R. D. Seppelt¹, P. A. Broady², J. Pickard³ & D. A. Adamson³

¹Antarctic Division, Department of Science, Kingston, Tasmania 7050, Australia; ²Department of Botany, University of Canterbury, Christchurch, New Zealand; ³School of Biological Sciences, Macquarie University, North Ryde, NSW 2113, Australia

Key words: Antarctica, algae, mosses, lichens, ecology

Abstract

Maps are presented showing the recorded distribution and species density of terrestrial plants in the Vestfold Hills. The distribution, biomass and species diversity of terrestrial lithic algae, mosses and lichens is influenced positively by availability of meltwater from drift snow and by additional nutrient supply (probably N and P) near bird nest sites. The terrestrial plants are affected negatively by exposure (including sand blast) and salinity. These four factors are probably the most important environmental characteristics exercising local control over plant distribution and abundance within the limits set by temperature.

Large changes in salinity, degree of exposure, water supply and nutrient supply occur across the Vestfold Hills, with the most favourable conditions generally occurring in the eastern half fairly close to the ice sheet.

Plant distribution and abundance are also discussed in relation to the length of time that particular areas have been exposed as a result of ice retreat. With increasing time of exposure, plant diversity and abundance rise but subsequently fall sharply as conditions become more arid, saline, or both. This temporal sequence can be explained by considering changes in the important factors that control plant growth.

Introduction

The Vestfold Hills comprise about 400 km² of icefree rock. The relief is generally low, the highest point being only about 160 m above m.s.l. The hills and valleys are draped with a variable cover of glacial till and support a flora of at least six moss species (Seppelt, 1986a), a minimum of 23 lichen species (Seppelt, 1986b), and at least 82 species of terrestrial algae, in which Cyanobacteria (about 34 species) and the Chlorophyta (about 36 species) predominate (Broady, 1986).

The eastern interior is generally more rugged and higher than the western half, with numerous hills and steep-sided valleys. Towards the coast there is a broad band of more gentle relief (up to 10 km in breadth) and wide valleys and open plains covered with moraines and tills. The geology of the region has been described by Crohn (1959), Law (1959), McLeod (1963) and Collerson & Sheraton (1986). A general summary was given by Johnstone *et al.* (1973). The country rock is chiefly gneissic with pyroxene-quartz-feldspar rocks predominating. Numerous basaltic dykes transect the whole area. The geological relationships between the Vestfold Hills and the neighbouring localities of Princess Elizabeth Land have been discussed by Wellman & Williams (1982), while a detailed discussion of the ancient metamorphics of the Vestfold Hills – Prydz Bay region has been given by Sheraton & Collerson (1983).

The climate is cold, dry and windy. Mean summer maximum temperatures rise to about $+2^{\circ}$ C but, as is typical of continental antarctic localities, temperatures are below 0°C for most of the year, falling to as low as -40° C in winter. Climatic data have been

summarized by Burton & Campbell (1980) and a general discussion of the climate is given by Streten (1986).

The area of exposed country rock in the Vestfold Hills has a significant effect on the climate. The low albedo of rock (compared with ice and snow) results in a mean annual temperature for Davis ($68^{\circ}35'$ S, $77^{\circ}58'$ E) of -10.2° C, compared with -11.2° C for Mawson ($67^{\circ}36'$ S, $62^{\circ}53'$ E) which, in contrast with the Vestfold Hills, is situated on a small coastal rock outcrop at the edge of the ice plateau in Mac.Robertson Land. Davis is, on average, warmer than other antarctic stations at similar latitudes.

The wind at Davis, 25 km from the ice plateau, has an annual mean velocity of 5 m s⁻¹, which is low for antarctic stations (Streten, 1968). Katabatic winds, present near the edge of the continental ice sheet, dissipate over the intervening hills and have little or no effect near the station (Lied, 1963). This contrasts with the marked katabatic component of the winds at Mawson (Seppelt & Ashton, 1978).

