18

PATTERN AND PROCESS IN A MACQUARIE ISLAND FELDMARK

By D. H. ASHTON and A. M. GILL
Botany Department, University of Melbourne

Introduction

The Feldmark or Fell-field formation has been defined by Beadle & Costin (1952) as 'an open sub-glacial community of dwarf flowering plants, mosses and lichens, usually dominated by chamaephytes'. Polunin (1960), however, has restricted the term to discontinuous communities of dwarf flowering plants which occupy less than 50% of the ground area in some arctic and alpine environments. Neither definition fully recognizes the fact that some of these communities may be completely dominated by bryophytes.

Pattern in Feldmark is striking and can be influenced by a number of factors such as stone nets and soil polygons (Bliss 1956), terraces (Taylor 1955), frost scars (Hopkins & Sigafoos 1951), scree (Warming 1909), and wind (Costin 1954).

The pattern in the Feldmark of Macquarie Is. is partly associated with terrace pattern, where material from frost sorting and creep has accumulated against stripes of vegetation (Taylor 1955). The present study, however, is concerned with the pattern on the windward slopes where terrace formation is very slight and discontinuous. It was undertaken in December 1964 while the authors visited Macquarie Is. with the Australian National Antarctic Research Expedition.

Environment

The Feldmark is the commonest formation on Macquarie Is. and occurs chiefly on gentle to moderate slopes above 600 ft (Pl. 28, fig. 1).

At its highest altitude, the Feldmark environment is marked by consistently low temperatures and high wind velocity. On the basis of 24 simultaneous readings of temperature over Macquarie Is., Taylor (1955) considered that the areas in which Feldmark occurs are likely to be 3-7°F cooler than at sea level. The reduction of temperature with altitude appears to be much more severe than usually encountred (Kittredge 1948). At its lowest limit, the Feldmark is suppressed by the shade cast from the vigorous rosettes of *Pleurophyllum hookeri* and tussocks of *Poa foliosa* (Taylor 1955).

Precipitation averages 40 in. per annum at the ANARE weather station. It is likely that precipitation increases with altitude, although the high winds on the plateau may offset this in some sites. Low cloud is common at Macquarie Is. and the plateau above 500 ft is frequently fog-bound.

Wind speeds of 20 knots are the most common at the weather station where the recorder is 33 ft above sea level (Law & Burstall 1956). Taylor (1955) estimates wind speeds in higher areas to be at least 25% greater than this.

The soils of the Feldmark have been called Dry Tundra soils by Taylor (1955), and the following brief account of them is taken largely from his work. Texture is variable due to varying quantities of stone and gravel throughout the profile.

Stones form a surface mat and may be frost-sorted into polygons on flat ground and parallel bands down slopes. Frost sorting is more intense on well drained soils, and the corrugations of the surface gravel have a counterpart as channels in the gravelly loam subsoil at depths of one foot or more.

Water relations vary markedly with the soil type and topography, and the poorly-drained soils may have a water-table close to the surface. The availabality of water to plants growing in these soils is further complicated by soil freezing, by mists and fogs, and by high winds. The hummocks of Feldmark vegetation are effective in intercepting rain and snow blown at high speed across the plateau (Pl. 28, fig. 2).

The Cushion Habit

The major Feldmark species, *Azorella selago*, forms a hard compact cushion. This habit is common to many families and genera of flowering plants and mosses. It is found not only in sub-glacial and alpine environments, but also in hot desert areas (Warming 1909). Rauh, cited by Troll (1960), calculated that 64% of all 'cushion plants' occur either in high tropical Andes or in the sub-Antarctic.

Spomer (1964) has shown that the cushion habit of some alpine plants may disappear when they are transplanted to lower elevations. He concluded from both field and laboratory experiments that temperature was perhaps the most important factor controlling the development of the cushion habit. Light, wind, and moisture-stress were considered to be less significant. However, wind as a factor has been emphasized by both Warming (1909) and Cockayne (1928). The former author connected wind effects with desiccation, particularly in cold climates where water deficits may develop in the plant due to retarded water absorption. Warming (1909) supports this theory by reporting cushion plants from 'arid, hot, but tolerably calm desert places' (p. 38).

At Macquarie Is. the cushion habit of *Azorella* was maintained on a relatively protected scree but, under the extreme protection of overhanging rocks, it may be more open and show etiolation. Hence, any one environmental factor does not explain all cases. Probably the habit is the result of a very slow growth rate and a prolific branching pattern resulting from a poorly developed apical dominance.

