas, there has been a progressive increase in air temperature, particularly during summer, since the late 1940s. This, together with an increase in precipitation, has resulted in the rapid retreat and thinning of many ice-fields and glaciers. Propagules, of local and exotic origin, are deposited by various means in the soil. These are the basis of future communities, if or when environmental conditions become suitable. Since the mid 1980s, the frequency of such favourable conditions has increased, permitting the process of colonisation and communitiy development to proceed more quickly. During a long-term research programme several experimental studies of colonisation by plants have been undertaken at a number of field sites, with complementary laboratory experiments. The purpose of this programme has been to investigate experimentally the effect of climate change, especially increased temperature, on the process of colonisation of soil by plants along a latitudinal (and hence climatic) gradient (from 54° to 74°S), by microclimate manipulation in the field and laboratory. The results of several of these experiments are reported here, all of which support the prediction that the rate of colonisation and the diversity of colonising species is greatly enhanced when environmental conditions become more favourable for the development of the soil propagule bank, growth and reproduction.

**KEY WORDS:** Colonisation - bryophytes - vascular plants - climate change - biological response - Antarctica

## INTRODUCTION

Most global circulation models predict that climate change effects will be greatest in the polar regions where mean annual air temperatures are expected to increase by up to 1°C per decade over the next *c*. 50 years (e.g. Cubasch, Cess, 1990; Mitchell et al., 1990; Kennedy, 1997). Throughout much of the maritime Antarctic (as defined by Lewis Smith, 1984) there has already been an increase in mean summer (November-February) of 1°C since around 1950 (King, 1994; King, Turner, 1997). This has caused substantial retreat and thinning of icefields and glaciers, creating new habitats for colonising terrestrial biota. At Signy Island in the northern maritime Antarctic, Lewis Smith (1990) reported a reduction of 35% ice cover between 1949 and 1989. Such situations are ideal for the study of colonisation processes and community dynamics, and of the response of individual species and communities to changing climate.

Botanical evidence of climate warming throughout the maritime Antarctic has been known since the mid 1940s, albeit by extrapolation. Observations by the author during the early 1960s revealed that ice recession was proceeding quite rapidly at several localities. On Signy Island and in the Argentine Islands (mid-west Antarctic Peninsula), lichen trim-lines were prominent on rock faces adjacent to glaciers, indicating that before the commencement of climate warming around the mid 20th century a colder period had allowed the extension and thickening of glaciers and icefields (Lewis Smith, 1972; Corner, Lewis Smith, 1973; Fenton, 1982). This resulted in substrata already colonised by plants to be buried and the vegetation killed and/or removed. When the ice began receding, the point at which the ice reached was marked by a prominent line above which healthy mosses and lichens remained, but below which there was no (or only dead) vegetation. Possible long-term effects of such climate change on Antarctic terrestrial ecosystems has been discussed by Adamson and Adamson (1992) and Kennedy (1995a).

The research reported here presents some results from a long-term investigation involving the manipulation of microclimatic and other environmental conditions in both the field and laboratory (see Kennedy 1995a, b, c, 1996). The main aim of this study has been to experimentally raise the temperature of recently deglaciated soils to induce the germination of buried spores and development of vegetative propagules, thereby initiating their establishment as pioneer colonists in an incipient fellfield community. Other environmental variables which were modified included relative humidity, UV-B irradiance and soil nutrients. To simulate some of the major changes (especially increased temperature) predicted to occur in the coastal Antarctic over the next few decades, several experiments have utilised miniature greenhouses (cloches) to enhance growing conditions (see Kennedy 1995b, c). The investigation has been undertaken at sites ranging from 54°S (South Georgia) to 74°S (Victoria Land). The eventual aim of the research is to predict changes in community stability and species composition, and in ecological and physiological processes and their effect on ecosystem dynamics, in response to climate change.

## STUDY SITES

Experimental sites were selected at seven locations, one in the sub-Antarctic, three in the maritime Antarctic, one intermediate betwen the southern maritime and continental Antarctic, and two in coastal continental Antarctica.

1. South Georgia (*c.* 54°S, sub-Antarctic), upper Husdal valley, *c.* 240 m alt. Site is a medial moraine ridge below a small receding glacier. The moraine is traversed by a series of at least 45 micromoraines and their associated narrow terraces, each deposited annually and thus allowing the precise age of each to be known. All are very sparsely vegetated with bryophytes, lichens and a few phanerogams, with an increasing number of species on the progressively older surfaces. [The numbers of phanerogam and bryophyte taxa recorded within study area were 6 and 15, respectively] .