Although cloud cover and snow precipitation are greater at coastal Davis than at the plateau edge, there is a higher incidence of drift show nearer the plateau. Drift snow is of considerable importance to the terrestrial vegetation in providing a source of moisture supplementing snow fall, which occurs mainly in winter. Snow accumulates only in the lee of ground relief where shelter from wind also reduces loss by ablation (Fig. 9a). As the antarctic climate is extremely arid, meltwater is a major factor governing plant distribution. On a local scale many distribution patterns reflect almost exactly the first accumulations of drift snow.

There is a general belief that antarctic terrestrial plant communities have a simple structure, e.g. Usher (1983), this belief presumably referring to the small stature, low biomass, low productivity and low species diversity of the vegetation. Antarctic terrestrial algal, moss and lichen communities lack the complex spatial structure and the many trophic levels of consumers in, for example, forest communities. However, there is a wide range of antarctic plant communities from endolithic algae and lichens (Friedmann, 1977, 1982; Friedmann & Ocampo, 1976; Broady, 1981c) to epiphytes (Longton, 1979; Seppelt & Ashton, 1978; Broady, 1981b), including multispecies assemblages displaying both vertical and horizontal complexity. Given the extent of plant abundance, some of the visually striking moss and lichen communities with their associated fungal, algal and invertebrate populations may be as complex as other physically larger communities elsewhere.

Methods

The distribution of lichens and mosses in the Vestfold Hills was determined initially by recording species presence in 1 km grid squares during the summer of 1978/79 with supplementary records obtained during 1980/81. Voucher specimens were collected for the verification of records and also for taxonomic studies. Specimens are currently housed in the herbarium of the Antarctic Division (ADT). Further analyses of lichen and moss distributions were undertaken on 70, 2 km squares. A total of 181, of a possible 635, 1 km grids were traversed for the lichen and moss survey.

Algal distribution was determined similarly with samples of epilithic, sublithic and chasmolithic algae, initially by direct microscopic observations of samples followed by culture of some of the taxa at the University of Melbourne.

Results and discussion

Lithic algal distribution

Lithic algae, or those associated with rock (Golubic *et al.*, 1981) may be categorized into five major groups (Friedmann & Galun, 1974): epilithic (on the exposed surfaces), chasmoendolithic (in cracks and fissures), cryptoendolithic (in structural cavities within porous rocks), euendolithic (organisms actively boring into rocks and forming tunnels) and sublithic (on the undersurfaces of transculent stones embedded on the soil surface). Chasmoendolithic and cryptoendolithic algae from continental Antarctica have been discussed by Friedmann & Ocampo (1976), Friedmann (1977) and Thompson (1979). Broady (1979, 1981b, 1981c) has studied chasmoen-

dolithic algae from the South Orkney Islands and coastal locations in Mac.Robertson Land and Princess Elizabeth Land as well as subaerial epilithic algae from these continental localities.

There are clear patterns in the distribution of terrestrial algae between habitats (Broady, 1986). Only seven species have been recovered from epilithic and nine species from chasmoendolithic habitats, reflecting the harshness of these habitats. Where there is a greater availability of water a wider diversity of algae is encountered, with a maximum of 48 species recovered from unenriched soils. From soils enriched in nutrients by animals 23 species have been recorded, while 24 sublithic species have so far been identified. Forty-one species have been identified as epiphytes.

Numerous taxonomic difficulties remain, however, and a great deal of further study of algal ecology is needed.

Figure 1 shows the distribution of epilithic algae, mostly Cyanobacteria, on rocks receiving percolation of meltwater. These epilithic communities do



Fig. 1. Distribution of epilithic algae in 1 km squares. Presence is indicated by closed circles. Open circles indicate that epilithic algae were not observed. Blank squares were not examined. The organisms were mostly Cyanobacteria which formed black encrustations on rocks receiving percolations of fresh meltwater.

not appear to be salt tolerant and have been found only in areas where snow drifting is frequent. They are probably more abundant in the north-eastern corner and along the interior margin of the Vestfold Hills than indicated in Fig. 1; but we are unable to verify this due to the limited number of field observations in these localities.