The growth rate of *Azorella selago* at Macquarie Is. has been estimated by Taylor (1955) to be ¼ in. per year. About 5-6 shortly-lobed sheathing leaves are produced each year with a density of 20-22 leaves per inch of stem. These die with the onset of winter and accumulate on the stem from year to year, gradually decaying into peat at the base of the cushion. Because of the branching habit and the stiff divergent leaves, the canopy is under considerable lateral pressure. The complex branching habit is shown in Fig. 1.

The streamlined surface of these cushions probably permits escape from the physical and abrasive effects of wind and the minimum area so exposed may prevent excessive transpiration and heat loss.

The long-roots of the *Azorella* (observed in summer) have a corrugated appearance, apparently due to contraction. The stele appears to be unaffected although the cortex is convoluted, and in transverse section contains large gaps. Although contractile roots are common in many species (Esau 1953), it is possible that their significance is greater in the Feldmark environment than elsewhere, as soil frosting occurs and strong winds prevail; the contraction may enable better purchase in the ground and prevent uprooting. Kokkonen (1927) found a correlation between the extensibility of the roots of four rye varieties and their ability to overwinter in frosted soils.

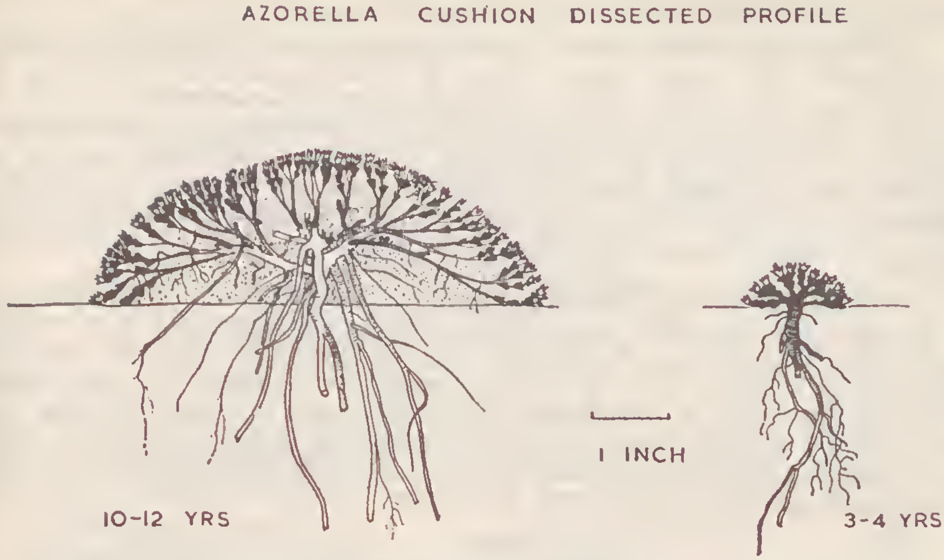


FIG. 1—Complex branching habit of *Azorella* cushions, showing large contractile roots and the accumulation of peat and fine soil.

Feldmark Vegetation

Taylor distinguished two alliances within this formation: the *Azorella selago* alliance and the *Dicranoweisia antarctica* alliance. The *Azorella selago* alliance was split into three associations depending on the proportion of the moss *Rhacomitrium crispulum*. This alliance occurs on the ramps of the leeward terraces and on the windward slopes. The *Dicranoweisia antarctica* alliance occurs on the flats or treads of the leeward terraces and on the most exposed saddles and mountain tops.

In the N. half of the island from Green Gorge to North Mt (800-900 ft), we have found that the dominant moss in the *Dicranoweisia antarctica* alliance is in fact *Ditrichum strictum* Hampe; no *Dicranoweisia* could be found, although it was collected by the ANARE from Wireless Hill in 1950. This alliance will be referred to henceforth as the *Ditrichum strictum* alliance.

The Feldmark consists of dense patches and stripes of vegetation which are separated by sparsely vegetated pavements of gravel and stones. The patches and stripes of vegetation can be considered as 'micro-associations' of species and, therefore, are only part of the whole vegetation of the site. The Feldmark shows variation in both the scale of patterning and floristic composition.

