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J. BASTOW WILSON
CAROL CULLEN*
Botany Department, University of Otago
P.O. Box 56, Dunedin, New Zealand

Abstract Cliff vegetation was sampled at five sites in the Catlins region, New Zealand. Ordination showed a vegetation sequence from the bottom to the top of the cliff, consistent in its overall pattern between sites. This was correlated with soil salinity and, from available information, with salt spray. There is evidence for the importance also of drought and of soil organic content. Some species show unexpected absences from particular sites; the explanation for this may lie in biogeographic history rather than in ecology. Generally, the vegetation is similar to that found on cliffs of islands lying off the coast of Otago.

INTRODUCTION

Cliffs are a major plant habitat of the New Zealand coast, but in contrast to sand dunes (Esler 1970, Sykes & Wilson 1983) and salt marshes (Partridge & Wilson 1975) they have been little investigated. There are descriptions of cliff communites on off-shore islands (e.g., Fineran 1973, Johnson 1976, Partridge 1983), but for mainland cliffs the only published comments are the general ones of Cockayne (1928).

This study describes the vegetation of coastal cliffs in the Catlins Region of southeastern South Island, New Zealand. Cliffs of early to middle Jurassic sandstones and mudstones, the latter often sandy mudstones (Speden 1971), are a feature of the Catlins coast (Fig. 1). They generally start from a rocky tidal platform, rising quickly to a height of 20–30 m. The False Islet cliffs are an exception, comprising conglomerate; this softer rock has given gentler slopes. Apart from the presence of a few exotic species the plant communities in many parts are essentially undisturbed by man.

The area has an equable climate. The most appropriate recording station is at Nugget Point, on the coast at the north of the area being considered. Mean annual temperature there is 9.9°C (New Zealand Meteorological Service 1983). At Tautuku (S. Beamish, pers. comm.) and Owaka there is frost on 13 and 43 days respectively per year, but on the coast on only 3 days. Yearly minimum temperatures are −6.1°C and −3.0°C at the two inland sites, but only −0.8°C at Nugget Point. Rainfall at Nugget Point is not particularly high at 852 mm, but further south at Tautuku it is higher at 1214 mm. Rain is evenly spread through the year, and occurs (> 1 mm) on an average of 151 days per year at Nugget Point, and 155 days at Tautuku. Winds are often strong, reaching gale force at Nugget Point on 53 days of the year. Moreover, the coast is oriented so that most cliffs are exposed to the prevailing southwesterly wind.

METHODS

Seven sites were visited (Fig. 2). Five of these were sampled by 2 m × 2 m quadrats, arranged in transects running up the cliff at its angle of steepest slope — a total of 10 transects and 62 quadrats. In each quadrat, species presence was recorded, and cover estimated subjectively. The data were analysed by one-dimensional Detrended Correspondence Analysis (D.C.A., Hill & Gauch 1980). The placement of transects was necessarily limited by accessibility, but the non-accessible parts viewed through bincoculars seemed similar.

A soil sample was taken from each quadrat if sufficient soil was accessible. In it, organic matter was determined by loss in weight of duplicate samples of oven-dry soil after ignition at 700°C for 2 hours. Soil salinity was estimated by conductivity. Deionised water equal to nine times the field water content of the soil was added, the conductivity of this solution was measured and adjusted to find the conductivity in the original soil solution.

A first approximation to salt spray estimation was made at some sites by suspending filter paper, held in mesh envelopes, from vegetation in selected quadrats. The estimation was made in autumn, during a period with no significant rain. After 4 days, the filter papers were leached in 100 ml of distilled water, and the conductivity of the leachate measured.
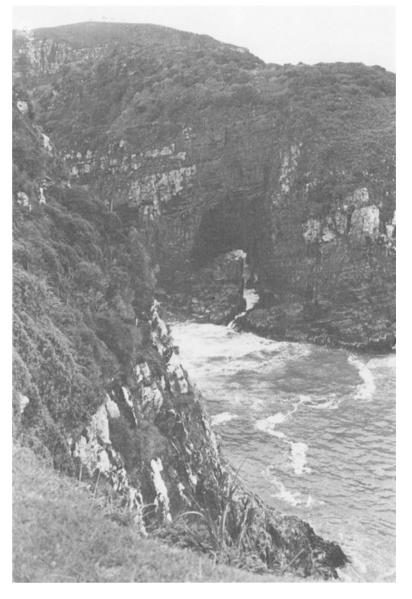
*Deceased

Fig. 1 Cliff communities in the Catlins (taken near Jacks Bay by Dr P. N. Johnson).

