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**SITE-VEGETATION MAPPING IN THE NORTHERN
JARRAH FOREST (DARLING RANGE).**

1. DEFINITION OF SITE-VEGETATION TYPES.

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PERTH

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ERRATUM

In Figure 20, *Lyginia tenax* is erroneously shown as the key indicator for Type F, when it should be shown as the key indicator for Type J.

SUMMARY

The ecological study described was designed as a basis for the sound management of a forested region of 10 500 km² in the south-west of Western Australia. A review of past ecological work in the region and of comparable studies, both local and overseas, was used to select a flexible approach combining both ordination and classification of the indigenous vegetation. The data basis comprised 320 observation plots capable of yielding not only ecological data but also information relevant to forest management. Each observation plot involved a complete basal area enumeration of all tree species on 0.16 ha, an estimate of cover of all perennial shrub and herb species on sixteen, one-metre quadrats and a description of associated topographic and edaphic features.

The basic data was converted, by means of auxiliary computer programs, into both quantitative and qualitative data. The former was analysed by means of principal component analysis, the latter by numerical classification of both divisive monothetic and agglomerative polythetic type.

The vegetation of the region was found to approximate most closely a multi-dimensional continuum. Classification, in particular divisive monothetic classification, was found to be least appropriate. By a process of successive approximations, involving the testing of the behaviour of the various species within a four-dimensional continuum, 55 species were chosen as indicator species. The continuum was broken up subjectively into 19 segments for the purpose of field mapping. Each segment was defined in terms of its component indicator species and the underlying environmental conditions.

Allocation of new observations, derived from large-scale surveys and consequently of a lower order of precision, to the continuum segments was attempted by visual matching, by computer-based decision making and by human judgment. All three approaches were found feasible, and differed chiefly in the time spent on preparation and on actual allocation.

SITE-VEGETATION MAPPING IN THE NORTHERN JARRAH FOREST (DARLING RANGE)

1. DEFINITION OF SITE-VEGETATION TYPES.

INTRODUCTION

In terms of basic concepts and techniques, the project described here is an extension of an earlier site study on the Swan Coastal Plain (Havel, 1968). However, it differs from it markedly in the complexity of environment and in the variety of land uses.

The earlier study dealt with the ecological basis of pine planting, and little consideration was given to alternative forms of land use. By contrast, this study covers an area renowned as a source of prime hardwood timber for over a century. It also contains the catchments of all the streams which currently supply the domestic, industrial and irrigation requirements of the southern portion of Western Australia. Scattered through the area are exotic plantations of both *Pinus radiata* and *Pinus pinaster*, established with varying degrees of success. Virtually the entire area is under long-term tenement for bauxite mining. As the nearest area of hilly, forested country, it is being used for recreation by the residents of the Perth Metropolitan Area. In addition, it acts as the last refuge for native fauna and flora threatened by agricultural clearing, both on the coastal plain in the west and in the wheatbelt in the east.

All these land uses are strongly interrelated. The relationships range from direct conflict, such as that between metropolitan water supply and water-based recreation, to relatively peaceful co-existence, such as that between hardwood silviculture and water supply.

Thus it seemed desirable to extend the investigation to cover all the interacting forms of land use, at least in so far as they influence forestry. One immediate implication of this decision is that the native vegetation ceases to be merely a means of assessing productivity, and warrants study for its own sake. This is because it is the basis of several forms of land use (hardwood silviculture, recreation, conservation of flora and fauna), and has considerable bearing on others (water catchments, rehabilitation of mined areas).

Whilst the necessary changes in objectives and methods may insure a wider applicability of the survey and its results, they bring in a very real danger that the ecological complexity will defy simplification and will diffuse the effort to the point of ineffectiveness. It was this consideration that influenced many of the decisions made in the course of the investigations.

Finally, it must be stressed that the investigation has a definite applied bias. It is undertaken to provide a basis for rational land use and to speed up the survey of natural resources. This influences the entire approach to the problem, in particular the location of sample areas; with few exceptions, these are tied to pilot plots of exotics or yield plots of native species. The few exceptions are chiefly remaining areas of virgin forest capable of providing information on the original structure of the tree stratum. Nevertheless, it is hoped that the investigation will also provide information of scientific interest.

The investigation has been divided into three sections:

- (1) Definition of site-vegetation types.
- (2) Location and mapping of site-vegetation types.
- (3) Relationship of site-vegetation types to land utilization.

Each will be the subject of a separate Western Australian Forests Department Bulletin.

SECTION I
GENERAL DESCRIPTION OF THE REGION

Location and area

The survey area is located in the south-west of Western Australia, between longitude 115° 50' E and 116° 50' E and latitude 31° 50' S and 33° 30' S. The overall area is approximately 10 500 km².

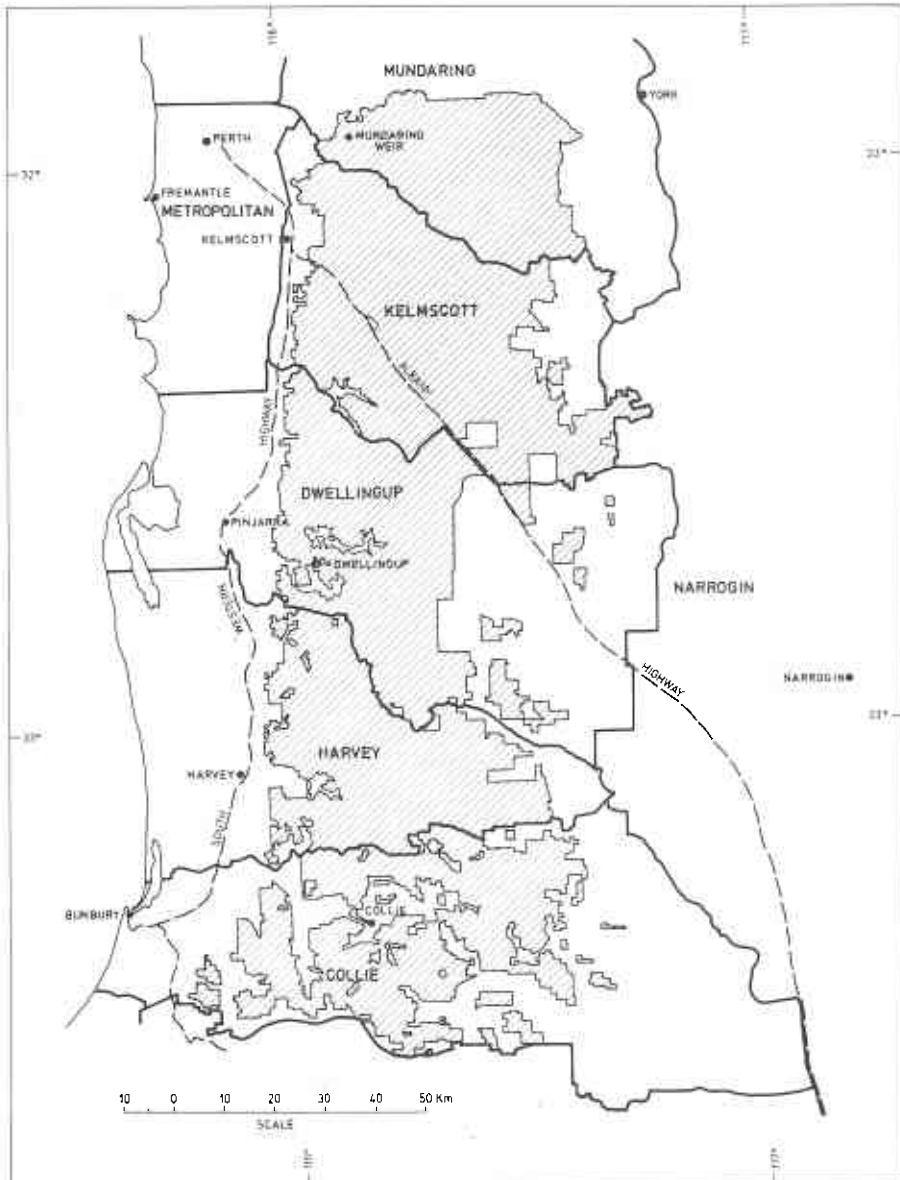


Figure 1

Map of the northern jarrah region, showing administrative subdivisions of the State Forest. (State Forest is shown diagonally hatched).

All detailed field work was located within the area designated as State Forest, which forms a solid block broken only near its southern end along the main road to Collie by a corridor of private farms. No sampling was carried out in the outliers of State Forest in the agricultural country to the north and east, such as Julimar and Dryandra, as these are ecologically quite different from the main block. Administratively the area is divided from

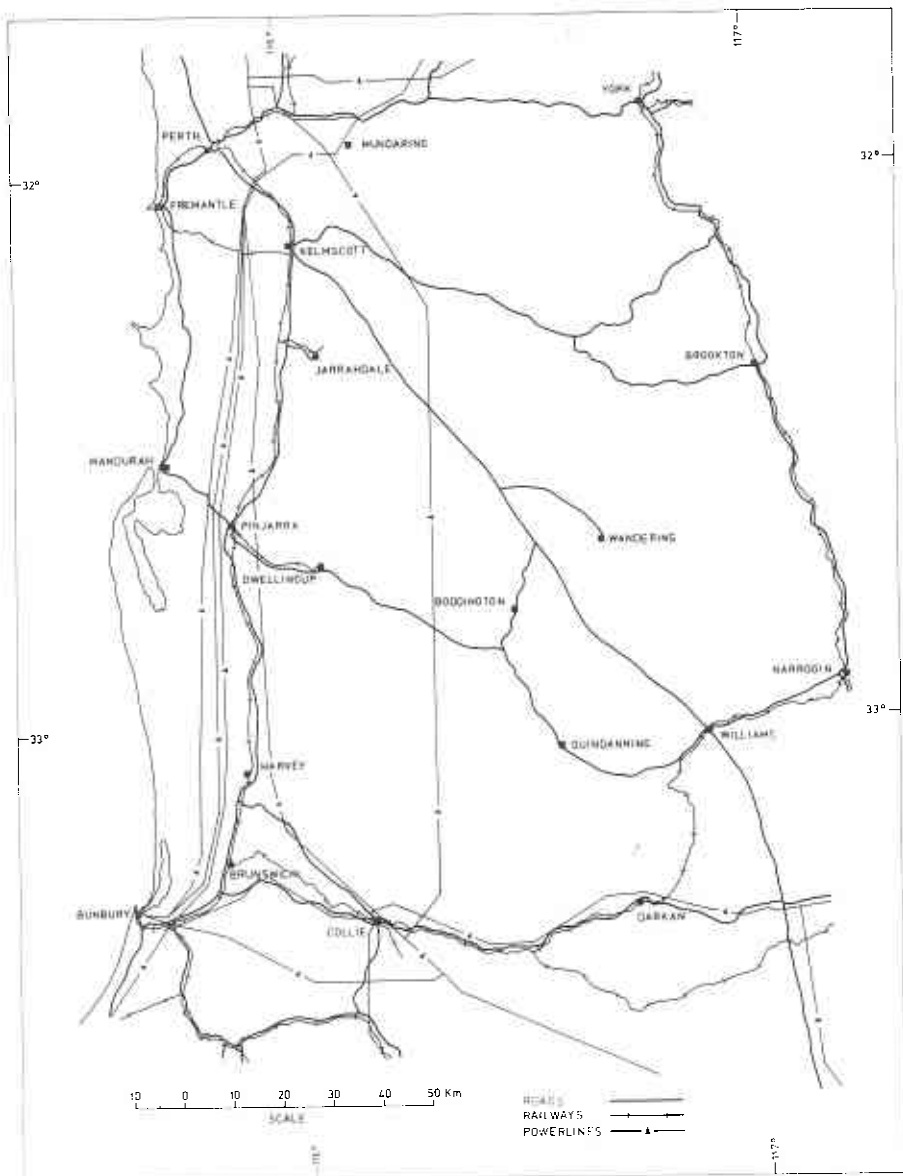


Figure 2
Map of the northern jarrah region, showing towns, railways, main roads and power lines.

north to south into five divisions (see Fig. 1): Mundaring, Kelmscott, Dwellingup, Harvey and Collie. Each division has its longest axis from west to east. The total area of State Forest involved is 732 600 hectares.

Population and economics

The capital of the State, Perth (population 641 800), is less than 32 km from the north-west corner of the survey area. The second largest town along the south-west coast, Bunbury (pop. 17 800), is approximately the same distance from the south-west corner. Several smaller towns, Armadale, Byford, Pinjarra, Waroona, Harvey and Brunswick Junction, generally of less than 2 500 inhabitants, are located near the western boundary of the State Forest. Four very small towns, Wandering, Boddington, Quindanning and Darkan, each with less than 500 inhabitants, are located along the eastern boundary. Within the area itself there are only four settlements of any size: Mundaring (580) in the north, Jarrahdale (390) and Dwellingup (480) in the centre, and Collie (6 730) in the south. However, the Perth Metropolitan Area now infringes on the north-western boundary.

Several highways cross the area from the coastal plain in the west to the agricultural region in the east (see Fig. 2). These are the Great Eastern Highway, the Brookton Highway, the Albany Highway, the Pinjarra-Boddington-Williams Road and the Brunswick-Collie-Darkan Road. East-west railway lines hem the northern and southern boundaries. Two minor railway lines terminate at Jarrahdale and Dwellingup respectively. One major north-south railway line follows the western boundary, another is approximately 30-50 km east of the eastern boundary.

