

VEGETATION OF A CANTERBURY SUBALPINE MIRE COMPLEX

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SUMMARY: The vegetation of a subalpine mire complex and the inter-relationships of the plant species in it are described. Particular emphasis is placed on the relationship of cushion plant vegetation to other types. Hypotheses are advanced to account for the differing vegetation patterns and evidence based on variations in micro-habitats is produced to support these.

INTRODUCTION

Cushion mire vegetation is peculiar to the cooler parts of the Southern Hemisphere and in New Zealand characteristically occurs in the upper montane and subalpine zones, descending to lower altitudes in Stewart Island and in the subantarctic region. There is no precise altitudinal limit for the occurrence of mires containing cushion vegetation but rather gradual transition into the *Sphagnum*-dominated mires of lower altitudes. On any one mire, however, it is unusual to find intermediate vegetation types; cushion vegetation being either completely dominant or very subordinate.

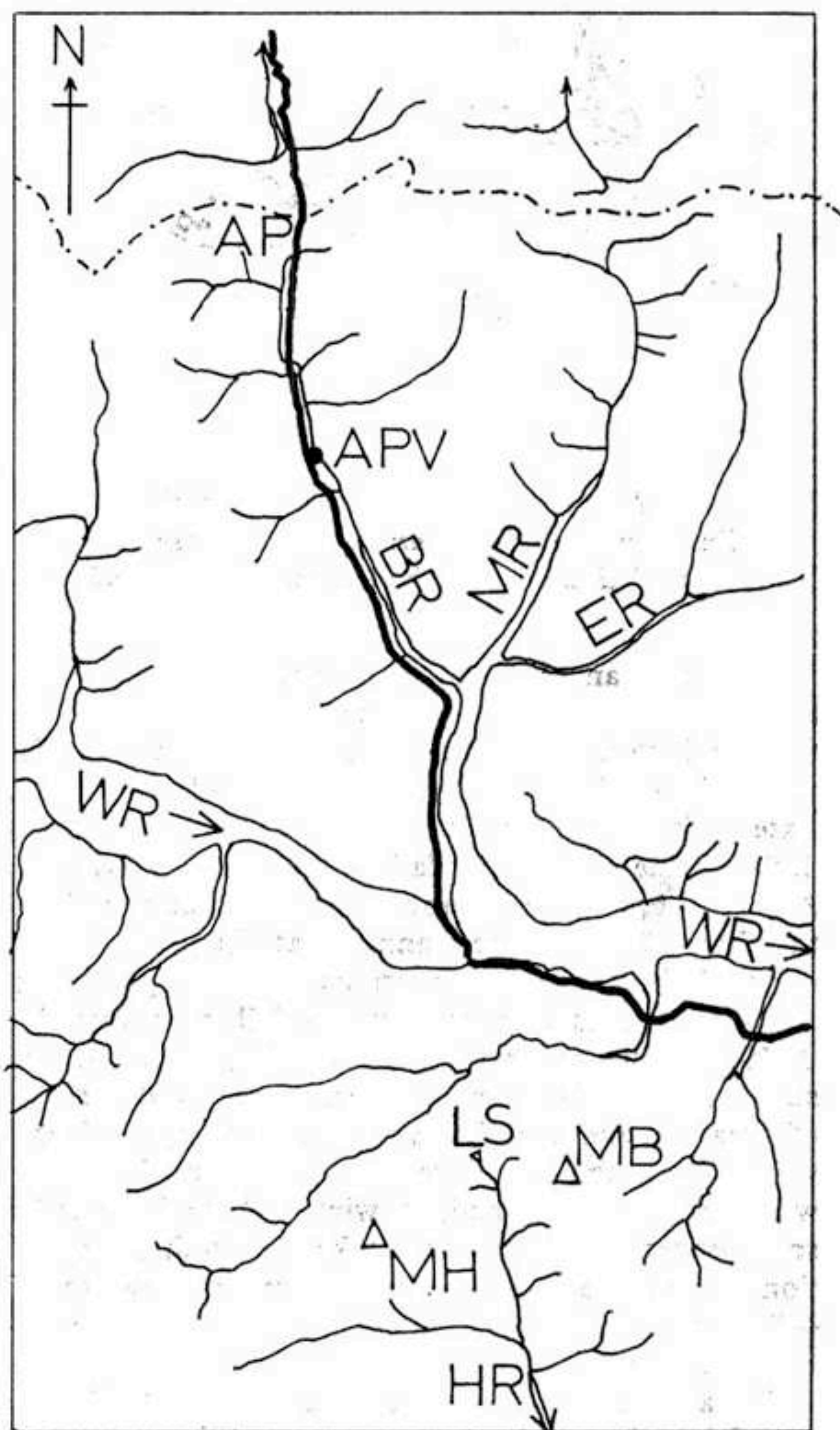
This account describes an investigation into the different mire types occurring on one site in the Canterbury Alps although reference is made to other sites in the vicinity. The main advantage of the study area was that it contained a complex mosaic of all the main subalpine mire types of that region, markedly different vegetation types often occurring directly adjacent to each other.

A brief description and photographs of the mire types of Canterbury have been provided by Burrows (1969) who included the site of this study in his survey.

