

**THE DISTRIBUTION OF *ACACIA* (LEGUMINOSAE-MIMOSOIDEAE)
IN WESTERN AUSTRALIA.
PART 3. NUMERICAL ANALYSIS OF PATTERN
AND ECOLOGICAL CORRELATIONS**

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ABSTRACT

The geographic distributions of the 481 species of Acacia have been analyzed to detect what patterns are present based upon joint occurrences of species in 147 1° x 1.5° grids covering 82% of Western Australia. At the broadest levels, the familiar south-western, northern, and arid central regions of the State were clearly defined, while subdivisions of these 3 regions into subunits were readily interpretable. The patterns detected bore strong resemblances to the Phytogeographic regions of Beard (1980) but only in the western part of the State. The main sections of Acacia were found to form a broad replacement series from north to south. The tropical Juliflorae and Plurinerves were found to define a northern element, whilst the temperate Pulchellae, Phyllodineae, and Alatae better defined south-western and western elements. There was an indication that winter temperatures may be more influential in controlling the distribution of Acacia species than rainfall.

INTRODUCTION

This is the third paper in a series on the distribution of *Acacia* in Western Australia. Previous papers of the series are published by Hnatiuk and Maslin (1980 and 1980a) while the fourth is in the present volume (pp. 23-55).

Taxonomically the genus *Acacia* in Western Australia is reasonably well known. Currently in the State there are 397 described species (Maslin and Pedley 1982) and an estimated 115 as yet undescribed. Of the 10 sections comprising the genus (Pedley 1978), 7 sections are recorded for Western Australia. The existing collections of *Acacia* are extensive with about 16,000 specimens currently housed at the Western Australian Herbarium

(PERTH). These collections are believed representative of the geographic distribution of most species (Hnatiuk and Maslin 1980).

Western Australia occupies about 1/3 of the Australian continent. Its north to south extent of about 2,700 km crosses nearly 21 degrees of latitude - from the tropics at about 14°S to the temperate zone at about 35°S. Its climate encompasses the monsoonal tropics, an extensive arid zone, a temperate mediterranean zone, and a cool, moist temperate zone. Nowhere are there high mountains, but low rugged relief is an important feature in some parts. Nevertheless, the landform is a complex mosaic of physiographic and edaphic variability, comprising uplands, plains, coastal strips, salt-lands, laterites, and gorges. *Acacia* species occur in all these areas, thus the study of their geographic patterns is likely to contribute to the understanding of major phytogeographic trends in Western Australia.

Previous phytogeographic studies in Western Australia date back to at least the writings of Mueller (1867) who first distinguished the southwestern part of the State as a floristic unit. Since then there have been several studies, but that of Diels (1906) was seminal in subdividing large portions of the State using botanic, edaphic, and climatic criteria. An excellent review of this and other classifications of the State is found in Gentilli (1979). The most recent, comprehensive attempt at recognizing phytogeographic regions has been that of Beard (1980) based primarily upon structural vegetation units but incorporating soils, geology and climatic data as well. Aspects of phytogeography of *Acacia*, not covered by the present paper, have been presented in Hopper and Maslin (1978). These aspects included the determination of areas of species richness as well as an investigation into the mechanisms of speciation.

The objectives of the present study were:

- (1) to determine the broad geographic patterns of *Acacia* in Western Australia;
- (2) to document how sections and species of *Acacia* contribute to these patterns;
- (3) to evaluate the relative contribution of several environmental factors to the distinguishing of these patterns; and
- (4) to evaluate the relationship of the patterns in *Acacia* to the current knowledge of phytogeographic districts in Western Australia.

METHODS

The data set used in this analysis comprises distributional information based on specimen records for the taxa listed in Part 4 (this volume pp. 38-55). These include 387 described species and 94 undescribed taxa. Distribution maps for the described species are given in Hnatiuk and Maslin (1980). For each undescribed taxon, a voucher specimen is cited and a distribution map is lodged at PERTH. Subsequent to completing this analysis a number of new W.A. species have been described. Also, the distributions of many species included in the present work have been updated. This new information is summarized in Maslin and Pedley (1982).

Details of the method of recording distributions are given in Hnatiuk & Maslin (1980) but briefly, the technique was to record which species had been collected in each of the 179 1° latitude x 1.5° longitude grid cells for the State. Each cell was treated as a sample site in a manner similar

to that used by Booth (1978) for eastern Australian forest species, by Bridgewater (1976) for certain species in Victoria, Australia, and by Proctor (1967) for British liverworts. Analyses discussed below used the 147 grids for which four or more species of *Acacia* were recorded. This restriction eliminated 32 grids and served to reduce the data matrix to a size that could be machine-analyzed at reasonable cost. The grids eliminated largely came from the remote, arid parts of the State where a combination of undercollecting and actual low species diversity contributed to the low number of species recorded.

Analysis was done using the TAXON library of computer programs at the CSIRO Division of Computing Research, Canberra. In particular, the following were used:

- a) classification using MULCLAS. The index of similarity chosen was the Canberra metric with "double-zero-matches" suppressed (which, for presence/absence data is equivalent to using the Jaccard coefficient - Clifford and Stephenson 1975). This metric was chosen because we wanted an index of similarity between sites which was based upon what was known about where *Acacia* species occurred and not influenced directly by information about where it had not been recorded (i.e. an asymmetric index). The absence of records for a species may be caused by either the fact that it does not occur naturally in a grid, or that it has not yet been collected there. We did not want these two possibilities to influence the results. The classification used the "flexible sorting technique" with $\beta = -0.25$. MULCLAS produces in a hierarchical structure of groups, with no *a priori* criteria for accepting or rejecting any particular number of groups at any particular level in the structure. The analytical procedure of MULCLAS is agglomerative, but, as the final sequence can be read in either direction, it is convenient here to report the results as divisions.
- b) MINSPAN: the determination of the Minimum Spanning Tree (Gower and Ross 1969);
- c) ordination of grids using GOWER and the same matrix of similarities used in MULCLAS analysis.

MULCLAS analyses were run on 3 sets of data that differed only in the species used: a) all 481 species, b) only species from the taxonomically closely related sections Plurinerves and Juliflorae and c) only species from the related sections Pulchellae, Phyllodineae and Alatae. The latter two analyses were done to see if these two major groups, largely tropical versus largely temperate, were contributing analysis.

A quantitative evaluation of the relative importance of environmental variables to the distinguishing of groups resulting from the MULCLAS analysis was done with discriminant function analyses (Klecka 1975). The method does not appear to have been used previously for this purpose in large-scale phytogeographic studies. The general objective of the discriminant function analysis is to "weight and linearly combine the discriminating variables in some fashion so that the groups are forced to be as statistically distinct as possible" (Klecka *ibid.* p. 435). The method assumes that the discriminating variables have a multivariate normal distribution as well as equal variance-co-variance matrices within each group. However, the technique is said to be very "robust" such that strong adherence to these assumptions is not necessary for its use (Klecka *ibid.* p. 435).