Despite the relatively well-developed communication system, population is sparse. This is largely due to the abandonment of former sawmilling and forestry centres which have been absorbed by the larger centres within, and especially on the periphery of, the area. Motorized transport, which has reduced the necessity of living close to work, is the major factor in population redistribution. There are five primary industries: bauxite mining at Jarrahdale and Dwellingup, coal mining at Collie, intensive agriculture along several river valleys penetrating into the area from the west, extensive grazing along the eastern boundary and forestry and sawmilling over the area as a whole.

Climate

The climate of the area has been described in several papers, and from several viewpoints, by Gentilli (1947, 1948, 1951 a and b). More recently, the Bureau of Meteorology (1965, 1966 a and b) has dealt in detail with the South-west, Great Southern and Metropolitan Regions of Western Australia, covering the southern and central portions, the eastern and the northern portions of the survey area respectively. The description of climate will be limited to a few points relevant to the ecology.

The climate is determined by its proximity to the Indian Ocean, by its latitude, and by local topographical configuration. It is a typical Mediterranean climate, oceanic with winter rain (Koeppens classification Csb), except that it is more equable than in other Mediterranean regions such as California, Chile, South Africa and Morocco. This is attributed by Gentilli (1948) to warm ocean currents along the coast. There is a predominance of winter rains, when moist westerly winds precipitate as they rise over the coast and the

Darling Scarp. The rainfall map (see Fig. 3), based on Bureau of Meteorology summaries (1965, 1966 a and b), shows the overall picture. The highest rainfall is recorded in the north-western sector at Churchman's Brook, where the special topographical configuration boosts the annual average to 1397 mm. Other areas of high rainfall (over 1250 mm) occur between Dwellingup and Collie. The usual pattern is a rise in rainfall from 1000 mm along the

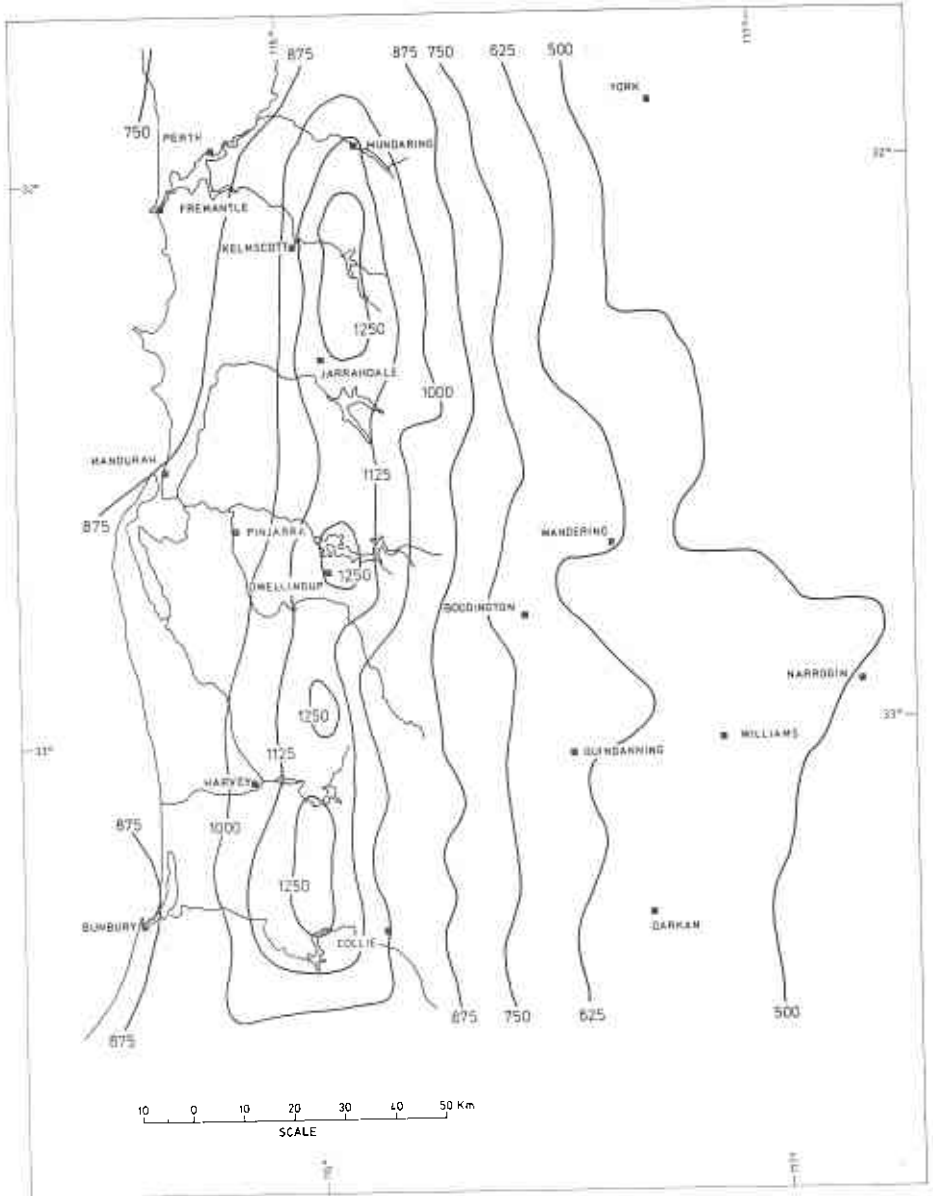


Figure 3
Rainfall map of the northern jarrah region. (Isohyets in mm/annum).

escarpment to the already-mentioned high point 5 to 10 km east of the escarpment, and then a relatively rapid drop in rainfall over the next 30 to 40 km to below 600 mm along the eastern boundary of State Forest. Figure 3 is probably an over-simplified picture of rainfall distribution due to paucity of recording stations. It is, for instance, probable that the chain of high monadnocks rising to 270 m above the plateau east of Jarrahdale has an impact on the rainfall.

The strongly seasonal rainfall is reflected in the ratio of winter (April to October) to summer (November to March) rainfall, which is 6:1 for most localities within the region. Thus summer drought is the chief limitation to plant growth. The rainfall is reliable, the variability being only of the order of ± 15 per cent of the mean figure. The number of wet days per annum ranges from 90 in the north to 120 in the south. The usually very light rain, averaging 0.75 cm per wet day, has a profound effect on soil formation and run-off.

To determine the growing season, the Bureau of Meteorology has used the following criteria: the season commences when rainfall of at least 12.5 mm in a day, or a number of consecutive days, is received, and when effective rainfall is exceeded continuously during the subsequent 30 days. It continues as long as effective rainfall (calculated by Prescott's Formula: $P = 0.54 \times E^{0.7}$, where P is effective rainfall and E is evaporation) is received in the months following. On this basis, the growing season commences in the first week of April at the southern boundary and in mid April in the north. The duration of the season ranges from six months in the north to seven months in the south. In climatic factors (total amount, variability, effectiveness) involving rainfall, there is a progressive deterioration towards the north-east.

Although in south-western Australia temperature has less influence on plant growth than rainfall, it was suggested by Diels (1906) that low temperatures may be a significant factor towards the eastern boundary of the survey area. There is a drop in the mean winter temperature from above 12°C in the north-west to 10°C in the south-east. More importantly, frosts range from less than 10 per annum in the north-west to over 50 per annum along the eastern boundary. The frequency of occurrence of frost is locally accentuated by topography, being highest in the upland depressions. Diels postulated that low temperatures did not lead to cessation of growth, but only to a slowing down. The number of hot days with temperatures exceeding 32.5°C ranges from 20 per annum in the south-western corner to over 40 in the north-east.

There have been numerous attempts to reconstruct the ancient climates of the region in view of their importance to soil formation and plant distribution. Fluctuations on both sides of the present climate have been postulated. It is assumed that laterization of the plateau surface took place under conditions warmer and more humid than at present. The presence of outliers of most of the forest species in climatically drier regions likewise points to a moister climate in the past. Drier periods between 500 BC and 300 BC and AD 500 and AD 1500 were postulated by Churchill (1968) on the basis of palynological evidence.

Burbridge (1960) claimed that greater aridity than that of the present would have eliminated the south-western vegetation, but this opinion was not shared by Gentilli (1951), who considered the jarrah forest to be very stable.

requiring a drop of 250 mm in annual rainfall to affect it markedly. A drop of 500 mm would be needed to change the vegetation to that of a desert. Gentilli (1947) also claimed recorded evidence of an increase in average annual rainfall of approximately 120 mm over the past century.

Physiography, geomorphology and geology

The features of the northern quarter have recently been reviewed by Mulcahy *et al* (1972). Where necessary, older sources are used in extending the description to the southern portion.

The area is locally known as the Darling Range. This is somewhat misleading, as it is merely the south-western margin of the Great Plateau of Western Australia. The term "Range" presumably arises from consideration of the dissection of the plateau margin by rejuvenated drainage following an epeirogenic uplift of the Plateau in relation to the narrow coastal plain to the west of it. The timing of the uplift has been the subject of much discussion: whereas Jutson (1934) postulated two major uplifts in the Pleistocene, Mulcahy *et al* postulated several successive smaller uplifts. The Plateau margin now consists of deeply incised valleys separated by broad uplands, but eastwards the dissection becomes progressively less pronounced. The highest remnants of the Plateau reach 400 metres, but evidence of former levels is to be found in several monadnocks which reach up to 582 metres. The western margin of the Darling Range is formed by the Darling Fault Scarp, which bifurcates to the south and to the north of the survey area, but within the area is a single north-south trending escarpment. The eastern margin of the Darling Range is far less clear cut. In the north and east, it is formed by the Avon Valley, and in the south-east by the Blackwood River and its northern tributary, the Hillman River.

The central portion of the Darling Range is cut by the Murray River, and its tributaries (Hotham, Bannister, Crossman and Williams) spread on to the main Plateau so that there is no clear demarcation. The Avon Valley coincides partially with a zone of seismic activity described as the Yandanooka-Cape Riche Lineament. The Swan Coastal Plain and the Avon and Blackwood Valleys thus tend to act as local base levels for all the streams draining the Darling Range.

In addition to the three major rivers already mentioned, all of which originate in the dry, agricultural belt east of the survey area, and as a consequence have brackish water, there are several smaller rivers. These are restricted for the whole of their course to the forested, high-rainfall portion of the area, and thus have fresh water. Most of these have been dammed, and are the principal sources of domestic, rural and industrial water in Western Australia. They flow only intermittently, in winter and spring (May to November). Their valleys mostly change from broad, shallow, mature forms in the head waters to deeply-incised, young, forms near the Darling Scarp.

The dominant rock type of the Darling Range is granite, in the form of batholiths, dykes and sills, which penetrate the older Precambrian whiststones, greenstones, schists and gneisses (see Fig. 4). The granite itself is penetrated by later dolerite and epidiorite dykes. Although these rocks underlie the entire Plateau, they are only exposed on the escarpment in river valleys incised into the Plateau and on residual monadnocks above the plateau. Over

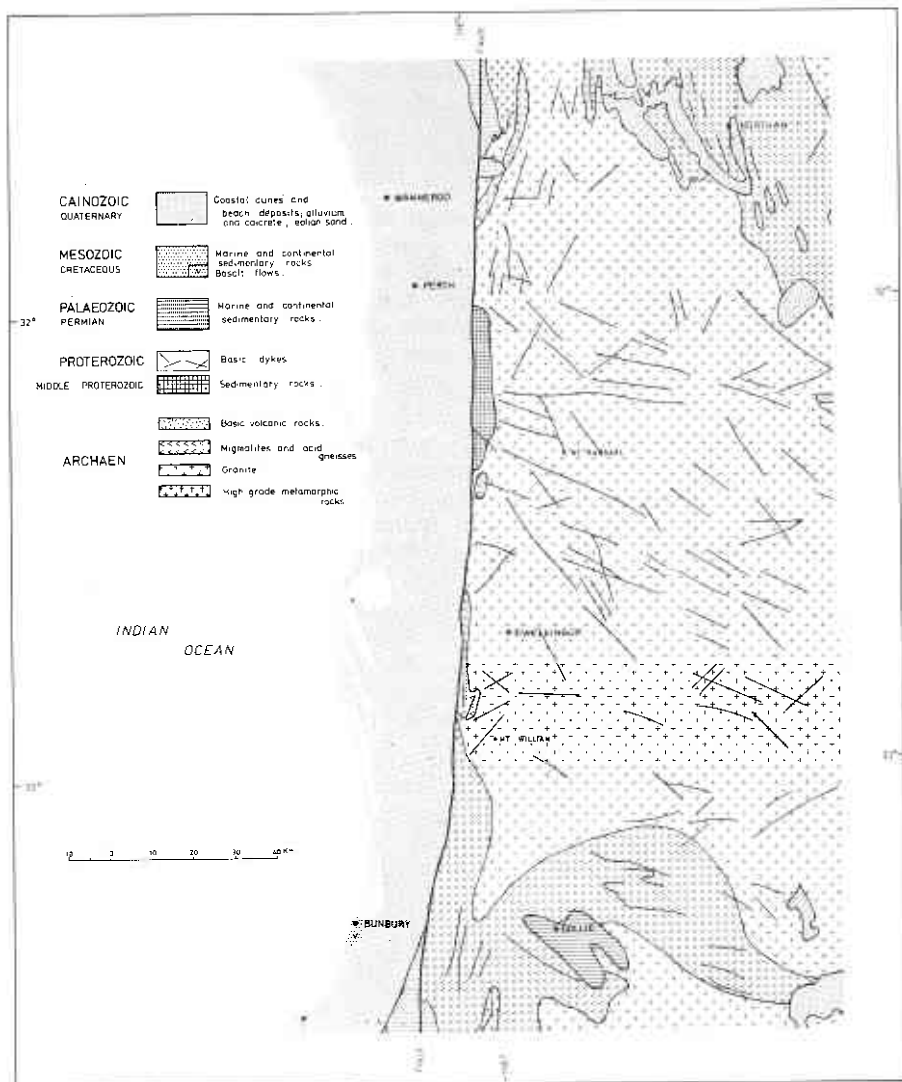


Figure 4
 Geology map of the northern jarrah region. (After Geological Survey of Western Australia, 1973).

much of the area, the bedrock is covered by a lateritic mantle, the age of which has been the subject of as much discussion as the timing of the uplift, to which it is related. Jutson (1934) postulated that the laterization preceded the uplift, whereas Playford (1954) and Mulcahy *et al* (1972) viewed it as contemporary with several successive uplifts. The only exception to the above generalization is the Collie Basin, which is filled with Palaeozoic (Permian) sediments, such as glacial tillites, shales, marine limestone, coal and continental sandstone.

