THE EFFECTS OF VOLCANIC ACTIVITY ON THE VEGETATION OF DECEPTION ISLAND

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Abstract. The results of the recent eruptions on the vegetation of Deception Island are described in the first study that has been made of the effects of an eruption on a largely cryptogamic flora. The consequences of burial by ash and factors controlling regeneration through thin layers of ash are discussed. The colonization of new surfaces is reported and the establishment of a vigorous colony of a species of the Funariaceae, not previously known from within the Antarctic botanical zone, is noted from fumarolic areas. The vegetation, as it can develop in inter-eruption periods, is described and reasons for its floristic poverty are suggested.

The vegetation of Deception Island has been described by Longton (1967), who pointed to its floristic poverty compared with other parts of the maritime Antarctic. An absence of certain community types was also noted, whilst in those that are present there are certain floristic differences from physiognomically similar communities occurring in the rest of the South Shetland Islands (personal communication from D. C. Lindsay), and throughout much of the maritime Antarctic. A well-developed fumarole vegetation has been reported from the volcanic South Sandwich Islands (Baker and others, 1964; Longton and Holdgate, 1967) but prior to the 1967 eruption no such vegetation was known on Deception Island. This is not surprising when it is realized that all the recently active fumarolic areas examined have been situated in the intertidal zone. The only other area of active volcanicity in the Antarctic is the crater of Mount Erebus on Ross Island, south Victoria Land, which is also known to be without macroscopic vegetation (Ugolini and Starkey, 1966).

The recent eruptions on Deception Island have afforded an example of more severe disturbance to Antarctic vegetation than normally occurs in the region from natural agencies, and a study of the effects of these eruptions was undertaken between 9 December 1968 and 9 January 1969 with a view to determining their influence on the island's terrestrial plant communities. It was also hoped that some evidence might be found to account for the island's floristic and vegetational poverty.

Effects of Other Eruptions

A number of studies has been made in the past of the effects of volcanic activity on vegetation. In the tropics, the catastrophic eruption of Krakatao, in 1883, resulted in much of the island's vegetation being destroyed. But within a few years it was revegetated, mainly from plants surviving on the undamaged part of the island, rather than by colonization from sources outside the island (Backer, 1929). The colonization by plants of Surtsey, the latest addition to Vestmannaeyjar, a group of volcanic islands off the coast of Iceland, has been studied in detail from the moment it emerged from the sea (Einarsson, 1965, 1967; Fridriksson, 1967). In this instance both ash and lava substrata were presented for colonization. The eruption in 1961 at Tristan da Cunha had relatively limited effects (Dickson, 1965). A lava flow destroyed and burnt some areas of vegetation, whilst the gases released damaged extensive areas. Eggler (1948, 1959) has discussed the consequences to vegetation of eruptions producing copious ash, and particularly pertinent to the situation on Deception Island are the investigations of Griggs and Smith (1932), Griggs (1933) and Griggs and Ready (1934) on the Katmai eruptions in Alaska. In the latter case, initial colonization of virgin ash was by species of the Jungermanniaceae, which the results of experimental work suggested are capable of growth on nitrogen-free media.

Plant Habitats on Deception Island

Most land above 100 m. is covered with ice which reaches sea-level at numerous places on the outer coastline and on the inner coast from Pendulum Cove to 2 km. north of Kroner Lake. Although not included in Fig. 1, the ice outline can be found by reference to the 1 : 25,000 map of Deception Island (Directorate of Overseas Surveys, No. 310, 1960).

Ice-free land on the island comprises three main types of substrata on which colonization by vegetation can occur, namely (a) the tuff of the main caldera wall, (b) the lava flows of varying

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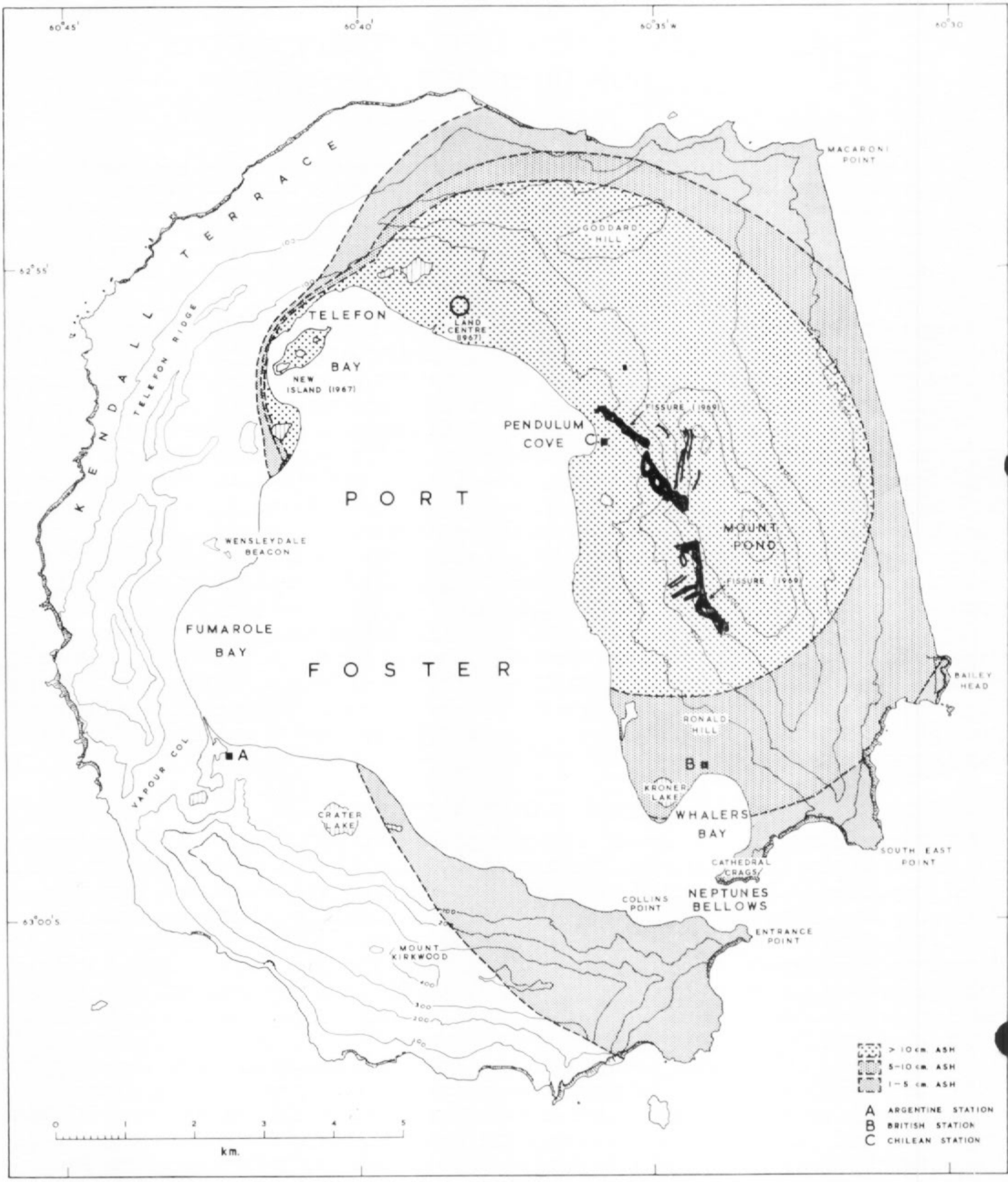