Nomenclature follows Allan (1961), Moore & Edgar (1970), and Clapham et al. (1981) for the groups they cover, or Edgar & Connor (1983) for recent suggestions, except where explicit author citations are given at the first use of a name.

RESULTS AND DISCUSSION

The vegetation sequence

Two transects are given in detail as examples (Fig. 3), one from Cannibal Bay and one from Purak-aunui Bay.

The ordination (Table 1) gives a vegetation sequence common to the five sites sampled. It is clear from Fig. 3 that quadrat position in the sequence is correlated with distance from the sea, quadrats with low scores (on the left of Table 1) being outer ones. The species with lowest scores on the ordination, at the bottom of Table 1, are therefore those that tend to occur nearer the sea. They are typical salt marsh species (Partridge & Wilson 1975) that are also able to grow on the lower parts of cliffs: *Selliera radicans, Samolus repens, Sarcocornia quinqueflora*, and *Schoenus nitens*. Hepburn

Fig. 2 The location of the sites. At sites marked O only overall floristic lists were compiled; sites marked ● were sampled by transects.

(1943) and Gillham (1960) found salt marsh species on cliffs, but did not note any tendency for them to occur more frequently towards the bottom.

Higher upslope (and higher in Table 1) are species typical of a variety of coastal habitats (Wilson 1982): *Disphyma australe, Apium prostratum, Myosotis rakiura, Crassula moschata, Scirpoides nodosa, Gentiana saxosa, Epilobium komarovianum, Colobanthus muelleri,* and *Blechnum banksii*. With them are two exotics whose distribution is wide, but includes dunes (Sykes & Wilson 1983): *Hypochaeris radicata* and *Cirsium vulgare*. Many species with such a distribution, and especially *Crassula moschata, Epilobium komarovianum,* and *Colobanthus muelleri*, seem to occur only in open sites, either in small crevices in rocks or on unstable banks. Perhaps such low-growing plants cannot compete when taller species are present. *Disphyma australe* seems to need loose well-drained soil. However, biogeographic causes may enter; it does have disjunctions in its distribution, being absent on the West Coast south of Greymouth (Chinnock 1971).

A few species are confined to the middle of the vegetation sequence: *Cotula dioica, Sonchus oleraceus* and to some extent *Pseudognaphalium luteoalbum*.

There are also species that are able to grow through most of the vegetation sequence, though often with a peak of abundance in the middle of the sequence: *Poa astonii, Hebe elliptica, Anisotome lyallii,* and *Asplenium obtusatum*. It is possible to find at least *P. astonii* and *H. elliptica* growing in the same 2 m × 2 m quadrat as the salt marsh species. Whether this represents environmental patterning on a small scale, or a wide range of tolerance for those species, remains to be deter-

mined. Possibly such species are tolerant of the salt load typical of the lower parts of cliffs, but are normally absent because they require a relatively deep, rich soil (T. R. Partridge, pers. comm.).

Other species appear only towards the end of the vegetation sequence furthest from the influence of the sea: *Pyrrosia serpens, Asplenium bulbiferum, Hierochloe redolens, Phymatosorus diversifolius* (Willd.) Pichi Serm., *Pimelea urvilleana,* and *Celmisia lindsayi*. Most of these are species also found in non-coastal situations. *Pimelea urvilleana* is an exception, as a species usually found on dunes. The other exception is *Celmisia lindsayi*, confined to coastal cliffs in the Catlins (Allan 1961). Its position in the ordination diagram therefore reflects a tendency to grow on the upper part of the cliff. It also occupies flat ground immediately behind the cliff. Since at undisturbed sites woody vegetation occupies such habitats, *C. lindsayi* may have invaded here after human removal of forest. Although *C. lindsayi* forms a pure mat only at the top of the cliff, individual plants can be found lower down, in this survey within 5 m vertically of high tide. It occurs as a mat only 8 m above sea level on the protected landward face of the stack on the Purakaunui Bay transect. This suggests that *C. lindsayi* is relatively intolerant of salt spray. Malloch & Okusanya (1979) suggested that some species are restricted to coastal cliffs by sensitivity to cold, but in the Catlins' equable climate it is more likely that *C. lindsayi* is prevented from growing inland by lack of suitable open, well-drained sites in the densely wooded Catlins landscape.