Soils

The systematic account of the soils of Western Australia began with Prescott (1931), who described as azonal the ferruginous and aluminous gravels so prevalent in south-western Australia. He considered them to be the remains of an ancient B horizon of a soil. This recognition made it possible to look for a soil which fitted the concept of the great soil groups. This he found on exposures of country rock below the laterite-capped Plateau.

This concept was further elaborated by Teakle (1938), who considered the survey area to be part of his zone of grey, yellow and red podzolised soils of the temperate sclerophyll forest delineated by the 620 mm isohyet. He distinguished these soils from northern temperate podzols by the lack of surface humus accumulation and relatively poor development of some other podzol features. He recognized the occurrence of acidic, red earths and solods, as well as the earlier-mentioned gravels, within the same zone.

Within this broad area he delineated the Darling Peneplain Region, which covers most of the survey area. He described it as a dissected granitic peneplain, whose former lateritic surface had been broken by erosion into ferruginous gravel. He considered the description of a typical soil profile of the region impossible, but referred to such common features as clayey, yellowish subsoil, grey and red mottling in the B horizon and the sandy and/or gravelly surface.

The eastern part of the area falls within Teakle's Dwarda Region of the zone of red-brown earths of the eucalyptus-acacia woodland, occurring between the 380 and 620 mm isohyets. He described the typical soil as a red-brown horizon overlying a reddish clay B horizon. On the broad uplands within this zone, ferruginous gravels persist.

Smith (1952) considered the soils in greater detail. He disagreed with Teakle (1938) on the use of the term podzol, claiming that many of the sandy-gravelly soils of the region had too low a content of organic matter, and should be more properly called sandy laterites or laterites, rather than podzols. He also renamed Teakle's red-brown earths non-calcic brown earths, on the grounds that they lacked one of the chief distinguishing features of the true red-brown earths, namely the accumulation of calcium in the B horizon. He renamed the zone within which the bulk of the survey area occurs as the zone of podzols, laterites and south-western brown soils.

In classifying the soils, he made use of soil families, defined as a group of related soil series. The families were grouped into three major groups, pedalfers, pedocals and peaty soils. For mapping purposes, the soils were grouped into soil combinations, and these in turn into soil zones. It is impossible to deal in detail with Smith's classification, as no attempt had been made to map the soils within the present survey area. Instead, they were grouped into three main combinations—Darling in the west, Avon in the north-east and Jingalup in the south-east. Some of the families of relevance are:

- Plantagenet (humus podzols)
- Mungite (meadow podzols)
- Willbay (deep sandy podzols)
- Kordabup (iron podzols)
- Wakundup (south-western laterites)
- Scotsdale (stony brown soils)

Gosnells (alluvial brown soils)
Punchmirup (stoney soils)
Camballup (solodized solonetz)

Of particular importance to the survey area was the higher iron content of the dolerite, which resulted in the formation of massive laterite; whereas on the neighbouring granite, poorer in iron, only pisolitic gravel was formed. Smith looked on the laterite of the Darling Range as an iron-rich bauxite, a mixture of gibbsite, diaspore and limonite, and claimed that removal of iron in solution and its redeposition in depressions, was still an active process. He attributed the weak acidity of most south-western soils to a combination of recycling of calcium and potash by trees, and the prevention of humus accumulation by recurrent bushfires.

Stephens (1962) and Stace *et al* (1968), in their description of Australian soils as a whole, did not treat the survey area in sufficient detail to contribute much to earlier work. Both adhered to the zonal concept of soil distribution, though Stace *et al* made cross-reference to Northcote's (1965) descriptive classification. The essence of the latter classification was a total abandonment of the zonal concept in favour of a classification based on observable soil features. The first order subdivision was into organic soils and soils with uniform, gradational or duplex profiles. There was no subdivision of the organic soils (O). The uniform soils (U) were subdivided on the basis of the texture, the gradational soils (G) on the presence of calcium within the profile. The duplex soils (D) were subdivided on the basis of the colour of their B horizon. Northcote *et al* (1967) classified the bulk of the survey area as KS-UC4.2, defined as ironstone gravels with sandy matrix. The soils derived from fresh rock on the scarp and in deep river valleys in the west were classified as Gn 2.14, that is red earths with an acid reaction trend. Soils occurring in similar situations in the north-east were classified as Dr 2.22, hard-setting, loamy, duplex soils with red, clayey subsoils, neutral reaction trend and an unbleached A2 horizon. The soils of the Collie Basin were classified as Uc 2.3, bleached, sandy soils with a compact or pan-like layer below the bleach. The upper valleys of the Darkin and Collie Rivers were classified as Dg 3.81, sandy duplex soils with grey, clayey subsoils and acid reaction trend. The eastern margin of the area, together with parts of the Helena Valley, was classified as Dy 3.81, hard-setting loamy, duplex soils with mottled, yellow, clayey subsoil, acid reaction trend and bleached A2 horizon. In the south-western corner, between Waroona and Collie, the red earths (Gn. 2.14) were replaced in analogous positions by two minor categories: Dy 2.21, hard-setting, loamy, duplex soils with yellow, clayey subsoils and acid reaction trend) and Dr 2.21 (identical, except for the red colour of the subsoil).

Several detailed soil surveys have also been carried out by Forests Department staff over the past four decades. Their chief deficiency is that they are not correlated, either between localities or with the more recent schemes of classification, other than for the references made to them by Smith. As a result, there is an excessively large number of minor categories of only local significance.

SECTION II

REVIEW OF ECOLOGICAL WORK

A review of past work is full of pitfalls, such as going too far into the past on one hand, and downgrading past work as worthless in the light of one's present knowledge on the other hand. Yet the extraction of worthwhile information is essential if futile repetition is to be avoided.

It is fortunate that "background noise", either in the form of information unsupported by sound observations or the reiteration of earlier work, is rather rare in the ecological literature of the south-west of Western Australia. Presumably this is because the task is so large, and the workers have been so few.

Early plant geography by Diels

The early work of Diels (1906) was essentially a study of the plant geography of the region. He gathered a wealth of data, and highlighted the relationship between plants and environment. The tall trees with their vertical leaves, the strongly-developed understorey of hard-leaved shrubs and the substitution of perennial Cyperaceae and Restionaceae for annual herbs and grasses add up to a vegetation type which has no counterpart in other regions with a Mediterranean climate. These outstanding features were used to define Diels' sclerophyll forest formation. The floristic richness of the vegetation, particularly on the extensive, infertile, sandy and gravelly soils, was emphasized.

Turning specifically to the jarrah (*Eucalyptus marginata*) forest, Diels delineated it by the 750 mm isohyet. He recognised that edaphically-favourable sites compensate for lower rainfall in the most easterly extension of the species. Jarrah is associated with gravelly uplands, but its extension on to the sandy, coastal plain, with a corresponding reduction in structure from tall forest to woodland, was recognised. Among the outstanding features of the forest, Diels lists its grey, dull appearance, except in valleys; the purity of its overstorey that, apart from marri (*Eucalyptus calophylla*), no species enters into; the uniformity of the small-tree understorey, restricted to eucalypt regeneration and a few Proteaceous species; and the diversity of the shrubby ground vegetation, which contrasts so strongly with the floristic paucity of the tree strata.

In dealing with individual tree species, he associated marri with moist, fertile sites, sheoak (*Casuarina fraseriana*) with sandy soils, *Banksia grandis* with gravelly uplands, *Melaleuca preissiana* and *Banksia littoralis* with swamps, and *Banksia attenuata* and *Banksia menziesii* with deep sands. Of the eastern species, wandoo (*Eucalyptus wandoo*) was considered to be restricted to heavy-textured soils underlain by clay, alternately wet in winter and baked hard in summer, and *Casuarina huegeliana* to granite outcrops. These were rather generalized conclusions, which could be made readily by anyone acquainted with the forest. Nevertheless, they were virtually overlooked in subsequent years. Even more surprising was his perception of the distribution patterns of the smaller perennials. He associated the genera *Petrophile* and *Isopogon* with sandy gravels, *Gastrolobium* with dry gravels, and *Viminaria*, *Cladium* (syn. *Baumea*), *Boronia*, *Astartea* and *Agonis* with swamps. Of the families, he considered Epacridaceae to be most restricted by external conditions, but

relatively poorly developed in the moister south; Myrtaceae to be bimodal, with strongest occurrence in swamps and sands; Restionaceae to be largely restricted to swamps; and Orchidaceae to be controlled more by fire than by edaphic conditions.

In dealing with structure, Diels emphasized epharmonic convergence, which he described as the possession of similar leaf types and forms of branching by widely different taxonomic units growing under similar environmental conditions.

Another of his remarkable perceptions was the recognition of a north-south trend in species distribution, as well as the more obvious east-west one. He considered that the optimum of the jarrah forest occurred in the middle Blackwood Valley. *Acacia nigricans*, *Hypocalymma cordifolium*, *Pteridium aquilinum* (syn. *Pteridium esculentum*), *Adiantum aethiopicum* and *Trymalium billardieri* (syn. *Trymalium spathulatum*) were listed as the under-growth associates of jarrah on optimum sites.

In the wandoo woodland east of the jarrah forest, he considered the undergrowth to be a depauperate version of the jarrah undergrowth, more xerophytic in nature. He named *Mirbelia spinosa*, *Gastrolobium obovatum* (syn. *Gastrolobium calycinum*?), *Hakea lissocarpa* and *Hakea marginata* as the main shrub species, and referred to the occurrence there of the herbaceous "everlastings" of the family Compositae, in particular *Helipterum manglesii*, *Helipterum cotula*, *Millotia tenuifolia* and *Waitzia acuminata*.

Apart from the forest formations, Diels also described swamp and granitic rock formations, giving a brief enumeration of species for each.

As a plant geographer, Diels was interested in endemism, which has considerable bearing on the detection of plant indicators. He considered the jarrah forest to be relatively poor in endemics amongst its 875 species, with the endemism at a maximum near its northern limit, where the climatic gradient is steepest. For the south-west province as a whole, he listed *Lyginia*, *Anarthria*, *Dasypogon*, *Kingia*, *Phlebocarya*, *Conostylis*, *Synaphea* and *Nuytsia* as first-class endemics, that is without any relations outside, and *Loxocarya*, *Diplolaena*, *Platytheca*, *Tremandra*, *Hypocalymma*, *Calothamnus* and *Andersonia* as second-class endemics, that is with some relations outside but markedly different from them.

Finally, Diels subdivided the south-west province into seven botanical districts. The survey area falls chiefly into the eastern upland portion of the Darling District, described as gravelly, hilly country within the 600 to 1 000 mm rainfall zone, also containing some swampy alluvium and sands. Jarrah is used as the character species. The north-east portion of the area falls into Diels' Avon District, and the south-east portion into the Stirling District.

Minor studies of Gardner and Holland

As far as the jarrah formation was concerned, little more was done in the field of broad-scale synecology for the next fifty years. Gardner's (1923) description was no more than a brief summary of Diels' work. The overall description of the vegetation of Western Australia by Gardner (1942) elaborated on the work of Diels, and added to the knowledge of areas not visited by him, but the scheme of classification was essentially that of Diels. The jarrah forest was mentioned only briefly, with no additional information.

In Holland's (1953) study of eucalypt distribution patterns, no new work was reported, apart from one transect and one small pot trial. The transect spanned the topographical gradient from lateritic upland to wet alluvium, that from jarrah through wandoo and marri to flooded gum (*Eucalyptus rudis*). Relatively few associate species were named. Marri was considered to be more flexible in its habitat requirements than jarrah, which was considered to be incapable of competing on good soils and to have a narrow tolerance to moisture fluctuations. A novel idea was the recognition of eroded valleys as migration routes. The present distribution of species was considered to be the result of past expansions and contractions. Presumably this was based on studies in the southern Eremean region as no detailed evidence was presented for the jarrah region.

Later synecological studies by Speck

The next study of south-western vegetation was that of Speck (1958), who worked within the framework established by Diels, but introduced several new methods and ideas. Although his work was not strictly quantitative, greater details are incorporated, particularly on Diels' Irwin Botanical District. From his data he attempted a classification of plant communities using the nomenclature of Beadle and Costin (1952), slightly modified for local conditions but retaining the emphasis on structure as the first criterion of classification. Three major formations were described: forest, woodland and scrub. The latter was defined as depauperate trees or shrubs in a continuous stratum, with subordinate shrub layer but poorly-developed herb stratum. The three formations were further subdivided into 24 subformations and 62 plant communities, largely, though not exclusively, described as associations. The association was defined as a climax community in which the dominant stratum exhibited a quantitatively uniform composition throughout its range. The dominants were used as the characteristic species. The associations were grouped by structure into formations, and by similarities in both floristic composition and structure into alliances. The use of profile diagrams to illustrate the structure of plant communities was one major advance on the work of Diels.