Fig. 1. Ash distribution on Deception Island resulting from the 1967 eruption, together with the new island, the land centre and the fissure of the 1969 eruption. (Based on information from Baker and others (1969).)

ages which may form cliffs and which in places are much fragmented and (c) the surfaces of the porous arid ash and lapilli plains, with their scattered bombs, mainly on the inner and southern outer coasts. There are a few permanent melt streams and occasional small lakes. As the surface layers of the porous ash dry out very rapidly, the finer particles are frequently redistributed over the island by wind, so that new surfaces are continually being made available for colonization by plants. Since Deception Island is composed of only basic volcanic rock

types (Hawkes, 1961), there is a reduction in the number of habitats when compared to other areas since acid rocks are absent.

Many new surfaces resulted from the recent eruptions but, as with the pre-eruption surfaces, only certain of these are amenable to colonization. The 1967 eruption produced ash and lapilli which, consequent upon the prevailing wind, were carried down-wind of the land centre (Fig. 1) and deposited in varying depths as far as the south-east corner of the island. In addition, a submarine eruption in the north-west corner of Telefon Bay produced a small new island separate from the main island. The 1969 eruption took place through an extensive fissure on Mount Pond and differed from the 1967 eruption in that mainly coarse lapilli but no fine ash were produced. Whilst neither of the eruptions appears to have given rise to any lava flows, both produced bombs of various sizes.

Fumarolic activity continued on the new island and in the floor of the new crater at the land centre after the 1967 eruption had subsided, but activity on the new island had almost completely ceased by December 1968. Whilst no analyses of fumarole gases have been made, it appears that only limited quantities of toxic gases might have been emitted at the time of the eruption. C. M. Clapperton (personal communication) noted yellowish sublimates around active fumaroles shortly after the eruption but none was observed around those active in December 1968–January 1969. By contrast, the 1969 eruption may have produced more toxic fumes, since there are extensive sulphur deposits on fumarolic areas in one section of the fissure (personal communication from P. E. Baker). Fumarolic areas appear to have afforded abnormal, relatively transient habitats in the past on Deception Island, as is discussed later with relation to *Philonotis gourdonii*, a species of moss so far described only from a single vegetative collection made on the "summit of Mount Pond" by Gourdon in 1909, and described as forming small carpets on calcareous and sulphurous deposits (Matteri, 1968). No snow-free substrata now exist on the summit of Mount Pond, apart from ash lying on top of the snow. Hawkes (1961) cited various authors who have described volcanic activity at Deception Island during the last century and a half, and from these it appears that there have been a number of transient habitats around fumaroles at various times in recent history.

Habitats suitable for terrestrial plants appear then to be normally relatively transient in nature, although habitats on vertical faces of tuff cliffs, and in some cases lava flows, might be more stable. During varying periods of time, however, some measure of stability is maintained from season to season, as for example, on ash once consolidation of the surface has occurred following the establishment of plant communities.

The Pre-eruption Vegetation

A description of the island's vegetation was provided by Longton (1967) and this was later amplified by R. I. L. Smith (personal communication), both of whom examined in some detail areas immediately accessible from the British station in Whalers Bay. The following description owes much to information gained from these two sources but it includes observations by the author in areas that were unaffected by the recent eruptions. Since the island is composed of basic volcanic rocks, many of the bryophytes and lichens colonizing the various substrata are found to be species that are regarded as mild calcicoles by Smith (personal communication) in the South Orkney Islands.

The fruticose lichen and moss cushion sub-formation is represented chiefly by communities in which species of *Bryum*, *Grimmia* and *Tortula* are predominant, while on the tuff cliffs small dense cushions of the genera *Barbula*, *Didymodon* and *Pottia* may also be frequent. *Usnea antarctica*, together with various crustose lichens, is usually abundant in these communities, although other species, including some of the genera *Andreaea* and *Dicranoweisia*, which are typical of many community types within this sub-formation elsewhere in the maritime Antarctic (Longton, 1967; Gimingham and Smith, 1970) are very uncommon on Deception Island.

The crustose lichen sub-formation, which has so far received inadequate attention, occurs in abundance locally on the tuff cliffs, with the *Caloplaca* association being well represented. These crustose lichen communities frequently intergrade with stands of the *Tortula–Grimmia* association of the former sub-formation. In contrast to this, a previously unrecognized

association occurs on lava flows and debris, where the *Caloplaca* association is replaced by stands dominated by *Placopsis contortuplicata* with several associated species, including *Bartramia* sp., *Grimmia antarctici*, *Leptogium* sp. and *Usnea antarctica*. The mosses do not commonly form cushions on the most exposed faces but with the species of *Leptogium* are confined to crevices.

Stands of *Polytrichum alpinum* replace the *Polytrichum alpestre–Dicranum aciphyllum* peat banks of the moss turf sub-formation which are so characteristic of many non-volcanic regions of the maritime Antarctic. The most extensive stands of *P. alpinum* are situated on the north-facing slopes of ash and weathered rock fragments between Collins Point and Entrance Point, where the coalesced hummock-shaped turves reach a depth of 30 cm. Various bryophytes may occur between these mounds with *Drepanocladus uncinatus* being the most frequent. On the level ash plains, strewn with fragmented bombs, and particularly on the floor of a shallow crater south-west of Ronald Hill, an open short turf is produced by *Polytrichum alpinum*, *P. juniperinum* and *P. piliferum*. Several short acrocarpous mosses together with fruticose and crustose lichens are frequent associates, while *Psilopilum antarcticum* is locally frequent on the floor of the shallow crater.

The encrusted moss sub-formation appears to be more or less restricted to ash substrata, where species of *Bryum* and *Ceratodon* are heavily encrusted with a reddish brown species of *Psoroma* and several other crustose lichens. In addition, *Drepanocladus uncinatus* and *Cephaloziella varians* are usually present. Longton (1967) pointed out that the moss cushions are impregnated with ash and often elongated and hollow in the centre, suggesting that they may be subjected to frost heave. Whilst a characteristic assemblage of plants makes up this sub-formation, species that occur in other sub-formations are also found to be encrusted with various lichens, as, for example, some cushions of *Grimmia antarctici* on Cathedral Crags.

