STUDIES ON PLANT COLONIZATION AND COMMUNITY DEVELOPMENT IN ANTARCTIC FELLFIELDS

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The Fellfield Ecology Research Programme (FERP) commenced at Signy Island in 1981 as a long-term series of integrated projects to investigate aspects of the environment and how it, and in particular the availability of water and the physical and chemical quality of the substrate, influences the biological processes of colonization, organism survival and community development in this stressed ecosystem, which predominates throughout the Antarctic biome. The short time available and poor weather conditions during January 1981 allowed little more than the selection and demarcation of seven study sites and a preliminary botanical and pedological survey of these. Three primary fellfield sites of varying age and degree of colonization, situated in Moraine Valley (35–60 m altitude), on the plateau above Factory Bluffs (110 m) and on Jane Col (150 m) were chosen as the locations where the majority of the projects would be concentrated (Fig. 1). The latter site has been uncovered by ice for only about two decades and it offers an ideal situation for studying colonization processes.

Samples of unvegetated soil were collected from the three main sites in 1981 to assess the composition of viable propagules present in these skeletal substrates. In order to test the colonization potential, replicate Petri dishes were filled with soil, sealed in the field, and maintained at −20°C until they were cultured in The UK. This was achieved on a thermogradient incubator at temperatures ranging from 2 to 27°C. The presence of plants was noted at regular intervals over periods up to 150 days. Within three to six weeks algae quickly became established, forming a gelatinous or filamentous skin over the soil, binding the particles and stabilizing the surface. Growth was quite rapid, especially at the higher temperatures. At least a dozen algal taxa were recorded but their identity has not been confirmed. Unicellular chlorophytes (cf. *Chlorococcum* and *Chlorella*) and desmids (e.g. *Cosmarium*) and short filamentous taxa (e.g. the xanthophyte *Heterothrix*) were especially abundant at the higher temperatures, with longer filamentous cyanobacteria (notably *Microcoleus*) and some unicellular taxa at the medial temperatures, and gelatinous cyanobacteria (cf. *Gloeocystis*) occurring at the lower temperatures; patches of brown and purple algae also developed on some plates at the medial and higher temperatures. Several bryophyte taxa appeared, usually after six to eight weeks, as individual shoots or as small colonies, arising sometimes from networks of brown protonemata which covered the soil surface. Species diversity did not increase after about ten to twelve weeks, but the density of the dominant taxa continued to increase. The species composition was similar at each of the three sites. The dominant taxon was an unidentified dicranaceous moss (possibly an ecotype of *Ceratodon*) which reached greatest densities at the higher temperatures (15–23°C). Several species were frequent at the lower and medial temperatures 3–15°C), including *Bartramia patens*, *Distichium capillaceum*, *Pohlia nutans* and the liverworts *Cephaloziella varians* and *Lophozia* cf. *propagulifera*, while *Bryum algens*, *Drepanocladus uncinatus*, *Pohlia cruda*, *Pottia austro-georgica* and species of *Tortula* also occasionally appeared. Most of these are mildly calcicolous taxa. All skeletal fellfield soils are at least mildly alkaline, which probably accounts