Although Speck rejected the use of edaphic complexes (for example, the swamp formation of Diels) as classification units, he recognized their usefulness in mapping. In order to cope with unmappable combinations of associations, he used the concept of "vegetation system", defined as an area of country in which there was a definite pattern of associations and alliances determined by a comparable pattern of soils and topography. In this aspect he came very close to the land system concept proposed by Christian and Stewart (1953).

Within the survey area, Speck recognized two vegetation systems. Of these, the Darling System, which covers the Darling Scarp and the western margin of the Plateau, contains some youthful streams and has an annual rainfall of over 890 mm. The Bannister System, which was restricted to the eastern margin of the area, away from the Scarp, lacks youthful streams and has an annual rainfall of between 500 and 1 000 mm. Each has a set of plant communities ranging from the *Eucalyptus marginata* to *Eucalyptus calophylla* high forest to *Eucalyptus wandoo* woodlands. However, whereas the Darling System was described as the "prime" jarrah forest, the Bannister

System was merely looked upon as its poorer eastern extension. The associations observed were: (i) *E. marginata*; (ii) *E. marginata-E. calophylla* and (iii) *E. wandoo* in both systems; (iv) *Eucalyptus patens* and (v) *Eucalyptus megacarpa* in Darling only; (vi) *Eucalyptus wandoo-Eucalyptus accedens* and (vii) *E. accedens* in Bannister only. Profile diagrams, structural formulae and brief species lists were used to illustrate the high forest of *E. marginata-E. calophylla* and the tall, temperate woodland of *E. wandoo-E. calophylla*. Only brief mention, without any species list, was made of *E. patens* and *E. megacarpa* associations.

It is obvious that Speck was aware of the continuous variation within the forest, as shown in his profile illustrating a xerosere from high forest on deep soils to mosses and lichens on granitic outcrops. However, he was limited in exploring this by the broad-scale nature of his study and his acceptance of Beadle and Costin's classification. The recognition of vegetational continuity was also implied in his climatic series, which arranged associations along gradients of decreasing rainfall. The relevance of Speck's work is that it provides a broad framework within which the more detailed survey of the northern jarrah forest can be fitted.

Detailed ecological work of Williams

The chief source of detailed ecological information is Williams (1932, 1945), who carried out two, small-scale site-vegetation studies in the north-western corner of the survey area. One of these was situated on Cohen Brook, a minor tributary of the Helena River, at the point where it descended from the Plateau on to the coastal plain. The other was situated in the valley of the Darkin River, the main tributary of the Helena River, approximately 27 km inland from the edge of the Plateau. The areas covered were 17.8 ha and 74.5 ha respectively. In both cases, the landscape was, by local standards, strongly dissected, the laterite capping occupying a very much smaller proportion of the total landscape than was true of the northern jarrah as a whole. Consequently, there was much outcropping of the underlying rocks, namely granite with epidiorite dykes. In the Darkin study, a narrow zone of alluvium was also encountered. Painstaking detail was collected, with the position of each tree being mapped and total enumeration of all perennials being carried out on one per cent of the area on a 20 x 20 m grid. The second survey was somewhat less detailed. On the basis of these surveys, Williams described several associations and consociations, the latter being communities dominated by a single tree species: *Eucalyptus calophylla*, *Eucalyptus wandoo*, *Eucalyptus marginata* and *Eucalyptus patens*. A successful attempt was made to relate these to underlying soils and rocks. Williams concluded that the units were too heterogeneous to be described as associations in the narrow sense. They could be better described as edaphic complexes. Regarding the plant indicators, he concluded that plant communities were indicative of soil conditions, but that individual tree species, and in particular individual shrub species, were of limited value for this purpose.

He found that the species complex of the lateritic uplands differed markedly from the species complex of the dissected landscape and soils derived from fresh-rock exposures. Within the latter group he found species with preferences for soils derived from granite and epidiorite respectively. Yet another set of species was associated with the moist alluvium. A number of species failed to show any edaphic preferences.

Soil surveyors of the Forests Department usually recorded, in the course of their work, plants considered to be associated with a particular site or soil type. The work has never been brought up to a stage of clear-cut conclusions similar to those of Williams. The reasons for this were the less-detailed and less-consistent recording, the milder environmental gradients, and the less-abrupt vegetational changes.

Study of tree distribution by Lange

Yet another relevant study is that of Lange (1960), who attempted to relate climatic and edaphic factors to distribution of tree species in the Narrogin district. Although his study area was east of the Darling Range, many of the tree species studied by him occur within the survey area, and their distribution in a drier climate throws considerable light on their site requirements. Lange found that the 500 mm isohyet was the main dividing line between the western species characteristic of acid, lateritic soils and higher rainfall, such as *Eucalyptus calophylla*, *Eucalyptus marginata*, *Eucalyptus rudis*, *Banksia grandis* and *Nuytsia floribunda*, and the eastern species characteristic of the calcareous, alkaline soils of the dry inland, such as *Eucalyptus salmonophloia* and *Eucalyptus longicornis*. However, a number of tree species, namely *Eucalyptus wandoo*, *Eucalyptus loxophleba*, *Eucalyptus astringens*, *Acacia acuminata* and *Casuarina huegeliana* straddle the 500 mm isohyet. Whenever the western species occur east of the dividing line, it is invariably as outliers on deep lateritic soils or on sandy soils in moisture-gaining depressions. He attributed the disjunct occurrence of the western species to an arid period in the late Quaternary, as postulated by Crocker (1959). The overall effect of increased aridity was the contraction of these species to favourable sites.

Palynological studies by Churchill

Past climatic fluctuations were the subject of palynological investigations by Churchill (1961, 1968), who was concerned primarily with the vegetation of the extreme south-west, in particular the balance between *Eucalyptus marginata*, *Eucalyptus calophylla* and *Eucalyptus diversicolor*. He found that the present distribution was largely determined by the rainfall of the wettest and driest months of the year, indicating that availability of water was a major influence. By contrast, no such relationship with temperature data was found. Major changes in pollen spectra were dated to 3000 B.C., 1200 B.C., A.D. 400 and A.D. 1200. He concluded that a drier climate, favouring the increase of *E. calophylla* at the expense of *E. diversicolor* (now largely restricted to high-rainfall areas along the south-western and southern coast) probably occurred between 3000 and 5000 B.C., and between A.D. 500 and 1200. Moister climatic conditions favouring *E. diversicolor* probably occurred prior to 3000 B.C., between 500 B.C. and A.D. 500 and from A.D. 1500 onwards. The incorporation of charcoal in the peat deposits indicated that fire has been part of the environmental complex for at least 7000 years. The three species discussed appear to have very wide edaphic tolerances within the high-rainfall belt. Churchill's conclusions about the northern limits of *E. marginata* and *E. calophylla* on the coastal plain were too sweeping, in that they ignored some of the less-accessible outliers. As a result, he tended to underestimate the ameliorating effect of shallow ground water and high organic matter in strongly-leached sands.

Ecophysiological studies of Grieve, Doley and Helmuth

Mention must also be made of the considerable amount of ecophysiological work of Grieve (1955, 1960), Doley (1967) and Grieve and Helmuth (1968). Grieve's former paper studied the water economy of sclerophyll plants, and placed them into the following categories:

- (1) Species that escape the summer moisture stress by loss of foliage (e.g. *Phyllanthus calycinus*).
- (2) Evergreen species that remain physiologically active throughout the summer (e.g. *Eucalyptus marginata*).
- (3) Evergreen species capable of restricting their physiological activity considerably, ultimately reaching a stage of near dormancy (e.g. *Hibbertia hypericoides*).
- (4) Evergreen species capable of restricting water loss before the deep water source is exhausted (*Eucalyptus calophylla*).

Doley studied the water loss in *Eucalyptus marginata* on lateritic gravels, and concluded that although the species was capable of some restriction of water-loss in midsummer at midday by partial stomatal closure, the deficits observed were due to either climate or redistribution of water within the tree. There was strong evidence that throughout the summer the tree was using water from deep layers in the soil, and that unbranched laterals descended through fissures in the laterite to kaolinitic horizons beneath.

Grieve and Helmuth stressed that despite the outward similarity of their leaves, plants may have markedly different rates of transpiration. They distinguished between plants that exhibit little seasonal variation in water loss (isohydric, e.g. *E. marginata* and *Phyllanthus calycinus*) and those that have marked seasonal variation (poikilohydric, e.g. *Hibbertia hypericoides* and *Stirlingia latifolia*).

Silvicultural studies of Podger, Kimber and van Noort

The opposite end of the moisture-availability scale was investigated by Podger (1968) whilst seeking for possible causes of the jarrah dieback disease. In seedling pot trials he found that the tolerance of south-western eucalypts to water-logging increased in the sequence *Eucalyptus marginata*—*Eucalyptus megacarpa*—*Eucalyptus patens*—*Eucalyptus accedens*—*Eucalyptus wandoo*—*Eucalyptus calophylla*—*Eucalyptus rudis*.

A recent study by Kimber (1974) showed how a tree species with virtually non-seasonal loss of water can exist under a strongly seasonal climate. Kimber showed that jarrah (*Eucalyptus marginata*) growing on a deep lateritic soil has two root systems—a dense lateral and feeder root system in the topsoil and a deep feeder root system near the ground water table, often 16 m below the soil surface. The two systems are connected by vertically descending, unbranched sinker roots. It is the deep feeder root system tapping ground water that enables jarrah to transpire throughout the hot, dry summer without drought death. Kimber did not observe any sinker roots in marri. There was, however, a tendency towards the development of a single large taproot.

Earlier work by van Noort (1960) demonstrated how the jarrah seedlings can persist until their root system is sufficiently deep to tap ground water. The jarrah seedling can persist in semi-dormant conditions under the mature canopy for as long as 20 years, during which time it is building up reserves

in its lignotuber and extending its root system. Development of a vigorous dynamic shoot only occurs when the overstorey is reduced by natural deaths or logging. The initial establishment of the seedling is favoured by baring of the soil by fires. Once established, the seedling can survive fires satisfactorily by virtue of the lignotuber, which serves as a source of new growing points.

The nutritional requirements of jarrah have been under investigation on several occasions. It is, for instance, possible to bypass the lignotuberous semi-dormancy by heavy fertilization of planted seedlings kept free of competition. Heavy nitrogen and phosphate fertilization of young jarrah stands results in a spectacular increase in density of foliage and in diameter increment. Some of the associated undergrowth species, in particular *Pteridium esculentum*, increase their relative cover; others, such as *Lasiopetalum floribundum*, decrease (Kimber, 1976).

Studies of the effect of fire on vegetation

The influence of fire on Australian vegetation has been discussed by Beadle (1940) and Mount (1964). Their studies referred, on the whole, to a moister and less seasonal climate than that of the survey area, but many of their conclusions are still relevant. Gardner (1957), in dealing primarily with the vegetation of south-western Australia, concluded that fires have been influencing local vegetation for a very long time and that it is in fact pyrophilous. This is reflected in underground woody stocks, in the structure of fruits and in the mode of germination of the seeds. The response of local flora to recurrent fires or to their absence indicates that the latter may have an adverse effect in that it leads to the locking up of a nutrient supply in woody debris, which in the local dry climate does not decompose sufficiently rapidly. Specht *et al* (1958) stressed the resistance of the vegetation on infertile soils in the mediterranean region of southern Australia to frequent firing and its capacity to regenerate readily from underground rootstocks, epicormic buds or seed.

The part played by fire in the jarrah forest has been discussed by Wallace (1966), who postulated that the fires prior to European settlement were relatively mild, but covered large areas each summer. By contrast, the post-settlement fires, which consumed logging debris, tended to be more intense. The more recent scheme of rotational prescribed burning tends to restore the former situation.

Peet (1971) studied the impact of fires on the undergrowth of the jarrah forest at Dwellingup. He concluded that mild fires encourage a more varied ground flora, whereas hot, wild fires decrease the variety, and increase the proportion of three leguminous fire-weeds, *Bossiaea aquifolium*, *Acacia strigosa* and *Acacia pulchella*. However, there was no evidence that a single wildfire eliminates any species, nor do the fire-weeds disappear entirely under a prescribed burning regime.

SECTION III

CHOICE OF STRATEGY

There are certain basic assumptions about site classification which Jenik (1956) describes as axioms. The first is the axiom of equivalence, which states that the aim of site classification is the definition of areas with the same or at least similar productive potential. The second axiom is that the vegetation and the environment form an integrated system. The third axiom states that the dominants of the forest phytocencse are the trees.

In practice, the choice of strategy for site classification of forests is dependent on many factors, which between them underly the result of the final analysis. One of the strongest reasons for adopting a given method, though not necessarily the most logical, is its past success. The successful methods of site classification fall into four main categories, which are discussed below.