The scale of patterning is determined by the size of the terrace formation on the site. On the windward slopes (W. and NW.) the terraces are slight and limited to the discontinuous stripes of vegetation. The intervening pavements contain scattered colonies of *Ditrichum*, *Andraea*, and the regenerating dominants of the stripes. On the leeward slopes (E. and SE.), the terraces are large and the ramps are clothed with continuous vegetation forming giant stripes which are separated by the gravel pavements of the flats or treads. The presence of scattered colonies of *Ditrichum* and *Andraea* on these latter sites may be related to the local severity of either wind (as suggested by Taylor) or frost. On intermediate aspects (NE.)

there may be a mixture of patterns due to the small scale stripes growing forward along the contoured flats of the large terraces.

A floristic simplification occurs in response to increased wind exposure on both the windward and leeward slopes. Thus, on relatively moderate exposure, the Herbfield associates of *Azorella* are diminished and *Rhacomitrium* becomes co-dominant. Wind exposure can exceed the limits of *Azorella* on the windward slopes, resulting in a community of *Rhacomitrium* stripes and *Ditrichum* colonies. On the most severe exposures *Rhacomitrium* disappears, leaving only the *Ditrichum* element of the Feldmark. The associations recognized by Taylor on the windward slopes are convenient points of reference in what is more or less a continuous gradation.

The classification of the Feldmark, therefore, presents considerable difficulties. We consider that the whole vegetation can be better interpreted as a complex *Azorella-Ditrichum* alliance, because *Ditrichum* is intimately mixed with the other dominants on so many sites. In this vegetation, the concept of the association should be broadened to encompass the whole pattern on any site. This then overcomes the objection of having a closed *Azorella* association (Taylor 1955) on the leeward slopes in a formation that is, by definition, an open one. This alternative classification of Feldmark associations is set out in Table 1.

TABLE 1

Feldmark Classification

According to Taylor (1955)	Alternative Scheme
Azorella alliance	*Azorella-Ditrichum* alliance
Azorella association	*Azorella* association
	windward facies
	leeward facies
Azorella-Rhacomitrium association	*Azorella-Rhacomitrium* association
	windward facies
	leeward facies
Rhacomitrium association	*Rhacomitrium* association
Ditrichum (*Dicranoweisia*) alliance	
Ditrichum association	*Ditrichum* association

The *Azorella selago-Rhacomitrium crispulum* Association (windward facies)

DESCRIPTION

This association consists of isolated cushions and stripes of *Azorella selago* and *Rhacomitrium crispulum* aligned at right angles to the prevailing wind. This alignment is usually along the contour but it may be inclined to this on the south-westerly slopes. The individual stripes may be 1-10 ft long, 3-30 in. wide, and up to 3-4 in. high. These micro-associations of either or both dominants may contain several species of mosses, liverworts and lichens, a prostrate fern, and stunted herbs and grasses. Liverworts in particular are more numerous than has been indicated by Taylor (1955). The species occurring in these micro-associations at North Mt are listed in Table 2. The percentage cover of the cushion areas and major component species has been determined by line transects and is summarized in Table 3 (J. F. Jenkin pers. comm.). As the degree of exposure to wind increases, the cushions of *Azorella* become more prostrate and less hemispherical, and *Rhacomitrium* becomes more and more prominent. On the gravel pavement between the stripes, isolated dark green cushions, balls and crescentic colonies of

Ditrichum strictum occur. Also scattered on these sites are the reddish tufts of *Andraea acutifolia* and the regenerating brown and green patches of the dominants, *Rhacomitrium crispulum* and *Azorella selago*.

TABLE 2

Species present in Azorella-Rhacomitrium *stripes, North Mountain*

VASCULAR PLANTS

Azorella selago (Umbelliferae)
Luzula campestris var. *crinata* (Juncaceae)
Agrostis magellanica (Gramineae)
Pleurophyllum hookeri (Compositae)
Acaena anserifolia (Rosaceae)
Coprosma pumila (Rubiaceae)
Grammitis billardieri (Filices)

