ORDINATION OF GRASSLAND AND RELATED COMMUNITIES IN OTAGO

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INTRODUCTION

Indigenous grassland and related vegetation covers most of Otago east of the lake district. The communities occur over a wide range of topography and altitude and are, in consequence, determined by a considerable variety of climates and soils. Additional variation has its origin in the complex grass and shrub successions which began after Maori fires removed montane beech-podocarp forests from much of the region within the last millenium (Holloway 1954, Molloy *et al.* 1963). These complicated patterns of stable and unstable vegetation have been subjected to further drastic change by the animals, plants and pastoral practices introduced by European man.

Extensive descriptions of the geography of the main plant communities in Otago were made early in this century by Cockayne (1928) and, later, Zotov (1938) assessed the condition of large areas of indigenous grasslands. Though a number of limited areas of the province were relatively well known, detailed descriptions began with the surveys by the Otago Catchment Board (Wardle 1956, 1960, Mark *et al.* 1959, 1960, and Mark 1965a). In this work little complete sampling was done, for the object was inventory mapping of main community types, their condition and agricultural potential. Mark (1955), however, made a quantitative study of grass and shrubland vegetation on Maungatua and, with Billings in 1961, related the alpine cushion vegetation to patterned ground in Otago mountains. More recently (Mark 1965b), has used point analysis and similarity comparisons of *Chionochloa rigida* grasslands on Maungatua, Old Man Range and Coronet Peak. In reporting on his detailed climate measurements, Mark (1965a) has successfully correlated contemporary climates with the broad zonation of mountain vegetation in Central Otago.

The only complete regional analysis of an indigenous grassland in New Zealand was made by Connor (1961, 1964, 1965) in the MacKenzie country and Upper Rakaia Catchment, Canterbury. His excellent description of the grassland communities, their main environmental features and present condition has allowed a plausible explanation of their history to be made.

Alpine grasslands in a part of Fiordland were described by Mark and Burrell (1966) who used Sorenson's similarity coefficients to group and separate stands in an altitudinal sequence. Ordination of stands of grassland based on their coefficients of similarity or dissimilarity has been little used in New Zealand. Techniques available for this quantitative analysis include those of the Wisconsin school (Bray and Curtis 1957, Loucks 1960) and, more recently, those developed at Bangor, North Wales (Orloci 1966, Austin and Orloci 1966).

In the analysis of Otago grasslands and related communities being made at present, the relatively simple Wisconsin methods are being used. This contribution reports a preliminary treatment of grassland stands using data gathered during 1965–66. An attempt has been made to relate variation in the grassland continuum to the principal environmental gradients.

METHODS

Stand selection

After reconnaissance of the region, 99 stands were sampled to represent the wide range of variation exhibited by the grassland and related vegetation. No attempt was made to select stands at random, though for future studies this would have some value. Samples were taken from 300 to 5,400 ft. altitude and from arid to semi-aquatic habitats. They varied in area from approximately half an acre for some graminoid swamps to hundreds of acres for some *Chionochloa* and *Festuca* grasslands.

No undisturbed indigenous vegetation was found within the region. Consequently, the only criteria for suitability of prospective stands were that:

(1) The vegetation was not visibly recovering from recent disturbance by fire or severe grazing.

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(2) The physiognomic dominant was represented throughout the stand.
(3) The stand had visibly uniform topography, soil, aspect and moisture status.

Sampling method

A rapid survey of the stand was made during which a list of the species present was compiled. Then an estimate of the relative cover by each species was made from hits recorded on a pointed steel wire placed at regular intervals along a 100 ft. tape. The initial placement of the tape was parallel to the contour and well within the stand. Subsequent tape positions were parallel to the first and separated from it by regular numbers of paces; usually 30 in such communities as *Chionochloa* grassland and shrubland or 20 in short-tussock and *Agropyron*/*Raoulia* grassland.

Point positions were separated by regular intervals along the tape — 2 ft. for cushion plant and low tussock stands and 4 ft. for *Chionochloa* grassland, shrubland and *Cortaderia* swamp. As 200 point placements were made per stand, the number of tape-positions was 4 in low vegetation and 8 where the physiognomic dominants were large. At each position of the pointed steel wire, two hits only were recorded — the first hit on a canopy species above 6 inches and the first hit on a ground species below 6 inches. Results obtained by this method are known not to constitute true species point-cover estimates and consequently the term relative cover has been used. True cover is difficult and time-consuming to measure; besides, a non-selective sampling method was required which combined light equipment with rapidity and accuracy, in vegetation varying from flat cushions to shrubland.

In practice, the results for all the single-layer communities and for some of those with a canopy correspond closely to true cover estimates. During point-sampling all new species encountered were added to the presence list. Additional species were recorded during the measuring of every stand and this demonstrates one of the intrinsic values of quantitative sampling.

For each stand a brief description of the soil profile was made and a volume-weight sample of surface soil collected. Additional notes taken at each stand included aspect, slope, condition and probable extent of past disturbance. All species not recognised in the field were given a field name and collected for positive identification later. Point-hits on bryophytes and lichens were recorded and a collection was made of all species encountered.

Analytical methods

Stands were sorted into groups representing communities recognised by particular physiognomically-dominant species. All species presence values, ground cover estimates and site records were then compiled and community averages obtained. The relative ground cover for leading physiognomic dominants and several prominent ground species was graphed so as to give an arrangement of the chief communities on mineral soils. These communities were placed along the ordinate in a linear continuum related to increase in altitude and moisture status.

Ordering of stands

For computation of the indices of dissimilarity between stands, 181 vascular species were chosen on the basis of their relatively high constancy in at least one community. Values of relative ground cover for the 181 species, plus relative estimates of canopy cover for 19 were used — after being put on to punch cards — in computing the value of the Index of Dissimilarity,

$$\left(C = 100 - \frac{200W}{a+b}\right)$$

for each stand. These calculations for a partial matrix of Dissimilarity values were performed in the IBM-360 computer at the University of Otago.

The partial matrix consisted of comparisons with stands likely to be the mathematical ends of the ordinates. From this matrix the stand having the highest sum of Dissimilarity values, i.e., the one most dissimilar from all the others, was selected as the first end of the primary axis. The stand most dissimilar from the first end stand was taken as the other end of the primary axis. All other stands were then placed between these two end stands according to their interstand distances, calculated by the geometric method of Beals (1960).