Use of a productivity index

The simplest of these is the mapping of the parameter which is considered most relevant to the object of management, such as timber production. Because volume increment is chronically difficult and slow to measure, some parameter which reflects productivity and yet can be measured rapidly is normally substituted. This parameter is usually the height of the dominants, either standardised by means of height curves to represent height at a standard age, or inferred from early growth by means of height intercept. Both approaches have been criticised. Curtis (1964) questioned the validity of the assumption that site quality is independent of age and that there is a constant proportional relationship between height curves for all sites and stand conditions. Wilde (1964) questioned whether early potential as determined by height intercept is the same as late site potential. Zahner (1962) and Mader (1963) maintained that the only accurate way of assessing productivity was by periodic measurements of volume increment. Nevertheless the method has been successfully applied both overseas and locally (Havel, 1968). Its chief limitation is that it only identifies productivity and gives little or no indication of the factors underlying productivity and how these could be used in silvicultural diagnosis and prescription. Furthermore, it only refers to the existing stands, and conveys no information on the likely performance of another species on the same site. Within the survey area, such an assessment has already been carried out by means of aerial-photo interpretation (API) using crown density, composition and stand height as parameters determining productivity of the native species (McNamara, 1959). The resulting maps are used as the basis for stratification of sample plots which cover one per cent of the total area of the forest. The individual plots are rectangular (400 x 20 m, 0.8 ha in size) and are used to obtain an estimate of marketable volume. In addition, there are a smaller number of permanent plots which are remeasured at five-yearly intervals. In view of the slow growth of native species and the periodic removal of a portion of the bark by fire, this estimate of volume increment provides an excellent check. Similar methods are used in the assessment of plantations of exotic pine species.

Use of combined vegetational and environmental features

Two alternative approaches to predict site quality involve the use of native vegetation or the direct measurement of environmental factors. The two approaches are not necessarily mutually exclusive. Hills and Pierpoint

(1960) developed an integrated approach incorporating the assessment of both physiographic and biotic features, which resulted in the definition of 'total type'. A 'total type' was defined as a particular forest type growing on a particular physiographic site type. A similar combination of environmental and biotic-factors was also implicit in the work of Pogrebnjak (1955) and Whittaker (1956). The former used an edaphic net, which was a combination of edaphic factors and associated vegetation types. The techniques of relating vegetation to environment were greatly elaborated by Loucks (1962), Waring and Major (1964), Bakuzis (1969) and Pluth and Arneman (1965). All these implied a better knowledge of the effects of environment than is available locally. The concept was taken further in the biogeocoenose concepts of Sukachev (1954), where not only the environmental factors of the site and the biological communities associated with them were considered as a single complex, but also their mutual interactions. The same reasoning lay behind the ecosystem theory pioneered by Tansley (1920). Integration of environmental and biotic factors is no doubt desirable for a proper understanding of the forest complex. However, mapping of all relevant (Sukachev's) parameters is out of the question.

Consideration of both environmental and biotic factors from the very beginning of classification, as by Walker and Wehrhahn (1971) and Norris and Barkham (1970), has further limitations. Because the two factors are considered concurrently, one cannot be used as a check on conclusions based on a study of the other. Whereas a purely vegetational classification can be compared with environmental data to test whether the hypotheses put forward regarding the influence of environment on vegetation are valid, this is no longer possible if environmental factors have been used in the construction of the classification. It is also likely that where there is any scope for subjectivity, the implicit assumptions regarding the effect of environment on vegetation will influence the conclusions. A further point of local importance is that it is easier to procure vegetational data than environmental data, which is often based on long-term records (climate) or on laboratory investigation (soils). Finally, the biological significance of physical factors is rarely known (Webb, 1969). It is therefore considered preferable to bring environment and vegetation together as a result of the investigations, rather than to use their relationship as a starting point.

Use of environmental features only

If it is decided to carry out the initial classification on either an environmental or vegetational basis, separately, rather than in combination, there still remains the choice of which one of the two methods is to serve as the basis of classification. This was the essential difference between the approaches of Coile (1952) and Cajander (1926), both of which have had many followers. It was pointed out by Havel (1968) and Jones (1969) that the past success of these diametrically-opposed systems depended largely on the characteristics of the regions in which they were applied. Cajander's use of vegetation as an integrator and indicator of environmental conditions has been most successful in regions with relatively simple and undisturbed vegetation, limiting climatic or edaphic conditions and lack of detailed data on environment, such as northern Europe, northern Asia and Canada (Daubenmire, 1961). Coile's approach has been successfully applied in regions with a disturbed, complex vegetation, favourable environmental conditions and ready availability

of detailed data on environment, such as the eastern United States. Further work by Coile and Schumacher (1953), Doolittle (1957), Jackson (1962, 1965) and Pegg (1967) largely relied on the use of multiple regressions, but Czarnowski (1964) and Idso (1968) recommended the construction of empirical models in which productivity is related to environmental factors having known relevance to plant growth. Czarnowski, Humphreys and Gentle (1967) actually developed a complex model for *Pinus radiata* plantations in New South Wales, which incorporates such edaphic factors as mean diameter of soil particles, ratio of gravel to total volume of soil and effective value of soil phosphorus, calcium and magnesium. Denmead (1968) related the photosynthesis and hence productivity of *Pinus radiata* to meteorological conditions in a model of comparable complexity. Both studies were desirable attempts, but their application to the current survey is precluded by the lack of data.

This limitation was recognised by Nix (1968), who developed a model for the prediction from basic environmental data of agricultural crop yield. Although considerable edaphic and topographic data are available for each of the plots on which the survey is based, no such information exists for the bulk of the area to be surveyed. Thus even if a valid relationship between productivity and environment could be developed by means of either multiple regression analysis or empirical modelling, it would still be impossible to apply it on a broad scale without a prohibitive amount of laboratory work and detailed measurement.

Nevertheless the environmental approach has been the basis of delineation of plantation areas within the region. The Departmental policy, as stated in the Western Australian Forests Department Bulletin 58 (1964), is that *Pinus radiata* plantations should be restricted to red and brown soils derived from basic igneous or metamorphic rocks. A phosphate level of above 250 p.p.m. P_2O_5 is also a criterion. Although no limiting specifications exist for physical features, plantations are normally restricted to areas with an annual rainfall in excess of 750 mm and adequate depth of soil, which is usually related to steepness of slope. Apart from initial samples, assessment is based on soil colour. There is no policy for soils failing to meet the phosphate specifications, and these are normally avoided. Excessively shallow but fertile soils have often been planted in the past with concomitant drought damage.

Use of vegetational features only

The acceptance of vegetation as the basis of classification for this survey is thus favoured by: (i) the successful application of this method on the nearby coastal plain (Havel, 1968), (ii) the lack of soil maps and (iii) the need to consider the vegetation itself as a factor influencing land use. Nevertheless there are several significant aspects in which the survey area differs from the coastal plain. It is far more complex in its climate, geology and topography, and so vegetation could be expected to be correspondingly diverse. This would be also true of any survey based on soils, which, because of their great depth and stoniness, are more difficult to sample and to describe than vegetation. A serious drawback to vegetation mapping could be the disturbance of native vegetation by a century of logging. The logging has, however, been mostly selective, and, apart from the greater development of understorey trees such as *Banksia grandis* and *Casuarina fraseriana*, the resulting disturbance is not very obvious. Disturbance due to fire also adds quantitative

rather than qualitative changes. Relevant to both is the relative paucity of seral species in the area. Local disturbance by disease is the most serious obstacle.

Choice of appropriate method of describing vegetation

The next decision to be made concerns the selection of the appropriate method for classification of vegetation. A review of the literature on this topic is entirely beyond the scope of this Bulletin, and in any case is quite unnecessary. An excellent review by Whittaker (1962) already exists. As regards coverage, it is only deficient with respect to Russian literature in this field, a deficiency which is made up for by a detailed though totally uncritical review of Russian forest typology by Svoboda (1949). Whittaker's review will thus be taken as a starting point, except where the special relevance of an earlier paper to forest site classification justifies its detailed reconsideration.

Whittaker's review emphasizes the early development of separate traditions, differing in their views on both the theory and practice of classification of natural communities. This is more than just history, for the various sources of argument are relevant in any present-day selection of methods. So far, the term "classification" has been used rather loosely to describe any effort to give a condensed systematized account of the vegetation of a given area. One of the basic arguments has been whether or not it is in fact possible to classify vegetation in the narrow sense of dividing it into more or less homogeneous classes which differ sufficiently from each other to be considered distinct. This cannot be separated from the question of level of classification, in that homogeneity can be expected to decrease as the size of the area to be classified increases. Closely related to the question of size is the question of what parameter is to be used as the basis of classification. If the consideration is restricted to vegetation alone, a decision must be made as to what aspect of vegetation is to be used—its floristic composition, its structure or its morphology. If the answer is composition, should it be measured qualitatively (by the presence or absence of the species) or quantitatively (by the proportion of the total area which they cover) or by some derived parameter (such as their abundance or constancy)? Further, what stratum of vegetation is to be used?

There is little point in detailing Whittaker's "ecology of ecological traditions", except in so far as a knowledge of the physical and intellectual environment which led to the development of a particular approach may help in selecting an approach which is best suited to local conditions.

Briefly, the large contiguous area of forest dominated by one or two tree species, containing a varied understorey vegetation, can be expected to fit the techniques of Cajander (1926) and Ilvessalo (1929) better than those of Braun-Blanquet (1932). The applicability of the former is reinforced by the variation in understorey appearing to be continuous rather than discreet, and its relatively undisturbed state. The broad-scale approach of the North American school (Weaver and Clements, 1938), with its accent on climate, physiognomy and dynamics, has little application in this relatively small-scale study of a near-stable forest formation. However, it was well suited for the earlier work of Speck (1958), which dealt with a much larger region in less detail and which spanned a much wider climatic and physiognomic range,

from tall forest formations in a high-rainfall zone to shrubland formation in a low-rainfall zone. Specks' study provides a useful framework for the present study.

The comparison of the newer American tradition typified by Curtis and McIntosh (1951), by Curtis (1959) and by Whittaker (1967), the essence of which is the view that vegetation is a virtually indivisible continuum, and the Southern European tradition (Braun-Blanquet, 1932), with its accent on clearly defined associations arranged into hierarchical classification, raises yet another question that needs consideration.

The "continuum theory" has been capably reviewed by Goodall (1954b, 1963), Whittaker (1962) and Langford and Buell (1969). The conclusion of the latter, that extreme views on this matter are out of place and that advance assumptions are best avoided, is accepted here. Locally the question has in fact already been answered by the work of Williams (1932), who was able to detect some discontinuities and loose associations in the vegetation of a restricted part of the survey area. However, the soil surveyors of the Forests Department searched for but never found any clearly defined, easily recognisable types within the jarrah forest. The truth obviously lies somewhere between the two extreme conclusions.

Practical implication of the choice of methods

Although the literature on the merits of the various methods of site and vegetation classification is voluminous, relatively little attention has been paid to their implication on subsequent use. If it is accepted that vegetation is continuous, and therefore cannot be classified, then the only alternative is ordination, either directly on environmental ordinates or on ordinates derived from an analysis of the vegetation. The advantage claimed for ordination is that it provides an integrated picture of the vegetation as a whole, rather than forcing upon it a formal hierarchical classification. However, it is not without disadvantages. As there are no discrete categories, new observations cannot be allocated to an association or a type, but can only be placed within the co-ordinate framework. This is not always easy, especially if the framework has more than two dimensions. By contrast, allocation of new observations to a hierarchical classification is rapid, even if not always correct. The extension of a hierarchical classification to newly surveyed areas is thus a very much simpler task than that of an ordination system. Although the claim that vegetation classes are only the construction of human intellect is probably correct, the fact remains that a class with a suitable name affixed is easier to describe, grasp and manipulate than a point or a cluster of points in a multi-dimensional co-ordinate framework. Finally, a vegetation class can be associated on a map with an area which it occupies, or on which it is dominant over other classes. By contrast, vegetation defined solely by ordination can only be represented by one or more series of isolines, depending on the number of dimensions involved. Although a precedent for this procedure exists in topographical and rainfall maps, these are based on more obvious and concrete parameters than the abstract, derived vegetational indices. The drawbacks of ordination described above can be reduced by subdividing the framework into segments (Pogrebnjak, 1955; Greig-Smith, 1964) which resemble classes, in that they can also be named and mapped as discrete areas. They differ from classes in that no precise definition is assumed

and in that the inter-connection between them would normally be determined by environmental control rather than by any desire for simple and easy classification. The problem of allocating new observations remains.

Final Selection

The reasoning underlying the selection of a method can thus be summed up as follows:

- (1) The need to consider several forms of land use precludes any classification based on a single parameter.
- (2) The initial use of a combined vegetation-site approach is not desirable, as no check would then be available on assumptions regarding their inter-relationship. In any case, environmental data is more difficult to obtain and at this stage is difficult to interpret biologically.
- (3) Any classification primarily based on environment would be handicapped by the lack of environmental data (e.g. detailed soil maps).
- (4) Vegetation thus offers the best basis for classification, both as an integrator and indicator of environmental factors, and as a factor in land use in its own right. This is particularly so because the vegetation is relatively undisturbed, and the relationship between soils and vegetation has already been demonstrated in a small portion of the area.
- (5) The present knowledge of vegetation indicates that it is neither one indivisible continuum, nor a mosaic of discrete units. The option should thus be left open for both ordination and hierarchical classification.
- (6) Inasmuch as past studies using physiognomic and structural approaches tended to view the vegetation of the area as one or at the most two formations, overwhelmingly dominated by one tree species, this approach cannot be used for more detailed classification. The floristic composition of the understorey thus appears to be the best basis of classification.
- (7) Because the only successful attempt to relate vegetation to soil was the detailed quantitative approach of Williams (1932), this will be followed in the current study.

SECTION IV

USE OF COMPUTERS IN ANALYSIS OF VEGETATION DATA

Computer Philosophy

The work of Williams (1932) covered two small areas, and so the subjective analysis of the data proved quite feasible, particularly as transitional plots were omitted from the final summation. A spectacular development of quantitative ecological analysis, however, has been made possible by the use of electronic computers over the past two decades. The task of reviewing all the recently developed methods is almost as formidable as the review of classification of natural communities undertaken by Whittaker (1962). The essential difference is that the problem of confused nomenclature has been replaced by the problem of involved, frequently disputed mathematical theory.