The following discriminating variables were scored separately for each

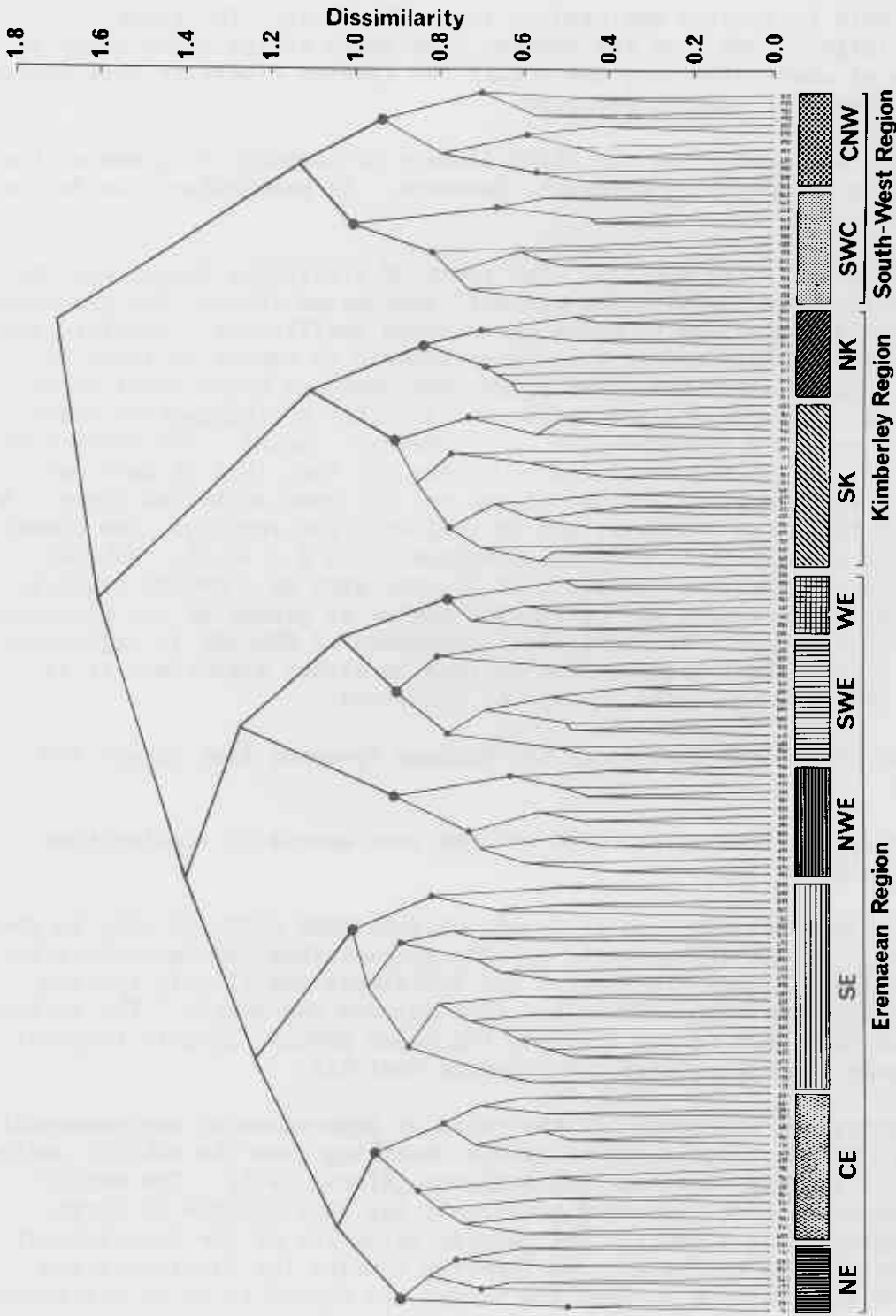


Figure 1. Dendrogram of results of MULCLAS analysis using all species. Numerals at bottom of dendrogram refer to 1° x 1.5° grid cell numbers as shown in Figure 2. Abbreviations for *Acacia* districts are as follows: South-West Region comprises the Central and Northern Wheatbelt (CNW) and South and West Coastal (SWC) Areas; Kimberley Region comprises the North (NK) and South (SK) Kimberley Areas; Eremaean Region comprises the West (WE), South-West (SWE), North-West (NWE), South (SE), Central (CE) and North (NE) Eremaean Areas.

Western Australia

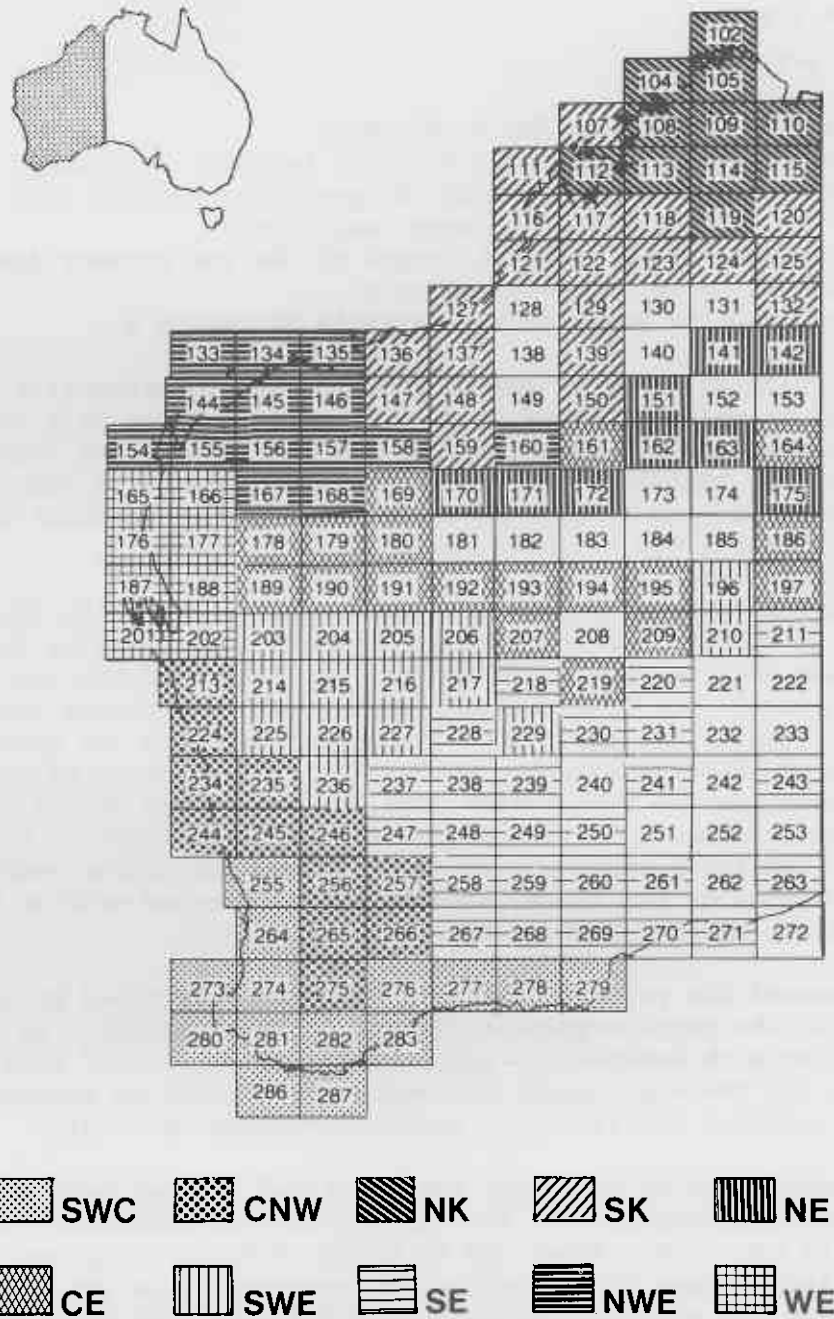
 CE

Figure 2. Map of Western Australia showing the 10 *Acacia* Areas derived from MULCLAS. Numbers for the 1° x 1.5° grid cells follow those given in Hnatiuk and Maslin (1980). Abbreviations for *Acacia* Areas are those given in the caption to Figure 1. Blank grid cells are ones not included in the analysis because they have fewer than 4 species recorded.

grid cell: mean annual rainfall, 10-percentile rainfall, season of rainfall, mean maximum temperatures for January and July, and mean minimum temperatures for January and July. The data were obtained from maps showing isohyets, thermoisopleths, and rainfall seasons for Australia (Anonymous 1975-77). On each map was drawn the $1^{\circ} \times 1.5^{\circ}$ grid and each variable was reduced to a single value for each cell as follows:

$$G = \sum_{a=1}^n p_a(m_a)$$

where: G = grid cell value for a variable;
 n = the no. of regions (i.e. areas between isopleths), which are crossed by the primary diagonals of a given grid cell;
 a = particular region between isopleths;
 p = proportion of a total length of the two primary diagonals of a grid which cross region a;
 m = mid-point value of the variable of region a.

