PROGRESS IN THE STUDY OF SOUTH ISLAND ALPINE VEGETATION

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INTRODUCTION

Since 1962, when the present writer outlined a broad physiognomic classification of South Island alpine grasslands, there has been progress in the study of the main grasses and grasslands. This permits a reassessment of some features of the description and ecology of the vegetation. An event of first importance was the revision of taxonomy of the New Zealand Arundinoideae by Zotov (1963). Plants formerly included in the genus, *Danthonia* were placed by him in several other more natural genera. The larger snowgrasses (and some smaller species) fall into *Chionochloa* and most of the smaller species into *Notodanthonia*. Two other advances made by Zotov were his clarification of taxonomy within the genus *Chionochloa* and the outlining of distribution ranges of the various species.

The study of alpine vegetation in different parts of the South Island mountains by Wraight (1963) (Wairau Valley, Marlborough); Connor (1965) (Rakaia Valley, Canterbury); Mark (1962) (Central Otago); Mark and Burrell (1966) (Humboldt Mountains, West Otago) and Mark and Baylis (1963) (Western Fiordland) has helped to clarify the nature of plant communities dominated by native grasses.

In the following account there is brief mention of some points of taxonomy of species of *Chionochloa* which indicate that more study is needed in some groups. The ranges of some species are extended further than was shown by Zotov (1963). Vegetation zones above the timberline in the South Island are defined. Information additional to that given by Burrows (1962) is presented in short descriptions of conditions in the habitats of the more important alpine grasslands. Discussion is confined to the grassland vegetation dominated by species of the genus *Chionochloa*, above the actual or potential timberline*. It should be understood that some of the species which dominate in alpine grasslands may also be common in subalpine, montane or lowland sites and some of the species more closely restricted to the alpine zone may occasionally descend to subalpine or montane sites.

TAXONOMIC AND DISTRIBUTIONAL NOTES

There are at least two widespread forms at present included under the name *Chionochloa rigida* (Raoul) Zotov. *Ch. rigida*, in the strict sense, is a species with leaves about 8 mm. broad at the base of the blade and with leaves up to 80 cm. in length. I have found it at altitudes of up to about 5,800 ft. but it descends to montane and lowland sites in the eastern South Island. Populations of the species have been observed in places from Marlborough and Banks Peninsula (the type area) to the Hector Mountains and Eyre Mountains, Western Southland.

The second form at present included under the name of *Ch. rigida* is probably a distinct species, and is hereafter called *Ch. sp. aff. rigida*. The two may be found growing together in parts of Canterbury and Otago but their full distributions are not yet known. *Ch. sp. aff. rigida* is smaller than *Ch. rigida*. Its leaves are up to about 50 cm. long and about 5 mm. broad at the base of the blade. The species occurs from at or just below timberline to 6,000 ft. I have found it in places from Nelson to the lower Rees Valley, West Otago. Both *Ch. rigida* and *Ch. sp. aff. rigida* dominate extensive areas of alpine grasslands east of the main divide in the South Island. The ecological interrelationships between these two forms and between both of them and other tall *Chionochloa* species await detailed study, but their altitudinal ranges suggest that *Ch. sp. aff. rigida* is better adapted to harsher, colder environments than is *Ch. rigida*.

Ch. pallens is a species differentiated into several regional forms. North Island populations differ from those of the South Island, and among the regional variants in the South Island there are some variable populations which may be the result of hybridization with *Ch. rigida* or *Ch. sp. aff. rigida*. At least four regional forms extending over

* Timberline was defined by Wardle (1965) as the upper limit of tall, erect "timber-sized" trees. Potential timberline, for the purposes of this paper, is regarded as the potential upper limit of timberline-forming trees in places where former forest has been destroyed. Altitudinal vegetation zones are discussed more fully later.

wide areas may be recognized. One extends from Nelson to Mt Cook and has a pale midrib to the leaf. Another similar form with a golden-coloured midrib is found from the Darran Mountains southward throughout Fiordland. Both of these have leaves from 30 to 75 cm. in length. Between the ranges of these two there is another—possibly a distinct species—with leaves less than half as tall as those of the others. The habitats occupied by this short form are similar to those of *Ch. pallens* in the northern and southern part of its range. Another form is present on the Seaward Kaikoura Range.