LOCALITY, HISTORY AND STRUCTURE OF THE LAGOON SADDLE MIRE

The main area of study was a mire at Lagoon Saddle in the Canterbury Alps (Fig. 1). Lagoon

FIGURE 1. *Locality map of Lagoon Saddle. Thick line—Provincial Highway 73; thin lines—rivers; dashed line—Main Divide; AP—Arthurs Pass; APV Arthurs Pass Village; BR—Bealey river; ER—Edwards river; HR—Harper river; LS—Lagoon Saddle; MB—Mount Bruce; MH—Mid Hill; MR—Mingha river; WR—Waimakariri river.*



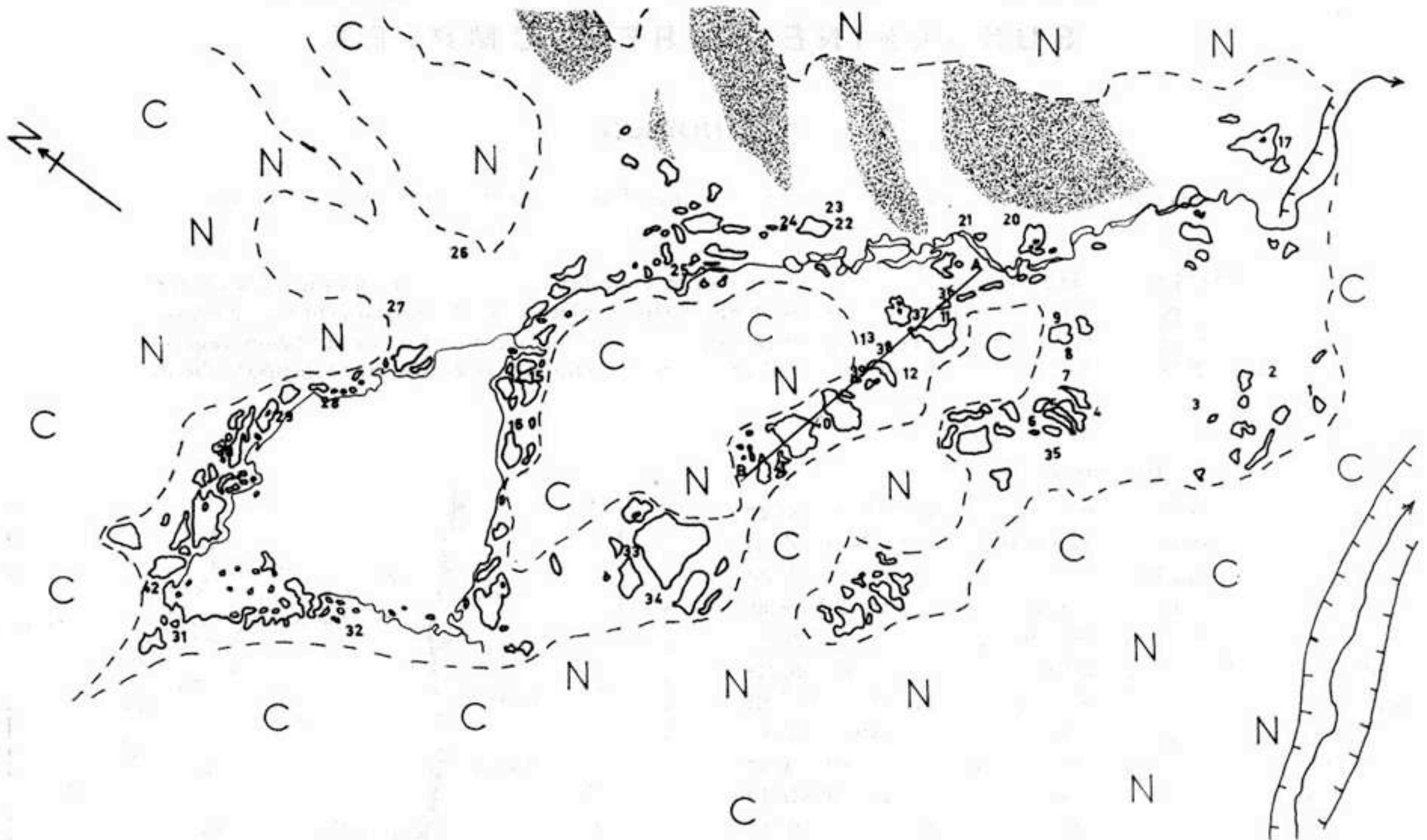


FIGURE 2. Map of Lagoon Saddle mire showing pool complex and sample sites. Dashed lines—mire margins; solid lines—pool margins and streams; Transect A-B; N—*Nothofagus* forest; C—*Chionochloa rubra* grassland; stippled areas—*Hebe-Chionochloa* scrub.

Saddle is at an elevation of about 1150 metres and separates the headwaters of the west branch of the Harper River, a Rakaia tributary, from the catchment of the Waimakariri River. The Saddle is about sixteen kilometres to the south-east of the main divide. The yearly rainfall on the main divide at Arthurs Pass averages about 500 cm but is reduced to about 200 cm per annum at Lagoon Saddle although long-term observations from nearby lower altitude stations suggest that rainfall may vary by $\pm 50\%$ of the mean in any year. Lagoon Saddle is subject, particularly in summer, to sunny dry spells of weather and the site is exposed to drying foehn winds from the north-west. However cool, cloudy weather is frequent and, in winter, there is periodic snow cover. Measurements taken beneath a vegetation cover give a winter minimum temperature of -7°C but presumably frosts are more severe on exposed sites.

The area was glaciated on several occasions during the Otira glaciation when tongues of ice from the

Waimakariri glacier flowed over the Saddle and a short distance down the Harper Valley (Gage, 1958). The retreat of the ice from the last of these episodes, possibly about 14,000 years B.P., left some ridges of morainic till which form well-drained areas within the mire complex, these moraines now carry mountain beech, *Nothofagus solandri* var. *cliffortioides*, and red tussock grassland, *Chionochloa rubra*. The uneven terrain was probably the cause of the impounding of the Lagoon and perhaps some of the other pools.

An unpublished pollen analysis by G. Mitchell shows that peat formation began some considerable time after the glacier retreated perhaps 10,000 years B.P. *Nothofagus* entered the area early and has maintained its dominance to the present. The mire is situated slightly below the local tree line, which is at 1200-1250 m, and until 1895 *Nothofagus* surrounded the mire on all sides although it was rather patchy and soon petered out on the ridges north and south of the Saddle. In 1895 a fire destroyed the

forest on the western side of the mire (Dick, 1956) and this area has subsequently been colonised by tussock and adventive pasture grasses. The exact limits of the burnt area are uncertain but the fire certainly reached the southern and western shores of the Lagoon. There has been negligible recolonisation by *Nothofagus* since the fire.