Chasmoendolithic algae (Fig. 2), although obviously widespread, have not been searched for comprehensively in the Vestfold Hills. Such algae may be more abundant in coastal regions than further inland but firm conclusions cannot yet be drawn.

Wind may have both direct and indirect effects on the local distribution patterns of these communities. Broady (1981c) found that in coastal chasmoendolithic communities *Prasiococcus calcareus* (Boye Petersen) Vischer occurred only in areas subjected to wind blown salt while a *Desmococcus* species occurred only in areas not affected in this way. Abrasion of the windward surfaces of rock substrata by



Fig. 2. Distribution of chasmoendolithic algae. Symbols as for Fig. 1. More extensive sampling is required but a wide distribution in the western part of Broad Peninsula is clear.

windborne sand and ice crystals inhibit colonization. Chasmoendoliths have generally been found only on leeward rock faces in the Vestfold Hills, the exposed northern to eastern aspects being both wind-affected and generally free of snow drifts. In contrast, Friedman (1977) reported that in the dry valleys of Victoria Land, cryptoendolithic communities were generally found on faces with northerly aspects where there is greater insolation.

Sublithic algal growths are widespread in the Vestfold Hills in nearly all areas visited (Fig. 3), even on the driest soils (Broady, 1981a). Absence of sublithic algae from grid squares may reflect sampling error rather than real absence. Abundance in grid squares varies widely. Twenty-four taxa have been identified (Broady, 1986) but only four are abundant: *Chroococcidiopsis* sp., and *Plectonema* sp., (Cyanophyta); *Desmococcus* sp., and *Prasiococcus calcareus* (Chlorophyta). Habitat selection by the different algae resulted in *Chroococcidiopsis* and *Desmococcus* favouring dry, raw mineral soils, *Plectonema* moist, raw mineral soils and *Prasiococcus*



Fig. 3. Distribution of sublithic algae on the undersurfaces of transculent quartz stones and the rare erratics of marble. Symbols as for Fig. 1.

calcareus seal and bird influenced soils. Chlorophyll *a* estimates showed sublithic algal growths to be considerably more abundant than growths in adjacent exposed soil surfaces but less abundant than superficial algal growths in favourable wet microenvironments (Broady, 1981a). Although not widely studied in continental antarctic regions, sublithic algae have also been reported from Ongul Island (Fukushima, 1959) and from the dry valleys of southern Victoria Land (Cameron, 1972; Thompson, 1979). Their distribution right across the Vestfold Hills reflects the sheltered sublithic environment which allows algal

growth even in the harsh conditions on the western part of the hills.

Lichen and moss distribution

Figures 4 & 5 show the distribution of mosses and lichens in the Vestfold Hills. In the initial surveys a total of 24 species was recorded. Further taxonomic studies have revealed the presence of an additional moss, *Ceratodon purpureus* (Hedw.) Brid (*C. minutifolius* Card., *sensu* Horikawa & Ando, 1963),



Fig. 4. Distribution of moss. Symbols as for Fig. 1.



Fig. 5. Distribution of lichen. Symbols as for Fig. 1.

and several additional lichens (*Verrucaria* sp., *Buellia* sp., *Lecidea* sp.) have been identified but none of these have been included in the analyses. Such taxonomic difficulties emphasize the necessity for the collection of voucher specimens not only for studies of taxonomy and phytogeography but also for ecological and physiological studies.

Analysis of distribution patterns has also been undertaken on 70, 2 km squares, indicating densities of between one and 21 species per square (Figs. 6, 7 & 8). Figure 6 shows concentrations of species in some localities, such as Ellis Rapids, Lake Zvezda and Lichen Valley, while in others, particularly in the seaward and southern perimeters and south-eastern corner, there are comparatively few species. Only one grid had more than 20 species; five grids had 16-20 species; 14 grids had 11-15 species; 12 grids had 6-10 species; 35 grids had between one and five species present. While these 67 grids represent a biased sampling which reflected collecting intensities, a reasonable effort was made to examine less favourable habitats by specific searches and by vary-



Fig. 6. Number of moss and lichen species in 2 km squares. Each spot is centered within each square rather than over sites.