The moss carpet sub-formation, characteristic of wet, low-lying coastal areas in the maritime Antarctic, is represented on Deception Island by *Drepanocladus uncinatus* only, none of its common associates elsewhere (certain species of *Calliergon* and *Brachythecium*) being known on the island. The stands of *Drepanocladus* are restricted to the infrequent moist habitats, few of which are extensive. Where the habitat is not too wet, species of *Bryum*, *Ceratodon*, *Tortula excelsa*, *Cephaloziella varians* and a species of *Psoroma* are occasional associates.

The moss hummock sub-formation is poorly developed, occurring only in a few suitable habitats, where slopes or rocks receive some degree of flushing. Here large cushions of a species of *Brachythecium* are associated with a species of *Bryum*, *Drepanocladus uncinatus* and *Tortula excelsa*.

As anticipated by Longton (1967), the thallose alga sub-formation was found to occur extensively around the chinstrap penguin (*Pygoscelis antarctica*) colony below Vapour Col on the outer coast. It probably occurs also at other more inaccessible colonies unaffected by the eruptions.

The grass turf and cushion plant sub-formation is uncommon on Deception Island, only a single locality being known for each of the native flowering plants. *Deschampsia antarctica* has been noted amongst the *Polytrichum* turf in the crater below Ronald Hill (personal communication from R. I. L. Smith), while an extensive stand of *Colobanthus quitensis* (=*C. crassifolius*) covered part of a sheltered north-facing gully between South East Point and Bailey Head (Longton, 1967).

A number of alien phanerogams have also been reported from Deception Island (Longton, 1966). Of these the most successful has been *Poa annua* which was established on the south side of the disused whaling station at Whalers Bay. The number of tufts increased considerably between 1963 and 1967, from "a single tuft approximately 10 cm. wide" in 1963 (Longton, 1966) to three tufts 15–25 cm. across lying close together, with many seedlings amongst and around them in 1967 (personal communication from R. I. L. Smith). *Poa pratensis* is also known to have survived for at least 4 years on Deception Island (Longton, 1966).

Post-eruption Changes in the Vegetation

It appears that the main effects of the recent eruptions on the vegetation of Deception Island can be attributed to the deposition of ash over large areas of the island. Dickson (1965)

has pointed out that it is very difficult to assess fume damage to vegetation after such activity has ceased but he noted that at Tristan da Cunha, although fume damage to bryophytes was not observed, vascular plants were extensively affected. It is thought that the maintenance of a moist micro-climate at ground level under the vascular plant canopy might have protected the bryophytes. This effect also allows growth of bryophytes, that are intolerant of pollution, in the heart of cities suffering from air pollution (Gilbert, 1968). Fume damage at Deception Island has not been observed but it is thought unlikely that harmful fumes were emitted between the eruptions of 1967 and 1969, as evinced by the growth of a moss species which had already colonized parts of the fumarolic areas at the land centre. The only species of cryptogam that might possibly have been affected is *Usnea antarctica*, which was frequently found to be free of ash but drooping, desiccated and pale brown in colour, being in a very fragile state and easily detached from the rock.

The phenomena associated with ash deposition that are of greatest biological significance may be considered under two headings: primary effects (i.e. direct burial by the initial fall of ash or burial following redistribution of wind-blown or water-carried ash) and secondary effects, in which ash deposition alters topography and hence melt-stream patterns, the latter also being influenced by changes in ablation rates caused by the deposition of ash over snow.

Whilst recognizing that ash can arrive at a locality in a number of ways, in order to survive burial a species usually has to grow through varying depths of ash to reach the new surface. Of the commonest mosses on Deception Island, *Polytrichum alpinum* is the most efficient at growing through ash, although the other two rarer species of *Polytrichum* were found to be equally efficient. In contrast, the pleurocarp *Drepanocladus uncinatus* seemed incapable of immediate shoot production or of regeneration when blown free of ash. It appears that the mechanism of their water relations and their growth forms directly affect the ability of these species to regenerate. Since most observations have been made on the commoner species, their regenerative performance is described in the context of the communities in which they are most commonly found.

Species of the fruticose lichen and moss cushion sub-formation have been less affected by the eruptions than those of other communities, as on the near-vertical faces ash can only lodge occasionally. The areas at and below the foot of cliffs, however, are generally adversely affected. Many cushions of *Grimmia antarctici* on Cathedral Crags were found to have been impregnated with ash throughout the previous year's growth, suggesting continued growth throughout the eruption and immediate recovery. Even in cushions of *Grimmia* that appeared moribund, live rhizoids were found when the cushions were dissected. Lichen encrustation of *Grimmia* was found to be quite common on Cathedral Crags and it was further noted that the encrusted parts were invariably fruiting, whilst, although capable of regeneration, the non-encrusted cushions were often infertile. Many very dry cushions were also noted on South East Point and, although impregnated with ash, appeared to still be alive.

Its occurrence on mainly vertical habitats has also resulted in the crustose lichen sub-formation appearing to have been little affected by the eruptions. It has been noted on excavation that crustose lichens on boulders at the foot of Cathedral Crags, buried in moist ash since the eruption, appeared to have been little affected. As mentioned above, *Usnea antarctica* appears to have been affected in some way and, whilst fume damage cannot be ruled out, it appears to be more likely that desiccation as the ash dries out and is redistributed, possibly with an allied effect of some toxic element in the ash, is the cause.

The dominant species of the moss turf sub-formation, *Polytrichum alpinum* and also the other species of *Polytrichum* found on the island, are some of the most efficient species at regenerating through ash. It is thought that the endohydric type of water conduction, and an ability to withstand desiccation, taken together with their sympodial growth pattern and the ability to produce shoots rapidly, are the attributes which enable these species to regenerate quite efficiently. Rhizoids are readily produced on the regenerant shoots, both on the stems (usually in an axillary position) and often on the margins of the vestigial leaves. In the Kroner Lake and Ronald Hill area it was found in a number of places where burial was not greater than 3 cm. that shoots, with terminal groups of fully expanded leaves, had already reached the surface, in places giving up to 10 per cent cover. In fact, all stages were noted from shoots with

mainly vestigial leaves which had almost reached the surface to fully developed, normal vegetative shoots, but as the aerial growth of the latter appeared rarely to represent a normal full year's growth, it seems that these shoots had reached the surface during the early part of the 1968–69 summer, rather than grown to the surface in the latter half of the 1967–68 summer, after the 1967 eruption. In a few places, as on ridge tops, the moss had been blown free of ash and in many places shrivelled shoots were found on the surface.