The use of computers makes it possible to deal with large quantities of data, and it provides the means of simplifying these data by detecting discontinuity and tendency to grouping. This tendency can be enhanced by maximizing discontinuities between groups and homogeneity within groups. Classification techniques are also a means of generating hypotheses about reasons for the discontinuity, which in this particular context would be the underlying environmental factors. They remove certain of the limitations of the human mind, such as the inability to store and manipulate a large quantity of data.

On the other hand, there are limitations associated with the use of computers (Williams and Dale 1965), which are sometimes not recognised and lead to exaggerated claims about the capacity of computers. It has frequently been claimed that numerical methods are objective and absolute. Williams (1968) points out that what objectivity there is in the use of computers arises out of their inability to store experiences and to use them in forming judgements. Though subjectivity in the processing of data is removed, it still enters into selection of the data to be analysed and of methods to be employed in its analysis (Ivimey-Cook, 1969). Any claims about the absolute nature of the classifications derived by computers are readily demolished by the fact that numerous answers can be extracted from the same set of data by using different methods (Sparek-Jones, 1970). Because of the above limitations, there is also no justification for claims or fears that numerical methods will replace human judgements.

Numerical classification employing computers does not eliminate the possibility of misclassification. In many cases the computer programs themselves have inherent weaknesses. The usual process of maximising discontinuities between groups is a process of distortion, which can lead to over emphasis of the discontinuities and thus to misclassification (Sneath, 1969). The objective rigidity of computer programs does not provide for eliminating or ignoring purely-chance occurrences of species on sites from which they are normally absent.

Although numerical classification is often an efficient method of generating hypotheses regarding the causes of discontinuities in plant distribution, it cannot generally be used to test hypotheses. There is in fact no null hypothesis to test (Williams, 1968). Once the possibilities and limitations of computers and numerical methods are realized, it is possible to specify the desirable properties that any method selected should have.

As the question of "absolutes" no longer arises, the key quality of the approach chosen should be its profitability or utility, that is whether its product fulfils the purpose of the study. It is also desirable that it should be economic. Most programs are economic short cuts which fall short of the ideal solution, namely the comparison of every individual with every other individual on the basis of all their observable characters. In this particular study, the purpose is twofold—to define vegetation types which can be assumed to be biologically equivalent irrespective of where they occur within the survey area, and to elucidate the reason for their occurrence in terms of controlling environmental factors. This points to two further characteristics considered by Williams to be desirable in any classification: stability and genetic basis. By stability is meant the capacity to absorb the addition of new information or the alteration of original information without major disturbance. By genetic basis is meant the ability to reflect the underlying generative system, such as the climate or the soil.

Similarly, if it is accepted that no classification can be completely objective, it is possible to increase the efficiency of the approach by judicious selection of parameters. Williams advocated the use of the simplest possible characters that lend themselves to ready definition and observation. In his view, any classification using characters that are difficult to observe was inferior or sub-optimal when compared to a classification based on readily observable characters. Nor did he see any objection to an efficient classification based on a small number of characters which are well chosen, even if chosen subjectively. Both Williams (1966) and Gibbons *et al* (1968) advocated interactions between men and computers to increase the efficiency of both.

Comparison of available computer programs

An important economic factor in the selection of programs is their availability. Locally-available programs can often be run more cheaply, especially if the user is part of the organization owning the computer. Ready accessibility maximizes opportunity for interaction, and avoids difficulties in specifying what is to be done.

There are numerous criteria by which computer programs used for the synecological study of vegetation can be compared (Williams and Lance, 1965, 1968). Perhaps the greatest polarity arises out of the acceptance or rejection of the continuum concept.

Ordination using quantitative data.

The protagonists of the former (Goodall, 1954a; Boyce, 1969; Whittaker, 1951) advocated the use of some forms of factor analysis of quantitative data. The commonest of these is principal component analysis, the essence of which is the arrangement of vegetation in relation to axes (components). These axes may or may not lend themselves to hypothetical interpretation in terms of environmental factors. To facilitate the interpretation, provision usually exists (e.g. Varimax of Cooley and Lohnes, 1962) for rotation of the axes, so as to maximise the coincidence between the position of the axes and the distribution of species within the component space. In earlier publications (Goodall, 1954a; Havel, 1968), the term 'factor analysis' has been used where 'principal component analysis' would have been more appropriate and more accurate.

The usual argument advanced in favour of this approach is that it is less subject to misclassification, in that all attributes (species) are used in deriving the position of each individual (plot) within the co-ordinate framework. The chief criticism of the method is that it is cumbersome, in terms of both collection and analysis of data, which are normally quantitative in nature. It has also been claimed by Orloci (1969) that it is not strictly applicable to populations which are not normally distributed. Qualitative data have occasionally been used, but the only values that it can take are either scaled values or else 0 for absence and 1 for presence.

A program (CFAC V8) for principal component analysis is available at the University of Western Australia. Although there are other forms of factor analysis capable of analysing quantitative data, such as the canonical factor analysis, they were not available locally at the time.

Classification using qualitative data.

Classification (in the strict sense), that is grouping of the population into discrete classes which differ sufficiently from each other, typifies the bulk of the remaining methods. There are several criteria on which these could be further subdivided. One such criterion is the nature of the data. Omitting purely quantitative data, which best lend themselves to principal component analysis, the chief choice is between purely qualitative data and mixed data, which can comprise quantitative, qualitative and multistate (e.g. ranked) data. The latter are more applicable to floristic taxonomy; as no mixed data were derived from the present survey, the case will not be considered any further.

For the purely qualitative data, there still remain several choices. It is possible to subdivide the total population progressively into smaller and more homogeneous classes so as to arrive at a classification which is divisive. Another approach is to build up the groups by fusion of individuals comprising the population into progressively larger but more heterogeneous groups, thus obtaining an agglomerative classification. Another difference arises from the employment of one single character (monothetic) or of a combination of several characters (polythetic). Finally it is possible to distinguish between a multiple level structure (hierarchical) and a single level structure of classification (reticulate).

It is claimed that hierarchical methods have the advantage that at each stage of subdivision or synthesis they seek the most efficient way of carrying out this task. This often results in a certain loss of homogeneity of the derived groups.

Of all the possible combinations of these (not all of which are feasible computationally), only two combinations were used in the present survey: the agglomerative polythetic hierarchical classification (Canberra program CLASS) and the divisive monothetic hierarchical classification (Canberra programs DIVINF and DIVINFRE). The existing reticulate or clustering methods were considered by Lance and Williams (1967a) to be open to serious objections.

The program DIVINF was developed by Lance and Williams (1968) as a modification of an earlier monothetic divisive program ASSO (Williams and Lambert, 1959, 1960) from which it differs by employing an information statistic instead of a derivative of Chi-square. Its advantages in comparison to ASSO are claimed to be its simple and rigorous stopping rules, absence of reversals in hierarchical levels and greater computational speed (Lambert and

Williams, 1966). It retains two of the weaknesses of ASSO. One of these is the formation of a heterogeneous residual group, the members of which only share the absence of all the species used as criteria for division. The other is the danger of misclassification due to an aberrant occurrence of one of the species (Sneath, 1969).

The program DIVINFRE is a modification of DIVINF designed to overcome these defects, though at the cost of much heavier computational load and reduction in the number of plots and/or species that can be handled. Greater group homogeneity is achieved by comparing each plot with the groups of plots created by the first run of the program, and allocating it to a group which it resembles most closely, which in most cases is the group to which it originally belonged. However, in this process some groups, especially the heterogeneous residual groups mentioned above, disappear. Plots which do not resemble any of the revised groups (the number of which is limited by prior definition) are placed in a renegade group. The re-allocation process can be repeated several times. Possibly the most serious drawback of the program is the loss of simplicity and speed in allocating new observations to the existing classification.

The program CLASS was also developed by Lance and Williams (1967b). Its aim is to fuse individuals (plots) into clearly defined groups by agglomeration based on all characters. Provision exists for a choice between several similarity-measures and sorting-strategies, of which squared Euclidean distance and flexible strategy were chosen. There is also provision for varying the clustering tendency. An intermediate level of clustering tendency, found applicable to most data, was chosen. The obvious advantage of the polythetic approach is that divisions have a much broader basis than in the case of the monothetic approach, and misclassifications described in the preceding paragraph are much less likely to occur. The main disadvantage is that the simplicity and speed of a monothetic divisive approach is lost, and allocation of new plots to an existing classification can be cumbersome. The capacity of CLASS in terms of plots and species tends to be less than that of DIVINFRE.

Normal and inverse analysis.

For simplicity, the discussion so far has been limited to ordination or classification of individuals, which in the case of ecological data are plots (sites), on the basis of the species occurring on them. However, most of the methods described can also be used for ordinating or classifying species (attributes) in terms of the plots on which they occur (Williams and Lambert, 1961a). In this case, the classification of individuals is described as normal, the classification of attributes as inverse.

Williams and Lambert (1961b) have combined normal and inverse association analysis into nodal analysis, which aims at determining how the various species groups are linked to plot groups. The first stage of the method is a two-way table in which the species groups are arranged vertically and the plot groups horizontally. By a further stage of refinement, each of the species-plot combinations, named nodum, is rearranged in such a way that it is defined by a plot containing the greatest number of the species within the species groups and by a species present in the greatest number of plots within the plot group. In this respect, nodal analysis could be of considerable use in defining site-vegetation types. Although it is not directly related to the nodum concept of Poore (1962), there is some similarity of purpose.

SECTION V

FIELD WORK

Establishment of plots

The earliest field work consisted of a broad-scale reconnaissance of vegetation and soils in the survey area to ascertain their range of variation. This was carried out intermittently from September to November 1967. The main field work commenced in late November 1967. Because of the practical bias of the study, sampling was linked to areas capable of yielding information about the management of the forest. They were:

- (1) Pilot plots of exotic species.
- (2) Growth plots of native species.
- (3) Restricted occurrence of virgin forest.

The reasoning behind this selection was very simple. The area contained 732 600 ha of State Forest, most of it only selectively logged, so that the understorey vegetation was not greatly disturbed. Most of the area was thus capable of yielding information on vegetation, but only a very small proportion of it, chiefly in the form of isolated pilot and growth plots, could yield management information. Random sampling on a co-ordinate system would not only have been difficult from the point of view of location and access, but would have missed the bulk, if not all, of the management plots. It was obvious from discussion with local administrative officers that in the selection of the plots they aimed at maximum coverage of site variation, which was also desirable. The sampling could not be called truly random, but neither was there any personal bias (by the writer) imposed upon it.

The linkage between the management information and site-vegetation information was achieved as follows:

- (1) In the case of pilot plots of exotics, which normally have a highly disturbed ground flora, a measurement plot was established in a portion of the pilot plot which had received standard treatment and was sufficiently far inside to be free of edge effects. Residual understorey vegetation was noted, a soil pit was dug and soil characteristics recorded. A search was then made in the neighbouring forest until a site with corresponding topographic and edaphic features was found. A comparison of the ground flora of this matching plot with the residual ground flora of the pilot plot was made, making allowance for seral and weed species. If the comparison with these characteristics indicated a high degree of similarity, the vegetation plot proper was then established. In view of the small size of most pilot plots, it was not usually necessary to go far to obtain a satisfactory match. A soil pit was dug, the soil profile features were recorded and samples were collected from each horizon for laboratory analysis. The danger of inadequate sampling from a single pit was recognized, but the prevalent occurrence of lateritic gravel and rock outcrops made digging so laborious that a higher level of sampling was out of the question. In addition, the topographic features of the plot, such as position, exposure, maximum slope and rock outcrops, were also recorded.
- (2) In the case of growth plots of native species, the vegetation plot was simply superimposed on the growth plot.

- (3) In the case of virgin areas, the plot was subjectively chosen so as to represent the area in terms of density of the overstorey. Where the virgin area was more extensive and variable, several plots were chosen to cover the full range of variation.

Recording of measurements and observations

In all cases, the dimensions of the vegetation plots were 40 m x 40 m (0.16 ha), established accurately by compass and chain with diagonals as check. Within the plot, a total enumeration of all tree species was carried out. Those trees greater than 7.5 cm diameter at breast height (d.b.h.) were measured, but all small trees and saplings below this diameter were merely recorded by numbers. Where any trees had been removed sufficiently recently for the re-occupation of the space by the ingrowth of saplings and suckers to be unlikely, diameters of the removed trees were also measured and included. This was assessed by the condition of the stump and closure of the canopy. In addition, the maximum height, co-dominant height and average length of bole were measured for the stand as a whole.

Within the larger plot, sixteen, one-square-metre quadrats were established on a 5 m x 5 m grid, and the cover contribution of each perennial shrub and herb species was assessed. The restriction to perennials was necessitated by the fact that by mid-summer all annuals had died and shrivelled up, making identification difficult if not impossible. It will be recalled from earlier accounts (Diels, 1906) that in most of the area annuals are a very minor proportion of the vegetation, particularly in terms of cover. Although the cover on individual sub-plots was expressed as a percentage of the area of the sub-plot, the summation of the percentage over sixteen quadrats of equal size provided a potential range from 0 to 1 600 and could thus be virtually considered a continuous variable. In quadrats with both tall shrubs and low shrubs or herbs, the sum of cover percentages for all species frequently exceeded 100.

The establishment and assessment took place in three stages:

- (a) 249 plots by March 1968;
- (b) a further 46 plots by May 1969;
- (c) a final 25 plots by January 1971, bringing the total to 320 plots.