Fig. 7. Number of moss species in 2 km squares, spots centrally located.

ing foot traverse routes across the hills. The pattern of distribution shows clear variation between moss and lichen in numbers of species and in geographic range (Figs. 7 & 8). Analysis of coarse distribution data in maps as well as by principal coordinate ordinations and canonical correlation analysis of the ordination vectors (Pickard, 1986) reveals several patterns worthy of closer investigation.

First, is the reduction in number of species close to the ice sheet and Sørsdal Glacier (as seen for example in Figs. 4 & 6) real or an artefact? The reduction may, in fact, be real, particularly in the area affected by the Chelnock Glaciation (Pickard & Adamson, 1983), when at about 1000-2000 a B.P., ice surged north from the Sørsdal Glacier, crossing Crooked Lake before it halted and retreated to its present position. As with the narrow easternmost strip of the Hills close to the ice sheet, there may have been insufficient time for complete colonization of the area and conditions may still be unsuitable for colonization.

Second, wind direction has remained essentially constant from the north-east over the last 4000-6000 a (Pickard, 1982) so that salt from the



Fig. 8. Number of lichen species in 2 km squares, spots centrally located.

open sea, marine embayments and saline lakes in the northern, central and western sectors of the Hills has been blowing over Long Peninsula, western Broad Peninsula and western Mule Peninsula for some thousands of years. Salt impregnated sediments have also been elevated above sea level by isostatic uplift along the western edge of the Hills.

Third, there is a clear east-west gradient of species



Fig. 9. a.Remains of ephemeral snow drift in lee situations at Ellis Rapids. Algae, lichen, and moss encrusted with algae, form a prominent dark zone. b. Crustose and foliose lichens on a sheltered ledge in a cleft near the eastern margin of the Hills. Remnants of drift snow lie on the foliose lichens along the back of the ledge. c. Moss turf with convoluted surface showing fragmentation into polsters. This is as luxurious a community of terrestrial plants as occurs in the Hills. d. Moss community at Lake Stinear near the limit of moss survival. It is one of the most westerly moss communities on the central part of Broad Peninsula. The plants are affected by wind-blown sand.

richness and complexity of communities. In the east, lichen assemblages close to the ice sheet (Fig. 9b) give way to moss beds with epiphytes and generally richer lichen assemblages (Fig. 9c). In the western half there is a rapid decline to simple lichen assemblages of only one or two species. Interpretation of this complex gradient as a classical succession following ice retreat is unsatisfactory. Species richness does increase with distance from the present edge of the ice sheet to reach a peak at about 1.5 km from the ice (Fig. 9c). Over this distance and at any particular site, species richness increases with the time elapsed since deglaciation. This pattern conforms to the classical succession model. However, the model breaks down with increasing distance from the ice sheet or, what is essentially the same thing, increasing time since deglaciation. Beyond 5-10 km from the ice sheet there is a sharp reduction in abun-



dance/richness. The land here has been deglaciated for 3000-5000 a or even longer, thus allowing accumulations of both salt and loose sand to reach toxic or detrimental levels (Fig. 9d). The climax crashes.

Fourth, areas relatively rich in mosses and lichens are frequently associated with elevated land. The main areas over 60 m above msl are shown in Fig. 8. This correlation may be related to two factors. In the eastern areas of higher relief there is an abundance of suitable nesting sites for birds, particularly snow petrels. As a result there are many localized areas rich in plant nutrients, particularly phosphorous. The higher land also traps abundant snow from the nearby ice sheet. In this way favourable nutrient and moisture conditions are provided for small sites which lic outside the more saline zone to the west and, in lee situations, are also sheltered from sand and snow blast.