Sheep, red deer and hares graze in the vicinity. Sheep and red deer usually avoid the mire but hares frequently venture on to its surface. *Carex sinclairii* and *Schoenus pauciflorus* are the mire plants usually eaten. The Lagoon and surrounds are grazed by nesting Canada geese during summer, and there are periodic visits from ducks.

The Lagoon Saddle mire is separated into several distinct spatial units by the Lagoon, the stream flowing from the Lagoon forming the source of the Upper Harper, and several morainic ridges (Fig. 2). There is a narrow band of mire vegetation surrounding the Lagoon and this contains the deepest accumulation of peat, 5.4 metres at Site 28. G. Mitchell's pollen analysis shows that the Lagoon originally contained abundant *Isoetes* but this rapidly disappeared probably as the bottom of the Lagoon acquired a covering of organic detritus. The Lagoon is now very oligotrophic (pH 7.05, Conductivity 13 micromhos/cm) and contains *Nitella* sp., *Potamogeton cheesemanii*, *Drepanocladus fluitans* and *Campylium stellatum*. Submerged peat banks show that the Lagoon has increased gradually at the expense of the mire.

The main areas of mire complex are on the slopes that drain into the stream that flows from the Lagoon. These wet areas are separated by drier outcrops bearing *Nothofagus* or *Chionochloa rubra* while the shady south-facing slope also has some patches of scrub and tussock grass, dominated by *Hebe odora* and *Chionochloa rubra* with a herbaceous ground flora, occurring on flushed, peaty soils. Apart from the scrub areas the transition from mire peats to mineral soils is abrupt.

The pool complex is a conspicuous feature (Fig. 2), some of the pools occurring on relatively steep slopes with a marked difference in water level between adjacent pools. Figure 3 illustrates a transect through one of the pool systems. In this system the overall slope approaches five degrees but attains thirty-five degrees at the steepest point. There is a general tendency for the pools to be related to depressions in the underlying topography and relatively narrow zones of peat retain the pools. The largest pool in this system seems to have been present since the initiation of the mire. There is no evidence that these pools are infilling to any appreci-

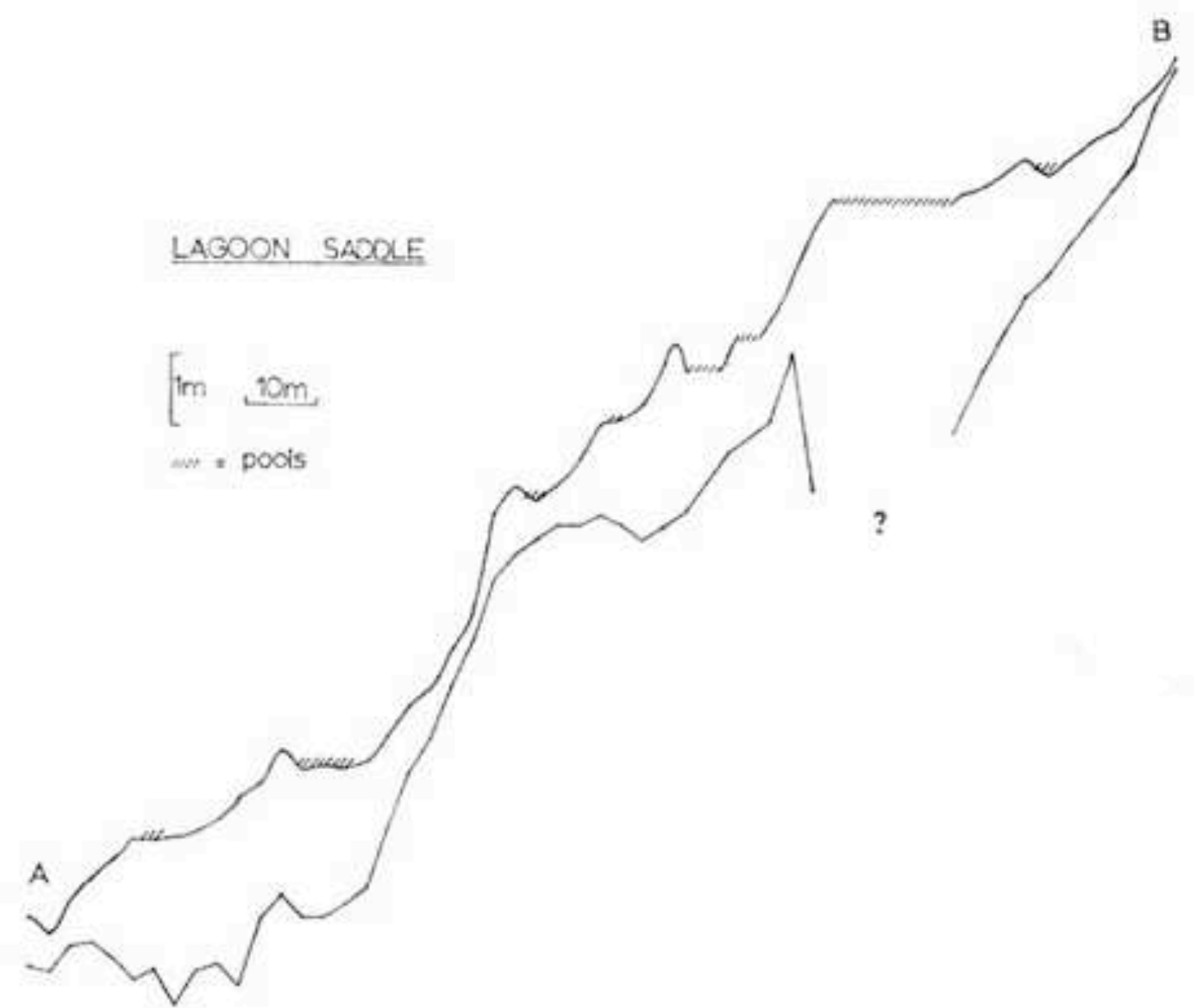


FIGURE 3. Transect A-B through pool complex showing surface and bedrock profiles.

able extent. Some shallow pools have sparse stands of *Carex sinclairii* or *Eleocharis acuta* and a few moss shoots but annual dry matter production per unit area by these species is very low and hence they are not accumulating peat. In mires at lower altitudes *Sphagnum falcatulum* may invade pools (Burrows and Dobson, 1972) but it shows negligible tendency to do so at Lagoon Saddle or in other sub-alpine mires.