Ch. pallens is prominent in alpine grasslands on and west of the main divide in the South Island. It also extends 10 to 30 miles eastward from the main divide until it is replaced by *Ch. rigida* and *Ch. sp. aff. rigida* along an elongated area of overlap. The eastern edge of this area approximates the 50 inch isohyet (Fig. 1). In the area of overlap there are complex patterns of pure and mixed populations of *Ch. pallens*, and the other species. A general distribution pattern is present in areas such as the Upper Clarence-Wairau watersheds in Marlborough, and the Craigieburn Range, Upper Rangitata and Godley watersheds in Canterbury. *Ch. pallens* extends farthest east at high altitudes and in shady, mesic sites in these areas. *Ch. rigida* wedges in below it, extending farthest west at lower altitudes near the timberline. It seems likely that differences in precipitation are responsible for this distribution pattern. The high rainfall which occurs on the Seaward Kaikoura Range appears to account for the presence of *Ch. pallens* there.

Ch. flavescens is commonest in the subalpine zone in association with scrub but it extends into the alpine vegetation in many places. It is another species with widespread distribution and is also differentiated into regional forms. That found in western Nelson has leaves about 8 mm. wide at the base of the blade with from one to several prominent veins. The form found from about Haast Pass southward and throughout Fiordland

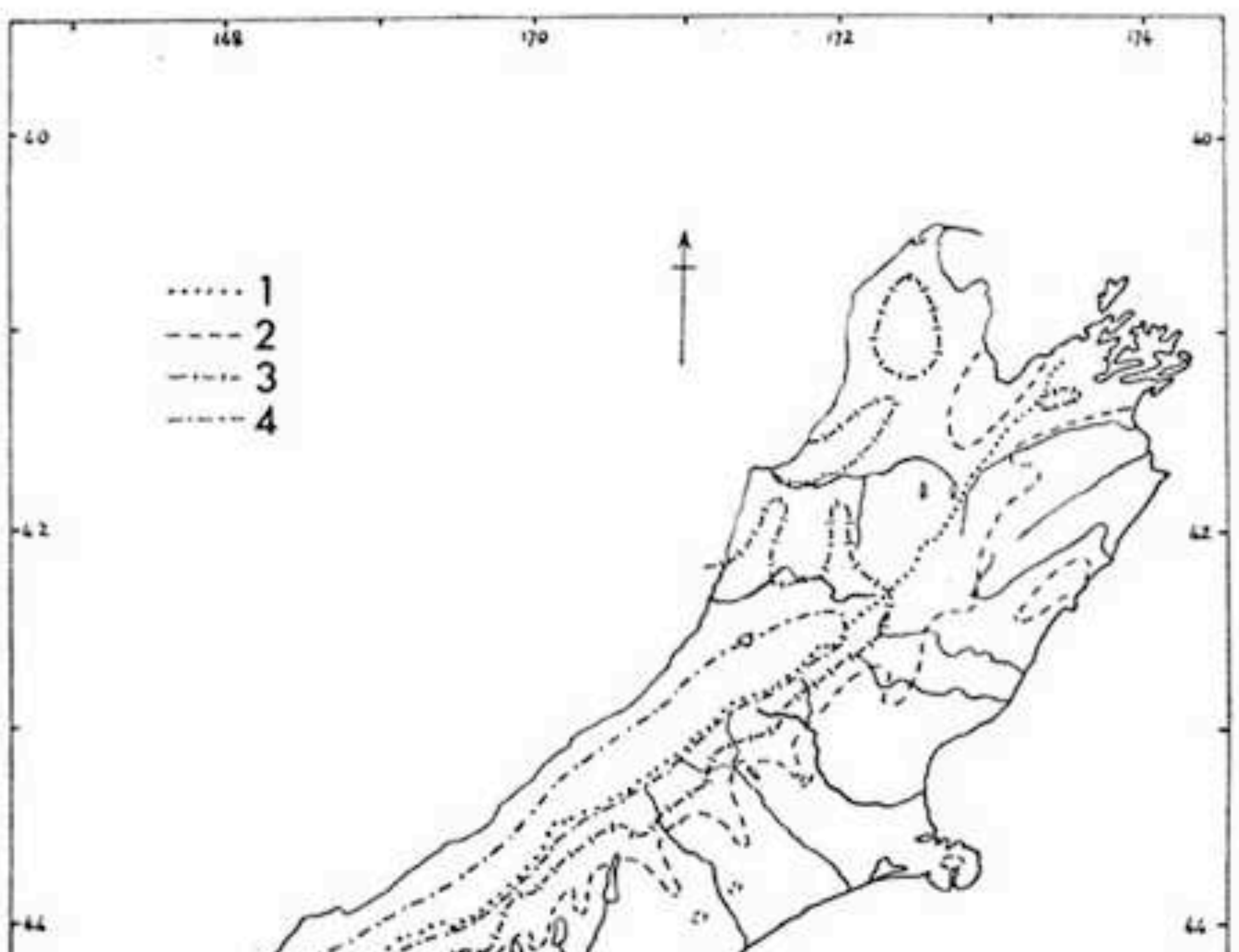

FIGURE 1. *South Island, showing Main Divide (1) and the 50 inch (2), 100 inch (3) and 200 inch (4) isohyets.*