2a. Signy Island, South Orkney Islands (*c.* 60°S, maritime Antarctic), Jane Col, *c.* 150 m alt. Site is a small level plateau adjacent to a receding icefield which is part of the island's ice cap. Soil is derived from quartz-mica schist, pH *c.* 5.4. Unvegetated ground close to the receding ice margins, but increasingly colonised by mosses and lichens on the older (15-45 years) ice-free ground. [Number of bryophytes within site *c.* 15].

2b. Signy Island, Marble Knolls, *c.* 10 m alt. Site is a series of small, low limestone hills with a calcareous soil (pH *c.* 8.0). About 200 m from a receding icefield margin, and with moderate bryophyte and lichen vegetation separated by unstable barren periglacial features. [Number of bryophytes within site *c.* 24]

3. Mid-west Antarctic Peninsula (*c.* 64°S, maritime Antarctic), Cierva Point, *c.* 150 m alt. Site is a level, unvegetated deglaciated area adjacent to receding icefield. [Number of bryophytes within site *c.* 8].

4. Adelaide Island, (*c.* 67°S, maritime Antarctic), Rothera Point, 5 m alt. Site is on a raised beach terrace, covered by boulders and deposits of sandy soil close to a receding icefield. Colonisation by mosses proceding rapidly. [Number of bryophytes within site *c.* 4].

5. South-east Alexander Island (72°S, intermediate maritime-continental Antarctic), Ares Oasis, 25 m alt. Site is a braided stream outwash of fine silty soil below a receding glacier margin. Mosses extremely sparse and mostly buried. [Number of bryophytes within site *c.* 3].

6. Wilkes Land (*c.* 67°S, continental Antarctic), Bailey Peninsula, *c.* 50 m alt. Site is a level terrace on a sparsely vegetated hillside with fine sandy soil and gravel. [Number of bryophytes within site 2].

7. Victoria Land (*c.* 74°S, continental Antarctic), Edmonson Point, *c.* 5 m alt. Site is fine, unstable, unvegetated alluvial silt at the margin of a permanently frozen lake. [Number of bryophytes within site 0].

## METHODS AND EXPERIMENTS

### 1. Response of *Deschampsia antarctica* and *Colobanthus quitensis* populations to increasing temperature (see Fowbert, Lewis Smith, 1994).

The long-term response of *D. antarctica* and *C. quitensis* was monitored between 1964 and 1990 on three islands in the Argentine Islands (Galindez I., Skua I., Winter I., 65°S, mid west Antarctic Peninsula, maritime Antarctic); the total numbers of individual plants were counted at intervals over the 27 years. *Colobanthus* was absent on Winter Island.

### 2. Response of colonising *Deschampsia antarctica* to increasing temperature (see Lewis Smith, 1994).

The short-term response of the grass to raised temperature, as well as to nutrient enrichment and reduced UV-B, was tested on Signy Island by simulating a mean increase in summer temperature of 3-4°C over eight years (1984-92). *D. antarctica* tillers with four to six visible leaves were transplanted to two contrasting sites on Signy Island. One (Factory Cove) was sheltered and near the shore (5 m alt.), with a loam-like soil enriched by nearby sea bird colonies, and close to a well-established population of grass from where the experimental tillers were taken. The other site (Site 2a) was a recently deglaciated inland plateau with nutrient-deficient fine glacial detritus. Such extreme habitats are not usually colonised by the grass. At each site 20 tillers were protected by each of two rigid, transparent, ventilated Perspex cloches (55x28x15 cm high), and a further 20 tillers were left uncovered in two identical plots as controls. One of each pair of cloches and control plots was treated irregularly with a NPK fertiliser solution (Phostrogen), while the other pair remained untreated. The spectral quality of the Perspex is unknown, but the cloches considerably reduced incoming UV-B.

### 3. Response of buried soil propagules to increased temperature *in situ*.

To determine the effect of increasing the soil and near-ground temperature above ambient, two cloches, as described above, were established on visually unvegetated soil at Sites 1-7, excluding 2b, and left *in situ* for at least three years. Uncovered control plots of the same area were marked within 50 cm of the cloches. However, for logistical reasons, they were not installed at the same time at each site. Because of the wide geographical range of the sites, the differences in altitude and years of the experiments were not considered to affect comparability of results to any significant degree. The percentage cover afforded by colonising plants, and the number of species, were monitored annually. Unfortunately, this was not possible at the Cierva Point and Bailey Peninsula sites, although close-up photographic records were obtained for the third year at the former site, and for the first and third years at the latter site. At these two sites both plant cover and species composition were estimated from photographs, but the data must be regarded with caution as they are less reliable than the *in* situ visual estimates.