VEGETATION AND SPECIES INTER-RELATIONSHIPS

Species abundance values were obtained from forty-two visually uniform sites on the Lagoon Saddle mire. Each site was approximately four square metres in area although because of the intricate nature of the vegetation complex it was not possible for the plots to be uniform shape e.g. between pools plots were elongated. At each site a water sample was taken and slope and aspect recorded.

A standard ordination using Principal Components Analysis (see Anderberg, 1973 or Williamson, 1972 for discussion of method) was performed on the forty-two sites, only the first two components provided information of ecological value (Fig. 4).

Notwithstanding the criticisms of Whittaker (1973) on the limitations of Principal Components Analysis, the analysis has provided a meaningful separation of the main vegetation types in this instance. This is because the species used in the above analysis have a high constancy.

The first component (I) separates the stands domin-

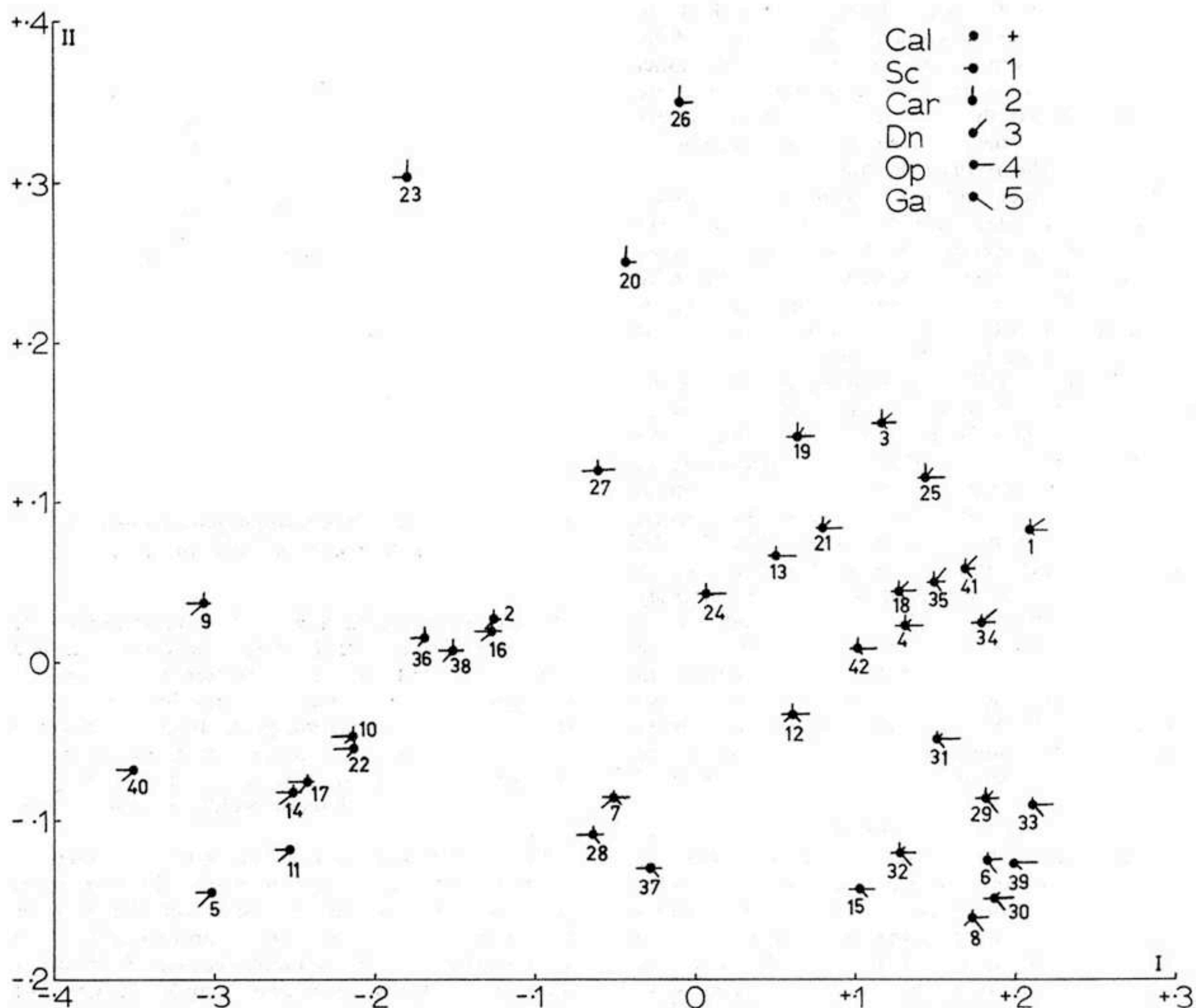


FIGURE 4. *Principal Components Ordination of sites using eight species as variables and indicating species abundance using Braun-Blanquet values: Calorophus minor, Sphagnum cristatum, Carpha alpina, Donatia novae-zelandiae, Oreobolus pectinatis, Gaimardia setacea, and not plotted, Chionochloa rubra and Drosera arcturi.*

ated by *Sphagnum cristatum* and its principal associate, *Calorophus minor*, from the cushion mire stands. On the second component (II) there is a strong positive loading for those stands dominated by *Carpha alpina* and *Schoenus pauciflorus*. The most extreme *Carpha-Schoenus* stands are clearly influenced by flush conditions, moving surface water often being visible in such communities. From observations at Lagoon Saddle and at other sites in the near vicinity, it is apparent that *Carpha alpina*

is a primary coloniser on skeletal mineral soil which is saturated with moving water. In these situations it will form an almost pure stand on a thin layer of raw humus directly overlying greywacke stones. It seems that as the peat layer develops the *Carpha* stand is invaded, the invading species depending upon peat quality: *Schoenus* on more fertile sites, *Oreobolus pectinatus* on less fertile.