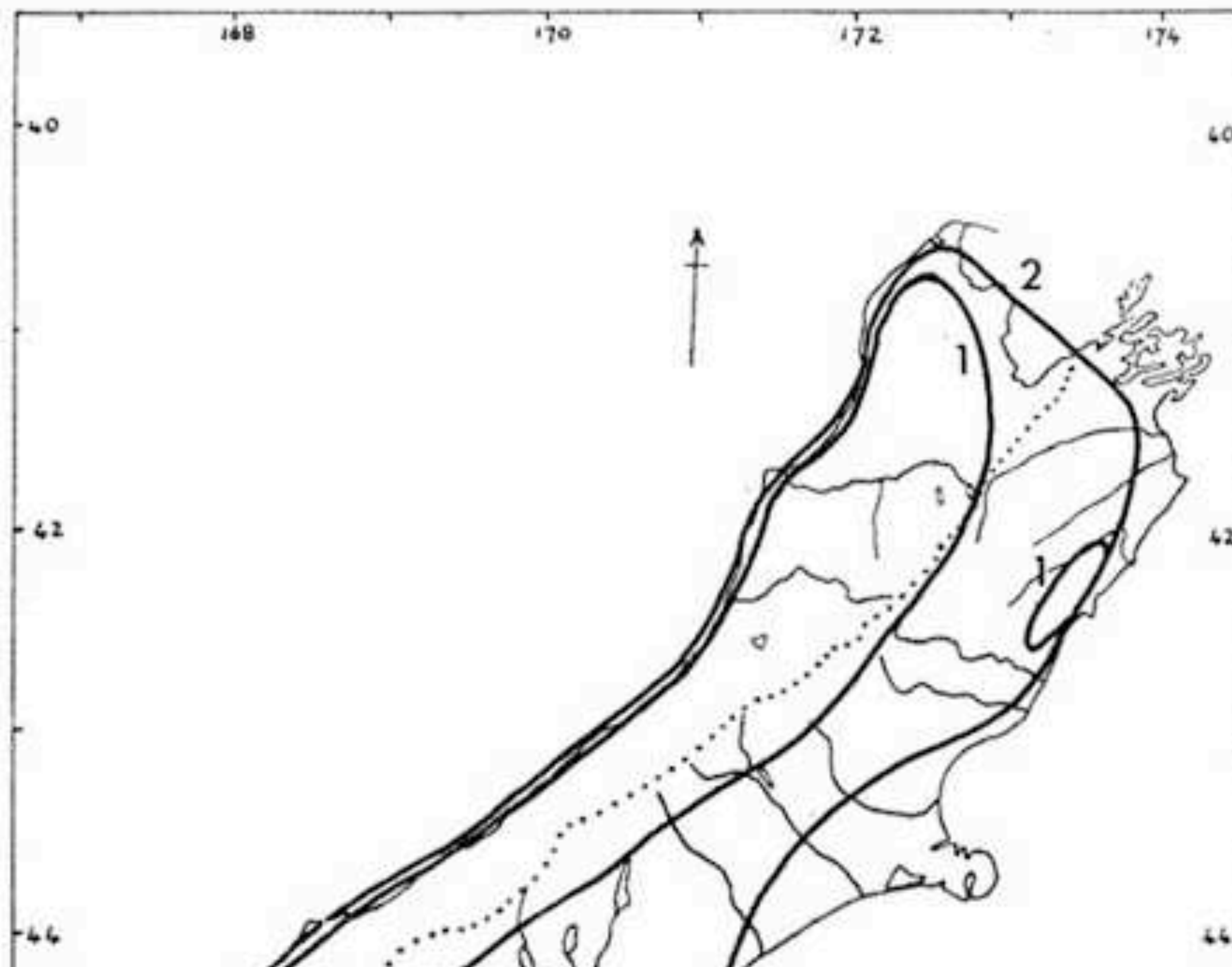

FIGURE 2. *South Island, showing the distribution of* Chionochloa pallens *(1)*, Ch. rubra *(2) and* Ch. acicularis *(3)*.

is very similar. In the central South Island there is another form of *Ch. flavescens* with leaves up to about 14 mm. wide at the base of the blade and with only one, less prominent, mid-vein. *Ch. flavescens* has a range similar to, but slightly more extensive than that of *Ch. pallens*. It is commonest on the mountains west of about the 50 inch isohyet and like *Ch. pallens*, is also present on the Seaward Kaikoura Range. Specimens of *Ch. flavescens* from Stewart Island are present in the herbarium of the Botany Department, University of Otago.

Figures 2 and 3 show outline distributions of those alpine species of *Chionochloa* not adequately treated by Zotov (1963). *Ch. oreophila* was found in the Cobb R. area in Nelson by Mr I. Ritchie, in 1967.