Calculation of midpoint values for mean and 10-percentile rainfall and temperature variables were straightforward, but for rain season a special procedure was necessary. Rain seasons Zones were numbered from 1 (for summer dominant, high rainfall areas) through 6 (for arid zone, uniform or non-seasonal areas) to 13 (for winter dominant, high rainfall areas). See Anonymous (1975-77) for detailed explanation of zones.

In order to determine how individual species related to the groups recognized in MULCLAS, an association-style table, following the general form of those used in the Zurich-Montpellier school of phytosociology for expressing composition of vegetation units, was constructed (see Appendix 1 in Part 4 - this vol. pp. 38-55). The order of sites was derived from the MULCLAS and MINSPAN results, whilst the initial order of species came from an examination of the species maps in Hnatiuk and Maslin (1980) whereby species were assigned to either one of the MULCLAS groups or to transition-al groups. The final order was determined from subjective evaluation of sequential copies of the table, produced via a program written by P. Bridgewater, Murdoch University.

We compared the pattern of *Acacia* Areas as determined by the MULCLAS analyses with the phytogeographic regions of Beard (1980). We selected Beard's system both because his map included the $1^{\circ} \times 1.5^{\circ}$ grid system, and because his was the most recent comprehensive attempt to examine the vegetation patterns and floristic variation within the State.

The method used to gauge the similarity of the two systems was as follows. By comparing maps of the two systems, we determined for each grid cell to which our *Acacia* Areas and to which of Beard's regions it belonged. For the latter we used the criterion of assigning it to the Beard Region which occupied the greatest proportion of the cell (Table 2). For each of our *Acacia* Areas, we calculated the Beard region composition in terms of percent. of the total grids for that Area. The Beard region with the largest percentage for each *Acacia* Area was noted at the bottom of Table 2.

In order to determine whether there was any geographic pattern to the degree of similarity, a map was constructed which showed firstly those Beard regions that represented greater than 50% of the grids of an *Acacia* Area (Figure 6). The 50% level was chosen, after subjective examination of

Table 2, as a level of similarity which was of medium strictness. A 25% similarity was then mapped to see if the same trend was to be found. These results were also shown in Figure 6.

RESULTS

The analyses using all 481 species (387 described and 94 undescribed) form the basis of most of the following paper, and it is this data set that is meant unless otherwise specified.

a) Geographic Patterns

The first division of MULCLAS split off the south-western grids (here called the South-West Region) from the remainder, whilst the second division separated the latter group into northern (Kimberley Region) and central (Eremaean Region) groups (Figures 1 and 2). At this level the three groups roughly represent the three Botanical Provinces of the State as recognized by many earlier workers.

The next split divided the Eremaean Region into a north western unit and an interior desert unit. The former was subdivided into a West Eremaean Area (WE), a North-West Eremaean Area (NWE), and South-West Eremaean Area (SWE) whilst the interior desert was subdivided into Northern Eremaean (NE), Central Eremaean (CE) and South Eremaean (SE) Areas. The South-West Region was divided into a South and West Coastal Area (SWC) and a Central and Northern Wheatbelt Area (CNW). The Kimberley Region was divided into a North Kimberley Area (NK) and a South Kimberley Area (SK). The three Regions and ten Areas thus recognized form the basis of the present paper. A description of these districts in terms of their *Acacia* flora is the subject of Part 4 of this series (this vol. pp. 23-55).

A comparison of the 10-group level of MULCLAS with the Minimum Spanning Tree shows two main features (Figure 3). Firstly, four of the Areas are well defined (SWC, CNW, NK and SK) and represent the extreme north and south-to-southwest parts of the State. Secondly, the six groups of the Eremaean region are not well defined as indicated by both the numerous links between groups and the fragmented nature of some groups when plotted onto the Minimum Spanning Tree.

The apparent distinctness of all the groups, fostered by the classificatory nature of MULCLAS is further modified by examining the first two axes of the GOWER ordination (Figure 4). The two features emphasized by these axes are firstly the continuous nature of the variation and secondly its curvi-linearity. The latter is highlighted by the fact that the first two axes account for only 5.69% and 4.54% respectively of the variance in the whole data set, while the first 5 axes only account for 18.02%. However, that there is a general trend with only two extremes (the south-west *versus* the north), with the arid regions in between, was evident from the plot of MINSPAN linkages on the ordination (not shown here). The distribution of grids when plotted against the first two Discriminant Functions showed a very similar pattern to that just described for the GOWER results.

MULCLAS analyses of grid cells using species grouped according to their major sectional affinities (i.e. combined sections Juliflorae - Plurinerves and combined sections Phyllodineae - Pulchellae - Alatae) produced results

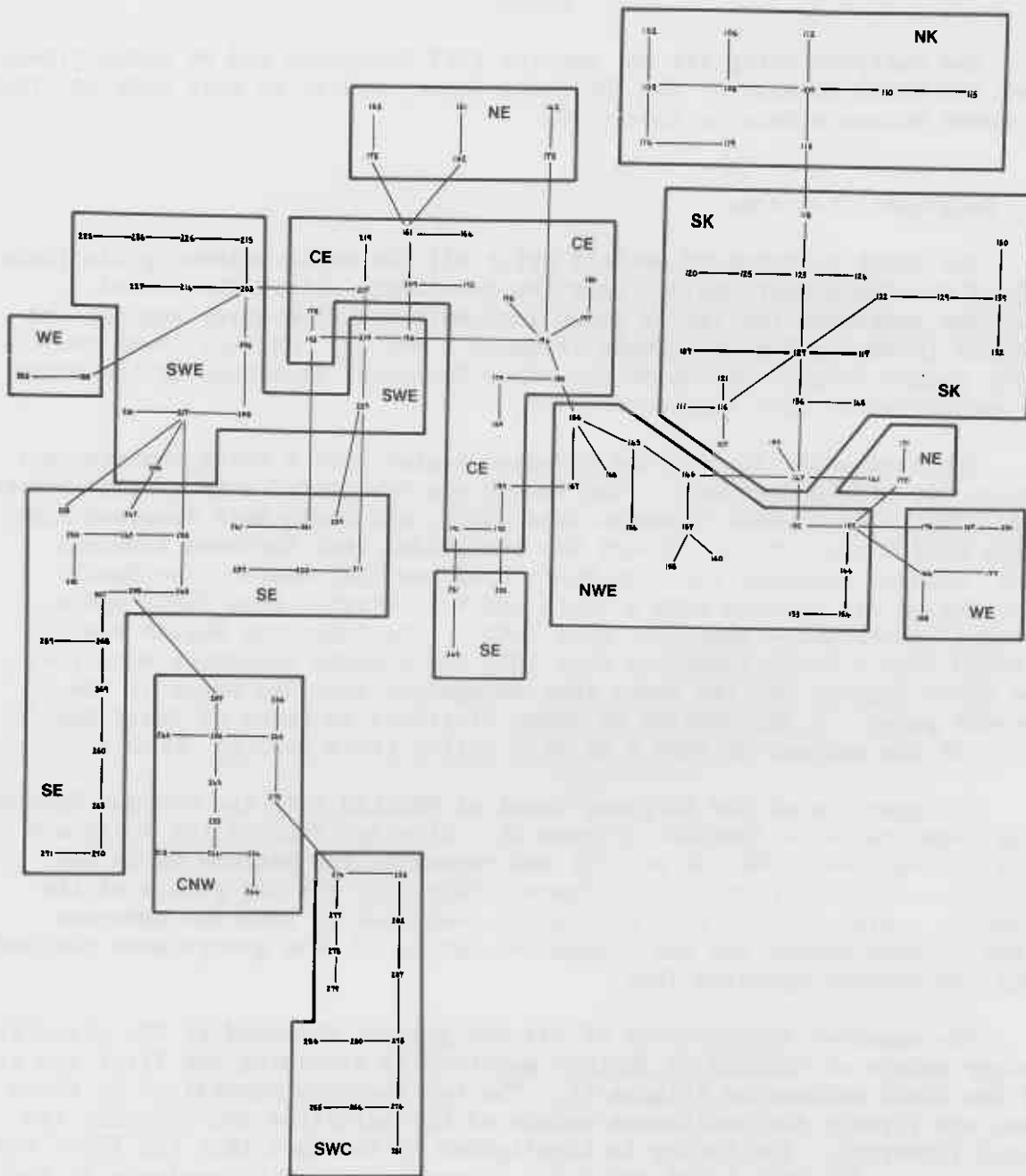


Figure 3. Minimum spanning tree for grid cells, based on the Canberra metric similarities between all pairs of the 147 grid cells. Numbers refer to $1^{\circ} \times 1.5^{\circ}$ grid cells as shown in Figure 2. Abbreviations for *Acacia* Areas are given in the caption to Figure 1.