Community structure

It is an interesting ecological question why some species are more or less restricted to the lower parts
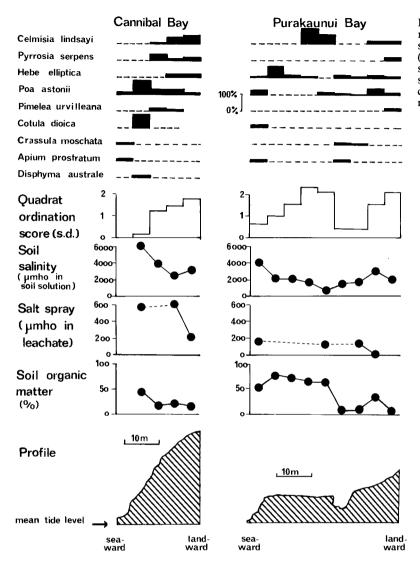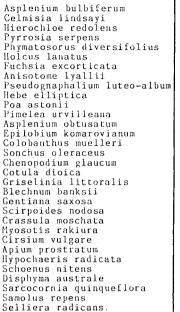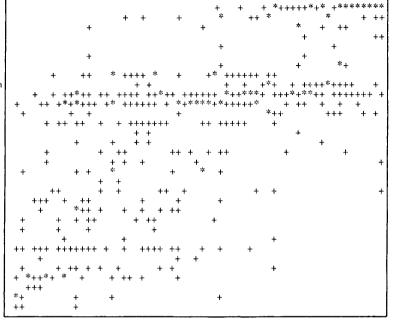
Fig. 3 Vegetation and environmental sequences along two transects. Individual cover values (estimated) are given for selected species. Ordination scores are in s.d., see Hill & Gauch (1980). For details of salinity and spray estimation see text.

of the cliff. Some extreme halophytes show a requirement of salt for maximal growth rate, but of those present here only *Sarcocornia quinqueflora* and perhaps *Samolus repens* are known to have salt requirement (Partridge & Wilson 1987). These two species tend to occur on the more saline, lower parts of the cliff, as is seen in their ordination positions (Table 1). Even for these species the salt requirement is not absolute; they can grow at two thirds of their maximal rate in fresh water. The other halophytes present show no salt requirement (Partridge & Wilson 1987, M. T. Sykes & Wilson, unpublished observations). It is more likely that the important feature for all species is their salt tolerance. *Samolus repens, Sarcocornia quinque-*

flora , and *Schoenus nitens* appear at the bottom of the ordination and can all grow at half of their maximal rate in salinities higher than 2.0% (Partridge & Wilson 1987). This suggests that the halophytes are present lower down because they can tolerate the salinity, and are absent higher up because they cannot compete with the less tolerant halophytes, and glycophytes, that can grow there. Most halophytes on salt marshes seem to have their upper limits determined in this way (Clarke & Hannon 1971). Many of the species found higher up the cliffs are taller, so competition for light is a possible cause. However, in many parts the cliff community is open. *Celmisia lindsayi* is short, but the dense carpet that it can develop may effectively

Table 1 Species pattern along the vegetation sequence. The species and quadrats are both arranged in order of their D.C.A. ordination score. * = cover estimated at 10% or more; + = present, but cover less than 10%.

sites, arranged by ordination sequence

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Asplenium bulbiferum                              +     +    + *+++++*+* +********
Celmisia lindsayi                      +   +    +     *   ++ *          *      + ++
Hierochloe redolens            +              +          *   +  ++
Pyrrosia serpens                                              +              ++
Phymatosorus diversifolius                        +             +
Holcus lanatus                 +                             +
Fuchsia excorticata                                     +         +    *+
Anisotome lyallii         +     ++   * ++++  *   +    +* ++++++ ++
Pseudognaphalium luteo-album              + +              +   +  +*+  + ++++*++++    +
Hebe elliptica            +  + ++*++ ++ ++++ ++*++ ++++++ *+++***+ +++*+*+*++ +++++++ +
Poa astonii            +  ++ +*+*+++ +* ++++++ + *+*+***+*+++++*   + ++  +  +  +
Pimelea urvilleana       +     + + +          +           *++          +++   + +
Asplenium obtusatum         + ++ ++  +   + +++++++    ++ +++++    +
Epilobium komarovianum                    + +                    +
Colobanthus muelleri           +      +  + +                  +
Sonchus oleraceus              +      +  ++      ++ +  + ++        +      +
Chenopodium glaucum            +         + + +         +                          +
Cotula dioica             +     + + *:        +    *  +
Griselinia littoralis            +   +
Blechnum banksii            ++       + +      ++ +     + +               +
Gentiana saxosa          +++   + ++       +    +    +
Scirpoides nodosa         +     *++ +   +  +  + ++
Crassula moschata      +    +  + ++     + ++        +
Myosotis rakiura       +    +  +  +        +
Cirsium vulgare             +          +              +
Apium prostratum       ++ +++ ++++++++ +  +  ++++ ++   +  +   +
Hypochaeris radicata      +                        +  +
Schoenus nitens        +     + ++ + +  +      + +          +
Disphyma australe     + *++*+  *  +    + ++ +      +
Sarcocornia quinqueflora   +++
Samolus repens        *+      +     +             +
Selliera radicans.     ++        +
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exclude most other species.