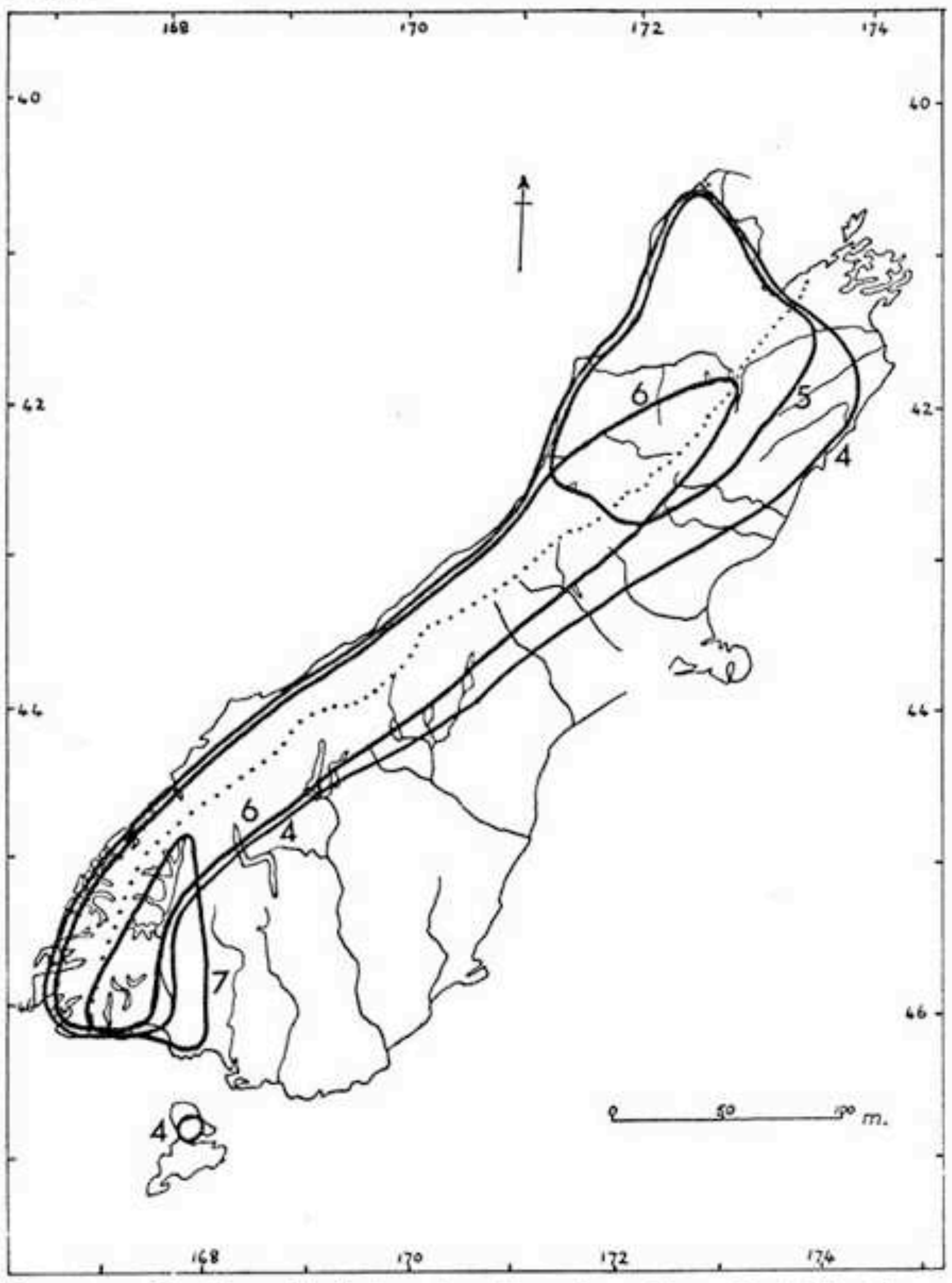

FIGURE 3. *South Island, showing the distribution of* Chionochloa flavescens *(4)*, Ch. australis *(5)*, Ch. oreophila *(6) and* Ch. teretifolia *(7)*.

ALTITUDINAL ZONATION

A scheme of altitudinal zonation to encompass the vegetation found above timberline in the South Island is presented in outline below (Table 1). It is a modification of that described by Wardle (1964). All such schemes are rather idealized and arbitrary because of variations in patterns of distribution of the species or kinds of vegetation used to delimit the zones. Also, zones are often not well marked where there is considerable disturbance or topographic irregularity. The division of the altitudinal sequence proposed by Wardle took into account floristics, physiognomy and broad climatic relationships.

TABLE 1. *Altitudinal zonation above timberline on and near the main divide, South Island (altitudes approximate)*.

	ALTITUDES IN FEET AT: 42°S.	43°S.	45°S.	
NIVAL ZONE				
	7500	7000	6000	Snowline
SUBNIVAL ZONE				
	5000	6000	5000	Grassline
		High alpine		
ALPINE ZONE	5000	5000	3800	
		Low alpine		
	4400	4200	3200	Scrubline
SUBALPINE ZONE	4200	4000	3000	Timberline (or Treeline)
	3000	3000	2000	

The zonation proposed here is physiognomic but also has some reality in a floristic sense. The *nival* zone is defined as that area above the lower limit of permanent firn snow, the *snowline*. Plants which grow here are lichens and a few highly specialized vascular species confined to rock faces, screes or rubble. The *alpine* zone has its upper limit at the *grassline*, the upper limit of continuous grassland vegetation. Between grassline and snowline is the *subnival* zone, where periglacial activity is very strong and only a sparse vegetation of cushion and tufted plants and lichens is found on the barren rocks, boulderfields, shattered finer debris and screes. The lower limit of this zone is variable in altitude and often diffuse. In many places on the more stable mountains closed alpine vegetation gradually grades into barrenland through progressively more open alpine cushion vegetation (Mark 1962) and fellfield (Burrows 1962). Where the substratum is less stable there may be a belt of erosion surface above the closed alpine grassland with scattered clumps of grasses and other plants in a matrix of predominantly bare ground. In many other places, however, the boundary between closed grassland and the subnival barrenland is very sharp. Within the alpine zone Wardle (1964) distinguished two subdivisions, the lower alpine belt, dominated by tall evergreen tussocks of *Chionochloa* spp., and a high alpine belt in which vegetation is low and less continuous.