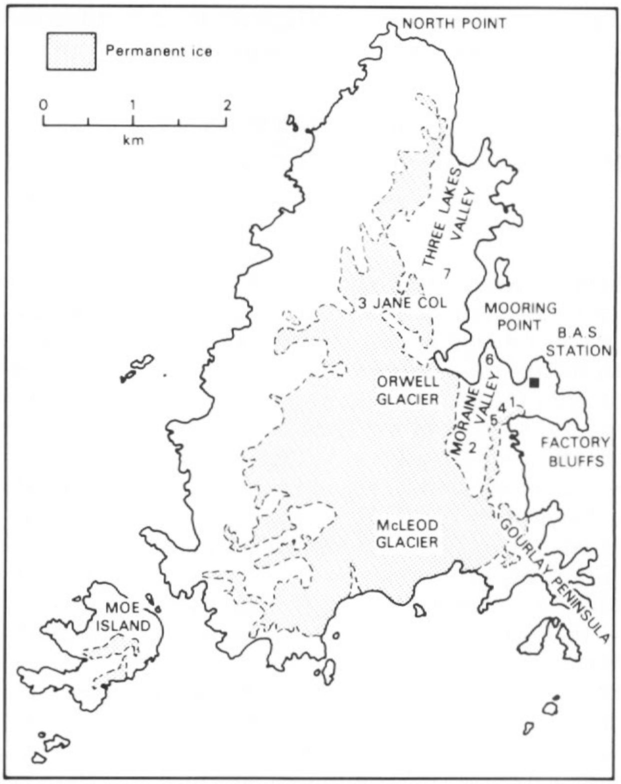

Fig. 1. Map of Signy Island showing sites 1–7 of the BAS Fellfield Ecology Research Programme. (1) Factory Bluffs: mature, densely vegetated plateau; (2) Moraine Valley: unstable, sparsely vegetated slope; (3) Jane Col: recently exposed, colonizing plateau; (4) 'Paal Col': lichen-covered, gravelly col; (5) 'Green Gable': densely vegetated, block scree; (6) Mooring Point: extensively patterned gentle slope; (7) Marble Knolls: moderately vegetated, calcareous ridge.

for the preponderance of calcicolous bryophytes developing on the soil plates and the apparent absence of calcifuge genera, such as *Andreaea* and *Dicranoweisia*, which are dominant in most Signy Island fellfields. They may be dependent on an autogenic process in which primary colonists, most likely algae, are required to stabilize the soil or enrich the soil or rock with an organic exudate. At least one species of moss (Funariaceae) and a basidiomycete fungus (*Coprinus* sp.), both unknown in the Antarctic flora, were recorded. Similar, but slightly more rapid, results were obtained using replicate samples treated with an NPK-rich fertilizer. Nutrient enrichment did not appear to enhance species diversity, shoot density or growth rate, but gelatinous algae tended to be more frequent than on the untreated soils. During 1984–85 similar experiments, using fresh soil material, have been conducted by Dr A. M. Coupar at Signy Island, using a two-tier thermogradient incubator with an alternating day/night temperature and lighting regime. Tests with samples from various depths showed a significant decline in viable propagules below 1 cm depth.

These trials indicate the likelihood of a considerable bank of propagules contained in the soil and on ice surfaces, including exotic taxa which are transported by wind over great distances, most probably from South America. The lack of appearance of these plants in the field suggests that, while viable propagules (spores, leaves, shoot or tissue fragments, etc.) exist in the substrate, conditions for germination and/or growth are not favourable. However, by increasing the temperature regime or nutrient status, or maintaining a high relative humidity and soil moisture content, colonization may proceed. These experiments have revealed the importance of micro-algae as the primary colonizers of apparently barren soils, and future studies will investigate the composition of the algal flora, the growth requirements and tolerances of the principal taxa, their role in stabilizing soil surfaces and the production of organic compounds and possible nitrogen fixation which may be critical prerequisites for bryophyte and lichen colonists.

During 1984 and 1985 attempts were made to assess the nature and source of propagules entering the fellfield ecosystem. The air spora close to the ground was sampled over several days at three-week intervals throughout the year using sticky slides attached to short posts and to the arms of Rotorod samplers. These have succeeded in trapping a variety of wind-dispersed moss leaf fragments and micro-propagules, although the identity of the latter has yet to be determined. Larger plant fragments were trapped using strips of sterile fibre matting held at different heights up to 1 m above the ground, sections of which will be cultured directly to test the viability of the propagules. Most of the few Antarctic bryophytes that reproduce sexually are fellfield species, but the majority rely primarily on vegetative means rather than on spores for their dissemination and establishment. In the laboratory on Signy Island spores of most of the fertile fellfield mosses were cultured at 15°C on nutrient-treated soil, rock fragments and on glass micro-fibre discs. Successful germination after several weeks was achieved only by calcicolous species, notably those with an ephemeral growth strategy (e.g. *Encalypta patagonica*, *Pottia austro-georgica*, *Pterygoneurum* cf. *ovatum*). However, failure to germinate by species such as *Andreaea regularis*, *Bartramia patens*, *Dicranoweisia grimmiacea* and *Schistidium antarcticum* may have been due to immaturity of the spores when sampled. Further experiments will be undertaken to test the requirements of germination.