The second component is clearly correlated with degree of flushing, those sites with a strong negative

loading on this component being the most stagnant. The abundance of *Carpha*, which occurs in most stands, is highly positively correlated with Component II and is evidently directly related to degree of flushing. However *Carpha* is independent of Component I and the *Sphagnum*-Cushion plant interaction. The differentiation of *Sphagnum*-*Calorophus* stands from Cushion plant stands is evidently not related to flushing. Indeed this interaction is apparently not related to overall nutrient status either. Figure 5 shows the distribution of stands in relation

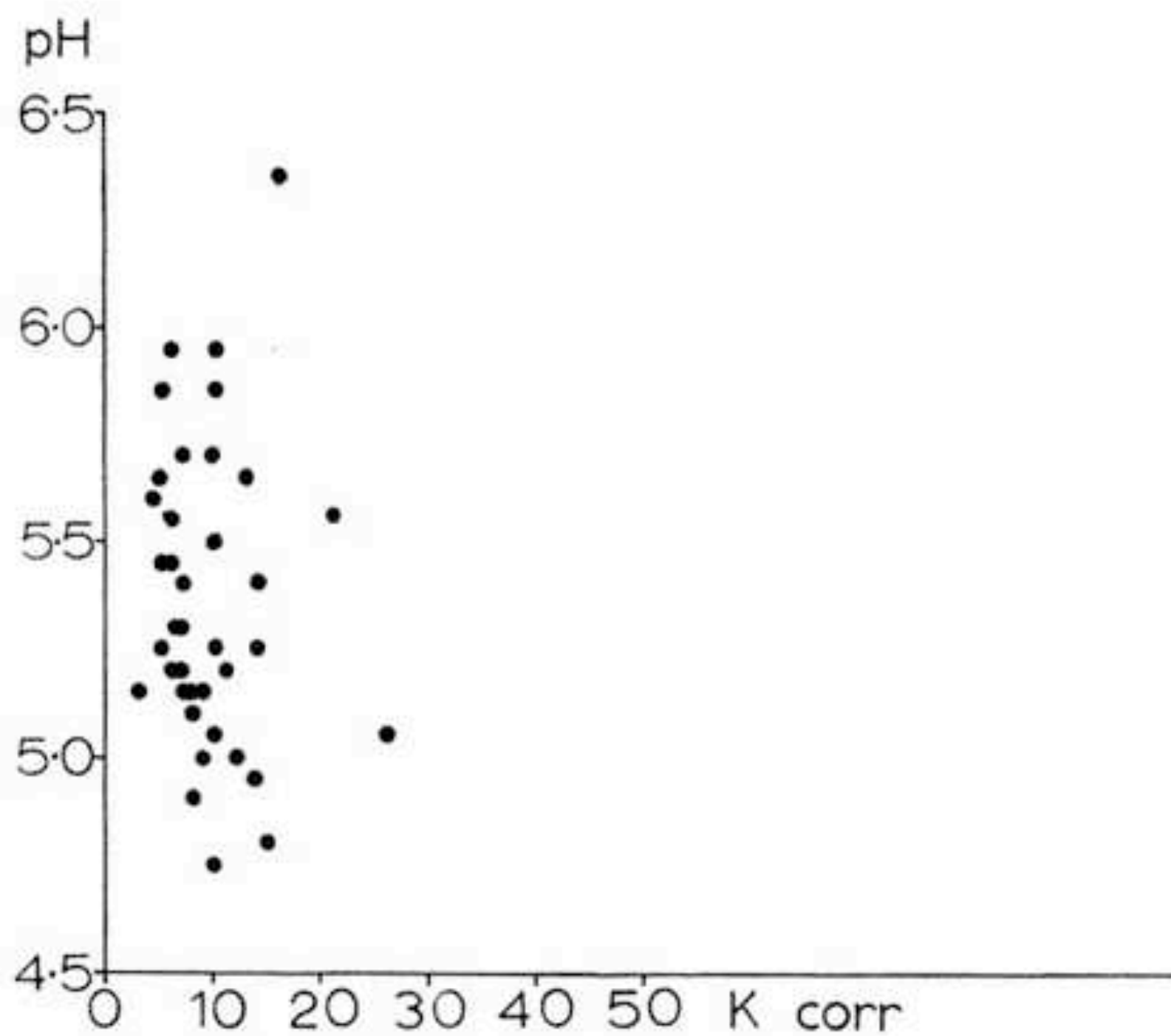


FIGURE 5. Distribution of pH values and corrected Conductivity (K corr) values in micromhos/cm on the Lagoon Saddle mire.

to pH and corrected Conductivity (K corr) values determined from the water samples. Even by the standards of oligotrophic mires, the Conductivity values of all sites are low. For a comparison of these values with those of a range of mire types see, for example, Sjors (1950) and Gorham (1956). The increased fertility of the flushed sites is therefore due to increased nutrient flux through the peat and increased aeration, compared with stagnant sites where nutrient flux is due to diffusion only. The water of flushed sites does not have an intrinsically higher nutrient status, a feature noted elsewhere (Sparling, 1966). Acidity of the mire water does not show any trends except that *Donatia* hummocks tend to be slightly more acid than other sites.

The most widespread and constant cushion plant is *Oreobolus pectinatus* (Fig. 6). The two other common cushion plants, *Donatia novae-zelandiae* and



FIGURE 6. Area dominated by *Oreobolus* cushions with small impermanent pools. Abrupt transition to *Chionochloa*-*Calorophus*-*Sphagnum cristatum* vegetation on either side.