It is suggested that the following sequence of events has taken place in turves composed of species of *Polytrichum*, although field observations suggest that they can be extended to include other acrocarpous species and certain pleurocarpous species that adopt a growth form more typical of acrocarps, as, for example, the hummock-forming species of *Brachythecium*. After burial of the former surface of the turf by a more or less even layer of ash, some redistribution of the latter would have begun immediately its surface dried out and was blown by wind. Wherever ash fell in depths through which regeneration was possible, it is considered most unlikely that it would have been at a temperature much above that of the air, since it had travelled some distance—up to 6·4 km. in the Kroner Lake area—and at some height, all the time passing through falling snow. Hence it is thought that regenerative growth could have started immediately, and that certainly some would have taken place before winter set in, particularly as the ash was damp and at depths of 4–6 cm. it is unlikely to have dried out completely before snow cover was established. The place of origin of the shoots in the buried turf varies but examination of a number of samples indicated that three main groups are recognizable—40 per cent of shoots are produced by continued growth of the apex of the old shoot, 28 per cent are deep sited (i.e. from deeper than 3 cm. in the old turf), while the remainder arise from between 1·5 cm. and the surface. Those that are from depths greater than 3 cm. represent a normal component of the branching system but those produced apically are a direct result of burial under ash.

In the following spring the ash would have been resaturated with melt water. Although no extensive experimental work was possible, the growth of shoots through ash that was placed on top of living material maintained in a saturated state, was quite rapid—up to 1 cm. in just over a month. With this speed of growth the shoots could be expected to reach the surface before the ash dries and give rise to new shoots of normal proportions. Drying of the surface and redistribution of the ash by the frequent strong winds can result in the shrivelling of the delicate shoots before they develop into normal shoots and once shrivelled growth cannot continue apically. Some re-exposure occurred in mid-January 1969, in the shallow crater below Ronald Hill and near Kroner Lake, and before growth can continue fresh branch shoots would have to be produced from deep in the old turf.

A similar sequence of events appears to have taken place in the two well-developed stands of the *Polytrichum alpinum* sociation that occurs between Collins Point and Entrance Point. As can be seen in Fig. 2, the micro-topography of the deep hummocks affects the regeneration of shoots and certain areas are protected from the wind, so that ash is not so rapidly dried out and redistributed. It will be noted that the consequence of this pattern of regeneration is a general levelling out of the hummocks.

As already noted, most acrocarpous species would appear to be capable of growing through ash layers but the more diminutive species can only recover where the layer remains thin. Species of *Bryum* seem, in general, to be very successful and where burial was to depths of 1 cm. or less the surface of the ash was often covered with what looked like minute green "spikes", the tips of the shoots that had just reached the surface. For this to happen, however, it is essential for the ash surface to remain moist and hence recovery of the encrusted moss sub-formation and other vegetation found on the more level even ground is unlikely because a shallow layer of the ash dries out very rapidly and starts moving over the pre-eruption surface. This very dry ash blowing over the former surface also absorbs further moisture from it and so provides an additional desiccating effect. When allied to the porous nature of the old ash, this results in large areas being killed off, notably those formerly covered by the lichen-encrusted moss sub-formation. The large flat area behind the beach to the east of Collins Point affords an example where only shallow burial had taken place but desiccation had occurred before shoot production and consolidation of the ash took place. Whole areas of the vegetation were loose on the surface and only a few patches showed any signs of life.

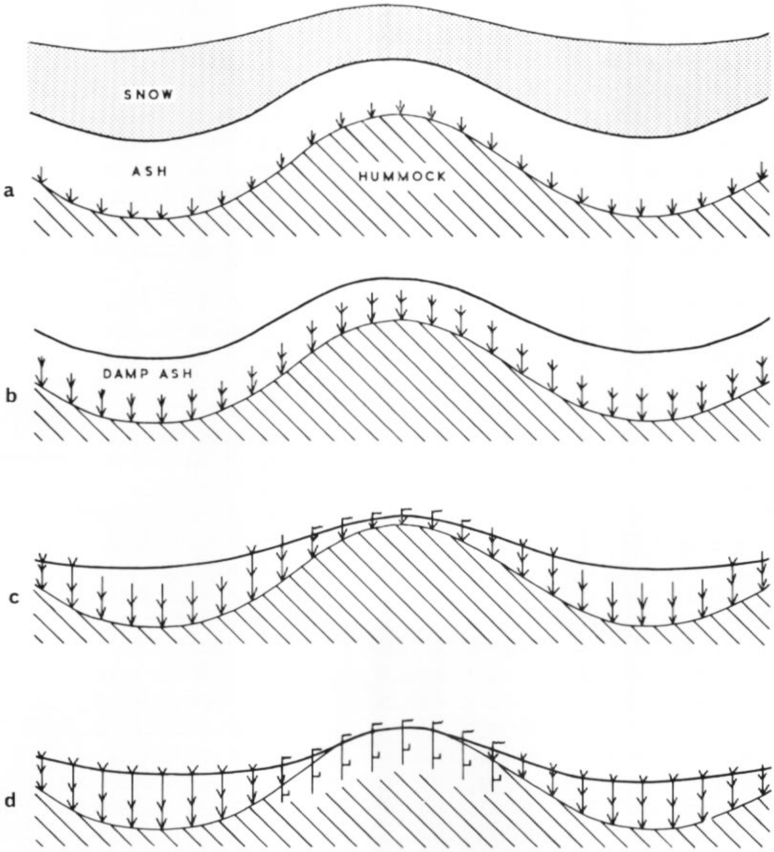

Fig. 2. Regeneration of *Polytrichum alpinum* hummocks; Collins Point, Deception Island.
a. Snow overlying ash, which evenly buries the old surface. Some shoot production may have occurred during the summer season of 1967–68, after the eruption of December 1967.
b. The spring melt of 1968–69 soaks the ash, which loses little water through drainage because of water-retaining hummock below. Shoots grow rapidly, becoming impregnated with ash.
c. Drying out of the ash and its subsequent redistribution by wind exposes the delicate shoots before they have time to expand to normal size at the surface and consolidate the ash.
d. The ash remaining is consolidated by shoots whose apices expand to more normal proportions on reaching the surface. Branch shoot production starts after the death of apical shoots.

Symbols:

Old shoot apex with extension shoot.
Old apex and shrivelled shoot.
Old apex and shoot with new normal growth.
Old apex, shrivelled shoot and branch shoot.