Field trials in the Jane Col site were initiated to test the ability of moss fragments to develop new plants and become established. The upper 5 mm of shoots of twelve fellfield species were homogenized and 'sown' within small plots in the field where their progress will be followed over several years. Replicate plots were covered by clear polystyrene cloches to enhance growth and development by creating a more favourable microclimate. The same species were also cultured on different fellfield soil types in the laboratory at 10–15°C. Fellfield soils typically have exceptionally low levels of nitrogen and other essential nutrients, and this may be partly responsible for the slow colonization and subsequent development rates experienced by fellfield plants. In another laboratory experiment, moss fragments were cultured on soil fractions of different particle size and treated with different nutrient regimes designed to provide nitrogen in various forms; replicates were also amended with 1% sucrose solution. In this way it may be possible to assess which form of nitrogen promotes optimum growth in each of the species tested, and whether growth is enhanced by the addition of carbohydrate.

To assess the effect of augmenting the nutrient status of the substrate and of modifying the microclimate by increasing the temperature and humidity and reducing the effects of wind, a long-term field trial to study the process of plant colonization was established at the Jane Col site. At each of six sub-sites, either visually barren or with a few small moss shoots present, four plots were marked with stakes on different categories of soil and gravel substrates, some of which are subjected to cryoturbation. Two plots at each sub-site were treated weekly with 0.2 Bold's complete nutrient solution. One treated and one untreated plot were covered by clear ventilated

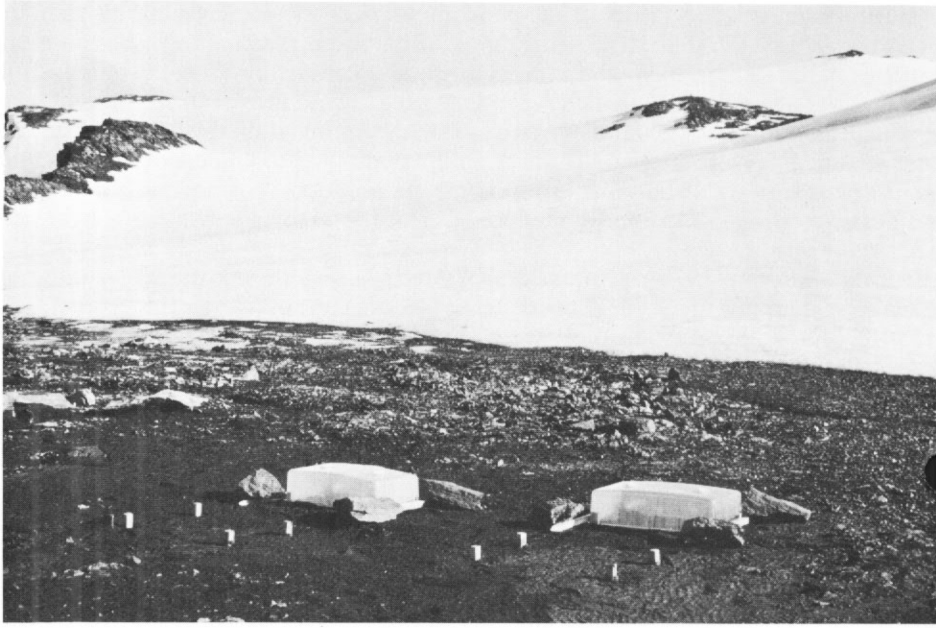

Fig. 2. Cloche experiment, Jane Col.

polystyrene cloches. The development of colonizing plants will be assessed annually, or more frequently if progress is rapid. Similar cloche experiments, designed to enhance microbial populations, at the three primary sites will also serve to provide comparative information on cryptogamic development.