This represents a total enumeration of all trees on 51.8 ha and cover assessment of all species on 5 120 one-metre square quadrats. As the average occurrence of shrub and perennial species per plot was approximately 30, the final data pool comprised approximately 9 600 individual records of shrubs and perennial herbs. To this could be added approximately 1 500 individual records of trees. When the census of species was carried out on the first 295 plots, 364 shrubs and perennial herb species and 18 tree species had been recorded within the plots out of approximately 600 species collected during the reconnaissance and the survey. It is not claimed that this mass of data gave a total coverage of the area; however, it appears at least to offer a solid basis for the analysis of vegetation. The distribution of the plots within the survey area is given in Figure 5.

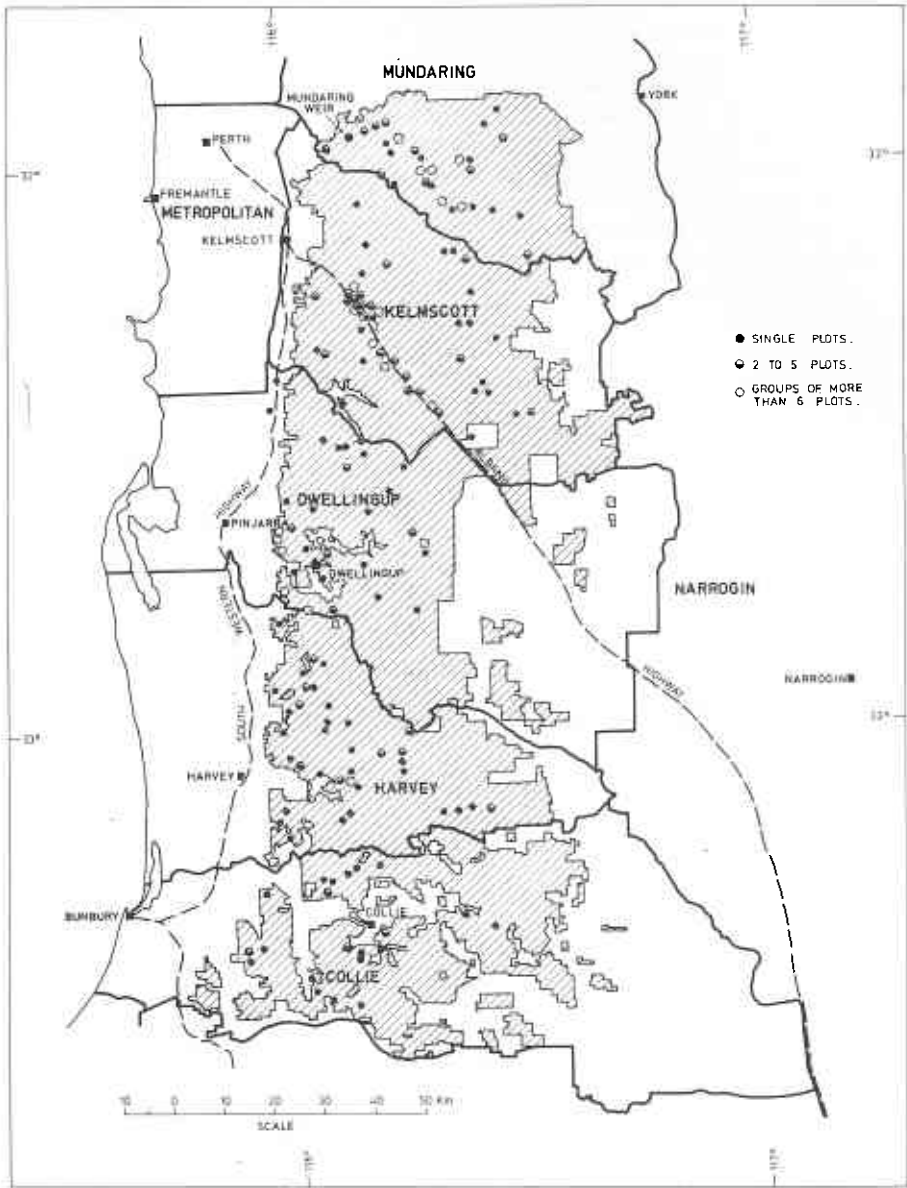


Figure 5
 Distribution of ecological sample plots within the northern jarrah region. Groups of plots generally form a topographical sequence.

In addition to detailed laboratory analyses of topsoil, field soil moisture sampling of 171 northern plots was carried out in the spring of 1970. On this occasion, the aim was to determine depth to ground water table (G.W.T.), depth to the wettest horizon (where G.W.T. could not be reached) and soil moisture at 30 cm intervals down to G.W.T. or to the limit of penetrability. Although the winter of 1970 was not particularly wet, the rains continued throughout the early part of the spring when moisture sampling was in process, and so the observations represented the end of the winter moisture regime. In addition, determination of soil moisture characteristics was carried out by the method developed by Fawcett and Collis-George (1967), which gave a laboratory approximation of field capacity, wilting point and moisture-holding capacity of the soil.

The field forms were designed on the basis of previous experience. The basic principle was that no data processing should take place in the field, assessors merely recording all measurements. In the case of tree data, the form provided for the recording of the plot number, species code number, maximum height, co-dominant height, average length of bole, number of saplings under 7.5 cm d.b.h. and girth at breast height (g.b.h.) of individual large trees with a precision of approximately 1 cm in diameter. The number of trees that could be recorded for any one species on one plot was quite flexible.

In the case of shrub and herb data, the form provided for the name of the species, plot number, species code number and individual records of cover on each of the sixteen quadrats. In practice, only the name of the species, or reference to its botanical collection (if it could not be immediately identified) was recorded. Coding was carried out in the office when all provisional identifications were completed and the full species list was available.

SECTION VI PROCESSING OF DATA

The magnitude of the data pool necessitated the development of auxiliary minor computer programs which could bridge the gap between the field records and the very rigid input specifications of the main classification and ordination programs.

1. INITIAL PROCESSING

The processing of the raw data took place along several lines:

(1) The processing of the raw tree data essentially amounted to a conversion of the diameters of large trees and the number of saplings to basal area per species per plot, and the determination of the total basal area and maximum height of the stand for all species combined. In this form, the data were suitable for input for principal component analysis as quantitative

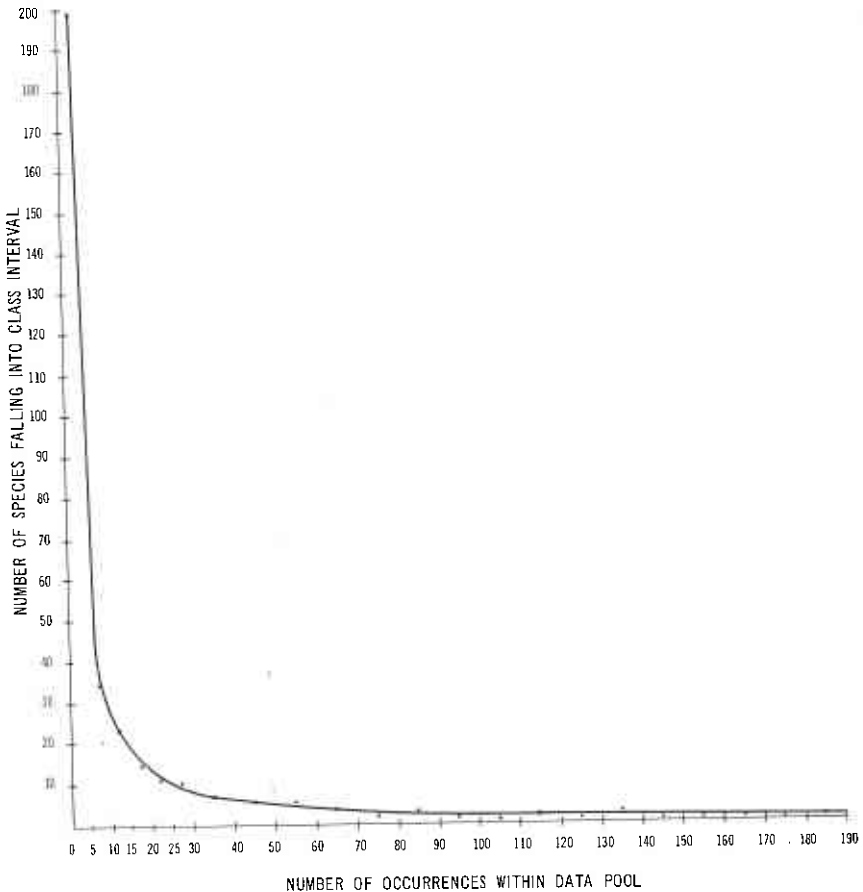


Figure 6
Distribution graph of the frequency of occurrence of potential indicator species.

floating point variables. All twenty-one tree species could be punched on a single card for each plot. The program was code-named STROP (Summary of Tree Plot data).

(2) Processing of raw shrub data for principal component analysis was even simpler, in that the summing up and averaging of individual quadrat entries was all that was necessary for a given species plot record. However, only a portion of the surveyed species could be used in any one analysis; it was necessary to build in flexibility. This was achieved by enumerating the code numbers of species which it was desired to sum up, by specifying their sequence for output, and by creating a corresponding set of arrays in the memory. As the species record was read by the computer, its code number was compared with the specified code list. Species not contained in the list were ignored. For those in the list, the summing up and averaging was carried out, and the result stored in the memory array. Upon completion of plot data, the average shrub cover was output in arrays of twenty species, preceded by plot number. Each array of twenty occupied one punch card and formed an independent unit suitable for use as a set of quantitative floating point variables. The program was code-named SPLOTS (Summary of PLOT Shrub data).

(3) From previous experience with divisive monothetic classification in general, and the program ASSO in particular, it was realised that the best result could be expected if all very rare or very common species were excluded from the input, as they tended to be separated out in the inverse analysis into meaningless, heterogeneous groups (Havel, 1968). Thus the first stage in the processing of qualitative data was an assessment of the relative abundance of the various species. This was achieved by summing up the individual counts within a computer memory array that contained every species code number.

The program was code-named NOSPOC (Number Of SPecies OCcurrences), and the results are shown in Figure 6.

(4) The conversion of the raw data to qualitative data suitable for input on the Canberra classificatory programs needed to conform to two requirements: restrictions as to what species were to be used, and the format specified.

Whilst provision existed in the Canberra programs to mask any species out of the species array, it was obviously inefficient to include those species which were unlikely to be used. An array of new code numbers, restricted to 130 species of medium frequency of occurrence, was established and matched with the corresponding species code numbers used on the field sheets. This matching and eliminating of species program was code-named CONVEG (CONversion of VEGetation data).

The net result of the processes described above led not only to simplification but also to loss of information. This was particularly so with the CONVEG program, where the quantitative assessment of cover on sixteen quadrats was collapsed into a single qualitative record of the particular species presence. The discarding in the array specification, of those species too rare, too common or too difficult to identify was also a major loss of information. However, it is doubtful if at present any computer program, except the simplest monothetic divisive one, could cope with a potential pool of 364 shrub species on 320 plots or 5 120 quadrats. It is even less likely that the full number of species could ever be used as indicators in an applied survey.

2. ANALYSIS OF DATA

First approximation on principal component analysis

Following completion of the first set of plot assessments in March 1968, it was decided to proceed with preliminary analysis to give a first approximation. This could later be improved by addition of further plots and re-analysis using the first approximation.

Initially, only the CFAC V8 program for principal component analysis (PDP6 computer) was used. Its limitations were set out in specifications—thus the number of individuals (plots) could not exceed 1 000, and the number of attributes (species) could not exceed 80. Of these, the limit on the number of attributes (species) was the only one of importance, because the number of plots at this stage (249) was well below the upper limit of 1 000.

Reduction in number of indicator species.

The reduction of the total number of species to less than one quarter was a formidable task. It was approached from the applied angle. Eight of the eighty spaces were allocated to trees. The list included all the main tree species. In the selection of the shrub species, the aim was to cover the widest possible environmental range, with species readily recognizable in the field on their vegetative characters. Thus any pairs of species whose identification depended on flower characteristics were discarded (e.g. *Daviesia polyphylla* and *Daviesia preissii*). Small, insignificant perennials, especially those with a tendency to shrivel partially in summer (e.g. some *Xanthosia* and *Gompholobium* species), were also rejected.

The analysis proceeded as far as the calculation of the correlation matrix between the 80 species, but did not proceed to the calculation of loadings on the components. Several runs were attempted, with similar results. It seemed likely that the second part of the program placed an excessive demand on the capacity of the computer, and a reduction in the size of the problem was attempted as follows.

Initial Species Grouping.

At this stage, the 80 x 80 correlation matrix offered an opportunity for the assessment of relationships between the species. Each of the species was examined for its tendency to associate with others. Some species showed little or no such tendency. Generally they were species of a relatively low frequency of occurrence and weak habitat preference, such as *Leucopogon oxycedrus*. Others were the nearest approximation in the jarrah forest to seral species, such as *Dryandra sessilis*. These were the obvious choices for rejection.

At the other end of the scale, strongly intercorrelated groups of species appeared. When these were studied in the light of field experience, it was obvious that they represented particular habitats. For instance, *Eucalyptus patens* was strongly positively correlated with *Baeckea camphorosmae*, *Hypocalymma angustifolium* and *Pteridium esculentum*, all species frequently seen on moist, loamy soils. *Sphaerolobium medium* was associated with *Daviesia pectinata*, *Isopogon dubius*, *Patersonia rudis*, *Styphelia tenuiflora*, *Synaphea petiolaris* and *Hakea cyclocarpa*, all of which were mainly found on sandy gravels in the eastern, low-rainfall zone.