As mentioned earlier, the moss carpet sub-formation is represented on Deception Island mainly by *Drepanocladus uncinatus* and a few associated species. It locally dominates extensive areas and yet this species has been found to be more or less incapable of immediate regeneration. The consequence of this is that, whilst shoot production in the ash might eventually occur, the ash is usually dried out and blown away before it can be consolidated, with the results described below. In the area south-east of Kroner Lake, Smith (personal communica-

tion) noted the development of extensive closed carpets of almost pure *Drepanocladus*. By mid-December 1968, the moss had not regenerated through the shallow layer of ash that covered it. Where the moss had been re-exposed at the upper margins of shallow hollows it was found to be fairly damp and a few delicate shoots had developed, this also occurring where the ash layer was a few millimetres thick. The very short shoots that had been produced turned upwards through the ash and were branch innovations or apical continuations of main axes. The presence of the moss was clearly indicated, even when it was buried under 5 or 6 cm. of ash, by darker moister areas. In mid-January 1969, strong winds blew for a number of days and dried out and redistributed much of the ash. The parts of the moss that were exposed and those under the thin layer were desiccated and cracked, and fragmentation of the carpet started. Because of the unevenness of the surface, very fine dry ash was packed against the windward side and baked hard.

From observations at other sites it appears likely that any other colonies of *Drepanocladus* that were dependent through most of the season on precipitation, and its retention in the carpet or mat, for their water supply are also likely to have been much reduced in extent.

The inability of *Drepanocladus* to produce shoots immediately has resulted in some change in community composition in a flushed area behind Collins Point. Here both *Drepanocladus* and a species of *Bryum* were buried, but only the latter has produced shoots in the moist ash and, because of some branching, had spread over a greater area than before the eruption.

Although the moss hummock sub-formation is not widespread on Deception Island, a few observations have been made. Certain of the species of wetter habitats appeared capable of extensive shoot production. A species of *Brachythecium*, for example, had produced a number of shoots from varying depths in an old hummock, which had mostly reached a level of 1 cm. below the surface, by late December 1968, through 2 cm. of ash. For those species growing in the wetter habitats recovery is often easier, since the ash is more stable and not removed to expose the delicate shoots, unless melt-stream patterns have been extensively disrupted. It was observed, however, that ash was continually being redistributed by melt streams and reburial sometimes occurred. Of the acrocarps growing in these situations, both *Bryum algens* and all the species of *Tortula* proved to be capable of producing shoots.

The thallose alga sub-formation appears to have been quite extensively affected by the eruptions. Whilst the colony at Vapour Col had a very luxuriant growth of *Prasiola crispa*, that at Bailey Head, where about 6 cm. of ash had fallen, had only a local development below the tuff of the headland. Judging from the buried nests in certain areas, with eggs *in situ*, allied to the reported observations at the time of the eruption that the penguins left the colonies (personal communication from O. H. S. Darling), it appears that the breeding cycle in 1967–68 was extensively disrupted. Whilst some contamination of the new ash would occur during redistribution, nitrogen levels would not have built up again until after the 1968–69 breeding season had started, and re-colonization of the area by *Prasiola* then had to occur from the cliffs of the headland, where it survived in sheltered vertical habitats around the nests of cape pigeons (*Daption capensis*).

The two localities known for the grass turf and cushion plant sub-formation have been adversely affected. There was no trace of *Deschampsia antarctica* in the crater below Ronald Hill, where ash reached depths up to 9 cm., whilst the extensive community of *Colobanthus quitensis* between South East Point and Bailey Head had been almost completely destroyed, with only a few of the old cushions still alive. It appears that the slightest burial will destroy this plant, since most of the patches still surviving were in sheltered situations or where ash had soon been blown clear. Elsewhere the stand was moribund but still moist.

Between 5 and 10 cm. of ash were deposited on the shores of Whalers Bay where the *Poa annua* population reported by Longton (1966) had been situated. When the area was first visited in December 1968 it was found to be devoid of vegetation. The chicken wire that had been used to fence off the area during the 1963–64 season, because of the dogs, had caused ash to accumulate to greater depths than elsewhere. No trace of the plants was found, although much of the site was excavated to the old surface. By the following day the whole area had been scoured to below the old surface by a new melt stream caused by the deposition of ash on the lower slopes of Mount Pond (Fig. 3).

Fig. 3. Former site of the alien grass, *Poa annua*, disrupted by a new melt stream resulting from the 1967 volcanic activity. The limits of the grass site are marked by the stakes; ash has drifted against the oil drums and fast-flowing melt streams, scouring to below the old surface, are sorting ash from lapilli.

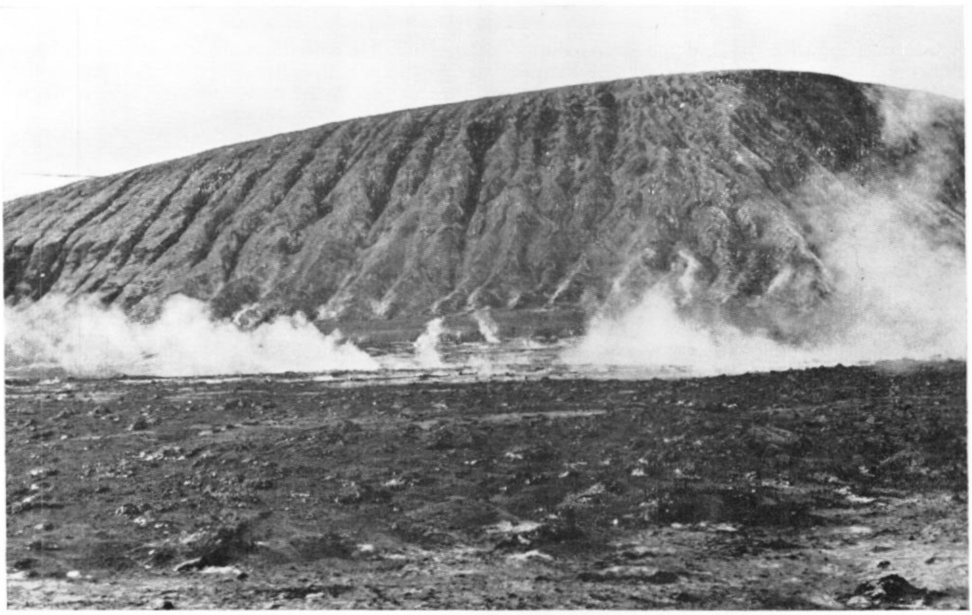

Fig. 4. Fumarolic activity at the 1967 land centre. A moss of the family Funariaceae occurred around fumaroles through fragmenting bombs and lapilli in the middle distance and less active fumaroles through partially consolidated ash on the lower slopes behind.