A detailed study of the nature and cause of pattern in vegetation at five of the fellfield sites has been undertaken by Dr A. M. Coupar during 1984–85. At each site, the micro-distribution of all plant species was recorded along five 5-m belt transects laid across areas of vegetation exhibiting distinct patterning, caused largely by the non-random sorting of the substrate by cryoturbic activity. Experimental studies of the colonizing strategies and growth requirements of the principal species will help to provide an understanding of how and why certain species occupy their particular micro-habitats and give rise to different forms of pattern in the vegetation. Also at the Jane Col site a series of twenty permanent quadrats has been marked out in which small colonies of cryptogams have very recently become established. The annual increase in plant stature, colony area and the appearance of new individuals will be monitored photographically.

Another study in progress at Signy Island overlaps with the FERP. Situated in mid-ocean on the the edge of the Antarctic, the environment of this small and relatively low-lying island is particularly sensitive to climatic change. The past twenty to twenty-five years have seen a very slight amelioration of the weather throughout the maritime Antarctic and at South Georgia. Marginally higher summer temperatures and rainfall have caused a relatively rapid recession of ice fields and glaciers. Examination of recently re-exposed areas of moribund vegetation on Signy Island indicate that, during the past two decades, the ice thickness has decreased by up to 7–8 m and has receded laterally by up to 50 m or more around icefield margins. These previously vegetated exposures, and rock faces with clearly demarcated trim-lines where lichens cease abruptly, indicate that the island was formerly less extensively covered by ice. Radiocarbon dates obtained for some re-exposed moss peat suggests that this vegetation was buried when there was a major ice advance caused by deteriorating climatic conditions during the 'Little Ice Age' of *c.* 150–200 years ago. During the past three years several new rock exposures have appeared in the island's ice cap and samples of moribund moss have been taken for further radiocarbon dating to provide a clearer picture of when the ice advance occurred. Some of these areas supported fellfield vegetation and they will serve as valuable baseline sites for monitoring regeneration and recolonization, since the date of the appearance of these substrates is precisely known. Accurate dating of substrates is particularly difficult, yet crucial, in understanding rates of colonization and development in the fellfield programme. In a few instances transects, originally analysed to demonstrate changes in plant species and community distribution along environmental gradients, have been reanalysed after twenty years to illustrate changes in species composition or diversity with time. One indication is that, in some situations at least, the vegetation is much more dynamic and the growth rate of colonizing lichens far greater than was previously supposed.

The terrestrial environment of Signy Island is also undergoing rapid change caused by a natural biological agent. During the past few years there has been a remarkable increase in the number of fur seals (*Arctocephalus gazella*) coming ashore on the island. These are almost entirely immature males originating from the population at South Georgia which has increased dramatically during the past ten to fifteen years. The annual population at Signy Island, which begins to build up in early January and peaks in late February to early March, has increased from only a few dozens of animals prior to 1969, to several hundred from 1970 to 1976, and from 1600 to 3000 from 1977 to 1983; in 1984 and 1985 there were over 8000 animals. The impact these seals have made on the island's environment has been sudden and locally devastating, especially along the more sheltered and accessible east coast. The fragile cryptogam-dominated vegetation in particular has suffered damage that may be irreparable. Some of the ice-free parts of the island are vegetated extensively and support a rich cryptogamic flora and a diversity of plant communities ranging from deep moss banks to wet moss carpets, lichen-rich fellfields and unique calcicolous fellfields on marble soils. Damage varies from complete removal of all macro-lichens and loosely attached moss cushions and the death of the deeper moss turves to the churning up of the wetter bryophyte mires. In all cases the communities become rapidly colonized by algae, notably *Prasiola crispa*, which favour the increased nutrient status of the substrata. The seals also frequent some of the island's freshwater lakes, while some venture several hundred metres inland and to over 100 m altitude on hillsides. In 1984 and 1985 over 40% of the fur seals occurred in the extensively vegetated low-lying north-east part of Signy Island where an estimated 75% of the vegetation (excluding precipitous areas) has been influenced by seal activity; about half of this area has been severely damaged within the past three years. This is seriously affecting some of the current FERP studies; one research site has been largely destroyed and four others have been penetrated by occasional seals. Six 5 × 5 m exclosures and adjacent unfenced control plots were established in representative stands of the principal plant communities in areas undergoing or expected to undergo perturbation from the seals. Marked quadrats will be photographed annually to follow deterioration caused by the seals in the control plots or recovery arising from the protection afforded them.

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