NON-VASCULAR PLANTS

BRYOPHYTES	LICHENS	
Mosses—	Foliose—	
Rhacomitrium crispulum	*Parmelia sublugubris*	(l)
R. lanuginosum var. *pruinosum*	*Sticta glabra*	(d)(l)
Ditrichum strictum	*Peltigera polydactyla*	(l)
Leptostomum inclinans	Fruticose—	
Breutelia pendula	*Cladonia fimbriata*	(d)
Rhacocarpus humboltii	*Cladonia aggregata*	(r)
Dicranoloma robustum var. *setosum*	*Sphaerophorus tener*	(d)(r)
Campylopus clavatus	*Usnea contexta*	(d)(l)
Psilopilum australe	Crustose—	
Polytrichum (*Pogonatum*) *australe*	*Psoroma versicolor*	(d)
Thuidium furfurosum	*Megalospora* sp.	(d)
Liverworts—	*Pertusaria tyloplaca*	(d)
Jamiesoniella colorata		
Adelanthus occlusus	(d) = on dead *Azorella*	
Lepidozia laevifolia	(l) = on living *Azorella*	
Lejeunia primordialia	(r) = with *Rhacomitrium*	

REGENERATION

(a) The *Azorella-Rhacomitrium* cushion.

Isolated seedlings of *Azorella* and small tufts of *Rhacomitrium*, one inch in diameter, occur on the erosion pavement in the micro-habitat provided by stones 2-4 in. in diameter. As these plants develop above this local protection, they are affected by the severe wind and grow as low tough discs of vegetation 1-2 in. high. As they become more dome-shaped they are liable to die back, lose coherence, and develop an erosion scarp on the windward side. They ultimately become asymmetrical and crescentic in outline, and continue to grow forward in their own shelter. The dieback on the windward crest of *Azorella* cushions, in part, may be due to the failure of the growing points to resume growth after the winter death of the leaves. Dieback patches are often slimy with blue-green algae and are frequently colonized by crustose lichens.

The older plants of the dominants are rarely pure colonies. Small plants of *Luzula campestris* var. *crinata*, *Agrostris magellanica*, *Grammitis billardieri*, and even *Pleurophyllum hookeri* are to be found, particularly on the lee sides of the

TABLE 3

Percentage cover of Feldmark estimated from progressive totals of intercepts on three 100 ft line transects downslope 5-6° to W., on North Mountain, April 1965 (J. F. Jenkin)

		0-100′	0-200′	0-300′
Azorella selago	living	13·6	15·8	14·0
Azorella selago	dead	1·5	1·2	1·8
Azorella selago	total	15.1	17·0	15·8
Rhacomitrium crispulum	living	19·7	21·5	20·2
Rhacomitrium crispulum	dead	1·7	1·8	1·7
Rhacomitrium crispulum	total	21·4	23·3	21·9
Agrostis magellanica		2·2	1·8	1·2
Luzula campestris var. *crinata*		1·2	2·0	1·3
Pleurophyllum hookeri		0·9	0·9	0·5
Lichens (6 spp.)		0·8	0·6	0·7
Acaena anserifolia var. *minor*		—	1·0	0·7
Pogonatum alpinum		0·1	0·1	0·1
Ranunculus biternatus		—	0·01	0·01
Andraea acutifolia		0·1	0·2	0·2
Ditrichum strictum		—	0·1	0·1
Coprosma pumila		—	—	0·04
Liverworts and other Mosses		—	—	0·1
Bare ground, stones		58·1	53·0	57·3
Total vegetation stripe		41·7	46·7	42·4
Between stripe vegetation		0·2	0·3	0·3
Total vegetation		41·9	47·0	42·7

cushions. The non-rhizomic plants, especially if long lived, will be gradually removed as the growth and subsequent erosion of the cushion proceed.

The tufts and cushions of *Ditrichum* and *Andraea* are intolerant of competition from the dominant plants and are soon suppressed if they are invaded by propagules or overrun by an advancing cushion or stripe.

The mats of *Rhacomitrium* are common sites for the establishment of *Azorella* seedlings. Often several seedlings establish in one mat, and their combined growth results in the peripheral displacement of the moss (Fig. 2). The moss is caught between the young expanding cushions and forms a hedge ½-1 in. higher than the surroundings (Pl. 29, fig. 1). The polymorphic nature of the mature cushion can be seen in the mosaic of colour and flowering times.

Erosion at this stage removes *Rhacomitrium* from the windward side and the structure becomes essentially a double stripe (Fig. 3). Proof of its forward movement is shown by the fact that *Rhacomitrium* has its origin beneath the *Azorella*, and the stems and roots of *Azorella* may protrude up to at least 18 in. from the eroding scarp on the windward side (Pl. 29, fig. 2). The fact that the *Rhacomitrium* forms a leeward strip to the *Azorella* hummock does not necessarily mean that it is less wind resistant.