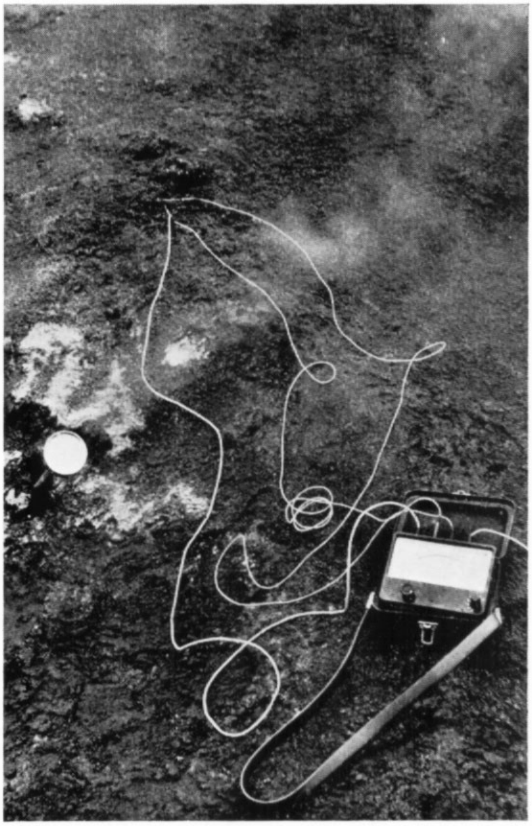

Fig. 5. Colonization by a moss of the family Funariaceae of the less active fumarolic areas through partially consolidated ash shown in Fig. 4. The thermometer to the left of the photograph is inserted in a vent surrounded by sublimates. The thermistor probes are inserted in the moss colony which is visible as a darker area against the surrounding ash.

Colonization of New Surfaces

As noted earlier, many new surfaces resulted from the 1967 eruption with additional ones arising from the 1969 eruption. At present on Deception Island there are four main situations where fresh colonization can occur: (a) the ash-lapilli and bomb-strewn surface of the new island, (b) areas where fresh ash, lapilli and bombs have fallen on to old surfaces, (c) where they have fallen on to snow, and (d) the sides of the fissure of the 1969 eruption running along Mount Pond, where certain areas are affected by active fumaroles.

The new island is barely 100 m. from the shore at its nearest point and on the slopes facing the island, which appeared to have been mostly unaffected by the eruption, a species of *Bartramia* and *Grimmia antarctici* were found fruiting, and a species of *Bryum*, which can spread vegetatively by means of detached apices, was common on the surface of some lava flows. The surface of the new island does not appear, at present, to provide any favourable sites as there is no water supply from melting snow and the bombs that cover much of it are in a very unstable fragmenting state. No trace of macroscopic vegetation was seen when the island was searched thoroughly in December 1968 and sticky slides exposed for varying periods of time up to an hour failed to trap either incoming vegetative propagules, or spores or fragments of macroscopic vegetation. These observations were corroborated in February 1969 by R. E. Cameron (personal communication). Although no incoming spores of macroscopic plants were detected, it would seem unlikely that the colonization of the island will be prevented by an inadequate source of propagules, when fruiting colonies occur at such short distances.

The surface of the island had cooled to normal temperatures by December 1968 and it is thought that lack of water was the main limiting factor.

In contrast, at the land centre, where extensive fumarolic activity occurred, extensive areas have been colonized by an as yet unidentified species of the Funariaceae. Two main areas were recognized, the first on ash and lapilli, the surface of which had been consolidated by fumarolic sublimates, and the second on a more level area to the south of this where bombs were being broken down to a fine grit by the continuous emission of steam from the vents (Fig. 4). The growth that had developed by early 1969 was patchy with local concentrations. No development of a mature growth form had occurred in the warm humid environment where single shoots grew to about 0·5 cm. above the ash surface, although a large number of the denser patches were fruiting (Fig. 5). In the areas between these patches the ground was covered with very young shoots which were growing from a fine weft of protonemata. Temperatures recorded in the vicinity of the moss are given in Table I. Whilst atmospheric humidity levels were not recorded, it seems likely, both from the continuous emission of steam from the fumaroles and from the amount condensing on the walls of the capsules, that humidity is maintained at a high level.

TABLE I. SUMMARY OF TEMPERATURE RECORDS FROM VEGETATION AROUND FUMAROLES AT THE 1967 LAND CENTRE, DECEPTION ISLAND

Temperature of vent nearest to vegetation at 5 cm. below surface (°C)	*Distance of vegetation from vent* (cm.)	*Position of probe above* (+) *or below* (−) *surface* (cm.)	*Height of vegetation* (cm.)	*Mean of ten temperature readings* (°C)		
				In slight wind and overcast	*In slight wind and strong sunlight*	*In strong wind and overcast*
A. Fumaroles through a predominantly ash surface						
80	3	− 0·5	0·3	36·0	—	—
	15	− 0·5	0·3	26·9	—	—
	18	+ 1·0	1·0*	15·2	—	—
	40	+50·0	—	5·0	—	—
85	50	− 1·0	—	36·7	—	—
	55	− 0·2	0·3	28·4	—	—
	55	0·0	0·3	21·2	—	—
	150	+50·0	—	5·5	—	—
90	3	− 0·5	—	32·5	—	—
	6	− 0·5	0·6	28·2	—	—
	6	0·0	0·6	21·0	—	—
	200	+50·0	—	5·5	—	—
B. Fumaroles through a surface of fragmenting bombs and lapilli						
>70	—	+ 5·0	—	—	42·0	37·5
	10	0·0	0·6	—	28·8	20·9
	10	+ 1·0	1·0*	—	20·4	12·9
	20	+50·0	—	—	5·2	3·7

* Amongst capsules.

It appears that in one area on the slopes north of the main fumarolic area, where there is still some slight fumarolic activity, although formerly more extensive, that there was some redistribution of the ash after growth had started and that the moss produced delicate shoots through the moist ash and then continued normal growth. The surface of the decomposing bombs was covered with the characteristic protonemata but there was no trace of any algal growth. Subsequent culture at Birmingham has resulted in the continued growth of the protonemata, with shoot production, but in addition there has also been extensive growth of a number of unidentified species of algae. It appears that this species of moss has not been recognized before on Deception Island (personal communication from S. W. Greene), but whether the initial propagules from which it has become established come from South America or the Falkland Islands or a more local source is unknown. Whilst long-distance aerial dispersal cannot be ruled out completely, it is possible that it was introduced accidentally by Man soon after the eruption had subsided, since many people were in the area within 10 days. Once fruiting had occurred, rapid spread by spores could take place from the point of introduction.