Wardle's high alpine belt continued to the snowline, whereas in the present scheme this area is divided into the subnival zone and the upper part of the alpine zone. There is no consistent physiognomic boundary between upper and lower parts of the alpine zone but there are some floristic differences. Short grasses including *Ch. oreophila* are often prominent in the high alpine zone, whereas tall grasses including *Ch. flavescens*, *Ch. pallens* and *Ch. rigida* (in pure communities) are more prominent in the lower alpine zone. The *scrubline* (equivalent to the *tree limit* of Wardle (1964) is the upper limit of the *subalpine* zone. This line is defined as the upper limit of continuous scrub vegetation. As with the grassline, the scrubline is variable in altitude and often the boundary between grassland and scrub is ill-defined so that a gradient exists from pure scrub to pure grassland. The timberline (or treeline) is usually well-marked.

At any given latitude the limits of snowline and timberline are usually higher some 20 miles or more east of the main divide than they are on and west of it. As examples there are the positions of timberline at about 5,000 ft. at lat. 42°S., some 20 miles east of the main divide and snowline at about 7,500–8,000 ft., 20 miles east of the divide at lat. 43°S. (cf. Table 1). The cause of the higher eastern limits appears to be the presence of drier, warmer climates found on that side of the divide. As Wardle (1964) has pointed out, however, the ecology of New Zealand timberlines is complicated by the absence of the main timberline-forming trees, *Nothofagus* spp., from some areas—notably on the western side of the main divide in the central South Island. The limits of grassline do not always rise consistently towards the eastern side of the divide. In Marlborough Wraight (1963) recorded alpine grassland up to 6,500 ft. about 20 miles east of it; but in central Canterbury the grassline may fall to about 5,500 ft., or even lower, where very active erosive forces depress the upper limit of alpine vegetation in ranges east of the divide.

VEGETATION AND ECOLOGY

Although it is not yet possible to give a synthesis of the plant communities dominated by all the various species of grass prominent in the alpine vegetation, some general points may be made. Communities extending over wide areas may be dominated by one species or by certain combinations of species. In parts of Fiordland the presence of all but one of the *Chionochloa* species prominent in alpine grasslands (the exception being *Ch. australis*) makes it possible to observe the combinations which may occur. Many of the combinations of dominants are distributed over relatively small areas and are not mentioned in this account. The commoner kinds of vegetation (named according to the principal dominants), are noted below. Commonly associated plants other than *Chionochloa spp.* are indicated in each instance and the habitats characteristic for the vegetation. Additions and amendments are made to the information given by Burrows (1962).

Before enumerating the kinds of vegetation some of the terminology to be used must be discussed. *Tall tussock grassland* is a term coined by Cockayne (1928) which was used by Burrows (1962) to include *Ch. crassiuscula* grassland along with other tall grasslands*. The division between the stature of *tall tussock grassland* and *short grassland* (in which the species are not strictly or not at all tussock-formers) may be placed at about 20 cm. Note that this usage applies only to alpine grasslands because lowland and montane *low tussock grassland* (Cockayne 1928) incorporates species which are often taller than 30 cm.

Tall tussock grassland

Ch. rigida (narrow-leaved snowgrass) in the strict sense (and *Ch. sp. aff. rigida*): Important associates include *Festuca novae-zelandiae, F. matthewsii, Poa colensoi, Ch. australis* (in Nelson-Marlborough-N. Canterbury). *Celmisia spectabilis, C. viscosa* and *C. lyallii*. A wide range of habitats on different slopes and aspects is occupied throughout the alpine zone and soils range from lithosols to mature yellow-brown earths and gleyed yellow-brown earths. Moderately deep winter snow is tolerated.