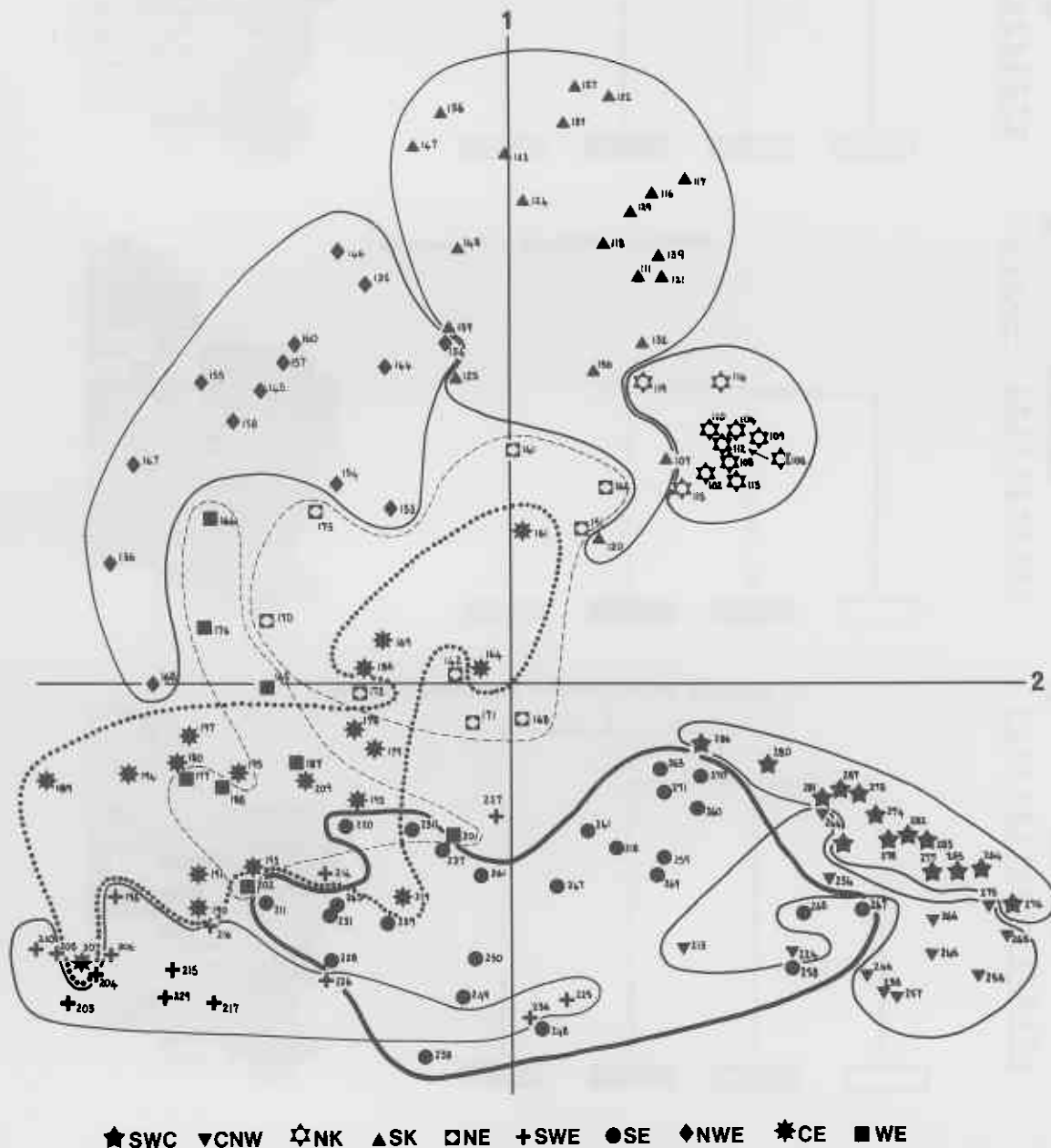


Figure 4. GOWER ordination of matrix of the Canberra metric similarities between all sites. Numbers refer to $1^{\circ} \times 1.5^{\circ}$ grid cells as shown in Figure 2. Abbreviations for *Acacia* districts are given in the caption to Figure 1. Proportion of variation accounted for by axis 1:5.69% and by axis 2:4.54%.