On areas of consolidated ash on the slopes north of the mainland area the moss was seen to be dying off where the fumaroles had ceased to be active. It was quite striking that colonization had been confined to the main fumarolic area and that no other species had succeeded in becoming established there by January 1969. It may be noted that the fumarolic activity in the area was little affected by the 1969 eruption and that no further ash fell (personal communication from P. E. Baker).

Ash fallen on snow can offer a suitable habitat for some species and a number of specimens, amongst them a species of *Bryum* and of *Ceratodon*, have been collected from the ash and morainic mounds lying on top of the glacier that flows down from Mount Pond to the inner coast. The glacier has been covered by ash for many years and during the 1967 eruption further extensive deposits were laid down, although these were later washed away by the excessive melt caused by the 1969 eruption. Provided some measure of stability is now attained, the occasional plant is likely to become established.

Whilst no details are available, it is worth noting that the 1969 eruption has also resulted in a number of new habitats, especially along the sides of the new fissure (Baker and others, 1969) running along Mount Pond, and certainly on its crater walls, where there is extensive fumarolic activity. In this area, however, there are more extensive deposits of sulphur that might discourage the development of vegetation.

Sites Marked for Future Investigations

Twenty-two sites, 50 cm.^{2} in area, have been staked out at a number of localities on Deception Island, selected to include representative areas and situations where there are likely to be changes in the vegetation in the future.

Sites over a variety of communities, buried to varying depths, have been marked, as well as a number of communities that have been re-exposed to differing extents. Sites on the new island have been marked and also on the fumarolic area of the 1967 land centre. At some sites a central 30 cm.^{2} quadrat was mapped in more detail and general notes made on the surrounding area. Likewise, in the vicinity of a few sites one or two reference stakes have been erected.

Extensive changes have already occurred at some sites as a result of the 1969 eruption. At least a quarter of them have been destroyed completely by the melt water and mudflows from the fissure and a number of them have been buried under coarse lapilli (personal communications from P. E. Baker and M. J. Roobol).

Discussion

There is an extensive literature on the colonization by plants of new land surfaces produced through volcanic activity and of recovery of plants that have been buried by ash but this pertains mainly to vascular plants (Backer, 1929; Griggs, 1933; Eggler, 1948, 1959; Dickson, 1965 (q.v. for further references); Einarsson, 1965, 1967; Fridriksson, 1967).

Regarding the burial of extensive areas of the vegetation, it appears that all areas on the isopach map (Fig. 1) that are covered by more than 6 cm. of ash are unlikely to be revegetated through regeneration from below, unless there is extensive redistribution and hence

a reduction of the ash thickness. Further deposition of lapilli has occurred on top of much of this ash at a number of areas during the 1969 eruption.

It has been found that various species of bryophyte react to burial by ash much as closely related species on sand dunes (Birse and others, 1957) and other unstable habitats in Britain (Leach, 1931). When burial occurs, delicate extension shoots are produced which grow vertically, and on reaching the surface the apices expand to produce shoots with normal foliage. The rate at which these shoots can grow varies greatly from species to species and this will partly determine whether the ash can be consolidated before it starts to dry out. Once drying out begins, re-exposure is usually rapid and, if, as normally happens, apices are damaged by desiccation, no further growth can occur without the production of new shoots and branches. In the deeper deposits, there is also the possibility that a shoot will not reach the surface before the plant is killed by compaction of the ash. Rhizoids that may be borne on the shoots, as well as vestigial leaves, may assist in water absorption in endohydric species but they certainly help in the consolidation of the ash, as has been described by Leach (1931) for species of *Polytrichum* growing on unstable ground.

The acrocarpous mosses of Deception Island all appear able to produce shoots rapidly but *Drepanocladus uncinatus*, the only common pleurocarp on the island, did not appear capable of immediate shoot production. Species of *Polytrichum* also contrast strongly with *Drepanocladus* in being able to tolerate the desiccating winds laden with dry ash, particularly on re-exposure of buried surfaces. These facts correlate well with the observations and experimental work of Gimingham (1967) on the water relations of some Antarctic mosses. The *Polytrichum* species are also able to draw on water that is held in the turf but the thin mats or carpets of *Drepanocladus* are soon desiccated. Also in accord with Gimingham's work is the observation that *Grimmia antarctici* can tolerate impregnation of the cushion by dry ash, and according to Longton (1967) it seems that this species has commonly been found on the island in this state.

Fruticose lichens, in particular *Usnea antarctica*, with their slow rates of growth, are unable to grow through ash and it appears that they suffer from the slightest and briefest burial. Whilst they appear desiccated, the colour change that has been observed means that toxic effects cannot be ruled out. On the other hand, crustose lichens have been buried in a number of places and on re-exposure always appear undamaged.

Table II summarizes the factors which determine regeneration of vegetation on Deception

TABLE II. FACTORS AFFECTING THE REGENERATION OF MOSSES AFTER BURIAL BY VOLCANIC ASH

Inherent in plants	*In the environment*
1. Growth form of species	1. Depth of burial
2. Water relations of species affecting	2. Water availability
a. tolerance to impregnation by ash	a. time in season
b. tolerance of the original colony to re-exposure	b. amount in relation to duration
c. tolerance of the regenerating shoots to exposure	3. Redistribution of the ash
3. Ability to produce rhizoids	a. may expose regenerating plants
a. for water absorption	b. may bury plants deeper
b. for consolidation of the ash	4. Toxic elements in air or ash
4. Growth rate of species determining whether or not it can consolidate the ash	5. Lack of certain nutrients
a. before the buried plant dies	6. Local modifications of the micro-environment, such as occur in fumarolic areas
b. before growing season ends	7. Wind, as a desiccating agent
c. before there is re-exposure	

Island and it will be noted that they fall into two groups: those that are inherent in the plants and environmental factors which affect them.

Colonization of new surfaces will take some time but is likely to be more rapid in fumarolic areas. It is interesting to note that the first species to colonize these areas of the land centre is a member of the Funariaceae, and this accords with the well-known ability for very rapid dispersal and colonization by members of this family. *Funaria hygrometrica* was one of the first two mosses found on Surtsey (Einarsson, 1967) whence it had probably been dispersed accidentally by Man, and also on the lava flow at Tristan da Cunha (Dickson, 1965), in fact the first record for that archipelago. As mentioned earlier, the Deception Island species has not been reported before from the Antarctic botanical zone, and it is the first instance where fruiting material has been seen. This is possibly an example of a species growing well outside its normal range, aided by a local modification of the micro-climate.