Gaimardia setacea, are ecologically separated (Fig. 4). *Gaimardia* occurs on wetter sites with the water table at the surface while *Donatia* hummocks are usually 10-20 cms above water table. The position of *Donatia* is apparently a result of its growth habit. Once established the *Donatia* hummock overwhelms and suppresses adjacent plants and individual hummocks may be a metre or more across. Several old hummocks which have coalesced will produce a polygon pattern, the boundary between hummocks being defined by a line of other species apparently the surviving suppressed plants (Fig. 7). The growth



FIGURE 7. Polygon pattern of *Donatia* cushions. Boundaries of cushions marked by *Chionochloa* and *Carpha*. Within cushions occur *Oreobolus*, *Pentachondra*, *Cyathodes* and *Drosera*.

of *Donatia* is extremely slow (evidence from pot-grown plants), its success in suppressing relatively large plants, e.g. *Chionochloa rubra*, being due to the formation of an extremely compact cushion.

Only the rhizomatous dwarf shrubs *Pentachondra pumila* and *Cyathodes pumila* are successful at penetrating the cushion (Figs. 7 and 8). Aeration of these hummocks by their rise above the water table probably causes increased humification and hence acidity. The fourth cushion plant at Lagoon Saddle, *Centrolepis ciliata*, is scattered throughout the cushion mire sites and is never abundant. Several other cushion species occur on the mires of the main divide at Arthurs Pass.

From the plexus diagram (Fig. 8) it is apparent that the cushion mires contain a rather loosely associated assemblage of species. Much of the lack of correlation between the cushion mire species is due to the physical exclusion of one cushion species

by another. There is a separation of species from wetter sites, *Gaimardia*, *Sphagnum falcatulum* and *Utricularia monanthos* and those from the drier hummocks (*Donatia*, *Pentachondra* and *Cyathodes*). The cushion mire species are rather tenuously connected to the central nodum of the plexus which is occupied by the species typical of flushed conditions. The typical flush species, *Carpha*, *Schoenus*, *Hebe pauciramosa*, *Gentiana corymbifera*, *Campylium stellatum*, *Bryum laevigatum*, *Anisotome aromatica* and *Viola cunninghamii* form a rather closely bound nodum which is also closely bound to a secondary nodum centred on *Sphagnum cristatum* by way of intermediate species such as *Calorophus* and *Chionochloa*.

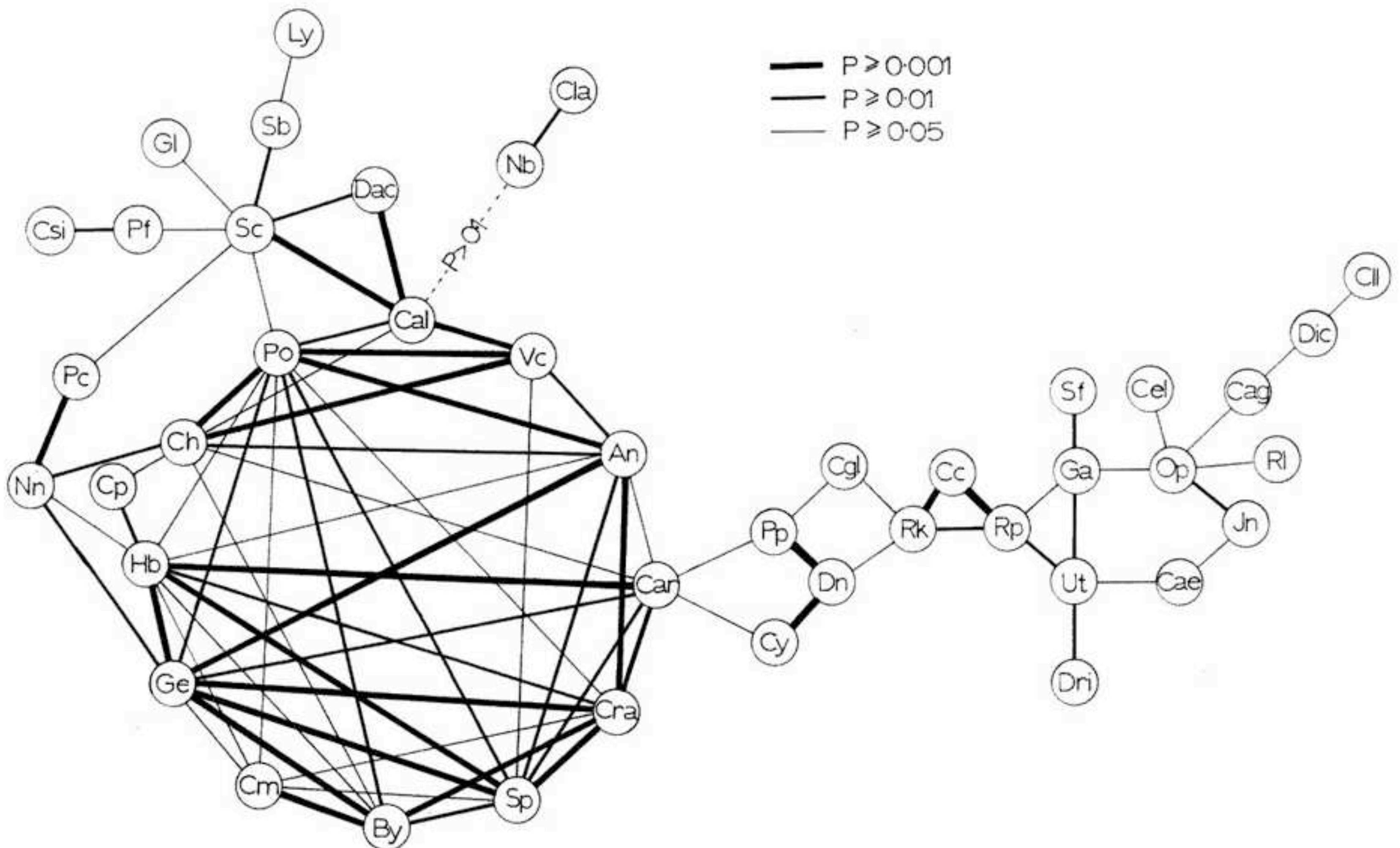


FIGURE 8. Plexus (=constellation) diagram of species occurring at more than one site at Lagoon Saddle based on significant positive correlation coefficients.