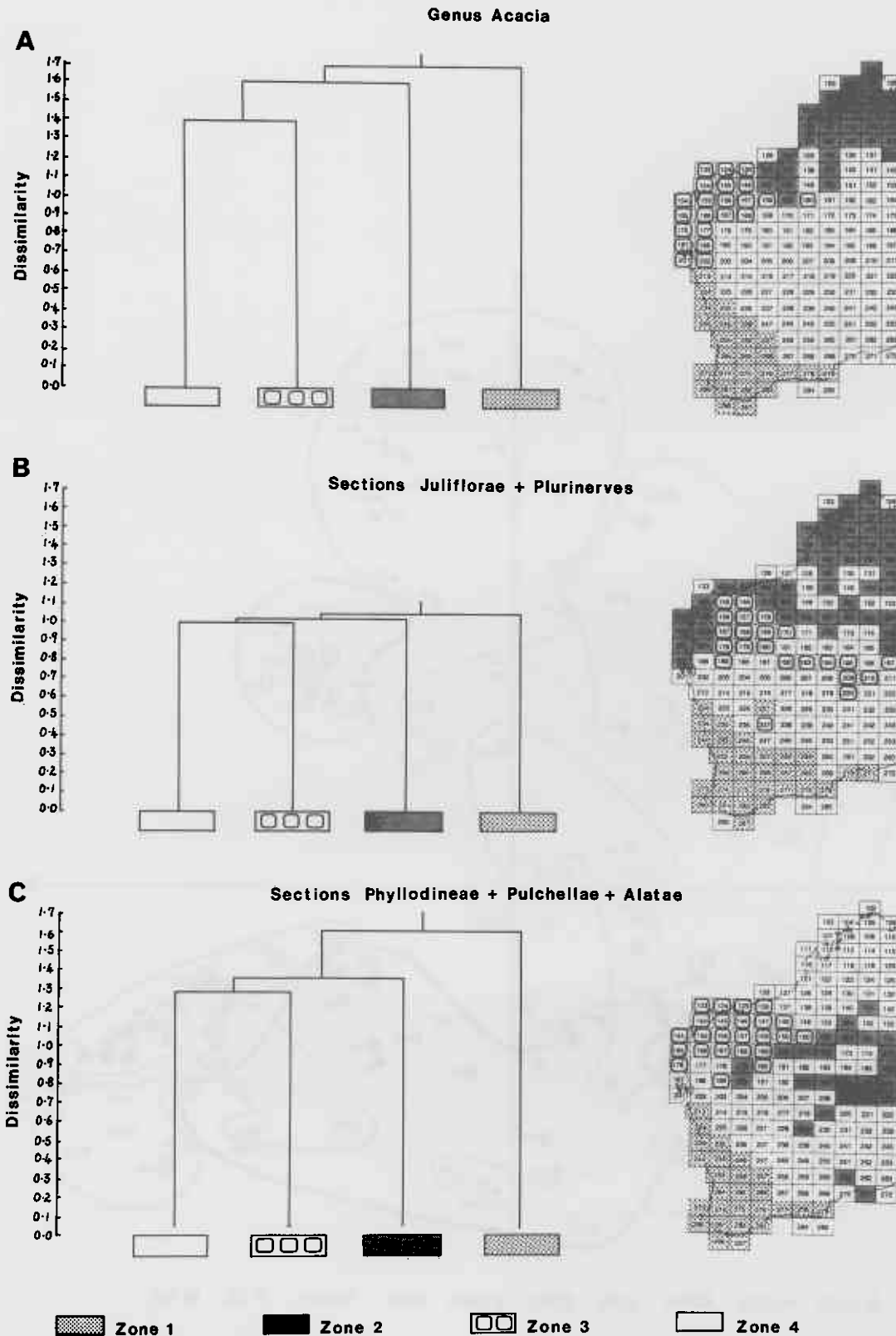


Figure 5. Simplified MULCLAS dendrogram and corresponding map of Western Australia for the genus as a whole (Figure 5A), the combined sections Juliflorae and Plurinerves (Figure 5B) and the combined sections Phyllodineae, Pulchellae and Alatae (Figure 5C). Zone numbers refer to the sequence in which zones (i.e. sets of $1^{\circ} \times 1.5^{\circ}$ grid cells as shown on the maps) were determined by MULCLAS. Grid cells not included in these analyses are shown on Figure 2.

partially comparable to that for the genus as a whole (compare Figures 5A, B and C). In both subsidiary analyses the South-West Region proved the most distinctive set of grids (Figures 5B and C). Except for minor difficulties involving a few grids along the inland, north-eastern margin of the South-West Region, these section-grouping analyses produced patterns for this Region which were the same as for the genus as a whole (Figure 5A). For the remainder of the State, however, there were substantial differences in the upper levels of the hierarchy although many of the subunits still distinguished the essential Areas as seen in the complete species data-set.

Figure 5B shows that following segregation of the South-West Region, the Juliflorae - Plurinerves analysis delineated a large northern zone which comprised the Kimberley Region and North Eremaean Area of the genus analysis but also included the coastal/near-coastal grids of the North-West and West Eremaean Areas. Inclusion of these coastal/near-coastal grids within the northern zone is somewhat surprising but is presumably accounted for by species such as *A. coriacea* and *A. xiphophylla*. The affinities between the Kimberley Region and the northern Eremaean Areas are expected and are discussed in Part 4 (this vol. p. 28). The next most important Juliflorae - Plurinerves MULCLAS zone was one essentially uniting the inland grids of the North-West Eremaean Area with the Central Eremaean Area. This relationship was expected and was accounted for by wide-ranging Arid Zone species from section Juliflorae e.g. *A. aneura*, *A. cuthbertsonii*, *A. kempeana*, and *A. stowardii*. The widespread, Arid Zone Phyllodineae species, *A. ligulata* is present in most of the peripheral grids of this zone e.g. 141, 151, 179, 190, 261 and 271, but is absent from a substantial number of the central grids. Most of these central grids have another widespread Arid Zone species, *A. dictyophleba*. These two species are undoubtedly contributing significantly to the discreteness of the zone.

Figure 5C shows that following segregation of the South-West Region, the Phyllodineae - Pulchellae - Alatae MULCLAS analysis then delineated a zone centred on the desert regions of central Western Australia. The third zone of this analysis represents the North-West Eremaean Area, peripheral parts of the adjacent South Kimberley Area, and the Central and Western Eremaean Areas of the whole genus analysis. This last zone includes many widespread Arid Zone Phyllodineae species but those which predominate here and which are less frequent elsewhere presumably contribute to its delineation e.g. *A. ampliceps*, *A. bivenosa*, *A. gregori*, *A. pyrifolia* and *A. sclerosperma*.

b) Discriminant Function Analysis

The discriminant function analyses (Table 1) indicated that the MULCLAS groupings of grid cells could be strongly distinguished by the four temperature and three rainfall variables used. About 90% of the variance between groups was accounted for by the statistically highly significant first 2 functions. It was the mean maximum temperature in July that dominated the first function, followed by the seasonal rainfall zone which was only about one half as important but opposite in sign. There was variation between analyses in variable scores on the second discriminant function. In the all-species analysis it was mean maximum July temperature that was most important, followed by the 10-percentile rainfall. For the temperate group of species (sections Phyllodineae, Pulchellae, Alatae) the dominant variable was 10-percentile annual rainfall, closely followed by mean maximum July temperature. The second function for the tropical group of species (Juliflorae, Plurinerves) showed mean minimum January temperature to be most

Table 1. Results of discriminant function analysis - first two functions.

Variable	All species		Combined sections Pulchellae- Phyllodineae- Alatae		Combined sections Juliflorae- Plurinerves	
	Function		Function		Function	
	1	2	1	2	1	2
50-percentile rainfall	0.02	0.11	0.10	0.16	0.14	0.28
10-percentile rainfall	0.02	0.60	<0.00	0.65	0.23	0.31
Rain season	-0.34	0.16	-0.43	0.24	-0.37	-0.17
Mean max. Jan. temperature	0.05	-0.09	-0.16	-0.15	0.02	>0.00
Mean max. July temperature	0.68	0.85	0.77	0.56	0.74	0.19
Mean min. Jan. temperature	0.05	-0.55	-0.02	-0.25	-0.02	-0.93
Mean min. July temperature	-0.07	-0.22	-0.12	-0.30	-0.19	0.19
% variance accounted for	67.5	22.4	62.5	29.6	64.8	25.9

important, followed by 10-percentile rainfall which was only about one third as important.

c) Phytogeographic District Correlations

A comparison of our *Acacia* districts with the phytogeographic regions of Beard (1980) showed that at the 3-group level (i.e. *Acacia* Region) of the MULCLAS hierarchy and the Botanical Province level there was an overall similarity, with the major exception that the Kimberley Region as defined by *Acacia* extends well south of the southern boundary of the Northern Botanical Province of Beard.

At the 10-group level (i.e. *Acacia* Area) of the MULCLAS hierarchy, the

agreement between the two systems was found to be best along the western and north-western half of the State, and worst for the arid interior (Table 2, Figure 6). Seven of Beard's Botanical Districts and our *Acacia* Areas were found to correspond reasonably well at the higher (i.e. 50%) similarity level (namely, and in decreasing order of similarity, the Carnarvon, Austin, Gardner, Darling, Avon, Fortescue and Ashburton Botanical Districts). For the Central Eremaean and North-West Eremaean *Acacia* Areas the western grids approximated Beard's Ashburton and Fortescue Botanical Districts respectively; the eastern extensions were not indicative of any particular Botanical District of Beard as might be implied by Figure 6. By relaxing the similarity criterion, it was found that three further Districts (the Dampier, Irwin, and Coolgardie) could be matched to sub-groups of the 10-group level MULCLAS results. For example, Beard's Irwin Botanical District approximated a subdivision of the Central and Northern Wheatbelt *Acacia* Area, while Beard's South-West Interzone and the Dampier Botanical District were subdivisions of the South Eremaean and South Kimberley *Acacia* Areas respectively. Only just missed by the relaxed criterion was Beard's Eyre Botanical District as a subdivision of the South and West Coast *Acacia* Area.

DISCUSSION

(a) Geographic Patterns

Our analyses of geographic patterns in *Acacia* in Western Australia have shown a number of geographically distinct districts that can be related to one another in a hierarchical manner. In the pattern shown by the three Regions recognized (i.e. the South-West (SWR), Eremaean (ER) and Kimberley (KR) Regions), there is a broad similarity to previously recognized phytogeographic subdivisions of the State and to several climatic variables (see below).