Many of the stands placed near each other on the primary axis were not very similar. The production of a second axis which separates them in two-dimensional space was therefore needed. The first end stand of the secondary axis was that which had the poorest fit on the primary axis, i.e., had the highest "e" value of Beals. The stand placed at the other end of the secondary axis had the highest Index of Dissimilarity relative to the first end stand and separated from it by less than 10% of the length of the primary axis. The primary and secondary co-ordinates were then constructed and stands plotted with respect to these in two-dimensional "vegetation space". Actually, tertiary and higher order axes may be calculated until there is no increase in the separation of highly dissimilar stands.

The method for calculation of coefficient of dissimilarity is such that stand position in the ordination is determined by composition of the vegetation. Vegetation structure and composition are largely under the control of environmental factors and the interactions between them. Consequently, by plotting environmental parameters and the performances of species on an ordination, correlations between vegetation and environment are obtained. The primary axis usually reflects the principal variation of the vegetation and thus the environmental factor or factors related to this variation. Secondary and higher order axes relate to progressively smaller amounts of variation in the vegetation as represented by the scatter of stand positions and therefore to environmental factors with commensurately less influence.

The environmental gradients

Available moisture and seasonal temperature appear to be the most important factors in the indigenous grasslands, though recent disturbance often obscures their controlling influence. At this time, soil analyses are incomplete and accurate climate records are available for the areas of only a few stands. Despite fragmentary data on the environment it is useful to obtain some idea of the general relationship between environment and stand position on the ordination. Consequently, the moisture status for each stand was estimated by a point-scoring system and altitude has been used as an indirect measure of ambient temperature.

With the valuable advice of Mr E. J. B. Cutler, Pedologist, Soil Bureau, D.S.I.R., each stand was scored between 0 and 4 for position on a drainage catena, average precipitation and the capacity for retaining soil moisture.

Using this system, a composite moisture score was derived for each stand. The moisture scores ranged from 0 for the driest, most well-drained stands to 12 for stands of semi-aquatic, poorly drained vegetation. Any broad relation between moisture supply and vegetation sampled should be revealed by plotting the scores on the stand ordination determined by the vegetation. Similarly, some impression of the importance of temperature should be obtained by plotting altitudes on the arrangement of stands in the ordination.

RESULTS AND DISCUSSION

The list of vascular species compiled in the study approached 400, including 50 exotic species. Over 100 species of bryophytes and lichens were recorded.

Relative cover values for species graphed according to a linear arrangement of communities are presented for important physiognomic dominants in Figure 1, some prominent ground species in Figure 2 and several important exotic species in Figure 3. The arrangement of communities along the ordinate combines the gradients in altitude and moisture status. The curves for species, therefore, demonstrate their ranges of tolerance of differing moisture and temperature levels. However, they demonstrate also the relative resistance or lack of resistance of canopy species to burning and grazing on different sites.

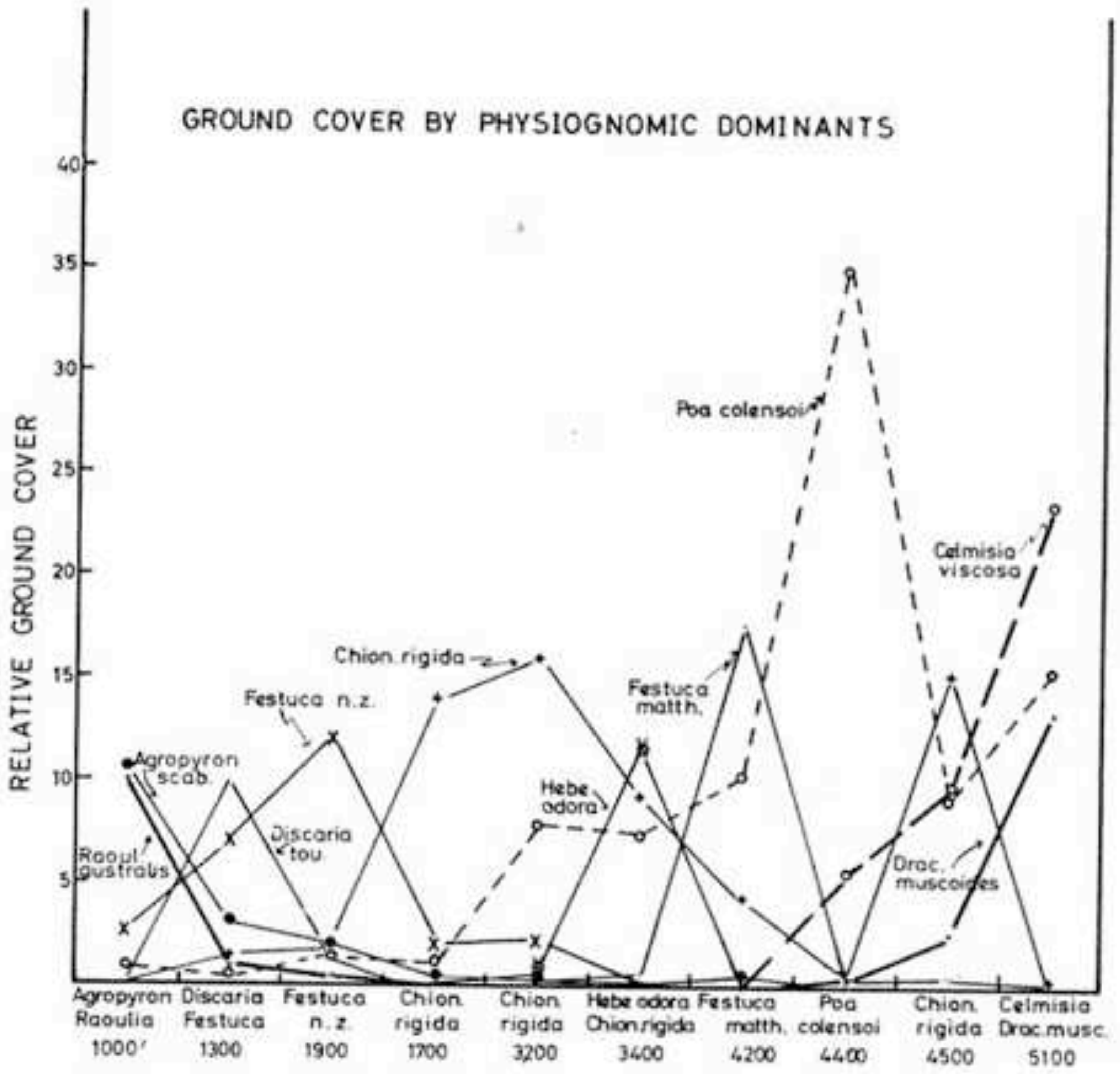

FIGURE 1. *Average relative ground cover contributed by leading physiognomic dominants to Otago grassland communities.*