The generalised vegetation sequence (Table 1) seems to be gradual, without the distinct zonation that others have claimed to find on cliffs (Hepburn 1943). At individual sites abrupt changes in community composition can be seen, coincident with sharp changes in the slope or possibly the nature of the substratum.

Hepburn found only three true coastal cliff species on Cornish cliffs, after eliminating five species characteristic of coastal cliffs but also found inland or in other coastal habitats such as salt marshes and dunes. In the Catlins there is about the same number of true coastal cliff species, perhaps only *Celmisia lindsayi* and *Myosotis rakiura. Poa astonii* is characteristic of coastal cliffs, but not only those directly exposed to salt spray. *Hebe elliptica* and *Asplenium obtusatum* are typically coastal, and appear most vigorous on cliffs, but they are not restricted to this habitat. However, even though most of the species are not restricted to cliffs the whole communities are usually characteristic of cliffs, as Malloch *et al.* (1985) also observed for Britain.

Vegetation and Environment

The ordination scores follow the topography closely (Fig. 3), even at Purakaunui Bay where the transect went over a stack, down to shore level, and then up the cliff again. There is clear environmental control of vegetational composition.

Salt spray is important in cliff communities (Hepburn 1943), but as it is difficult to measure little is known of its intensity, distribution and variability (Rozema *et al.* 1983). Our preliminary investigation here shows the expected (Goldsmith 1973b) pattern of a lower salt load higher up the cliff. The records indicate some difference between the two sites, that is not reflected in the vegetation. However, salt spray will be very variable and a survey over many months, through varying weather conditions, would be necessary before any correlations could be made. It is possible that the vegetation patterns are determined by salt spray conditions that occur only infrequently, say once a decade.

We do not know whether the species differ in their tolerance of salt spray, though this is commonly assumed to be the cause of species zonation on cliffs. In South Africa *Scirpoides nodosa* is very tolerant of salt spray, especially beyond the seedling stage (Lubke & Avis 1982), but in New Zealand *Phormium tenax* and *Pseudognaphalium luteo-album* have been found to be even more tolerant (M.T. Sykes & Wilson, unpublished observations).

All the sites sampled were above high tide level, so all salt input must be by spray and splash. The soil salinity therefore provides a more integrated

measure of salt input than immediate spray catches, and might be expected to show a better correlation than the spray measured in any short period. It also follows the expected (Gillham 1960) pattern of lower salinity further from the sea. The Purakaunui transect is particularly interesting in showing low salinities behind the stack, where the vegetation is growing at low elevation but sheltered from the sea. The ordination scores indicate that the vegetation responds to this shelter. Even soil salinities can be expected to vary with salt spray input, evaporation, and rain dilution (Hepburn 1943), like those of salt marshes (Chapman 1939) and sand dunes (M.T. Sykes & Wilson, unpublished observations). However, the ordination scores provide a community phytometer that correlates well with the soil salinity at the time of sampling, so we can have some confidence that the relative differences of the salinities reported are typical. Goldsmith (1973a) also found such a correlation of soil salinity and ordination score in Anglesey cliff vegetation, and Malloch *et al.* (1985) in a survey of British cliffs.

Soils on cliffs tend to be shallow, except in clefts. Along most transects the greatest depth that could be measured was in the range 4–6 cm. An exception was seen on the stack at Purakaunui Bay (Fig. 3). On the flat top, depth of the soil reached 25 cm; it was mostly an accumulation of peat as indicated by the percentage of organic matter. The greater depth of soil here did not have major impact on the vegetation; the species found on the stack such as *Hebe elliptica*, *Asplenium obtusatum* and *Hierochloe redolens* are typical of mid-upper cliffs. However, their tall dense growth excluded species such as *Crassula moschata*, *Epilobium komarovianum*, and *Colobanthus muelleri* which grew at a similar elevation on the cliff behind, in vegetation with a similar ordination score but a more open canopy. *Hebe elliptica* grew more vigorously on the top of the stack than on other parts of the two transects that seem to have similar salt input. This is some confirmation of the idea mentioned above that it requires a deep soil. On the other hand, *Poa astonii* is absent there. It seems to occur mainly on steep faces, and might be excluded from the top of the stack by a requirement for good drainage, or by competition. Yet, Wilson (1982) records *P. astonii* from shrubland and open scrub on Stewart Island.