**4. Response of buried soil propagules to increased temperature and nutrients *in situ* (see Lewis Smith, 1993).**

At Site 2a on Signy Island pairs of cloches, with adjacent uncovered control plots, were set up at two subsites. Subsite A was an accumulation of dark mineral detritus washed down from an adjacent receding ice slope. At the beginning of the experiment (1985) it was 5-10 m from the ice margin and about 25 m from the nearest very sparse visible vegetation. It had an estimated age of *c*. 5-10 years since becoming exposed. Subsite B, *c*. 50 m from the ice edge and towards the centre of the site, comprised fine soil subjected to cryoturbation. Colonisation here had already commenced, and the soil within each of the cloches and control plots had 1-3% bryophyte cover. The age of the surface was postulated to be about 30 years since exposure at the beginning of the experiment. At each subsite two cloches were treated with a NPK nutrient solution at irregular intervals during each summer. A corresponding pair of cloches received no treatment, or occasional distilled water if the plots appeared to be very dry. The development of mosses was recorded over the next seven years.

**5. Response of buried soil propagules to increased temperature in laboratory cultures.**

To determine the effect of temperature on the composition of the soil propagule bank, five samples of visually uncolonised surface soil (0-0.5 cm) were taken from each of the seven field sites (including 2b). Those from each site were mixed and *c*. 0.5 cm depth of soil placed in five 100 $cm^2$ plastic dishes per site, and cultured on thermogradient incubator plates at the British Antarctic Survey laboratories in Cambridge. [Earlier culture experiments had shown that the propagule bank decreased rapidly with increasing soil depth (Lewis Smith, 1987; Lewis Smith, Coupar, 1987)]. Several experiments were undertaken, with incubation temperatures varying from 15°C (the optimum temperature for development of the soil propagule bank, as determined in earlier experiments, see Lewis Smith, 1987; Lewis Smith, Coupar, 1987) to a range of temperatures from 2-25°C. However, only those conducted at 15°C are reported here. The experiments continued for 16-26 weeks. The number of bryophyte shoots, and their identity, was recorded every few days.

**6. Response of detached moss fragments to colonise soil *in situ* under an increased temperature regime at a maritime Antarctic site (see Lewis Smith, 1993).**

To test the ability of vegetative propagules to colonise bare ground and establish populations, the apical 0.5 cm of aggregations of 14 fellfield mosses were macerated using a microhomogeniser. The experiment was undertaken at Site 2a (Signy Island). Each species was cultivated within 30 $cm^2$ open-ended cylindrical Perspex tubes pressed into the soil. Two sets of replicates were covered by cloches (see above), and a duplicate series left unprotected as a control. No nutrients were applied. Approximately 200 fragments per species were sown in each cloche and control plot. The experiment was monitored over four years. A complementary experiment was carried out over 12 weeks using soil from the site, cultured at at 15°C in the laboratory, but with very low survival. These results are not reported here.

**7. Response of soil propagule bank in a glacier foreland to increased temperature (see Lewis Smith, in press).**

To study the effect of increasing temperature on the colonisation potential of the buried soil propagule bank deposited on and integrated into the surface layer of soil in a glacier foreland, a series of cloches were emplaced on known-age micromoraines at Site 1 (South Georgia). Pairs of cloches were positioned on uncolonised soil on five micromoraine terraces (5, 15, 25, 35, 45 y old). Adjacent to each cloche was an uncovered control plot of the same area. The experiment was set up in 1991 and continued for the following three years. In each year colonising species were recorded photographically and percentage cover estimated. Small samples of bryophytes were collected for identification after years one and two, and a thorough collection made in the third year.

**8. Response of the colonisation potential of detached moss apices to increasing temperature at a continental Antarctic site (see Lewis Smith, 1999).**

A short-term experiment was set up at Edmonson Point (*c.* 1 km from site 7) to determine the ability of vegetative propagules of the three dominant moss species in Victoria Land to establish colonies quickly during the short continental growing season. The process was accelerated by increasing the temperature by the use of cloches, and the effect of screening the plants from ambient UV-B was also assessed. The upper 2-3 mm of shoots from colonies of *Bryum pseudotriquetrum* and *Ceratodon purpureus* were cut using a scissors. Detached buds and apices of *B. argenteum* were collected from dense accumulations on a film of melt water below a stand of this moss. All material was air-dried for several hours. Using a small portable balance, aggregations of *c.* 10 mg of shoot apices of each species were weighed in the field and sown onto the moist soil *in situ*. For each species, 50 replicates were given two treatments: within transparent acrylic plastic cloches which allowed UV-B radiation to penetrate (+UVB), and which filtered out UV-B (-UVB); a control plot for each species had no cloche treatment. After 5 weeks the colonies were harvested and each „colony" washed, air-dried (24 h), weighed and the increase in dry mass recorded.