The physiognomic dominants form a replacement series in Figure 1. For example, *Festuca novae-zelandiae* is weakened at the dry end to be replaced by *Agropyron scabrum* and *Raoulia*. *Chionochloa rigida* at low altitudes tends to be maintained against shrub encroachment following fire and heavy grazing but on drier sites gives place to *Festuca novae-zelandiae*. Throughout a wide subalpine zone of weakness the narrow-leaved snow tussock has been removed or greatly reduced by fire and grazing. In moist situations, however, both the *Chionochloa* grassland and *Hebe odora* shrubland remain as remnants. Drier, exposed situations now carry *Festuca matthewsii* grassland, and the fire-resistant *Poa colensoi* has increased to overriding dominance in most of the zone. On the exposed, cold and windswept alpine plateaux, the highly adapted *Celmisia viscosa, Dracophyllum muscoides* and other mat and cushion plants have long dominated. The scattered *Chionochloa* tussocks in such vegetation may, however, remain from former alpine grassland.

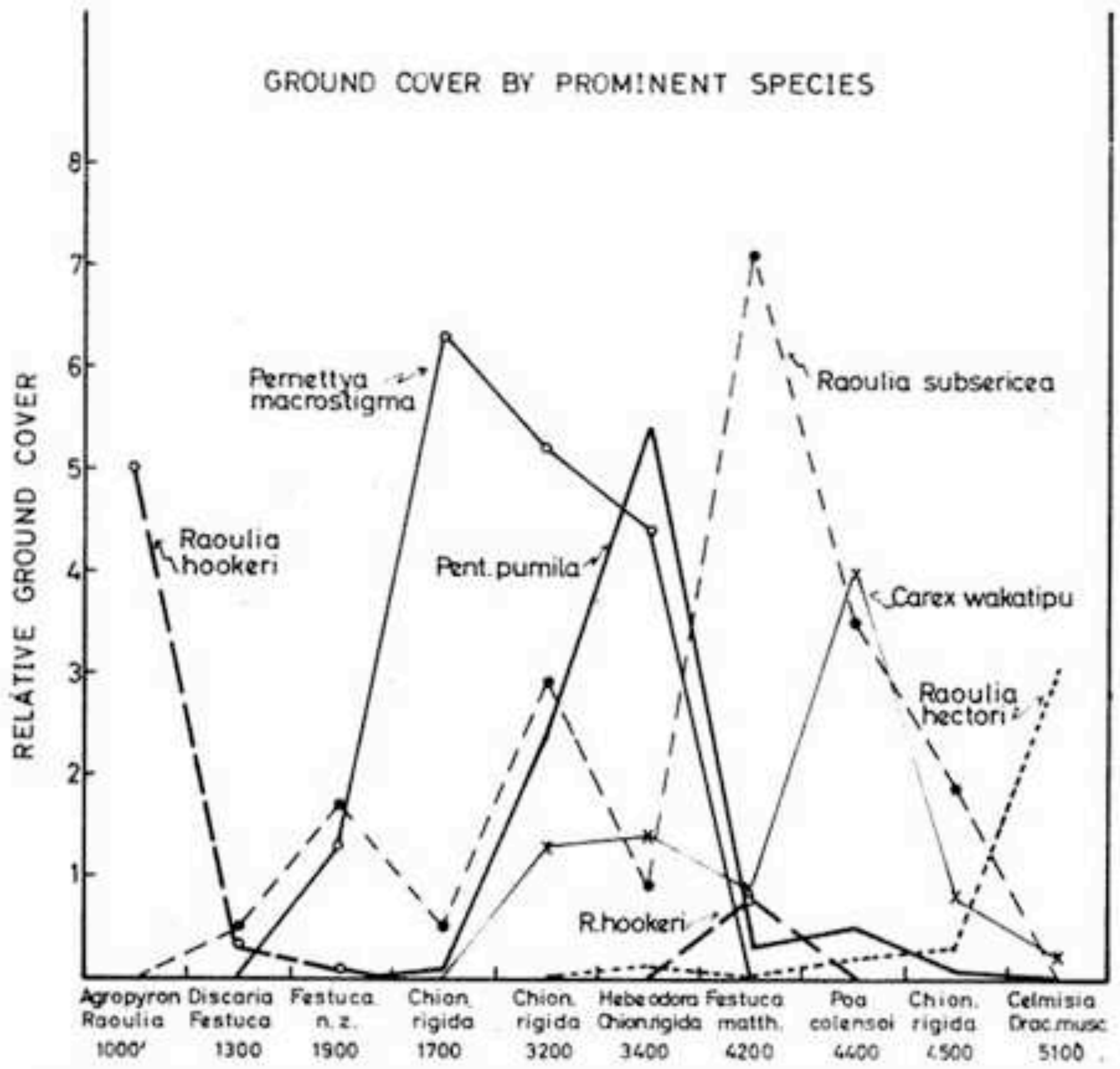

FIGURE 2. *Average relative ground cover contributed by some prominent ground species to Otago grassland communities.*

The cover by ground species fluctuates with both degree of cover by canopy grasses and shrubs and the environmental gradients. For example, *Raoulia hookeri* is prominent in dry, eroding short grassland, *Raoulia hectori* in moist, cold, eroding alpine cushion/herbfield. *Pernettya macrostigma* and *Pentachondra pumila* contribute their highest cover to low- and mid-altitude *Chionochloa rigida* grassland and *Hebe odora* shrubland. Such vegetation flourishes on leached yellow-brown earth soils, containing abundant charcoal from former forests. The wide range of *Raoulia subsericea* is clearly seen in Figure 2 but this species, together with others such as *Carex wakatipu*, is most prominent in the low tussock swards at subalpine altitudes. These ground species may have increased on being released from unfavourable conditions of illumination beneath previously-intact snowgrass canopies.

In Figure 3 a line representing the average percentage of bare soil in communities has been superimposed. The driest and the most elevated communities have today the least vegetative cover and appear to offer conditions too severe for vigorous establishment and growth of introduced species. Grasses such as *Anthoxanthum, Agrostis* and *Holcus* reach their highest cover values in *Discaria*-dominated grassland. The presence of abundant *Discaria* may indicate relatively fertile soil and less severe competition for light from canopy species.