The terrestrial flora of the Vestfold Hills may be considered as representative of much of continental Antarctica. Differing taxonomic interpretations make overall biogeographic comparisons difficult, particularly in regard to the moss genus *Bryum* and lichen genera such as *Buellia*, *Lecidea*, *Caloplaca*, *Xanthoria* and *Rinodina* (Pickard & Seppelt, 1984; Seppelt, 1986a, 1986b). Of particular interest is the occurrence of a species of the marine lichen *Verrucaria*, the only record of this genus from continental antarctic regions (Seppelt, 1986b).

The Vestfold Hills, while not possessing a unique terrestrial flora, provide a wide range of contrasting habitats which, coupled with the Holocene history of deglaciation of the oasis, provide an ideal opportunity for the study of terrestrial polar ecosystems. At scales ranging from kilometres to fractions of a metre, extreme environmental gradients exist in important variables such as moisture, nutrients, salinity and exposure. However, exploiting the ecological and physiological potential of the area requires the prior resolution of important taxonomic problems.

References

Broady, P. A., 1979. The terrestrial algae of Signy Island, South Orkney Islands. Br. antarct. Surv. Sci. Rep. 98.

- Broady, P. A., 1981a. The ecology of sublithic terrestrial algae at the Vestfold Hills, Antartica. Br. Phycol. J. 16: 231–240.
- Broady, P. A., 1981b. Ecological and taxonomic observations on subaerial epilithic algae from Princess Elizabeth Land and Mac.Robertson Land, Antartica. Br. Phycol. J. 16: 257-266.
- Broady, P. A., 1981c. The ecology of chasmolithic algae at coastal locations of Antarctica. Phycologia 20(3): 259-272.
- Broady, P. A., 1986. Ecology and taxonomy of the terrestrial algae of the Vestfold Hills. In J. Pickard (ed.), Antarictic Oasis. Terrestrial environments and history of the Vestfold Hills. Academic Press, Lond.: 165–202.
- Burton, H. R. & P. J. Campbell, 1980. The climate of the Vestfold Hills, Davis Station, Antarctica, with a note on its effect on the hydrology of hypersaline Deep Lake. ANARE Sci. Rep., Publ. 129. Aust. Govt. Publ. Service, Canberra, 50 pp.
- Cameron, R. E., 1972. Ecology of blue-green algae in antarctic soils. In T. V. Desikachary (ed.), Taxonomy and Biology of Blue-Green Algae. Centre for Advanced Studies in Botany, University of Madras, Madras: 353-384.
- Collerson, K. D. & J. W. Sheraton, 1986. Bedrock geology and crustal evolution of the Vestfold Hills. In J. Pickard, (ed.), Antarctic Oasis. Terrestrial environments and history of the Vestfold Hills. Academic Press, Lond.: 21–62.
- Crohn, P. W., 1959. A contribution to the geology and glaciology of the western part of Australian Antarctic Territory. ANARE Rep. Publ. 49. Antarct. Div., Dept. External Affairs, Melbourne, 104 pp.
- Friedmann, E. I., 1977. Microorganisms in antarctic desert rocks from dry valleys and Dufek Massif. Antarct. J. U.S. 12: 26-30.
- Friedmann, E. I., 1982. Endolithic microorganisms in the antarctic cold desert. Science 215: 1045-1053.
- Friedmann, E. I. & M. Galun, 1974. Desert algae, lichens and fungi. In G. W. Brown (ed.), Desert Biology, 2. Academic Press, Lond.: 165-212.
- Friedmann, E. I. & R. Ocampo, 1976. Endolithic blue-green algae in the dry valleys: primary producers in the antarctic desert ecosystem. Science 193: 1247–1249.
- Fukushima, H., 1959. General report on fauna and flora of the Ongul Island, Antarctica, especially on freshwater algae. J. Yokohama munic. Univ. Ser. C Nat. Sci. 31: 1-20.
- Golubic, S., E. I. Friedmann & J. Schneider, 1981. The lithobiontic ecological niche, with special reference to microorganisms.J. Sediment. Petrol. 51(2): 475-478.
- Horikawa, Y. & H. Ando, 1963. A review of the antarctic species of Ceratodon described by Cardot. Hikobia 3(4): 275–280.
- Johnstone, G. W., D. J. Lugg & D. A. Brown, 1973. The biology of the Vestfold Hills, Antarctica. ANARE Sci. Rep. Publ. 123. Antarct. Div., Dept. Sci., Melbourne, 62 pp.
- Law, P., 1959. The Vestfold Hills. ANARE Rep. Publ. No. 47. Antarct. Div., Dept. External Affairs, Melbourne, 50 pp.
- Lied, N. T., 1963. Notes on sastrugi and sand dune observations, A.N.A.R.E. Satellite Station, Vestfold Hills, 1961. Aust. Meteorol. Mag. 40: 35-46.
- Longton, R. E., 1979. Vegetation ecology and classification in the antarctic zone. Can. J. Bot. 57: 2264–2278.
- McLeod, I. R., 1963. An outline of the geology of the sector from