Ch. flavescens (broad-leaved snowgrass): Associates include many shrubs and herbs such as *Dracophyllum uniflorum, Olearia* spp., *Senecio* spp., *Hebe* spp., *Coprosma* spp., *Phormium colensoi, Ch. pallens* and *Celmisia coriacea*. In Fiordland *Ch. teretifolia* or *Ch. acicularis* may be associated. The most characteristic habitats are warm slopes just above timberline or on cliffs and

* Printers' errors in the table included in Burrows (1962) were corrected by an erratum note. The main change to be made there is to place the division between tall tussock grassland and short grassland below *Danthonia* (*Chionochloa*) *crassiuscula*.

ridges exposed to the sun. On such sunny sites the species may ascend to 5,000 ft. (43° S.) and 3,800 ft. (45° S.). The substratum is frequently well-drained because of position on bluffs, ridge-crests or rock falls but the grassland may also be present on poorly-drained (but relatively warm) slopes and in some places the vegetation containing *Ch. flavescens* grades into bog. Mark and Burrell (1966) recorded the species from a community with *Ch. crassiuscula* on poorly-drained soils in the Humboldt Mountains. The soils most commonly occupied are lithosols but in wetter sites soils are gleys and shallow peats. Only light snow in winter is tolerated.

Ch. pallens (midribbed snowgrass): Important associates are *Ch. australis* (in Nelson-North Westland) and *Ch. crassiuscula* (both frequently co-dominant), *Celmisia discolor, C. armstrongii* and *Poa colensoi*. A wide range of habitats is occupied on different slopes and aspects throughout the alpine zone, and sites ranges from well-drained to poorly-drained. The area occupied by *Ch. pallens* in Fiordland is limited, presumably because of the very wet peaty soils. Pure *Ch. pallens* vegetation is best developed on young, and probably relatively fertile, well-drained colluvial and alluvial soils. It is associated with *Ch. crassiuscula* on poorly-drained soils and with *Ch. australis* on soils ranging from moderately well-drained to poorly-drained. The soils occupied are therefore lithosols, as well as mature gleys and gleyed yellow-brown earths. The species tolerates moderately deep snow in winter.

Ch. rubra (red tussock): The main associates are species such as *Schoenus pauciflorus, Carpha alpina* and *Oreobolus pectinatus* but in Nelson-Marlborough *Ch. australis* is often associated. The areas occupied by *Ch. rubra* above timberline are limited and the species is restricted to Nelson and North Westland and parts of Southland and South Otago as an important component of alpine grassland. Elsewhere the species is commoner in subalpine, montane and lowland valley-floor sites. The usual sites in the alpine zone are very poorly-drained, flat to gently-sloping areas on cirque floors or flat-topped ridges and mountain-tops up to about 5,000 ft. at 41°S. and 4,000 ft. at 45° S. Where sites are somewhat better-drained in the northern South Island the vegetation grades into *Ch. australis* vegetation and in wetter sites *Ch. rubra* vegetation grades into bog. The soils occupied are mature gleys and shallow to deep peats. Light snow in winter is tolerated but the sites are usually cold.

Ch. crassiuscula (curly grass): *Ch. pallens* is the only consistent prominent associate of *Ch. crassiuscula* although *Celmisia haastii* and *Caltha novae-zelandiae* are commonly found with it. Fiordland is the only region where the species occupies extensive areas as the sole dominant. Elsewhere, limited patches of the grass are found round the margins of late-snow areas. In western Fiordland *Ch. crassiuscula* vegetation may be found on a wide range of altitudes, slopes and exposures but it is always commonest at altitudes above about 4,800 ft. (43° S.) and 3,500 ft. (45° S.). All sites are poorly-drained and *Ch. crassiuscula* is often found as a minor component in bog. Soils under *Ch. crassiuscula* are immature shallow to mature deep gleys and shallow to deep peats. The species tolerates deep winter snow.