The distinctness of the south-western corner of the State is emphasized in our analyses, whether based on the total species set or upon the major sectional groupings. The interior boundary of the SWR follows that first defined, in general terms, by Mueller (1867) as extending from Shark Bay south-eastward to Israelite Bay. It is similar to the South-West Botanical Province of Beard (1980) but lies within the SW Interzone of Burbidge (1960). It follows approximately the "7-8 dry months" line of Gentilli (1970) except in the northwest where our area extends further north than his line does.

The subdivision of the SWR at the 10-group level of MULCLAS, into the South and West Coastal (SWC) and North and Central Wheatbelt (CNW) Areas is an oversimplification of the complexity of patterns that appear to exist there. The northwestern extreme of the CNW, the western end of the SWC, and the eastern SWC represent areas that have been variously recognized by several authors using very different criteria - zonal climatology (Gentilli 1970), soil and ecological regions (Teakle 1938), regional landscapes and landforms (Holmes 1944), physiographic regions (Gentilli and Fairbridge 1952) (these references all from Gentilli 1979). The south-eastern and inland northern parts of the CNW are not well represented in the works noted above, but together they have a reasonably strong correlation with the Avon Botanical District of Beard (1980).

The Kimberley Region appears to represent the western end of pan-

Table 2. A comparison of Beard's (1980) Botanical Districts (BD) with the 10 *Acacia* Areas derived from MULCLAS. Each grid cell was assigned firstly to an *Acacia* Area, then to the one BD which occupied the greatest proportion of the grid cell area. Abbreviations for *Acacia* Areas are given in the caption to Figure 1.

Beard Botanical District	Acacia Area										Totals	Acacia Area with highest proportion of similarity to BD in each row	
	SWC	CNW	SWE	SE	CE	NE	WE	NKE	SK	NK			
Darling	9	1	-	-	-	-	-	-	-	-	-	10	SWC 90%
Eyre	3	-	-	-	-	-	-	-	-	-	-	3	SWC 100%
Roe	2	1	-	2	-	-	-	-	-	-	-	5	SWC/SE 40%/40%
Avon	-	7	-	-	-	-	-	-	-	-	-	7	CNW 100%
Irwin	-	3	-	-	-	-	-	-	-	-	-	3	CNW 100%
Eucla	-	-	-	5	-	-	-	-	-	-	-	5	SE 100%
Coolgardie	-	-	-	7	-	-	-	-	-	-	-	7	SE 100%
Austin	-	-	13	6	-	-	-	-	-	-	-	19	SWE 68%
Carnarvon	-	-	-	-	-	-	-	2	-	-	-	10	WE 80%
Ashburton	-	-	-	-	10	-	-	3	-	-	-	13	CE 83%
Fortescue	-	-	-	-	-	-	-	8	4	-	-	12	NWE 67%
Keartland	-	-	-	-	1	3	-	1	-	-	-	5	NE 60%
Helms	-	-	-	4	1	-	-	-	-	-	-	5	SE 80%
Giles	-	-	1	1	2	-	-	-	-	-	-	4	CE 50%
Carnegie	-	-	1	-	2	3	-	-	-	-	-	6	CE/NE 40%/40%
Mueller	-	-	-	-	1	1	-	-	1	-	-	3	-
Canning	-	-	-	-	1	2	-	-	4	-	-	7	SK 57%
Dampier	-	-	-	-	-	-	-	-	7	-	-	7	SK 100%
Fitzgerald	-	-	-	-	-	-	-	-	2	2	-	4	SK/NK 50%/50%
Hall	-	-	-	-	-	-	-	-	2	-	-	2	SK 100%
Gardner	-	-	-	-	-	-	-	-	1	9	-	10	NK 90%
Total no. of grids	14	12	15	25	18	9	8	14	21	11		147	
BD with highest proportion of similarity to Acacia Area in each column	Darling 64%	Avon 58%	Austin 87%	Coolgardie 28%	Ashburton 56%	Keartland/ Carnegie 33%/33%	Carnarvon 100%	Fortescue 57%	Dampier 33%	Gardner 82%			

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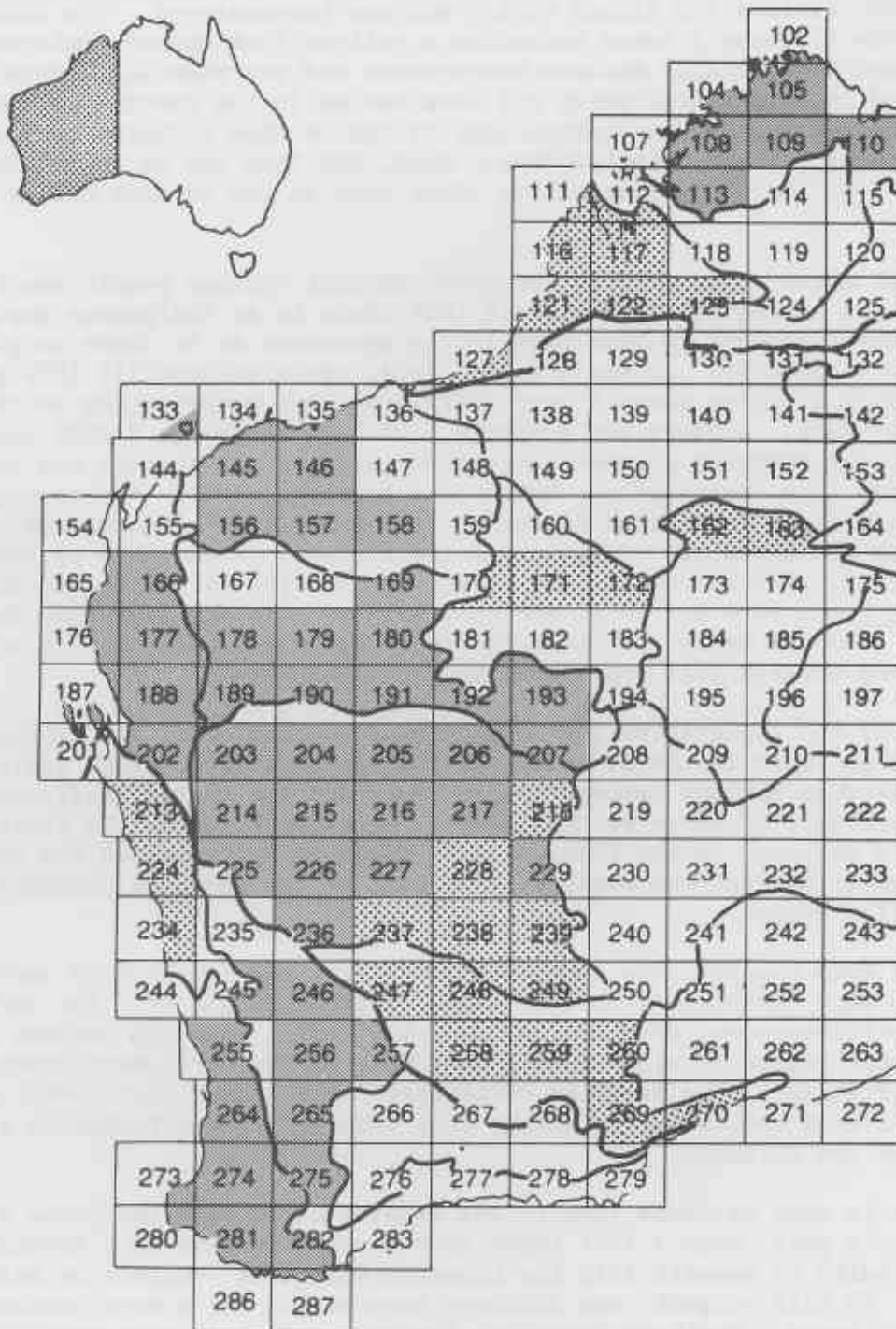


Figure 6. Results of a comparison between the *Acacia* districts derived from the MULCLAS analysis (see Figure 2) and the phytogeographic regions defined by Beard (1980). Beard's Botanical Districts (bold lines) are superimposed on the $1^{\circ} \times 1.5^{\circ}$ grid used in the MULCLAS analysis. Correspondence between the two systems is shown by cross-hatching (for more than 50% similarity) and stippling (25-50% similarity).

continental, tropical suites of *Acacia* species. The pattern of *Acacia* Areas within the Kimberley Region is that of northern and southern elements. The North Kimberley Area (NK) is climatically distinguished from the South Kimberley Area (SK) by its higher and more reliable precipitation, and by lower summer maximum and higher winter minimum temperatures. The MULCLAS subdivisions of these 2 Areas emphasize a pattern that appears related to the combined average July maximum temperature and the rainfall (annual average and 10-percentile) which all show maxima in the central part of the North Kimberley Area. The subdivisions of the SK show eastern, central and western groups, rather than concentric ones, but this may be an artifact due in part to the truncation of our study area at the eastern border of the State.