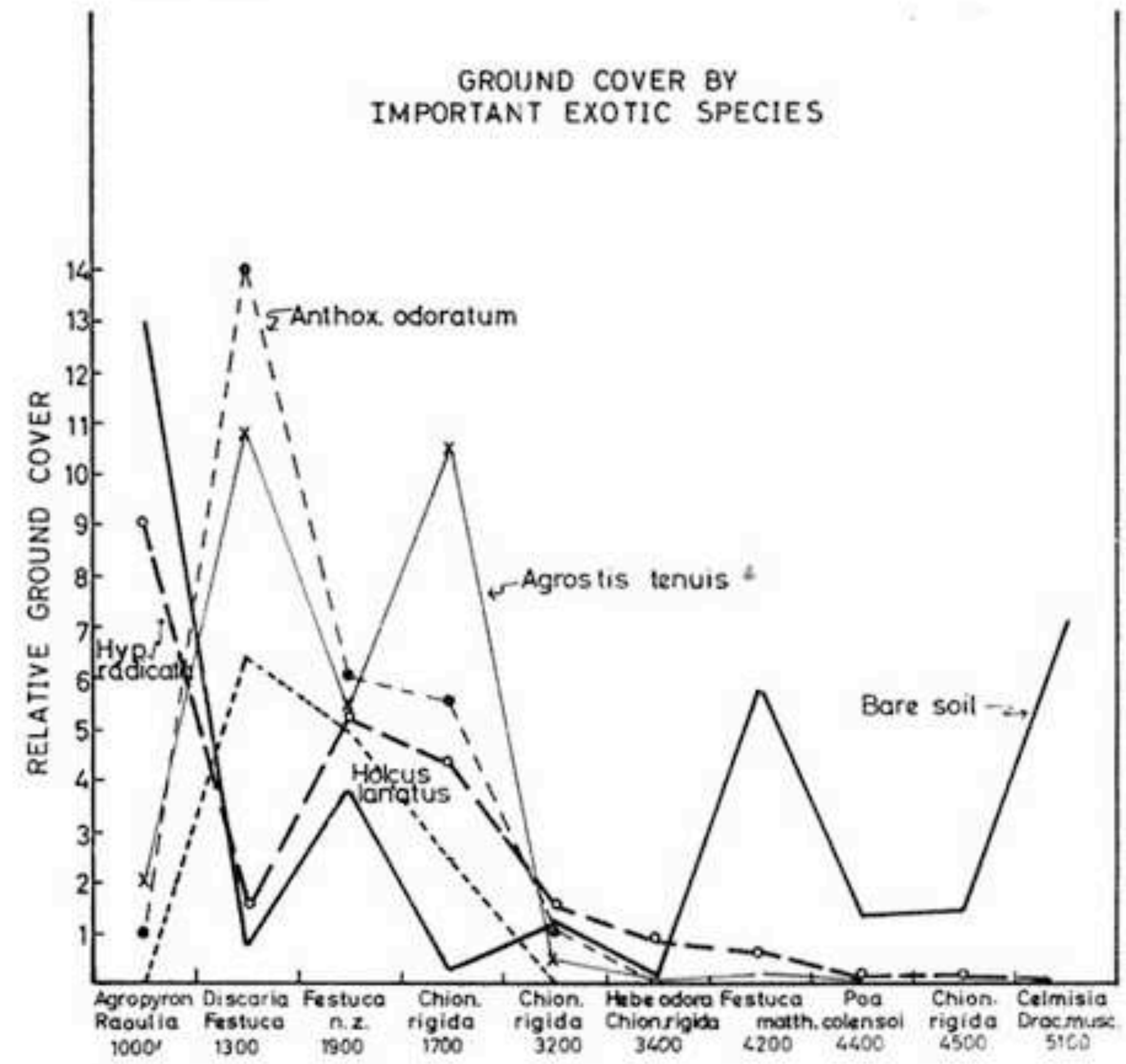

FIGURE 3. *Average relative ground cover of some important exotic species in grassland communities of Otago. Average percentage of bare soil has been superimposed.*

The flatweed, *Hypochaeris radicata* has the distribution of a species able to exploit open soil but with low competitive ability in closed swards. The curves of Figure 3 show clearly that these introduced plants reach their ecological limit in subalpine vegetation. Bare soil areas on alpine plateaux thus remain largely unoccupied as indigenous species, with few exceptions, appear unable to re-establish.

Ordination of stands

Figure 4 provides the ordination of stands according to the two principal axes of variation. Symbols representing stand positions identify them with the accompanying key to the physiognomic dominants. For the ordination to be an adequate abstraction of the vegetation, stands appearing