## RESULTS

**1. Response of *Deschampsia antarctica* and *Colobanthus quitensis* to regional warming in the maritime Antarctic (see Fowbert, Lewis Smith, 1994).**

The long-term monitoring of *D. antarctica* and *C. quitensis* populations in the Argentine Islands showed a dramatic increase in the number of live (or with partial necrosis) individual plants, excluding seedlings. Thus, in 1964 a total of *c.* 710 *Deschampsia* plants and 72 *Colobanthus* plants were recorded. By 1990 these numbers had increased to *c.* 17,000 and 390, respectively. The grass, in particular, had established many more populations than existed at the beginning of the study. The relatively rapid increase in the abundance and distribution of these species is interpreted as a response to the increasing summer air temperatures being experienced in the northern maritime Antarctic. If this had been the normal rate of population expansion over the past few centuries, these species would now be very much more abundant than they in fact are. In particular, there appears to be improved success in reproductive behaviour (i.e. viable seed production) resulting from warmer and/or longer growing seasons.

**2. Response of colonising *Deschampsia antarctica* to increasing temperature (see Lewis Smith, 1994).**

This cloche experiment was designed to raise the temperature of the summer growing environment by 3-4°C. Six years after transplanting the *Deschampsia* tillers the number of plants surviving from the original 20 was: Factory Cove (sheltered, 5 m) cloches with nutrients 16, without nutrients 13, control with nutrients 17, without nutrients 15; Jane Col (exposed, 150 m) cloches with nutrients 5, without nutrients 5, control with nutrients 2, without nutrients 0.

At the sheltered site, after an initial loss of a few plants during the first two years those surviving increased substantially in size and tiller production over the next four years withoout much further mortality. There was little difference in survival between those protected by cloches and those exposed to the prevailing ambient microclimate in the control plots. Most losses in the cloches resulted from periods of high temperature and desiccation in summer. There was also little difference between the nutrient-treated and untreated plots, since the nutrient status of the soil was already optimal due to the proximity of cliff-nesting sea birds. After six years most of the surviving plants had in excess of 50 tillers, and most produced inflorescences by the third year.

After two years, survival at the exposed site was high only in the nutrient-treated cloche, whereas there was substantial mortality in the untreated control plot. Over the next four years numbers declined steadily and by year 6 only five of the original 20 plants survived in each cloche treatment, and two in the fertilised control and none in the untreated control. The experiment was allowed to continue for a seventh year, when only a single very unhealthy plant remained in each cloche, and zero in the controls. This decrease resulted from a combination of frequent exposure to low temperatures and freeze-thaw cycles (numerous plants were uprooted by frequent formation of needle ice in the top 1-2 cm of soil), long periods of water-logging of the clay particles (despite its low water content), nitrogen deficiency and lack of organic content in the soil. There was a marginally greater survival in plots treated with nutrients than in the untreated plots. All plants were very small and none exceeded eight tillers after six years; no inflorescences were produced.

**3. Response of buried soil propagules to increased temperature *in situ*.**

The development of bryophytes from buried propagules in the soil at the seven recently deglaciated field sites over three years is given in Table 1. Data for the Cierva Point and Bailey Peninsula sites are incomplete. It should be noted that this experiment was not conducted over the same time period, and the sites are at different altitudes. However, neither of these factors is considered to have had a significant effect on the results.

At each of the maritime Antarctic sites (including the Alexander Island site) there was a steady increase in plant cover over the three years, reaching >70% at both South Georgia and Signy Island. This was two to three times the cover attained at the three more southerly sites. The number of species correspondingly increased with time, but declined with increasing latitude. At all but the South Georgia site the peak number of species was more or less reached by the second year. The two continental sites yielded only two species (*Bryum pseudotriquetrum* and *Ceratodon purpureus* at Site 6, and *B. argenteum* and *C. purpureus* at sitre 7). No bryophytes were recorded in the adjacent control plots at any of the sites. Clearly, the enhanced conditions provided by the cloches stimulated rapid development of the buried soil propagule bank, except at the continental site. In all cases the species appearing in the cloches were the same as those in the vicinity of the experiment.

**4. Response of buried soil propagules to increased temperature and nutrients *in situ*.**

The percentage cover and number of moss species which appeared in the cloches and controls at Jane Col subsites over seven years are given in Table 2. Within the cloches at both subsites there was rapid colonisation by several species after only one year and, by year 2, over 55% cover was attained in both nutrient treated and untreated cloches at the younger subsite (A); by year 7 there was complete cover. The trend was very similar at subsite B, with more species appearing, but much less cover afforded by these. At subsite A there was very little development in the control plots, with only *Ceratodon purpureus* appearing. However, at the more mature subsite B, several species, including *Ceratodon*, were slowly beginning to colonise. In all the treatments, *Bryum pseudotriquetrum* and *C. purpureus* were the dominant colonists. The addition of NPK fertiliser did not significantly stimulate faster or greater development. At subsite A slightly higher moss cover was attained over the first two years in the treated cloches, but subsequently there was no difference, although a larger number of species appeared. At Subsite B the nutrient-treated cloches showed a very slight increase in cover, but not in number of species, but this was not evident in the controls.