Why these stripes develop at right angles to the wind is not understood. It is possible that erosion is less severe at the edges of the cushion due to eddy effects. Lateral expansion may not be as great as leeward growth, but over a long time may lead to the formation of an elongated stripe. The pattern at Macquarie Is. differs from the *Rhacomitrium lanuginosum-Empetrum* erosion complex at 3,000-3,500 ft

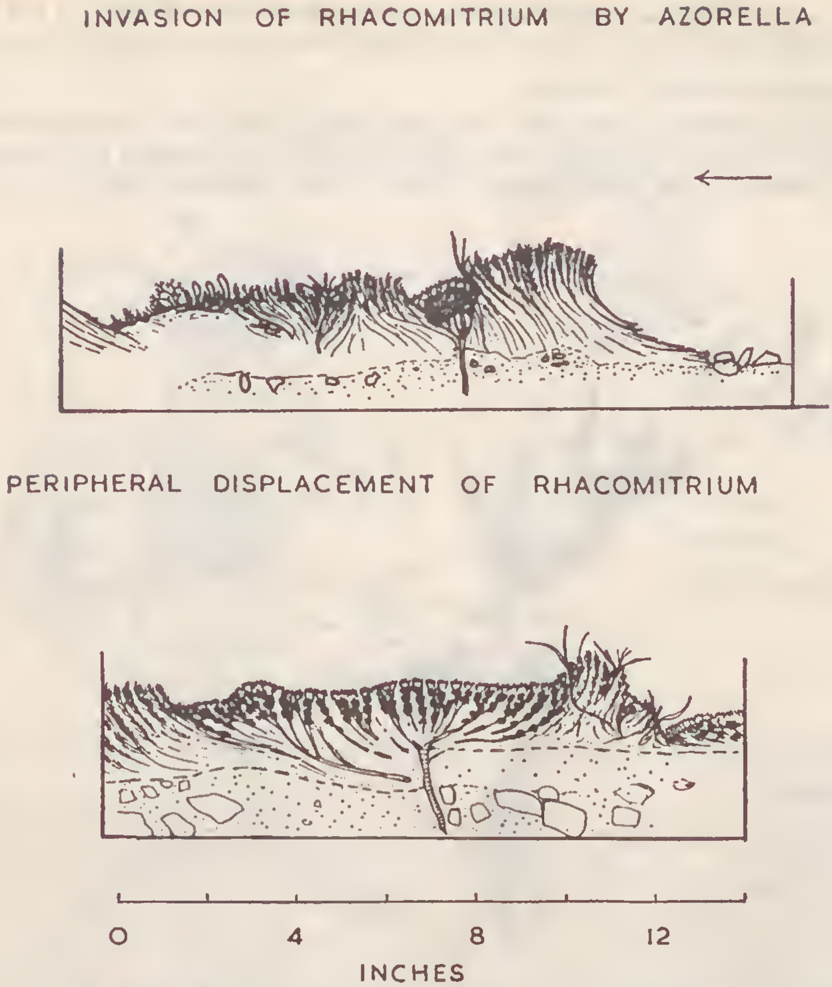


FIG. 2—Two stages of the invasion of *Rhacomitrium crispulum* mats by *Azorella selago*; *Luzula campestris* and *Agrostis magellanica* are common associates. In the upper example the simple leaves of the fern *Grammitis billardieri* protrude through the moss shoots.

in the Cairngorms (Burges 1951, Watt 1947) in that the vascular dominant occurs on the exposed side of the stripe. From leaf scar measurements, the age of the stripes is of the order of 20-80 years. The total life span of the plant is not known, but it is eertainly not indefinite, sinee the whole of the hummock may die simultaneously and the dcbris, peat aeeumulation, and any small associated plants are seoured away by the wind. Living *Rhacomitrium* is often blown away at this stage although, if it is large and firmly establishcd, it may remain and continue growth. It may then be subjeet to further eolonization by *Azorella*.

In some eases, the diebaek of tall *Azorella* eushions starts at the exposed summit and spreads to the base, lcaving only a ring of living *Azorella*. Whether adventitious roots would sustain these shoots during severe storms is not known.

Whether or not *Rhacomitrium crispulum* establishes in *Azorella* mats is not known with certainty, but some evidence from shallow stem depths suggests it can do so.

(b) *Ditrichum strictum* cushions.