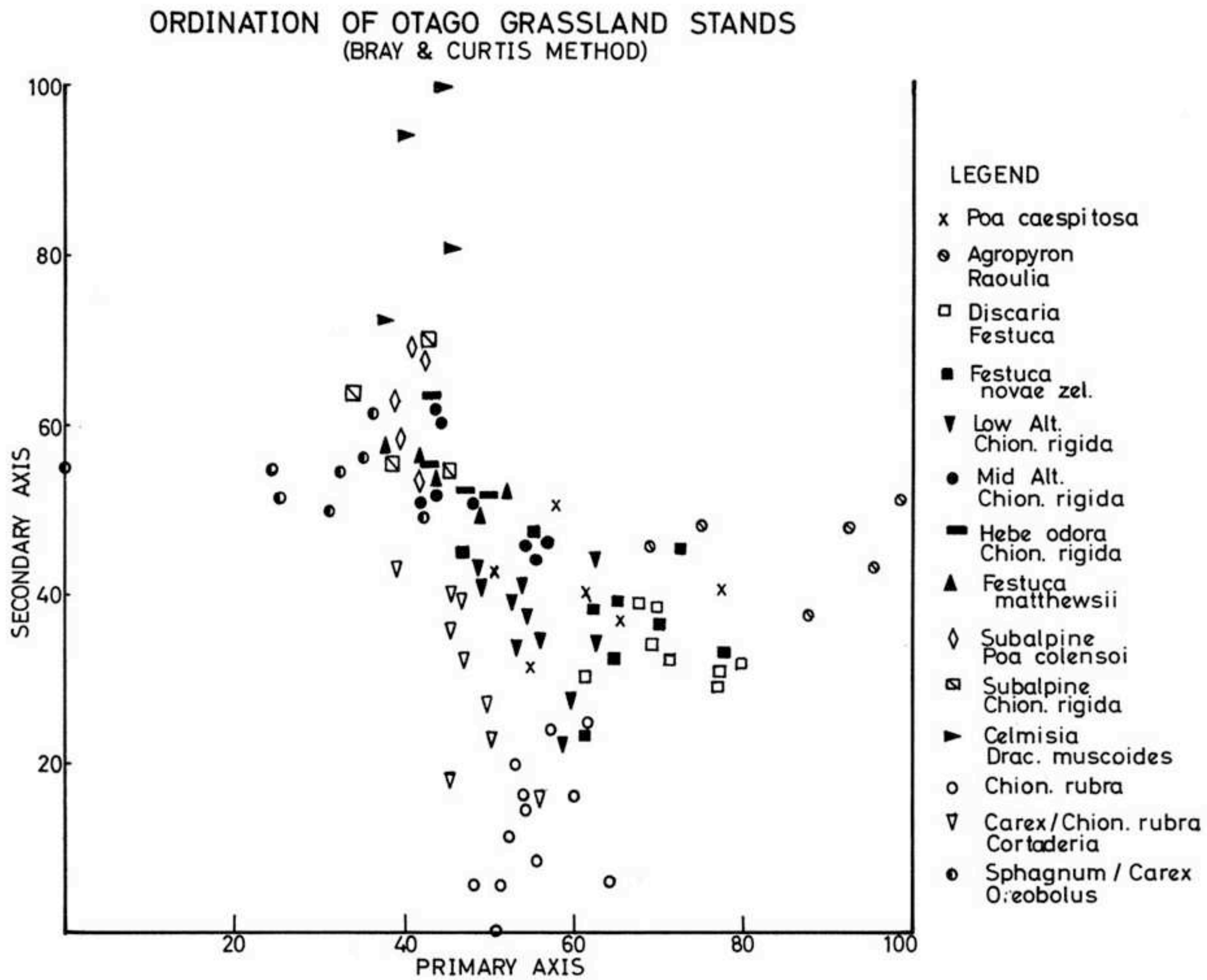

FIGURE 4. *A two-dimensional ordination of stands of grassland and related vegetation in Otago. Symbols identify stand positions with the key to physiognomic dominants.*

close together should be very similar in composition. In general this appears to be so. For some stands such as those dominated by *Poa caespitosa*, a third axis might provide a more efficient grouping. The ordination shows clearly that these communities form a continuum with both gradually merging and with relatively clear changes from one community to another. It is as well to note, though, that the Bray and Curtis method of ordination usually over-emphpasises the continuum and is less efficient than the more recently devised techniques of Orloci (1966) and Austin and Orloci (1966).

The ordination places most of the subalpine stands in an apparently mixed group. This appears to result from the inadequacy of grouping according to the physiognomic dominants when there is considerable similarity throughout in ground species composition. The ordination thus lends support to the possibility that most subalpine communities of mineral soils are stages in modification of *Chionochloa rigida* grassland.

An interesting feature of New Zealand's indigenous grasslands is the large group of species with broad ranges of tolerance. Connor (1961, 1964, 1965), in his studies of indigenous grassland in the Mackenzie Country and Canterbury, has defined them as "widespread species". In this preliminary ordination of grasslands in Otago some of the lack of discontinuity between communities is very likely caused by the degree of

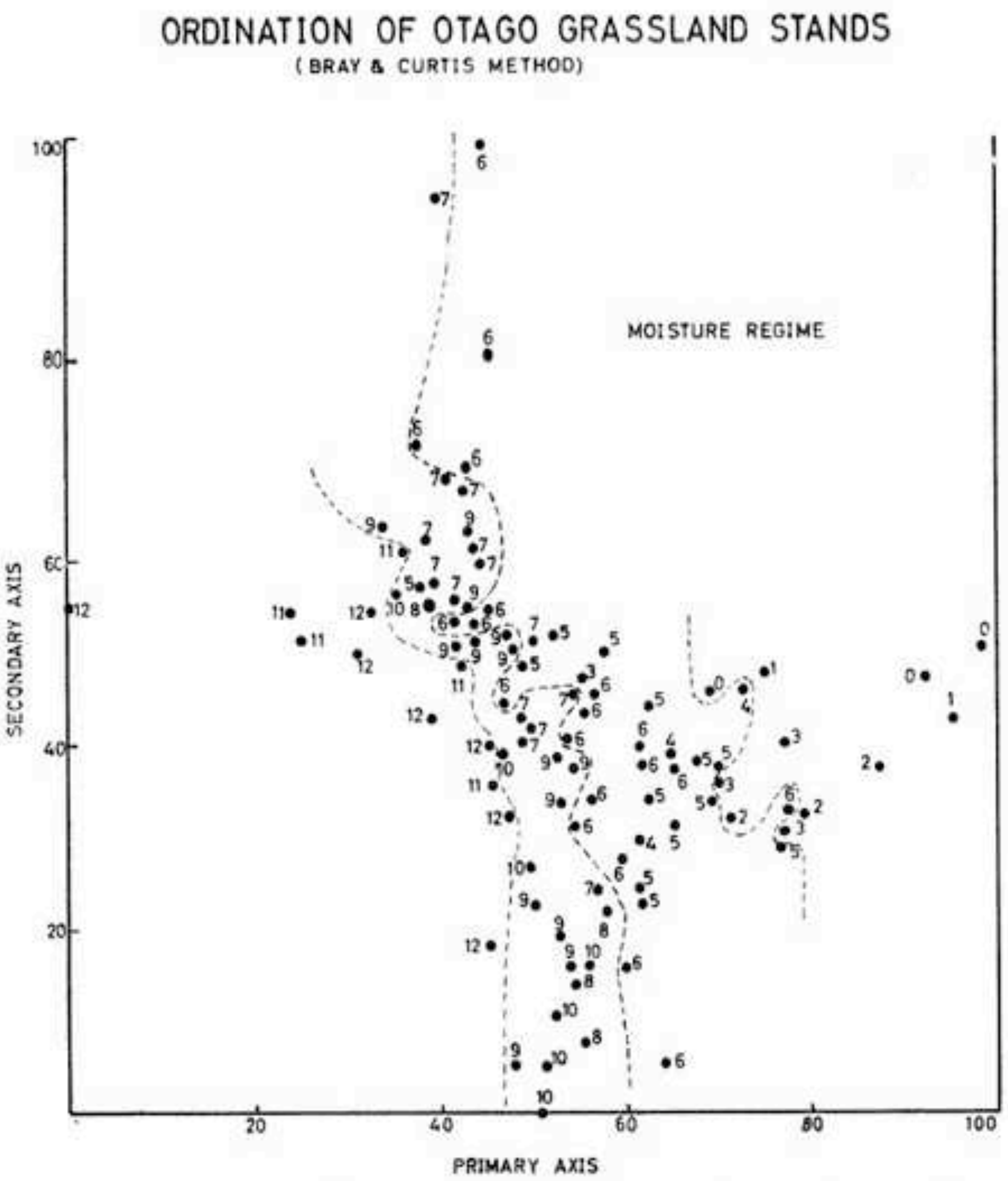

FIGURE 5. *Stand moisture scores plotted on the ordination of stands of grassland and related vegetation in Otago (Range: 0 — arid, excessively drained to 12 — semi-aquatic, poorly drained).*