The more rapid development at Subsite A, close to the receding ice slope appears to have resulted from a larger propagule bank, washed down in the meltwater from the ice slope in spring and being deposited on the soil close to its receding edge. As proposed by Lewis Smith (1993) icefields and glaciers serve as an important reservoir for wind- and water-dispersed propagules. These remain encased in ice until released in meltwater and deposited onto favourable substrata. The driving force in the colonisation process is the activation of dormant propagules by a stimulus whic, as yet, is largely unknown and unquantified. Germination of spores or development of vegetative structures may be a response to a single stimulus, or to a combination of stimuli, of which temperature and moisture are probably the most important, although light quality, organic or inorganic nutrients, substrate stability and texture, may be equally important.

**5. Response of buried soil propagules to increased temperature in laboratory cultures.**

All samples of soil from the eight sites and cultured under the same controlled conditions yielded numerous bryophyte species (Table 3). As with the previous experiment, the number of species generally declined with increasing latitude, although the site at Bailey Peninsula produced only two species. In the field, only three species (*Bryum pseudotriquetrum, Ceratodon purpureus, Schistidium antarcticum*) were recorded in the vicinity of this site, and the author has never noted *S. antarctici* to develop from cultured soil from any Antarctic site, even if it is an abundant component of the local flora. Both South Georgia and Signy Island (Site 2b, calcareous soil) had a high biodiversity (18 and 15 species, respectively) although only eight were common to both sites. The cosmopolitan *B. pseudotriquetrum* was the only species common to all sites tested. Again, the diversity of species in the cultures reflected the composition of the local flora from where the samples were taken, although many more developed under laboratory conditions than appeared witnin the cloches at the same field sites. In separate laboratory culture experiments using soil samples from Site 2a (Lewis Smith, 1987, 1993; Lewis Smith and Coupar, 1987; Kennedy, 1996 using data from these), it has been shown that the optimum temperature for the development of the soil propagule bank is 10-15°C, although shoots of a few species can develop at as low as 2°C, and also at 25°C. At the lowest temperatures, such development takes at least eight weeks before shoots appear, whereas at the optimal temperatures they appear after 2-3 weeks.

**6. Response of detached moss fragments to colonise soil under an increased temperature regime at a maritime Antarctic site (see Lewis Smith, 1993).**

The survival of detached fragments of 14 species of moss sown onto soil at the exposed Site 2a on Signy Island is indicated in Table 4. Small colonies of all species developed within the cloches, while several failed to establish (*Andreaea gainii, A. regularis, Hennediella antarctica*), or <5 shoots survived, in the uncovered control plots. These results are important because the experiment showed that several species (notably *Andreaea* spp., *Dicranoweisia grimmiacea* and *Schistidium antarctici*) were capable of establishment on soil *in situ* if conditions are favourable. By comparison, several attempts to culture these taxa on soil and on agar with various nutrient enrichments under controlled laboratory conditions failed. For all species within the cloches at least 6-50 shoots were counted after four years, and for *Bartramia patens, Bryum pseudotriquetrum, Ceratodon purpureus, Sanionia uncinata, Schistidium antarctici* and *Syntrichia princeps*, over 100 stems survived or developed additional shoots. The most successful species in the control plots were *B. pseudotriquetrum, C. purpureus* and *S. uncinata. B. patens* and, especially, *H. antarctica* are typically opportunistic colonists, but neither proved very successful in th experimental control plots. Clearly, the conditions provided by the cloches enhanced the ability of stem fragments to act as vegetative propagules and become established.

**7. Response of soil propagule bank in a glacier foreland to increased temperature (see Lewis Smith, in press).**

The pairs of cloches placed on terrain dated at 10-year intervals, produced an increasing number of species from the buried propagule bank, and correspondingly increasing plant cover, with increasing age of the substratum (Table 5). After three years, the youngest surface (5 y) had only two species (mostly the liverwort *Marchantia berteroana*) providing an estimated 11% cover. On progressively older substrata, the amount of plant cover increased significantly, although the number of species on the three oldest surfaces was similar (8-10 species). On the 25 and 45-year old micromoraines the introduced grass *Poa annua* provided a substantial amount of the cover. This species, accidentally introduced at the former whaling stations, has become widespread in many parts of the island, and is sometimes the first vascular plant to become established in exposed fellfields and on glacier forelands. Once again, all species which appeared also occurred in vegetated areas some distance from the site. There was no colonisation occurred in any of the control plots over the three years. This was partly because the substratum remained unstable due to freeze-thaw activity, exposure to frequent katabatic winds and desiccation, all factors which were largely eradicated within the cloches.