.*Ditrichum* tends to form pure units, but older plants may be associated with the leafy liverwort *Jamiesoniella colorata*. The growth form appears to be dependent on the vagaries of the environment. When a small cushion grows to 1-2 in. in

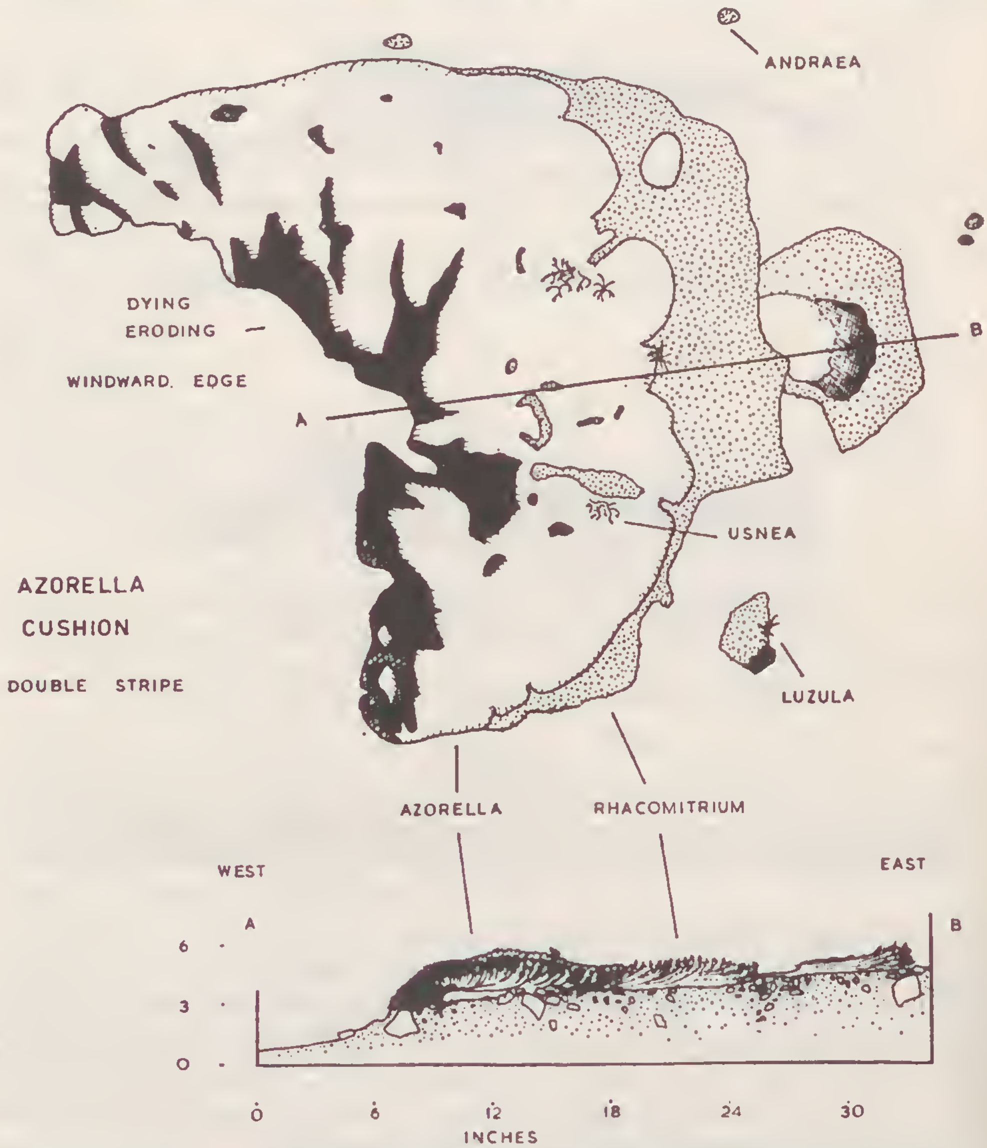


FIG. 3—Plan and profile of a double stripe of *Azorella* and *Rhacomitrium* showing pattern of die back on the windward side (shaded). This forms terraces in the surface of the cushion in some places. An independent colony of *Rhacomitrium* to the right is also showing erosion on its windward side.