An	Anisotome aromatica Hook. f. (s.l.)	Apiaceae	rosette herb
By	Bryum laevigatum Hook. f. & Wilson	Bryaceae	moss
Cal	Calorophus minor Hook. f.	Restionaceae	rhizomatous juncoid
Cm	Campylium stellatus (Hedw.) Lange & C. Jens.	Amblystegiaceae	moss
Cae	Carex echinata Murr.	Cyperaceae	caespitose graminoid
Cag	C. gaudichaudiana Kunth	"	rhizomatous graminoid
Csi	C. sinclairii Boott	"	rhizomatous graminoid
Car	Carpha alpina R. Br.	"	caespitose graminoid

Cgl	<i>Celmisia glandulosa</i> Hook. f.	Asteraceae	rhizomatous rosette herb
Cel	<i>C. gracilentata</i> Hook. f.	"	rosette herb
Cc	<i>Centrolepis ciliata</i> (Hook. f.) Druce	Centrolepidaceae	cushion herb
Ch	<i>Chionochloa rubra</i> Zotov	Poaceae	caespitose graminoid
Cl	<i>Cladia aggregata</i> (Eschw.) Nyl.	Cladoniaceae	lichen
Cl	<i>Cladonia leptoclada</i> Des Abb.	"	lichen
Cp	<i>Coprosma pumila</i> Hook. f.	Rubiaceae	woody chamaephyte
Cra	<i>Craspedia uniflora</i> Forst. f.	Asteraceae	rosette herb
Cy	<i>Cyathodes pumila</i> Forst. f.	Epacridaceae	dwarf shrub
Dac	<i>Dacrydium laxifolium</i> Hook. f.	Podocarpaceae	dwarf shrub
Dic	<i>Dicranoloma billardieri</i> (Schwaegr.) Par.	Dicranaceae	moss
Dn	<i>Donatia novae-zelandiae</i> Hook. f.	Donatiaceae	cushion herb
Dri	<i>Drosera arcturi</i> Hook.	Droseraceae	insectivorous rosette herb
Ga	<i>Gaimardia setacea</i> Hook. f.	Centrolepidaceae	cushion herb
Ge	<i>Gentiana corymbifera</i> Kirk	Gentianaceae	semi-rosette herb
Gl	<i>Gleichenia dicarpa</i> R. Br.	Gleicheniaceae	rhizomatous herb
Hb	<i>Hebe pauciramosa</i> (Ckn. et Allan) L. B. Moore	Scrophulariaceae	dwarf shrub
Jn	<i>Juncus novae-zelandiae</i> Hook. f.	Juncaceae	caespitose juncoid
Ly	<i>Lycopodium fastigiatum</i> R. Br.	Lycopodiaceae	lycopod
Nb	<i>Nertera balfouriana</i> Ckn.	Rubiaceae	herbaceous chamaephyte
Nn	<i>Notodanthonia nigricans</i> (Petrie) Zotov	Poaceae	caespitose graminoid
Op	<i>Oreobolus pectinatus</i> Hook. f.	Cyperaceae	cushion herb
Po	<i>Pentachondra pumila</i> (J. R. et G. Forst.) R. Br.	Epacridaceae	dwarf shrub
Pp	<i>Pimelea oreophila</i> Burrows	Thymelaeaceae	dwarf shrub
Pc	<i>Poa colensoi</i> Hook. f. (s.l.)	Poaceae	caespitose graminoid
Pf	<i>Polytrichum formosum</i> Hedw.	Polytrichaceae	moss
Rl	<i>Racomitrium lanuginosum</i> (Hedw.) Brid.	Grimmiaceae	moss
Rp	<i>Rhacocarpus purpurascens</i> (Brid.) Par.	Hedwigiaceae	moss
Rk	<i>Rostkovia magellanica</i> (Lam.) Hook. f.	Juncaceae	caespitose juncoid
Sp	<i>Schoenus pauciflorus</i> (Hook. f.) Hook. f.	Cyperaceae	caespitose juncoid
Sb	<i>Senecio bellidioides</i> Hook. f.	Asteraceae	rosette herb
Sc	<i>Sphagnum cristatum</i> Hampe	Sphagnaceae (—sphagnum)	moss
Sf	<i>Sphagnum falcatulum</i> Besch.	Sphagnaceae (—cuspidata)	moss
Ut	<i>Utricularia monanthos</i> Hook. f.	Lentibulariaceae	insectivorous herbaceous chamaephyte
Vc	<i>Viola cunninghamii</i> Hook. f.	Violaceae	rosette herb

Although Component II of the Principal Components Analysis is related to degree of flushing, this component is not correlated significantly with slope as might be expected. However Component I is highly significantly correlated with slope ($P > 0.001$). *Sphagnum-Calorophus* stands occur frequently on steep slopes (often ten degree slopes and up to thirty-five degrees) while cushion stands tend to be on relatively flat sites. The *Sphagnum-Calorophus* stands are typically immediately below pools, forming dams (Fig. 9). These *Sphagnum-Calorophus* stands are particularly associated with the deeper pool complexes and also the Lagoon margins near where the Harper Stream leaves the Lagoon. Smaller shallow depressions rather than true pools are associated with the cushion species but in summer these frequently dry out. They are typically occupied by the mosses *Rhacocarpus purpurascens* and less commonly *Sphagnum falcatulum*. This is related to a

basic difference in the peat types underlying *Sphagnum-Calorophus* vegetation and cushion vegetation. *Sphagnum* and *Calorophus* are vigorous peat-formers and produce a spongy water-retentive peat. In some lowland mires *Calorophus* is known to be a vigorous peat former even in the absence of *Sphagnum* (Campbell, 1964). This type of peat is very resistant to waterflow. The cushion species produce a fibrous peat which is relatively much more pervious to water and does not exhibit good capillary properties. Cushion species peat would be incapable of restraining the large quantities of water that are impounded by relatively narrow zones of *Sphagnum-Calorophus* peat. The Lagoon and deeper pools quite clearly have deepened over a long period of time as a result of the upward growth in thickness of *Sphagnum-Calorophus* peat. The water from the pools does not drain through the impervious *Sphagnum-Calorophus* peat but rather a well-defined overflow channel is