**8. Response of the colonisation potential of detached moss apices to increasing temperature at a continental Antarctic site (see Lewis Smith, 1999).**

The mean dry mass increase of colonies of the three mosses after five weeks in UV-B transparent and UV-B screened cloches at Edmonson Point is presented in Table 6. There was highly significant growth between the control and both cloche treatments ($P<0.001$). *B. argenteum* readily became established and proliferated by producing many new, although very small clusters of shoots. The mean biomass of the control colonies increased by 22%, while those in the cloches increased by 93% and 137% in the +UVB and -UVB treatments, respectively. The other two species failed to establish successfully in the controls, several of the colonies losing biomass through death and probably also by loss of material due to wind. However, some growth was recorded in the cloches, that in the +UVB cloches being almost equal in the two species (*c.* 25% increase), while in the absence of UVB biomass production increased by 28% in *B. pseudotriquetrum*, but only 18% in *Ceratodon*. The difference between the growth of *B. argenteum* in the two cloche types was highly significant ($P<0.001$), but for *C. purpureus* it was only slightly signficant ($P<0.05$), and not significant for *B. pseudotriquetrum* ($P>0.5$). In *Ceratodon* in the -UVB cloche the shoots had become green by the loss of much of the dark carotenoid pigments, but in the +UVB cloche the shoots remained dark reddish-brown (see also Post, 1990).

Daytime soil surface temperatures in the cloches were usually about 10-15°C higher than the soil outside the cloches, the difference reducing to *c.* 1-3°C at night. The much greater colony growth of each species in the cloches, compared with that in the controls, was most likely attributable to the increased temperature and retention of soil moisture.

## CONCLUSIONS

The current trend in climate change in coastal Antarctic sites is causing increased (i) air (and substrate) temperature, (ii) length of „growing season", (iii) precipitation (especially in summer), (iv) ice melt, and recession of ice fields, (v) extent of ice-free habitat, (vi) availability of soil moisture, (vii) release or input of nutrients into the ecosystem, (viii) springtime ozone depletion (resulting in increased UV-B), and (ix) frequency and changes in direction of severe weather events (affecting the provenance, dispersal and deposition patterns of propagules, e.g. Lewis Smith, 1991; Marshall, 1996).

The ecological and physiological consequences of these changes in climate include (i) overall increase in favourable conditions for colonisation, community development, reproduction and dispersal, (ii) more frequent and effective stimuli for the development of buried propagules, (iii) increased rate of development of the buried soil propagule bank, (iv) potential for establishment of species new to region (including higher plants), (v) possible shift in community stability due to change in dominance and/or species abundance and in species composition, (vi) increased reproductive success (sexual and asexual), (vii) increased local propagule dispersal, (viii) increased physiological activity and production of photoprotective pigments, enhancing survival of some species and possibly favouring new colonists, (ix) possible reduction in resilience of modified communities to brief periods of reversed climate trend.

## ACKNOWLEDGEMENTS

I am indebted to M. Chalmers, M. Edworthy, H. MacAllister, A. Rossaak, M. Smithers (all British Antarctic Survey), L. White (Wye College, University of London), O. Benitez and G. Mattaloni (Instituto Antartico Argentino, Buenos Aires), all of whom provided data from the various field experiments. I am also grateful to Dr. M. R. Worland for maintenance of the thermogradient incubator during the laboratory experiments.

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**Tab. 1** Percentage cover and number of bryophyte species recorded after one, two and three years in cloches on recently deglaciated unvegetated soil at five coastal Antarctic sites along a latitudinal gradient.

* increasing to 100% by 5th year.
Data are means of two cloches per site.

| | S. Georgia 54°S Site 1 1991-94 | | Signy I. 60°S Site 2a 1985-88 | | Cierva Pt. 64°S Site 3 1991-94 | | Rothera Pt. 67°S Site 4 1994-97 | | Bailey Pen. 67°S Site 6 1986-89 | | Ares Oasis 72°S Site 5 1994-97 | | Ed. Pt. 74°S Site 7 1995-98 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. |
| Year 1 | 12 | 3 | 5 | 3 | - | - | 2 | 2 | 2 | 1 | 1 | 1 | >1 | 1 |
| Year 2 | 36 | 6 | 39 | 7 | - | - | 18 | 4 | - | - | 13 | 3 | 1 | 2 |
| Year 3 | 75 | 10 | 72* | 8 | c. 25 | 4 | 32 | 4 | 5 | 2 | 28 | 3 | 2 | 2 |

**Tab. 2** Percentage cover of bryophytes recorded in cloches and controls, with and without nutrient treatment, at Signy Island (Site 2a) after two, four and seven years. No species were present at subsite A in 1985, but there was 1-3% cover at Subsite B.