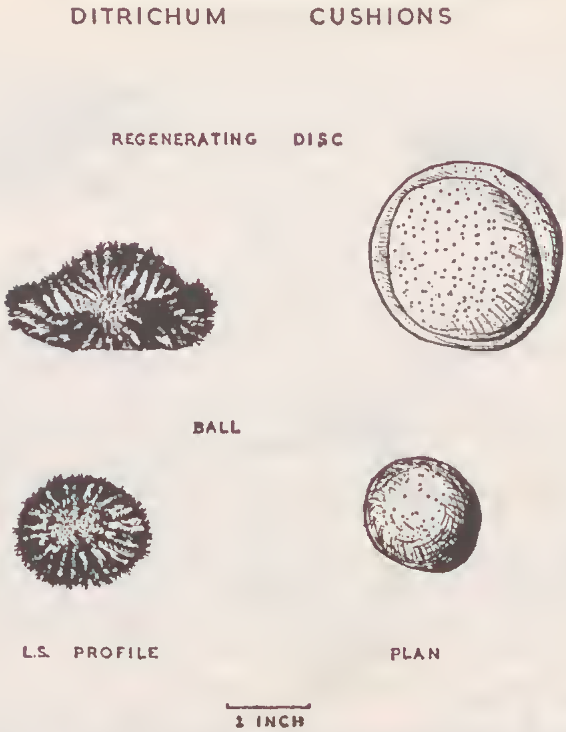


FIG. 4—The 'ball and button' types of *Ditrichum* colony showing longitudinal sections.

diameter it may be dislodged by wind or frost action. However, it has the ability of continuing growth even though overturned. By a repetition of overturning and regeneration, a complete ball of moss up to 3 in. in diameter may form with a core of fine accumulated mineral soil and peat (Fig. 4). If a large unit remains in a stable position for sufficiently long to kill the underneath shoots, then, on overturning, the regeneration may not proceed fast enough to offset erosion of the dead area. A ring of moss can thus be formed. However, it is possible that the rings of moss could also develop by the death and erosion of the centres of the cushions. Such death can be due to fungal attack (Warren Wilson 1951) although this has not been observed at Macquarie Is.

One very large ring of *Ditrichum*, 11 in. in diameter, showed active erosion in the centre, due to direct and eddying wind effects. Whether the rate of radial growth can keep pace with such erosion is not known, but crescentic fragments (Pl. 29, fig. 3) growing before the wind are common.

Conclusion and Summary

It is proposed to consider the Feldmark community as one large unit, the *Azorella-Ditrichum* alliance.

The *Azorella-Rhacomitrium* association within this framework consists of complex isolated cushions of *Azorella* and *Rhacomitrium* and very scattered *Ditrichum* and *Andraea* tufts in the intervening pavement.

Although *Rhacomitrium* mat is more wind-resistant than the *Azorella* cushion,

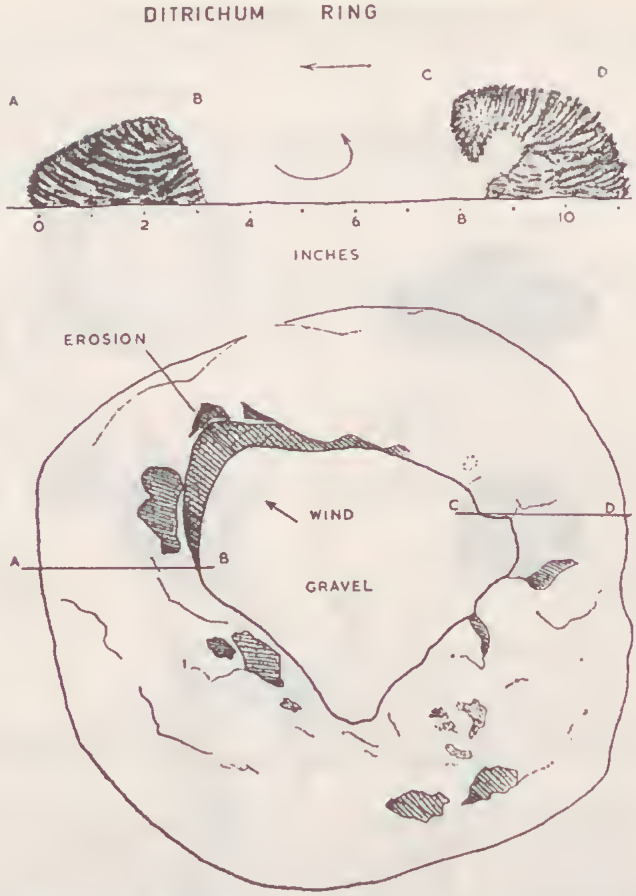
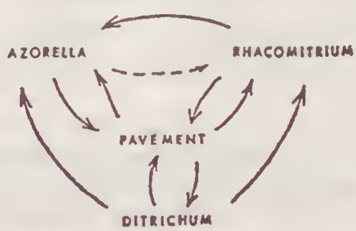