Examples of these types of situation are known from other regions of active volcanicity. At the Paricutin volcano, in a primary succession on lava flows, Eggler (1959) noted crustose lichens, algae, mosses and ferns in depressions between lava blocks. Of the mosses, a species of *Physcomitrium* (Funariaceae) was most common. He also noted the concentration of mosses that occurred around gas vents in solfataras. At Jorullo volcano he recorded that some lava flows had a 100 per cent cover of mosses of the genus *Campylopus*, the dominant species being *C. introflexus* mixed with *C. flexuosus*. It is, therefore, interesting to note that one of the mosses that has been found on the South Sandwich Islands in the characteristic zoned fumarole vegetation is *Campylopus introflexus* (Longton, 1967; Longton and Holdgate, 1967). Longton and Holdgate pointed out that *Campylopus* affords an interesting example of a temperate species restricted to fumarolic areas in the Antarctic botanical zone, and they suggested that it is the generally prevailing low temperatures which restrict the further spread of the species. At the time, its nearest known locality was the Falkland Islands but it has now been collected on South Georgia (personal communication from S. W. Greene). A further example of a plant growing outside its normal range is that of *Lycopodium cernuum*, a plant of the tropics and warm temperate zone, which is known in the cool temperate zone of Japan in association with fumaroles (Yoshioka, 1968).

The establishment of a vigorously growing bryophyte species in a land fumarolic area on Deception Island is also of interest in relation to the sole collection that has been made of an apparently endemic species of moss, *Philonotis gourdonii* Card. from the summit of Mount Pond. Matteri (1968) recorded that the label of the type collection indicates this species forms small carpets on calcareous and sulphurous deposits, and that it was collected on 28 December 1909. During the latter half of the nineteenth century it appears that the top of Mount Pond had a number of active fumaroles and that at the time of collection of the specimen these were almost quiescent. At the present time there are no snow-free substrata on the summit of Mount Pond, other than ash lying on snow. The material of *Philonotis gourdonii* was sterile and, as it bears a close resemblance to *Philonotis acicularis* (C. Muell.) Kindb. from South Georgia from which it differs only slightly in leaf shape and size and cell structure, it might well be that these differences are phenotypic responses caused by the abnormal environment. Whatever the explanation, it is noteworthy that this is the only authenticated occurrence of a species of this genus within the Antarctic botanical zone (personal communication from S. W. Greene).

Volcanic ash, while potentially giving rise to very fertile soils, is initially free of nitrogen, although it will quickly become contaminated by wind-blown or water-carried ash of greater age that will contain nitrogen-fixing micro-organisms. Ammonia is often emitted by fumaroles and this could be one of the factors that has aided the rapid colonization of parts of the fumarolic areas. Griggs and Smith (1932), Griggs (1933) and Griggs and Ready (1934), working on the effects of the eruption of Katmai, have shown that the two members of the Jungermanniaceae that colonized the ash as an almost continuous mat after 16 to 18 years were able to grow in effectively nitrogen-free soils (0·05 p.p.m.) and that while ammonia in the rainfall could provide a source of nitrogen for the plants, they concluded that they were capable of some measure of nitrogen fixation. Blue-green algae were reported from Krakatao by Ernst in 1909 (Backer, 1929), but these have not been noted so far on any new ash surfaces on Deception Island. Fogg and Stewart (1968) have demonstrated nitrogen fixation *in situ* on

Signy Island associated with *Nostoc commune* and lichens in which it is the phycobiont, so that it will be of interest to see if any such lichens or algae become established on uncontaminated new ash.

The lichen-encrusted sub-formation seems to be associated with the desiccating environments of volcanic islands (Longton, 1967), although colonies of *Sarconeuron glaciale* growing in very arid areas at McMurdo Sound are also usually heavily encrusted (personal communication from S. W. Greene). Epiphytic lichens are common on mosses in the Antarctic but the characteristic assemblage of species recognized by Longton (1967) is restricted to the ash plains of volcanic islands. Encrustation could arise through the establishment of the lichen weakening the moss or the performance of the latter being lowered through intrinsic effects such as crowding, or through extrinsic factors, such as arise during volcanic eruptions.

Buried mosses, including species of *Polytrichum*, excavated in the Kroner Lake area, were sometimes covered with abnormally high concentrations of *Collembola* and at other times with apparently freshly growing crustose lichens. It is suggested that the buried turf with dark humid conditions existing amongst its stems may provide a substratum favourable for the establishment of new lichen growth and an environment suitable for collembolan activity, where micro-fungi could also multiply. If blown free of ash, mosses that have become lichen encrusted while buried might form the basis of the lichen-encrusted moss sub-formation.

From the foregoing observations it is possible to suggest some factors which, in part, at least, appear to be responsible for the depauperate nature of the vegetation of Deception Island.

The flora will inevitably be rather limited in number of species since only some of those known within the Antarctic botanical zone can grow on basic substrata. Furthermore, there has been sufficient frequency of major volcanic activity in the last 150 years (Hawkes, 1961; Baker and others, 1969) to cause periodic direct destruction of habitats bearing such vegetation as develops during periods of quiescence. These latter periods are characterized by an initial phase during which ash is being redistributed, often by wind, and hence large areas of vegetation otherwise unaffected become buried or desiccated. Moreover, after consolidation of the ash surface much of the snow-free areas of the island are composed of porous substrata, which result in rapid drainage and arid soils, initially, at least, with low levels of nitrogen. The almost total absence of regularly moist habitats such as permanent melt streams, small lakes and dripping rocks, etc. is another feature of this volcanic island.

The persistence of these very unstable conditions has meant that a number of species that might have become established on the island have been precluded, both because of the lack of suitable moist habitats and because of their own inherent inability to regenerate efficiently when buried by ash. Gimingham (1967) has noted that *Brachythecium "antarcticum"* and *Acrocladium* (*Calliergon*) *"austrostramineum"* both lose and take up water very rapidly and so they are restricted to habitats with a permanent water supply. That they have not so far been reported from Deception Island where such habitats are very limited in extent is, therefore, not surprising. It also seems likely that these two species, with their need for a permanent water supply, would be no more efficient than *Drepanocladus uncinatus* at regenerating after burial. The form of *Drepanocladus* found on Deception Island corresponds to Gimingham's "small type from drier habitats", which is generally the hardier form.

Finally, reference should be made to the possibility of vertical or sheltered rock faces of cliffs, little affected by ash, acting as sources for re-colonization of more horizontal exposed areas. It has been observed in the case of *Prasiola crispa* that re-colonization of a penguin colony had started from tuff cliffs nearby and, as it seems that this phenomenon might be more widespread, it is worthy of further investigation.

It is, therefore, to be expected that much of the island's flora will be composed of species that are best able to withstand the prevailing arid conditions, often with periods of extreme desiccation, and also are capable of regeneration when buried. The evidence so far points to such a conclusion but it is hoped that by following the changes in vegetation at the sites marked out for future study additional information will be gained which will provide a clearer understanding of the factors involved.

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