* With sporophytes
Data are means of two cloches per subsite.

| | With nutrients | | | | | | No nutrients | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cloche | | | Control | | | Cloche | | | Control | | |
| Species Year | 2 | 4 | 7 | 2 | 4 | 7 | 2 | 4 | 7 | 2 | 4 | 7 |
| Subsite A | | | | | | | | | | | | |
| *Bartramia patens* | <1 | <1 | 1 | 0 | 0 | 0 | <1 | 1 | 1 | 0 | 0 | 0 |
| *Bryum pseudotriquetrum* | <1 | 5 | 5 | 0 | 0 | 0 | 5* | 20* | 20 | 0 | 0 | 0 |
| *Cephaloziella varians* | 0 | 0 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ceratodon purpureus* | 65 | 80 | 95 | 0 | 0 | <1 | 50 | 65 | 80 | 0 | 0 | <1 |
| *Pohlia nutans* | 0 | 0 | <1 | 0 | 0 | 0 | <1 | <1 | <1 | 0 | 0 | 0 |
| *Polytrchum juniperinum* | 0 | <1 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sanionia uncinata* | 0 | <1 | <1 | 0 | 0 | 0 | <1 | <1 | <1 | 0 | 0 | 0 |
| *Warnstorfia sarmentosa* | <1 | <1 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Percentage cover (total) | 65 | 85 | 100 | 0 | 0 | <1 | 55 | 85 | 100 | 0 | 0 | <1 |
| Number of species | 4 | 6 | 8 | 0 | 0 | 1 | 5 | 5 | 5 | 0 | 0 | 1 |
| *Andreaea regularis* | 0 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bartramia patens* | 0 | 0 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bryum pseudotriquetrum* | <1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Cephaloziella varians* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Ceratodon purpureus* | 20 | 28 | 35 | 2 | 5 | 5 | 18 | 25 | 35 | 5 | 8 | 12 |
| *Ditrichum* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | <1 | 0 | 0 | 0 |
| *Pohlia cruda* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | <1 | <1 | 0 | 0 | <1 |
| *Pohlia nutans* | 2 | 7 | 10 | 0 | 1 | 1 | 2 | 5 | 10 | <1 | 1 | 2 |
| *Polytrichum juniperinum* | <1 | <1 | <1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Sanionia uncinata* | <1 | 12 | 18 | <1 | 2 | 2 | <1 | 3 | 12 | 0 | <1 | <1 |
| *Syntrichia princeps* | 0 | <1 | <1 | 0 | 0 | 0 | 0 | <1 | <1 | 0 | 0 | 0 |
| *Warnstorfia sarmentosa* | 0 | 0 | <1 | 0 | 0 | 0 | 0 | <1 | <1 | 0 | 0 | 0 |
| Percentage cover (total) | 22 | 49 | 65 | 2 | 8 | 8 | 20 | 36 | 60 | 5 | 9 | 14 |
| Number of species | 5 | 8 | 9 | 2 | 3 | 3 | 3 | 9 | 10 | 2 | 3 | 4 |

**Tab. 3** Diversity of bryophyte species cultured at 15°C for 16 weeks from unvegetated surface soils from recently deglaciated sites along a latitudinal gradient.

S.G.: South Georgia (Site 1); Sig.: Signy Island, Jane Col (Site 2a); Sig.*: Signy Island, Marble Knolls (Site 2b); Cierv.: Cierva Point (Site 3); Roth.: Rothera Point (Site 4); Bail.: Bailey Peninsula (Site 5); Ares: Ares Oasis (Site 6); E.P.: Edmonson Point (Site 7).