FIGURE 9. A pool system looking downslope, a dry moraine with *Chionochloa* grassland in middle distance and beech forest and scree beyond.



FIGURE 10. Close view of vegetation of pool barrier. *Sphagnum cristatum* obscured by dense growth of *Calorophus* and *Chionochloa*.

present. This channel usually is delineated by a narrow band of *Schoenus* and *Carpha*.

It is a conspicuous feature of *Sphagnum cristatum* at Lagoon Saddle that it is mostly to be found growing beneath taller species usually *Calorophus* but sometimes *Chionochloa rubra* and rarely *Carpha* or *Schoenus* (Fig. 10). Where *Sphagnum* is growing in more open communities it has a high mortality and patches of bare peat occur. These are usually invaded by *Polytrichum formosum* (Sites 7, 28 and 37 on the ordination). *Sphagnum cristatum* is restricted at Lagoon Saddle to sheltered sites as it suffers from frost and/or wind desiccation where exposed. A species growing towards its upper altitudinal limit would be expected to occupy the warmer micro-habitats and certainly the slopes on which the *Sphagnum-Calorophus* stands occur predominantly face north and east and are in relatively sheltered positions which supports this. However, I have collected *Sphagnum cristatum* at 1500 m on Mid Hill (Fig. 1) where it was occurring on a very sheltered site: a snow hollow at the margin of a tarn.

Although the Lagoon Saddle mire has a complex structure, individual stands are evidently stable and replacement of one vegetation type by another is negligible. There are some indications that *Sphagnum* and *Calorophus* are invading cushion mires in a few places. The rhizomatous *Calorophus* is able to penetrate the cushions while *Sphagnum* in sheltered positions clearly grows faster than the cushion plants, the hummocks of the former slowly overwhelming the latter. Similarly there is observational evidence that *Donatia* hummocks can slowly overwhelm other species. Following a drought in the summer of 1973 there was considerable mortality of the upper parts

of *Oreobolus* cushions in one part of the mire. This part of the mire has a number of *Donatia* cushions and the death of *Oreobolus* may provide suitable conditions for the establishment of *Donatia*.

The boundary of the whole mire complex at Lagoon Saddle is characterised by an increase in *Chionochloa rubra* which eventually dominates the surrounding vegetation. From its stature and vigour it is evident that conditions for *Chionochloa rubra* on the mire itself are suboptimal. It is distributed in all vegetation types at Lagoon Saddle but is noticeably less abundant in cushion vegetation. *Gleichenia dicarpa* is locally abundant on the drier margins. In places there is a very abrupt transition from peaty to mineral soils and here there is a narrow zone of shrubs, *Phyllocladus alpinus* and *Dacrydium bidwillii* passing directly into *Nothofagus* forest.

CONCLUSION

The mire vegetation at Lagoon Saddle may be conveniently divided into three main types:

1. *Sphagnum cristatum-Calorophus minor* type.
2. Cushion vegetation type in which the main cushion-forming species are *Donatia novae-zelandiae*, *Oreobolus pectinatus* and *Gaimardia setacea*.
3. A sedge type in which the most conspicuous plants are *Carpha alpina* and *Schoenus pauciflorus*.

Intermediates between these types can be found but in general a particular site will fall readily into one of the three categories and abrupt boundaries between different types frequently occur (Fig. 6).

The peat water at all sites is acidic and oligo-

trophic, however, it is apparent that *Carpha-Schoenus* vegetation receives flushed water and is therefore both better aerated and has an increased nutrient flux. *Carpha*, although preferring more fertile sites, is to be found in all but the most infertile sites and its relative abundance is perhaps a better indicator of nutrient status of a site than water analysis. Pure *Carpha* communities occur on very shallow peats directly overlying mineral soils.

Sphagnum-Calorophus communities apparently occur in warmer and more sheltered micro-habitats. *Sphagnum cristatum* shows high mortality in the absence of sheltering vascular species. Its local abundance at Lagoon Saddle is probably due to the chance occurrence of *Calorophus* on this mire. In Canterbury, *Calorophus* is a relatively rare species (Burrows, 1969). It is noticeable on other cushion mires, such as those at Arthurs Pass, where *Calorophus* is not present, that *Sphagnum cristatum* is usually a very subordinate species. *Sphagnum* and *Calorophus* are vigorous peat formers usually forming deeper peats than the cushion plants. This community type often occurs on north-facing slopes and forms peat barriers separating and restraining the larger pools. The depth of these pools reflects the degree of peat accumulation. There has been negligible infilling of the pools with organic matter.

On the shallower peats cushion plants predominate but within these areas, *Gaimardia* occupies the wetter sites and *Donatia* the drier, while *Oreobolus* is more catholic in its requirements. There is however evidence that *Donatia* can suppress both the other cushion species and taller herbs but this is a very slow process.

The mire vegetation at Lagoon Saddle, although intricate, is clearly stable and changes in species composition and abundance at any site are negligible at the present time.

ACKNOWLEDGMENTS

I am grateful to Dr Colin Burrows for additional information and his criticism of the manuscript and Mrs Hilary Langer and Dr R. McCammon for their considerable assistance with the computation. My wife and Mr G. Mitchell assisted with the field work.

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