Most of the soils were high in organic matter, as Hepburn (1943) found in Cornwall. Nevertheless, organic content does not seem to be a requirement for cliff species, since *Hebe elliptica* and *Poa astonii* are abundant on mineral soil elsewhere (Partridge 1983).

Another environmental stress experienced by plants on cliffs is drought (Hepburn 1943). The most obvious indication of its importance, even in the high-rainfall Catlins, is an increase in species diversity and of cover in areas of fresh water seepage. Such areas were found at False Islet and Cathedral Caves. Drought may be less important on the flat top of the stack at Purakaunui Bay, since more vertical rain will be caught on a horizontal surface, and drainage will be much slower than in many crevice sites.

Biogeographic relations

The vegetation described here is clearly similar to that found on Wharekakahu, about 100 km to the north (Partridge 1983). Wharekakahu has a more limited range of species, but does bear *Lepidium oleraceum*, not found on the Catlins cliffs. The Catlins cliff vegetation is also similar to the vegetation of the Mutton-bird Islands (Fineran 1973), Bird Island (Fineran 1966), and Womens Island (Johnson 1976) 100–200 km to the south, but without a number of species present there, such as *Olearia angustifolia*, *Lepidium oleraceum*, *Poa foliosa*, *Linum monogynum*, or *Tetragonia trigyna*. The Catlins is north of the geographical range of *P. foliosa*, and the answer to its absence may lie more in geological history than in ecology. The palatable *L. oleraceum* was once common on the South Island; its present rarity is due to grazing. It is possible that *T. trigyna* and *L. monogynum* are absent here because the cliffs are too exposed (T.R. Partridge pers. comm.).

The geographical distribution of some of the species is interesting (Table 2). *Celmisia lindsayi* is abundant at some sites. It is absent from others that are apparently suitable ecologically and still within its limited (65 km) geographic range of Clutha River mouth to Waikaia. The climate of its limited range does not seem unique, so it is unlikely that ecological factors prevent its occurring outside the Catlins, which points to biogeographic history as the cause of its overall distribution. It is logical to suspect that the same process explains its absence from some sites within the Catlins. *Gentiana saxosa* and *Sarcocornia quinqueflora* were found only at False Islet. Both species are widespread round the coasts of southern New Zealand and beyond. Perhaps they occur at False Islet because of the softer rock and gentler slopes. This may be part of the reason for the distribution of *Disphyma australe*. Its absence at the four southern sites could indicate climatic intolerance towards a southern climate, though *Disphyma* occurs also on Stewart Island and surrounding islands (e.g., Fineran 1973), where the climate is of an even more southern type. The presence of *Pimelea urvilleana* at some sites and its absence at others also needs investigation. Since it is primarily a sand dune species, its absence may reflect the non-availability of suitable microhabitats.

Table 2 Abundance, subjectively determined on the "dafor" scale (dominant, abundant, frequent, occasional, or rare), of selected species, at the Catlins cliff sites visited.

Species	site 1	2	3	4	5	6	7
Agrostis capillaris	–	–	–	r	o	–	–
Anisotome lyallii	a	f	o	o	f	–	f
Celmisia lindsayi	d	d	–	a	d	–	–
Chenopodium glaucum	o	o	o	o	–	o	o
Colobanthus muelleri	o	–	–	–	o	o	–
Disphyma australe	o	d	o	f	–	–	–
Gentiana saxosa	–	f	–	–	–	–	–
Myosotis rakiura	–	o	–	r	–	r	–
Pimelea urvilleana	f	o	–	–	–	–	–
Samolus repens	r	o	–	–	–	o	–
Sarcocornia quinqueflora	–	o	–	–	–	–	–
Schoenus nitens	–	o	o	–	–	o	o
Scirpoides nodosa	–	o	–	–	–	o	o
Selliera radicans	o	o	–	–	–	o	–
Sonchus oleraceus	o	o	o	o	–	–	o

Key: 1 = Cannibal Bay
2 = False Islet
3 = Jacks Bay
4 = Hinahina Cove
5 = Purakaunui Bay
6 = Picnic Point
7 = Cathedral Caves

This work gives only a preliminary description of the coastal cliff vegetation of the Catlins. It points to the need for further work, on the macro- and micro-distribution of the species, on the environment, especially in relation to spray, and on the environmental tolerance of the cliff species.

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