Data are total for five samples per site, mixed, and cultured on five 10 x 10 cm dishes.

| | Site and latitude | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | S.G. 54° | Sig. 60° | Sig.* 60° | Cierv. 64° | Roth. 67° | Bail. 67° | Ares 72° | E.P. 74° |
| *Anisothecium cardotii* | x | - | - | - | - | - | - | - |
| *Bartramia patens* | x | x | x | x | x | - | - | - |
| *Bryum argenteum* | x | - | x | - | - | - | x | x |
| *Bryum pseudotriquetrum* | x | x | x | x | x | x | x | x |
| *Cephaloziella varians* | x | - | x | - | - | - | - | - |
| *Ceratodon purpureus* | - | x | x | x | x | x | - | x |
| *Distichium capillaceum* | x | - | x | - | - | - | x | - |
| *Ditrichum* sp. | x | - | - | - | - | - | - | - |
| *Encalypta procera* | x | - | - | - | - | - | x | - |
| *Encalypta rhaptocarpa* | x | - | x | - | - | - | - | - |
| *Hennediella antarctica* | - | - | x | - | - | - | - | - |
| *Hennediella heimii* | - | - | - | - | x | - | x | x |
| *Marchantia berteroana* | x | - | x | - | - | - | - | - |
| *Notoligotrichum trichodon* | x | - | - | - | - | - | - | - |
| *Platydictya jungermannioides* | - | - | x | - | - | - | - | - |
| *Pohlia cruda* | x | - | - | - | - | - | - | - |
| *Pohlia nutans* | - | x | - | x | - | - | - | - |
| *Pohlia wahlenbergii* | x | - | - | - | - | - | - | - |
| *Polytrichastrum alpinum* | x | x | - | - | - | - | - | - |
| *Polytrichum piliferum* | x | - | - | - | - | - | - | - |
| *Pterygoneurum ovatum* | - | - | x | - | - | - | - | - |
| *Sanionia uncinata* | x | x | x | x | x | - | - | - |
| *Schistidium* sp. | x | - | - | - | - | - | - | - |
| *Syntrichia arenae* | x | - | - | - | - | - | - | - |
| *Syntrichia filaris* | - | - | x | - | - | - | - | - |
| *Syntrichia princeps* | - | x | x | x | - | - | - | - |
| *Syntrichia saxicola* | - | x | x | - | - | - | - | - |
| Total no. species | 18 | 8 | 15 | 6 | 5 | 2 | 5 | 4 |

**Tab. 4** Establishment after four years of 14 mosses from c. 200 leaf and stem fragments sown on fellfield soil in situ on Signy Island.

1 = 1-5 shoots; 2 = 6-10; 3 = 11-25; 4 = 26-50; 5 = 51-100; 6 = >100
Data are means of two cloches.

| | Mean no. live shoots per 30 $cm^2$ | |
|---|---|---|
| Species | Cloche | Control |
| *Andreaea depressinervis* | 4 | 1 |
| *Andreaea gainii* | 2 | 0 |
| *Andreaea regularis* | 4 | 0 |
| *Bartramia patens* | 6 | 1 |
| *Bryum pseudotriquetrum* | 6 | 5 |
| *Ceratodon purpureus* | 6 | 6 |
| *Dicranoweisia grimmiacea* | 6 | 4 |
| *Hennediella antarctica* | 3 | 0 |
| *Polytrichastrum alpinum* | 3 | 2 |
| *Racomitrium sudeticum* | 4 | 1 |
| *Sanionia uncinata* | 6 | 5 |
| *Schistidium antarctici* | 6 | 1 |
| *Syntrichia princeps* | 6 | 2 |
| *Syntrichia saxicola* | 4 | 2 |

**Tab. 5** Percentage cover of plants and number of species, derived from buried propagule bank, recorded in cloches on a South Georgia micromoraine chronosequence after three years.

* Includes *Poa annua*.
Data are means of two cloches per site.

| | Age of micromoraine (years) | | | | |
|---|---|---|---|---|---|
| | 5 | 15 | 25 | 35 | 45 |
| Total plant cover (%) | 11 | 26 | 43 | 53 | 75 |
| Number of species | 2 | 5 | 8* | 8 | 10* |

**Tab. 6** Mean dry weight biomass of colonies of detached moss shoot apices after five weeks in control plots and in UV-B transparent (+UVB) and UV-B opaque (-UVB) cloches at Edmonson Point, Victoria Land. (n = 50; initial mean colony dry wt. 10 mg).

| | Biomass as dry wt. (mg ± S.D. and range) and percentage increase | | |
|---|---|---|---|
| | Control | +UVB | -UVB |
| *Bryum argenteum* | 12.2 ± 2.1 | 19.3 ± 3.9 | 23.7 ± 6.3 |
| | (7-16) | (12-28) | (9-37) |
| | 22% | 93% | 137% |
| *Bryum pseudotriquetrum* | 10.6 ± 0.9 | 12.6 ± 2.1 | 12.8 ± 2.3 |
| | (9-12) | (9-20) | (9-20) |
| | 6% | 26% | 28% |
| *Ceratodon purpureus* | 10.4 ± 0.8 | 12.5 ± 1.7 | 11.8 ±1.5 |
| | (9-12) | (9-17) | (9-16) |
| | 4% | 25% | 18% |