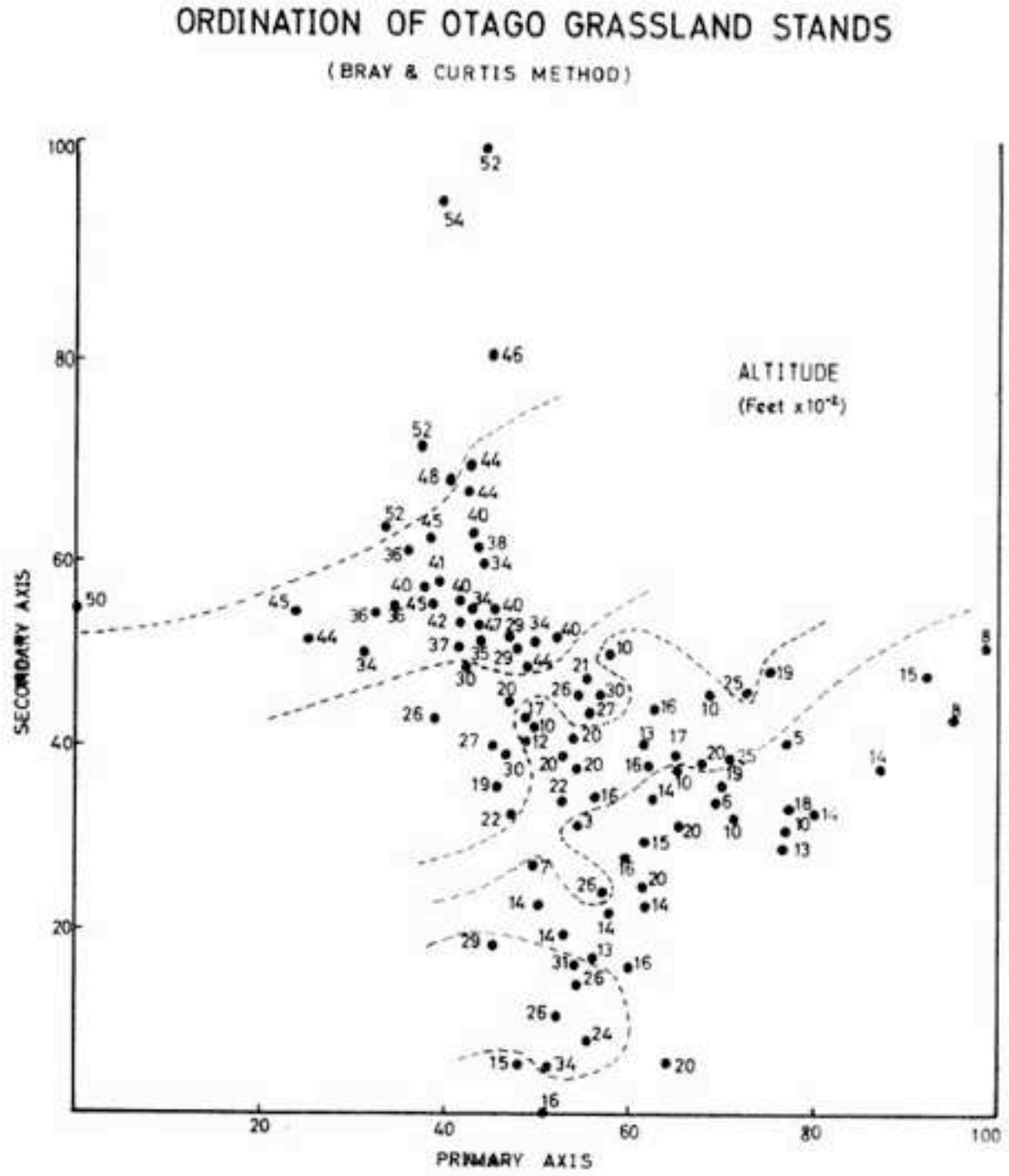

FIGURE 6. *Stand altitude plotted on the ordination of grassland and related vegetation in Otago. Altitude is related to variation along both axes as it influences both temperature and precipitation.*

similarity between many stands conferred by these widespread species.

In Figure 5 the moisture scores have been plotted on the stand ordination. Moisture scores increase from right to left along the primary axis. Altitude appears more strongly related to the secondary axis as seen in Figure 6. However, the two environmental variables are not independent, each being associated with both axes, thus causing a skew in the orientation of the cluster of points representing stands. Effects of local variation in topography and cultural modification probably obscure some of the indirect influence of altitude on vegetation-level climates, particularly in montane areas. The relatively small number of stands sampled in alpine communities probably magnifies the divergence of extreme stands from the point-cluster.

The distributions of relative cover by individual species according to stand position emphasises the usefulness of the ordination. For example, *Bulbinella angustifolia* achieves its highest ground cover in montane grasslands of moderate moisture status (Fig. 7). There is an interesting discontinuity in its distribution, as it appears to be successful also in wet *Chionochloa rubra* grassland.