Ch. teretifolia (hairy snowgrass): Associates are *Dracophyllum uniflorum, Celmisia petriei, C. verbascifolia* and *Ch. crassiuscula*. The most characteristic sites are sunny slopes and ridge-crests up to about 3,800 ft. In such sites it is sometimes associated with *Ch. flavescens* but pure stands of *Ch. teretifolia* always occur on less well-drained slopes where impedance of drainage is enhanced by the peaty soil. Soils occupied are invariably shallow to deep peats. Only light winter snow is tolerated.

Ch. acicularis (needle-leaved snowgrass): Associates include *Dracophyllum* spp., *Hebe* spp., *Celmisia petriei, C. verbascifolia* and *Ch. crassiuscula*. The species is sometimes associated with *Ch. flavescens* on very steep exposed, sunny sites such as cliff faces up to about 3,800 ft. where drainage is potentially free; but pure stands are usually on less well-drained slopes. With *Ch. crassiuscula* it occurs on poorly-drained but convex sites and it is also frequently found in subalpine bogs. The soil is invariably shallow to deep peat. The species tolerates light winter snow.

Short grassland

Ch. australis (carpet grass): The commonest associates other than the taller grasses *Ch. pallens, Ch. rigida* and, less often, *Ch. rubra* are *Celmisia petriei, C. discolor,* and *C. spectabilis*, but the species may occupy areas almost to the exclusion of other prominent species. In pure stands the most characteristic sites are warm exposed ridge crests and other convex slopes, up to about 6,000 ft. Soils under *Ch. australis* range from mature yellow-brown earths, and gleyed yellow-brown earths to gleys. The species tolerates light to moderately deep winter snow.

Ch. oreophila (snow patch grass): Important associates are *Poa colensoi, Anisotome imbricata, Marsippospermum gracile, Celmisia sessiliflora* and, in places from Mt Cook to southern Fiordland, *Celmisia hectori*. The grassland is confined to sites with late-lying snow. These are concave sites and lee-slopes protected from radiation, above about 4,800 ft. (43° S.) and 3,800 ft. (45° S.). The soils occupied by *Ch. oreophila* vegetation range from well-drained young lithosols to gleys, shallow peats and shallow podsols. Deep winter snow is tolerated.

Other short grasslands found in the alpine zone dominated by *Festuca matthewsii, Poa colensoi* and *Notodanthonia setifolia*, are briefly dealt with by Burrows (1962), Mark (1962) and Wraight (1963). The more extensive areas of these grasslands seem to have been induced by fire and overgrazing.

ACKNOWLEDGMENTS

Grateful acknowledgement is made of financial support for field study from the Miss E. A. Hellaby Indigenous Grasslands Trust, The N.Z. University Grants Committee, the Royal Society of New Zealand and the Botany Department, University of Canterbury.

I am grateful to Mr. J. Allen for helpful criticism of this paper.

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EXPERIMENTS CONCERNING CAUSES OF TIMBER LINE—A PROGRESS REPORT

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Experiments are being carried out on the Craigieburn Range (in Canterbury, New Zealand) with mountain beech (*Nothofagus solandri* var. *cliffortioides*), which is the local timber line species, and with timber line species from other parts of the world. The aims are to compare growth at different altitudes, to demonstrate symptoms of failure in seedlings set out above their natural limit, and to show whether timber lines in New Zealand are climatically equivalent to those in other lands.

The experimental sites are on a slope facing north-east, at the altitudes of 3,600 ft., 4,200 ft. (which is just below the natural mountain beech timber line before it was depressed by fire), 4,800 ft. and 5,400 ft. There is also a site on a tussock flat at 3,000 ft. for the purpose of testing whether lower or valley timber lines are governed in the same way as alpine ones. At each altitude 3 degrees of shading, i.e., full exposure and two-thirds and one-third of full exposure, are provided by appropriate spacing of laths. The plots are covered with bully netting, to exclude grasshoppers which nearly destroyed the earlier trials; this reduced the light intensity by an additional 20%. Other environmental variations are minimized in order to keep experiments to manageable size. The seedlings are grown in waxed paper pots, which allow small seedlings to be transplanted with minimum disturbance but do not inhibit the root