Whilst there appears to be consensus amongst various people who have produced maps of regions in the State that there is an indigenous northern element, there appears to have been little agreement as to where to place its southern boundary. Jutson's (1914, 1934, see also Gentilli 1979 p. 12) physiographic division shows a very restricted area as belonging to the northern element. Gardner and Bennetts (1956) and Burbidge (1960) each extended their northern element to include parts of the coastal and inland Pilbara area (i.e. parts of our North-West Eremaean Area). The geological map of the Western Australian Department of Mines (1979) does not provide a basis for the botanical extension of the Kimberley Area south of the Fitzroy River. Neither do the soil maps of the Atlas of Australian Soils (sheets 6, 9 and 10 N.W.) correlate well with an extended Kimberley in botanical (*Acacia*) terms, but then the soil maps were based in part on correlations between soil types and geological substrate.

Part of the explanation for the southward extension of our Kimberley Region can be found in the discriminant function analyses, which indicated that the average maximum temperature for July was the most significant climatic variable of those we considered. An examination of the isotherm map of this variable showed that the 27°C isotherm approximated the central, southern parts but not the south-western part of the southern boundary of our Kimberley Region.

Apart from the SWR, the responses of the two major groups of sections of *Acacia*, were different from each other (Figures 5B and C). The sections Juliflorae-Plurinerves, define a northern Australian zone and include a broad coastal region across the north and west of the North-West Eremaean Area (the Pilbara). The sections Pulchellae-Phyllodineae-Alatae well define separate Pilbara and Carnarvon areas, thus restricting the Kimberley in the vicinity of the Pilbara.

There is some evidence from recent studies of mammals (McKenzie 1981, plus McKenzie pers. comm.) that there is a clear extension of a tropical, Kimberley suite of mammals into the Eremaean Botanical Province as defined by Beard. In this respect, our findings support his for a more southern boundary of Beard's Northern Botanical Province. Clearly more work is required before a definitive statement can be made on the position and nature of boundaries, if they exist.

The Eremaean Region of our analyses is very complex. It is also the Region for which we have least data. It covers a vast area approaching nearly two thirds of the State or about 840,000 km². Only in the western part of the Eremaean Region do our *Acacia* Areas bear correspondence to Beard's (1980) Botanical Districts. The MINSPAN, GOWER, and discriminant function analyses showed variations in how the MULCLAS units of the Eremaean

Region related to one another (see Figures 3 and 4). The differences between the two *Acacia* sectional analyses further underlined the complexity of variation in this Region.

Despite the large variation between analyses, there appears to be a broad pattern, or set of interacting patterns, influencing the composition of suites of *Acacia* species in the Eremaean Region. Firstly, from north to south there appears to be a gradual change both in the total species composition (see Appendix 1 in Part 4 - this vol. pp. 38-55) and in the proportion of species from different sections of *Acacia* (Figures 7 and 8). Secondly, there is an area that centres on the North-West Eremaean Area (the Pilbara) which perturbs the north-south trend seen in the deserts further east (see Appendix 1 in Part 4 - this vol. pp. 38-55). Finally, there are the peripheral intergradations wherein south-western species extend obliquely north-eastwards and northern species extend southwards into the Eremaean. An analysis of *Acacia* biogeography of the arid/semi-arid centre of the Australian continent (Maslin and Hopper 1982) showed somewhat similar north to south trends, even though their basic units were much larger.

The geographic patterns of *Acacia* in our analyses bear some resemblance to the pattern of species richness in *Acacia* shown in Hopper and Maslin (1978). In both studies, the south-western part of the State is clearly conspicuous, the Kimberley or northern part is distinguished from the adjacent Eremaean area to the south, and a weak distinction within the Eremaean, of the western and south-western rim from the remainder, are indicated. The similarity is not likely to be due to the methodology used in detecting patterns because species composition played no part in the richness analysis, and species richness was unlikely to influence significantly the MULCLAS results since the Canberra metric was used as the similarity coefficient. Rather, the similarity of these essentially independent analyses strengthens the case for the reality of the phytogeographic patterns detected.

Upland areas in the Eremaean Region were noted as being areas of locally increased species richness by Hopper and Maslin (1978). In our analyses, such areas do not show particularly strong affinities to each other and often have rather different suites of *Acacia* species.

(b) Species Contributions to Geographic Patterns

The general picture of geographic variation in *Acacia* species composition is that of a finely-graded replacement series which has steepened gradients of change which we here have used to delineate *Acacia* Areas. These intergradations are discernable from a detailed study of Appendix 1 given in Part 4 (this vol. pp. 38-55) and also in the results of the numerical classifications and ordination.

Individual species were found to contribute less than 4% towards information gain on group fusion in the GROUPER results. Our analyses thus strongly emphasize suites of species as determinants of phytogeographic pattern rather than a few character species. Such a conclusion, if it is true, needs further investigation, particularly because our results fail to recognize such a well known vegetation unit as the "mulga zone" (e.g. Nix and Austin 1973) or a less well known but important vegetation unit of the Murchison area called "Acacia scrub" by Beard (1976). The large size of our sample units must contribute to these differences, but other factors are also likely to be important. For example, these two vegetation units are defined