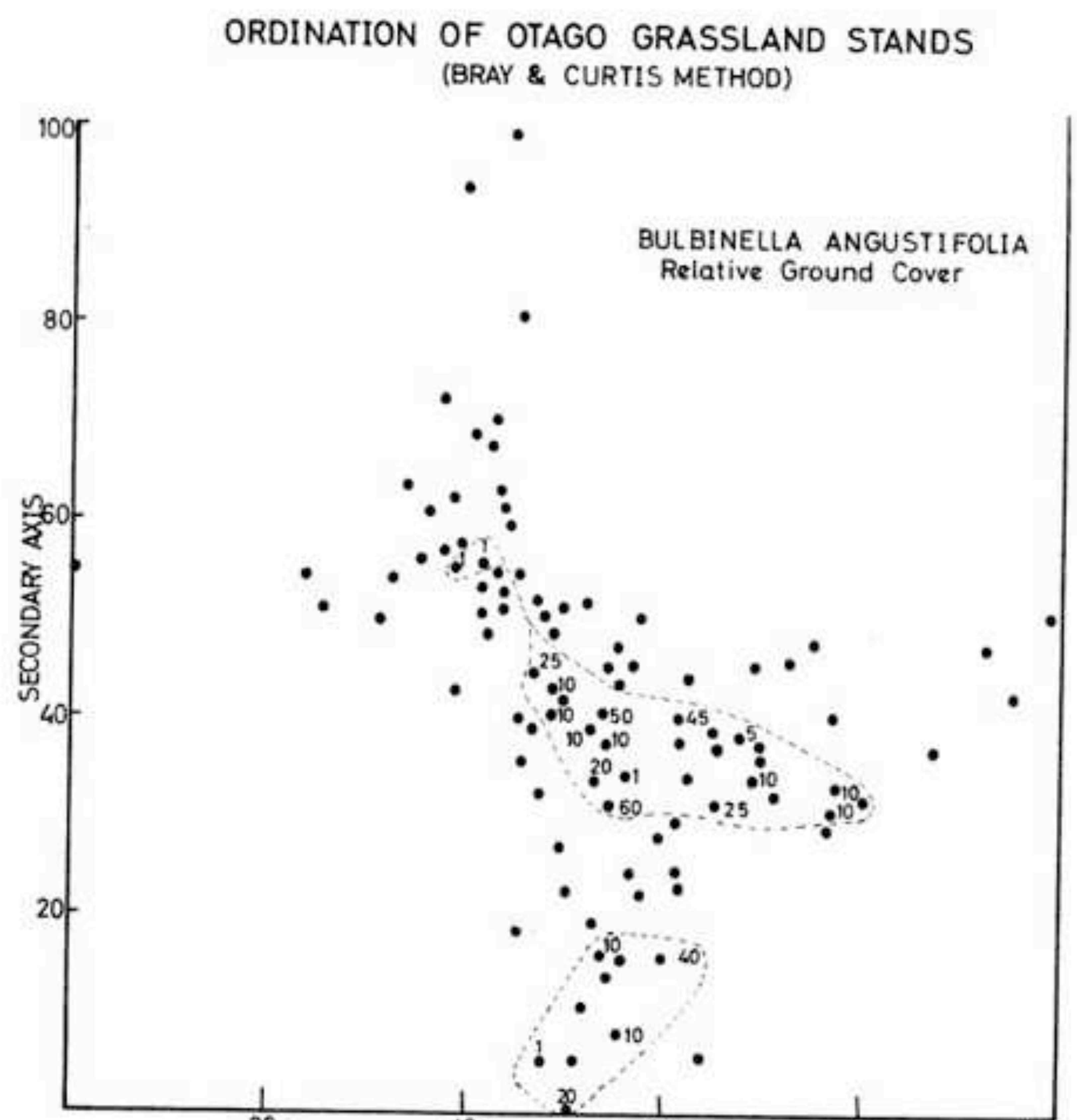

FIGURE 7. *Distribution of* Bulbinella angustifolia *on the stand ordination.*

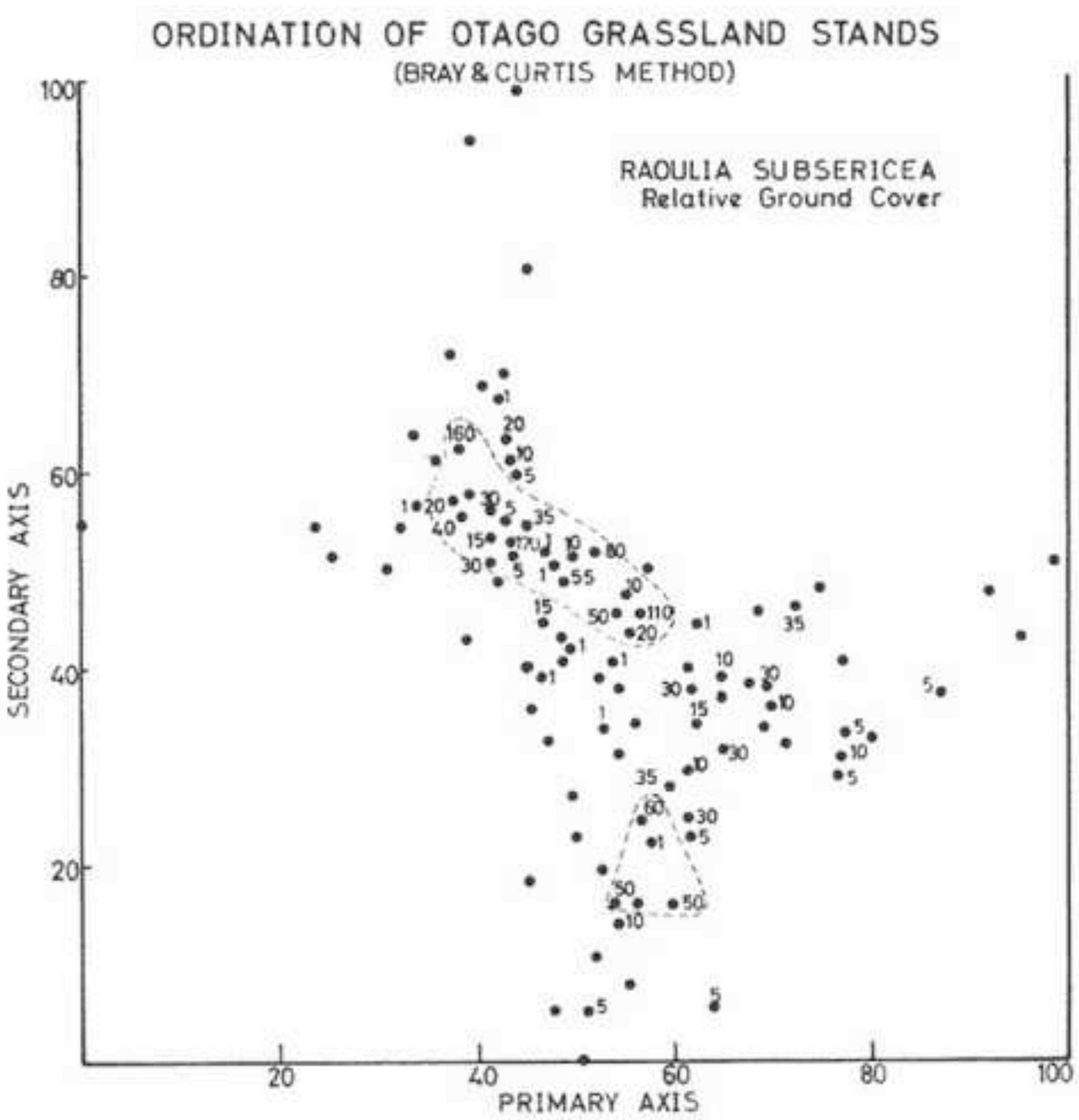

FIGURE 8. *Distribution of* Raoulia subsericea *on the stand ordination. The grouping of stands in which* R. subsericea *reaches high relative cover has been emphasised.*