FIG. 5—Large ring of *Ditrichum strictum* showing erosion on the windward surfaces. The liverwort *Jamiesoniella colorata* is shown in the section at the right-hand side. Arrows indicate predominant wind direction.

it is usually found on the leeward sides of the vegetation stripes. This is due to the mode of regeneration of *Azorella* in the moss mats, and the subsequent erosion on the windward sides. These communities may be linked in a series of regeneration cycles which are to some extent due to chance establishment and subsequent growth before the prevailing winds. On the gentle W. slopes of North Mt the sequence of vegetation may be summarized as follows:



Acknowledgements

We would like to express our sincere thanks to Dr P. G. Law for permission to join the ANARE to Macquarie Is. in December 1964. We would also like to thank Mrs A. E. Hodgson for the determinations of the liverworts, Messrs J. H. Willis and K. N. Allison for the determinations of some of the mosses, and Mr R. Filson for the determinations of the lichens.

References

BEADLE, N. C. W., and COSTIN, A. B., 1952. Ecological classification and nomenclature. *Proc. Linn. Soc. N.S.W.* 77: 61-82.

BLISS, L. C., 1956. A comparison of plant development in microclimates of arctic and alpine tundras. *Ecol. Monog.* 66: 303-337.

BURGES, A., 1951. The ecology of the Cairngorms III. The *Empetrum-Vaccinium* Zone. *Jour. of Ecol.* 39: 271-284.

COCKAYNE, L., 1928. *The Vegetation of New Zealand.* Leipzig.

COSTIN, A. B., 1954. *The Ecosystems of the Monaro Region of New South Wales with special reference to Soil Erosion.* Sydney.

ESAU, K., 1953. *Plant Anatomy.* New York.

HOPKINS, D. M., and SIGAFOOS, R. S., 1951. Frost action and vegetation patterns on Seward Peninsula, Alaska. *U.S. Geol. Surv. Bull.* 974-c.

KITTREDGE, J., 1948. *Forest Influences.* New York.

KOKKONEN, P., 1927. (On the relationship between the hibernation of rye and the extensibility and tensile strength of its roots.) English summary—*Acta Forestalia Fennica* 33: 1-45.

LAW, P. G., and BURSTALL, T., 1956. *Macquarie Island. Interim Reports* 14.

POLUNIN, N., 1960. *Introduction to Plant Geography.* London.

SPOMER, G. G., 1964. Physiological ecology studies of alpine cushion plants. *Physiol. Plant.* 17: 717-724.

TAYLOR, B. W., 1955. The flora, vegetation and soils of Macquarie Island. *ANARE Reports Series B,* 11: 1-190.

TROLL, C., 1960. The relationships between the climates, ecology and plant geography of the southern cold temperate zone and the tropical high mountains. *Proc. Roy. Soc. Series B* 152: 529-532.

WARMING, E., 1909. *Oecology of Plants.* Oxford.

WARREN-WILSON, J., 1951. Observations on concentric 'fairy rings' in an arctic moss mat. *Jour. of Ecol.* 39: 407-416.

WATT, A. S., 1947. Pattern and process in the plant community. *Jour. of Ecol.* 35: 1-22.

Explanation of Plates

PLATE 28

Fig. 1—General view of Macquarie Is. plateau at 800 ft above sea level, looking S. to Mt Ifould and Mt Hamilton. The Feldmark is the windward slope facies dominated by stripes of *Rhacomitrium* and *Azorella.*

Fig. 2—*Azorella selago* Feldmark cushions and stripes at 750 ft altitude showing collection of snow driven by high winds during a storm in December 1963.

PLATE 29

Fig. 1—Hedges of *Rhacomitrium crispulum* in a developing *Azorella* cushion.

Fig. 2—Eroded cushion of *Azorella-Rhacomitrium* forming a double stripe. The old stems and roots of *Azorella* occur in the eroded pavement on the windward side.

Fig. 3—Small eroding cushions of *Ditrichum strictum* between the cushions of *Azorella* on the windward slope Feldmark.