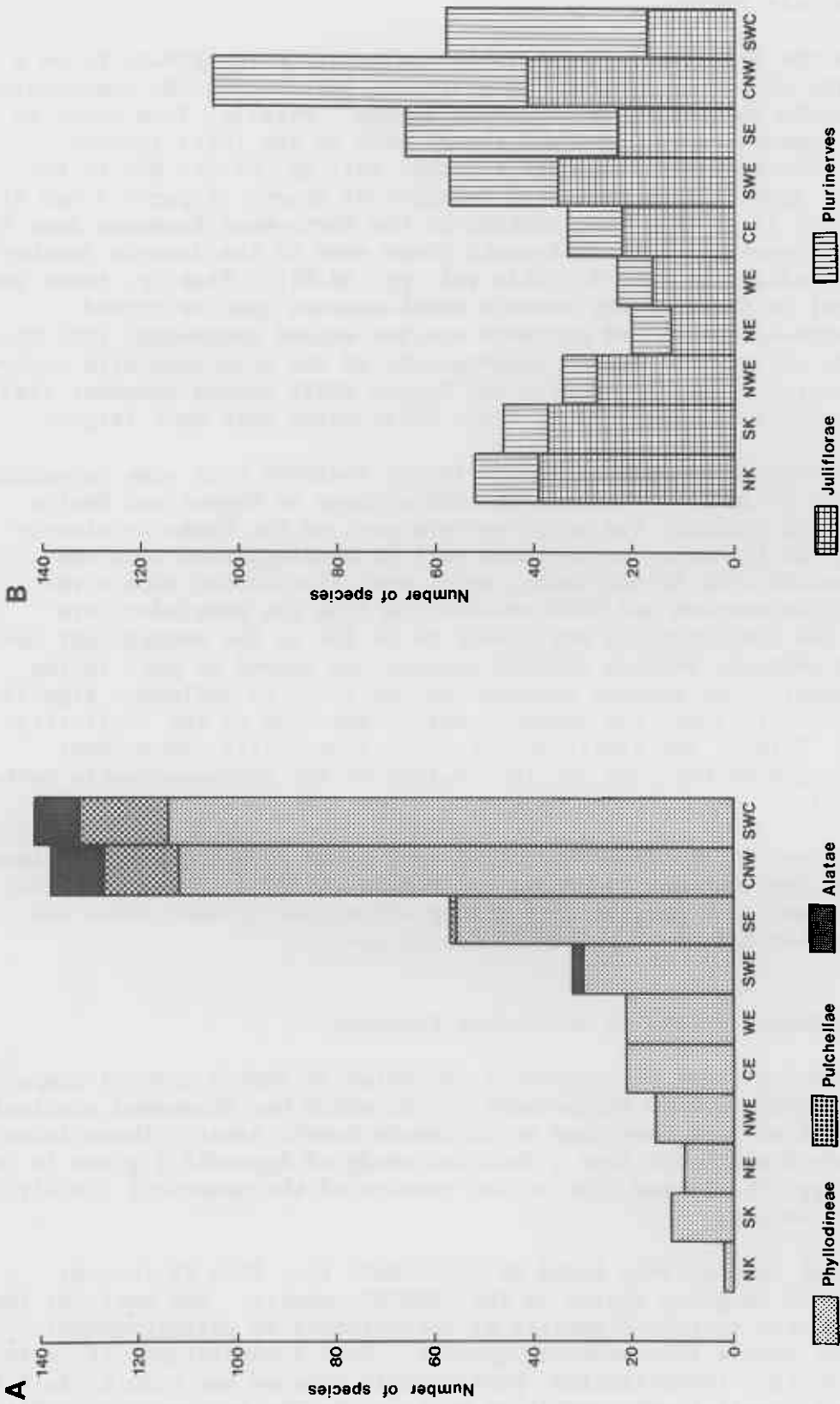


Figure 7. Histograms showing numbers of *Acacia* species within the related sections *Alatae*, *Phyllodineae* and *Pulchellae* (Figure 5A) and the related sections *Juliflorae* and *Plurinerves* (Figure 5B) for the 10 Western Australian *Acacia* Areas as derived from MULCLAS. The Areas are arranged approximately north (left of histogram) to south (right). Abbreviations for Areas are given in the caption to Figure 1.

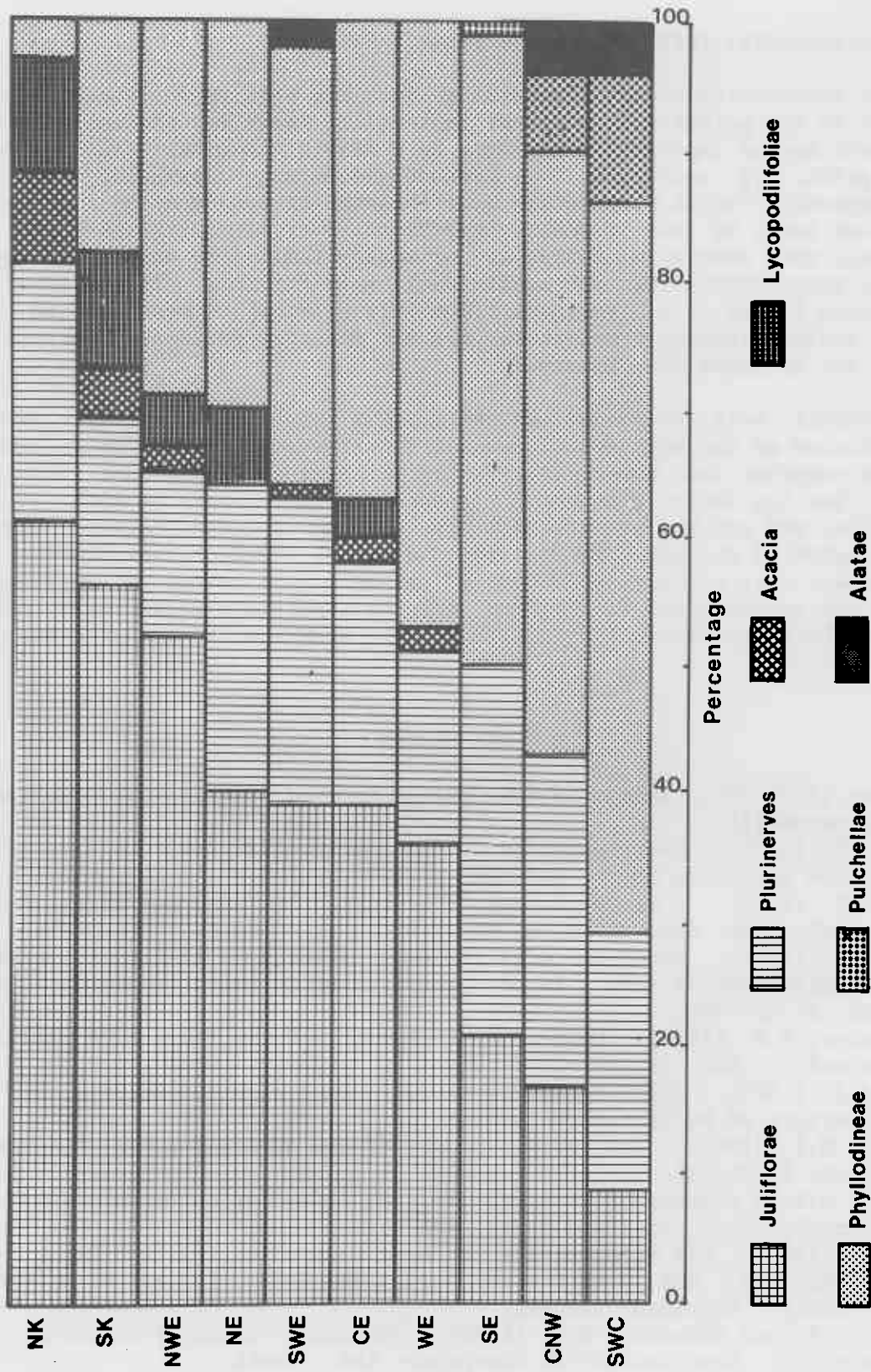


Figure 8. Histogram showing the percentage of *Acacia* sections within each of the 10 Western Australian *Acacia* Areas as derived from MULCLAS. The Areas are arranged approximately north (top of histogram) to south (bottom). Abbreviations for Areas are given in the caption to Figure 1.

by the physiognomically dominant species, whereas our Areas are floristically based.

(c) Environmental Influences on Geographic Patterns

Our examination of environmental factors has been very limited in scope. Not many of the potentially relevant factors are known for the entire State, and others appear impossible to reduce to a single numerical value for each of our grids, e.g. soil type. The present preliminary estimation suggests that temperature might be a better discriminator of *Acacia* Areas than rainfall which seems to rank second in importance. Our studies suggest the hypothesis that species of *Acacia* are primarily limited in where they may occur by temperatures that are sufficiently warm for them. If the lower temperature limits (i.e. average maximum July (winter) temperature and average minimum January temperature) are not met then presumably certain species are excluded from an area.

Rainfall, both its season and its drought levels (10-percentile amounts), was indicated as the next most important discriminator of our *Acacia* Areas. It is no surprise that water, in a distinctly semi-arid continent, is still a major limiting factor even for a widespread genus. That the 10th percentile, and not the average rainfall, was the important factor, suggests a high degree of drought tolerance for the genus. However, our simple analyses are only broadly indicative of possible rank orders of importance. We have not compensated, for example, for the complicating fact that rainfall increases both northwards and southwards away from the Eremaean Region.

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