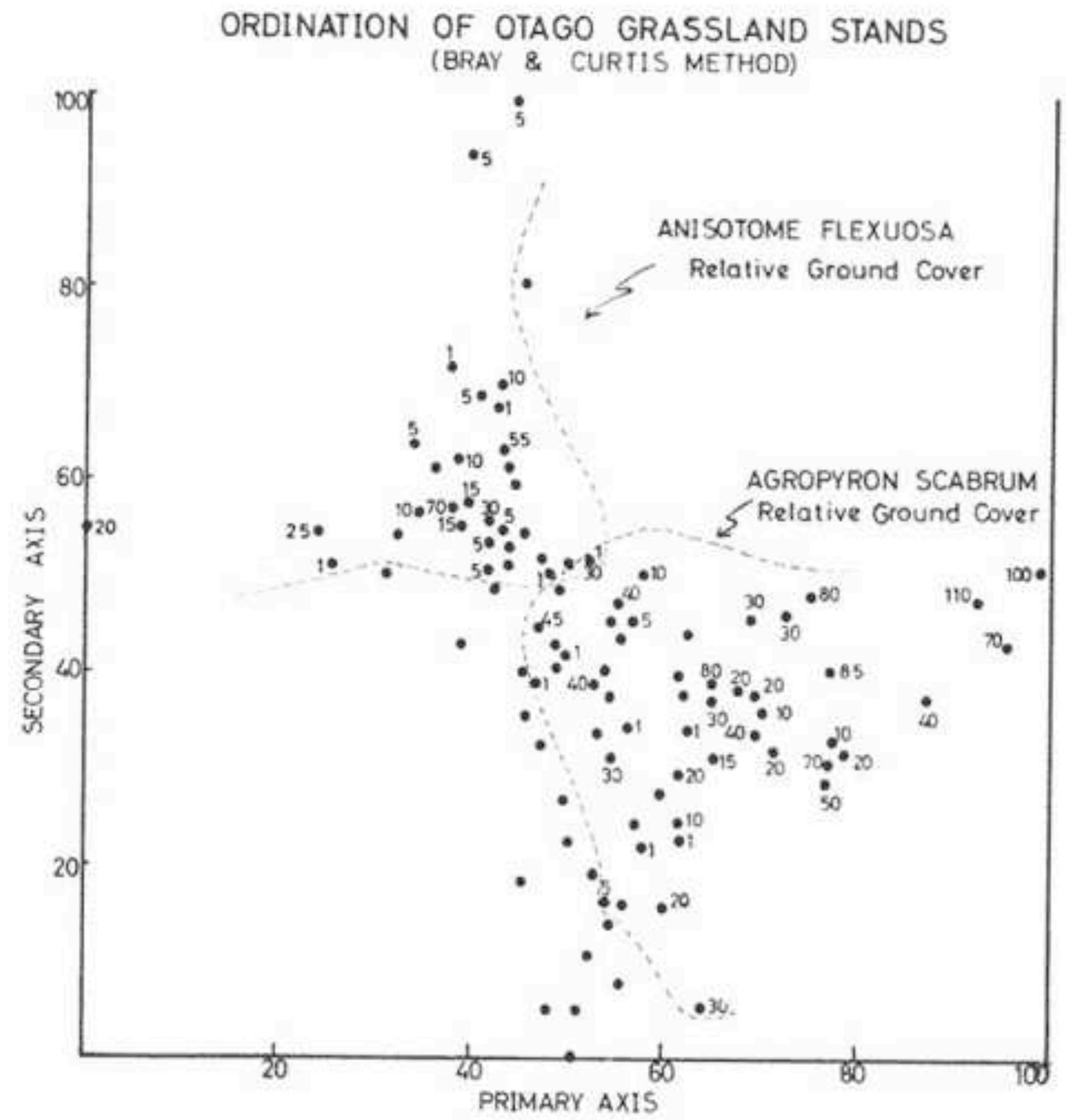

FIGURE 9. *Relative ground cover by* Anistome flexuosa *and* Agropyron scabrum *on the stand ordination, showing the almost discontinuous distribution of the two species.*

The soils vary in moisture level but those in which *Bulbinella* thrives are all likely to have good drainage and aeration.

The wide range of *Raoulia subsericea* is clearly demonstrated in Figure 8, as is the grouping of stands where the species has high cover values. Again, to demonstrate the almost discontinuous distribution of some montane and alpine species, the relative cover estimates from *Agropyron scabrum* and *Anisotome flexuosa* have been plotted in Figure 9. These two species were recorded together in only one stand. The dwarf herb *Anisotome flexuosa* is limited to vegetation at higher altitudes but over a wide range of moisture. The lax tussock grass, *Agropyron scabrum* is most prominent in the montane sites but it, too, may grow successfully in moist grassland, though limited possibly by competition.

Conclusion

Ordination techniques such as those used in this paper appear to have considerable value in the ecological analysis of New Zealand grasslands. More detailed sampling and methods of treatment of data such as the weighted similarity ordination of Orloci (1966) could be used to relate variation in vegetation with accurately measured environmental parameters.

SUMMARY

This report forms part of a study of indigenous grasslands of Otago using continuum analysis. An attempt has been made to relate variation in grassland and related vegetation to the principal environmental gradients.

Stands were sampled throughout the grassland and related vegetation west of the coastal hills and east of the Cromwell Gorge. In each stand rapid point-records were taken to obtain relative values of cover for all macroscopic plants. Average relative values of ground cover for the leading physiognomic dominants and some prominent ground species are graphed for an arrangement of communities. These performance curves emphasize species optima and ranges of tolerance. The overlapping distributions indicate the continuum of vegetation along a gradient of increasing altitude and changing moisture.

Coefficients of dissimilarity between stands were computed as a partial matrix and these dissimilarity values formed the basis for the construction of a two-dimensional ordination using the method of Bray and Curtis.

The relationship between stand position and moisture and altitude is very marked. The ordination appears to be an adequate characterisation of the vegetation. Cover values for *Bulbinella angustifolia, Raoulia subsericea, Anisotome flexuosa* and *Agropyron scabrum* have been plotted and their distributions discussed.

From these preliminary results it is considered that ordination methods are of value in the presentation and analysis of causal relationships between indigenous grasslands, component species and their environments.

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