45°E to 80°E, Antarctica. Sci. Comm. Antarct. Res. Bull. 15: 262–275.

- Pickard, J., 1982. Holocene winds of the Vestfold Hills, Antarctica. N.Z. J. Geol. Geophys. 25: 353-358.
- Pickard, J., 1986. Spatial relations of the vegetation of the Vestfold Hills, Antarctica. In J. Pickard (ed.), Antarctic Oasis. Terrestrial environments and history of the Vestfold Hills. Academic Press, Lond.: 275-308.
- Pickard, J. & D. A. Adamson, 1983. Perennially frozen lakes at glacier/rock margins, East Antarctica. In R. L. Oliver, P. L. James & J. B. Jago (eds.), Antarctic Earth Science. Aust. Acad. Sci., Canberra: 470–472.
- Pickard, J. & R. D. Seppelt, 1984. Phytogeography of Antarctica. J. Biogeog. 11: 83-102.
- Seppelt, R. D., 1984. The bryoflora of the Vestfold Hills and Ingrid Christensen Coast, Antarctica. ANARE Res. Notes 20. Antarct. Div., Dept. Sci., Hobart, 30 pp.
- Seppelt, R. D., 1986a. Mosses of the Vestfold Hills. In J. Pickard (ed.), Antarctic Oasis. Terrestrial environments and history of the Vestfold Hills. Academic Press, Lond.: 221–246.
- Seppelt, R. D., 1986b. Lichens of the Vestfold Hills. In J. Pickard (ed.), Antarctic Oasis. Terrestrial environments and history of

the Vestfold Hills. Academic Press, Lond.: 247-274.

- Seppelt, R. D. & D. H. Ashton, 1978. Studies on the ecology of the vegetation at Mawson Station, Antarctica. Aust. J. Ecol. 3: 373-388.
- Sheraton, J. W. & K. D. Collerson, 1983. Archaean and Proterozoic geological relationships in the Vestfold Hills – Prydz Bay area, Antarctica. J. Aust. Geol. Geophys. 8: 119–128.
- Streten, N. A., 1968. Some features of mean annual wind speed data for coastal East Antarctica. Polar Rec. 14: 315-322.
- Streten, N. A., 1986. Climate of the Vestfold Hills. In J. Pickard (ed.), Antarctic Oasis. Terrestrial environments and history of the Vestfold Hills. Academic Press, Lond.: 141–164.
- Thompson, K., 1979. Plants in antarctic rocks: adaptation to the most extreme environments. 49th Aust. N.Z. Assoc. Adv. Sci. Conf., 63 pp.
- Usher, M. B., 1983. Pattern in the simple moss-turf communities of the subantarctic and Maritime Antarctic. J. Ecol. 71: 945-958.
- Wellman, P. & J. W. Williams, 1982. Extent of Archaean and Late Proterozoic rocks under the ice cap of Princess Elizabeth Land, Antarctica, inferred from geophysics. J. Aust. Geol. Geophys. 7: 213–218.