Eucalyptus marginata was positively correlated with *Adenanthos barbiger*, *Bossiaea ornata*, *Macrozamia riedlei*, *Lasiopetalum floribundum*, *Leucopogon capitellatus*, *Leucopogon verticillatus*, *Hibbertia montana* and *Hovea chorizemifolia*, all of which were common on lateritic uplands in the high to medium-rainfall zone.

Adenanthos obovata was strongly correlated with *Dasyogon bromeliaefolius*, *Leptospermum ellipticum*, *Lyginia tenax*, *Patersonia occidentalis*, *Petrophile linearis*, *Hakea ceratophylla* and *Melaleuca preissiana*, all normally found on moist, leached sandy podzols. All but one member of the latter group (*Hakea*) were also found in analogous positions within the Bassendean Dune System on the coastal plain in the earlier study (Havel, 1968).

Some negative correlations were also highly informative. *Eucalyptus marginata* was negatively correlated with *Hypocalymma angustifolium*, a contrast between well-drained, infertile gravels and moist, loamy, fertile soils. At this stage it could be concluded that several groups of positively correlated species existed, and that these could be related to the more extreme habitats. It was also possible to reject several species which appeared unlikely to serve as indicators. This was particularly important because the number of species had to be reduced so that principal component analysis could be completed.

The analysis was repeated with a progressively smaller number of species until, at 55 species, the full output, comprising means, standard deviations, correlation matrix, normal component loadings and rotated component loadings, was obtained. The first four components accounted for only 25 per cent of the total variation in the vegetation data, the first twelve components for 50 per cent and the first twenty-five components for 75 per cent.

Distribution of species within component space.

The normal loadings of the 55 species on the first four components were then plotted to obtain a picture of their inter-relationships. The results are shown in Figures 7 and 8. It will be seen that they form essentially two triangles, the apices of which are formed by the groups of strongly inter-correlated species discussed earlier, that is the species of the well-drained, infertile, lateritic gravels; those of the moist, neutral, fertile loams of the lower slopes; those of the dry sandy gravels; and those of the moist, strongly-leached, acid sands. In the centre of the triangles are found the species which either occupy intermediate habitats, or whose relationship to site is not immediately obvious.

However, as the purpose of the study was to find indicators capable of defining biologically-equivalent sites, it was desirable to extend the analysis to the ordination of plots. This was accomplished by developing a minor program (FACVA) capable of combining the loadings of the species on the component axes with their cover or basal area values on individual plots to obtain scores which could be used as plot co-ordinates. The program was a local adaption of the Cooley & Lohnes (1962) program. Essentially, the plot co-ordinate (score) on any one component axis is the sum, for all species, of the products of their loadings on that component and the deviation of their cover value on that plot from their mean cover value in the study as a whole. It is thus a summation of the trends of all individual species occurring on that plot.

Testing of indicator species.

The plotting of the plot co-ordinates was at first carried out manually. An attempt was made to study the distribution of the individual species within space, in order to ascertain their suitability as indicators. It was reasoned that the best indicators would be the species with a restricted range of occurrence, and with consistent occurrence within that range. Loadings of individual species give some indication of their tendency to be associated with one or other extreme of a particular component, but provide no indication of how well-defined or precise that tendency is.

It soon became obvious that to test the suitability of the species by reference to their performance on 249 plots would be an impossible task if done manually. A program, code-named *CORD*, was therefore developed to perform the task rapidly. The inputs on the program are an array of 20 species names, a set of cards with arrays of cover values of these twenty species on individual plots, and the set of plot co-ordinates.

The set of plot co-ordinates is examined for maxima and minima on any two chosen components, thus setting the extreme negative and extreme positive limits for the component framework. The first of the components is used as the horizontal, the second as the vertical axis, and the full range on each of these is subdivided into twenty equal segments, thus giving 400 (20 x 20) cells which are best visualized as pigeon holes. Within each cell provision is made for the accumulation of twenty separate species records or sub-cells, which can be visualized as envelopes within the pigeon holes. The co-ordinates of the plots are now re-examined and used to allot a particular plot to its appropriate pigeon hole within the framework. A record is kept of the allotment, because from this stage on the cell becomes the basic unit. The number of plots falling within a particular cell, and their identity, are thus known. As the cover values on individual plots are read, they are accumulated in appropriate cells on the basis of plot number, and in appropriate sub-cells according to species, implied by its position within the array. When all plots have been dealt with, the values accumulated in the individual sub-cells are averaged. The output consists of 20 separate distribution diagrams, one for each species. Each diagram consists of four hundred cells, in which the mean cover value of the species and the number of plots contributing to the mean are given. Cells into which no plots have fallen are left blank to avoid congestion of the diagram. It is thus possible to determine rapidly from which portion of the component framework the particular species is totally absent, and at what level it occurs in the remainder, that is whether it is scattered or concentrated. As the dimension of the diagram is determined by the extreme values, removal of extreme plots enlarges the diagram covering the central group of plots. This is valuable if there is a congestion of plots near the centre. The adjustment is of course done at the cost of seeing the picture as a whole.

The use of the program is not restricted to data on which principal component analysis is based. Once the position of the plots within the component framework is established, any other quantitative data relevant to the plots can be displayed within the same framework (e.g. cover values of additional species or soil analysis data).

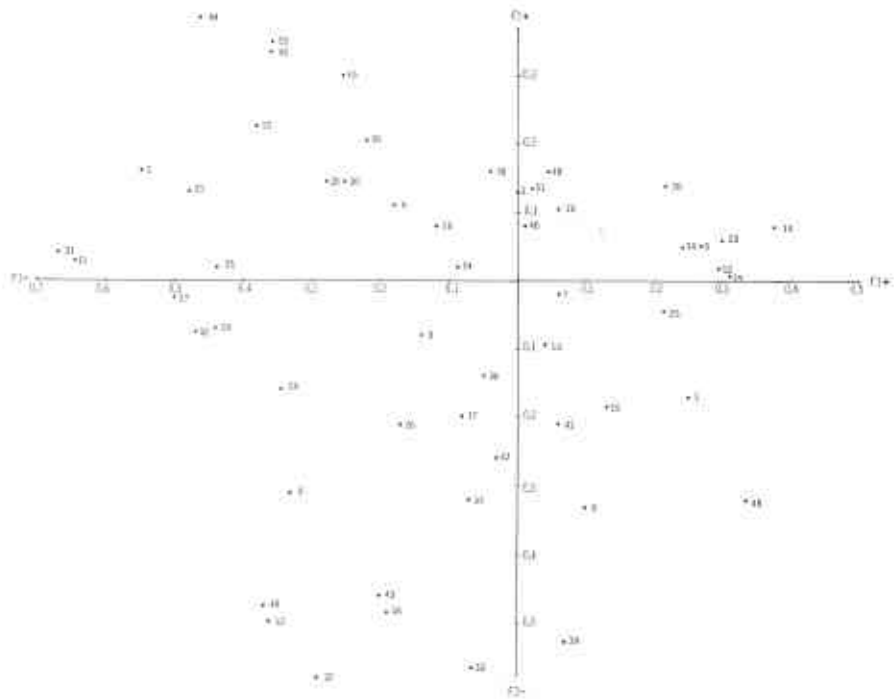


Figure 7

Distribution of indicator species within component space derived by principal component analysis—first approximation, normal loadings, 55 tree and shrub species, components 1 and 2.

- | | |
|---------------------------------------|------------------------------------|
| 1. <i>Adenanthos barbiger</i> | 29. <i>Lyginia tenax</i> |
| 2. <i>Adenanthos obovata</i> | 30. <i>Lysinema ciliatum</i> |
| 3. <i>Agonis linearifolia</i> | 31. <i>Mesomelaena tetragona</i> |
| 4. <i>Baeckea camphorosmae</i> | 32. <i>Patersonia occidentalis</i> |
| 5. <i>Bossiaea aquifolium</i> | 33. <i>Patersonia rudis</i> |
| 6. <i>Bossiaea ornata</i> | 34. <i>Phyllanthus calycinus</i> |
| 7. <i>Bossiaea pulchella</i> | 35. <i>Petrophile linearis</i> |
| 8. <i>Casuarina humilis</i> | 36. <i>Pteridium esculentum</i> |
| 9. <i>Conospermum stoechadis</i> | 37. <i>Sphaerolobium medium</i> |
| 10. <i>Dampiera alata</i> | 38. <i>Stirlingia latifolia</i> |
| 11. <i>Dasyopogon bromeliaefolius</i> | 39. <i>Styphelia tenuiflora</i> |
| 12. <i>Daviesia pectinata</i> | 40. <i>Synaphea petiolaris</i> |
| 13. <i>Daviesia longifolia</i> | 41. <i>Grevillea wilsonii</i> |
| 14. <i>Macrozamia riedlei</i> | 42. <i>Grevillea pulchella</i> |
| 15. <i>Hypocalymma angustifolia</i> | 43. <i>Hakea cyclocarpa</i> |
| 16. <i>Isopogon dubius</i> | 44. <i>Hakea ceratophylla</i> |
| 17. <i>Kingia australis</i> | 45. <i>Hakea varia</i> |
| 18. <i>Kunzea micromera</i> | 46. <i>Hakea lissocarpa</i> |
| 19. <i>Lasiopetalum floribundum</i> | 47. <i>Hakea rusciifolia</i> |
| 20. <i>Leptidosperma angustatum</i> | 48. <i>Eucalyptus marginata</i> |
| 21. <i>Leptocarpus scariosus</i> | 49. <i>Eucalyptus calophylla</i> |
| 22. <i>Leptospermum ellipticum</i> | 50. <i>Eucalyptus patens</i> |
| 23. <i>Leucopogon verticillatus</i> | 51. <i>Eucalyptus wandoo</i> |
| 24. <i>Leucopogon cordatus</i> | 52. <i>Banksia grandis</i> |
| 25. <i>Lomandra sonderii</i> | 53. <i>Melaleuca preissiana</i> |
| 26. <i>Lomandra caespitosa</i> | 54. <i>Nuytsia floribunda</i> |
| 27. <i>Loxocarya fasciculata</i> | 55. <i>Casuarina fraseriana</i> |
| 28. <i>Loxocarya cinerea</i> | |

As soon as the program was operational, testing of species commenced. In addition to the 20 tree species and 72 shrub species already cited, a further 40 shrub species were converted from raw data and tested. As four of these were duplicates of species already assessed, the total number of species tested was 128.

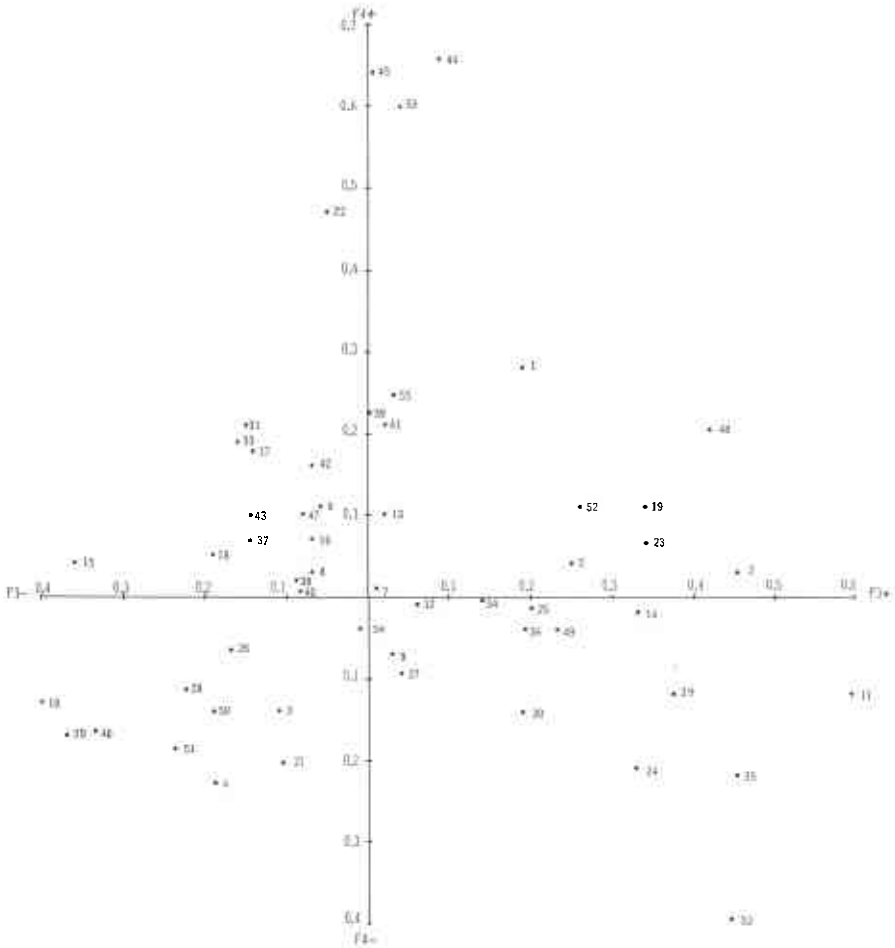


Figure 8

Distribution of indicator species within component space derived by principal component analysis—first approximation, normal loadings, 55 tree and shrub species, components 3 and 4. (Species/number sequence is the same as in Figure 7).

It was necessary to separate a group of extreme sandy plots from the remainder, as the distances between these plots and the bulk of the plots were too large, and dwarfed all comparisons. The testing of the species on the first four gave a much better appreciation of their potentialities.

Ordination based on trees only

In the earlier attempt at ordination, tree species had definite positive and negative loadings on the various components. This, combined with the fact that to foresters trees are of greater economic interest and are better known than shrubs, prompted an attempt to establish an ordination system based on trees alone.

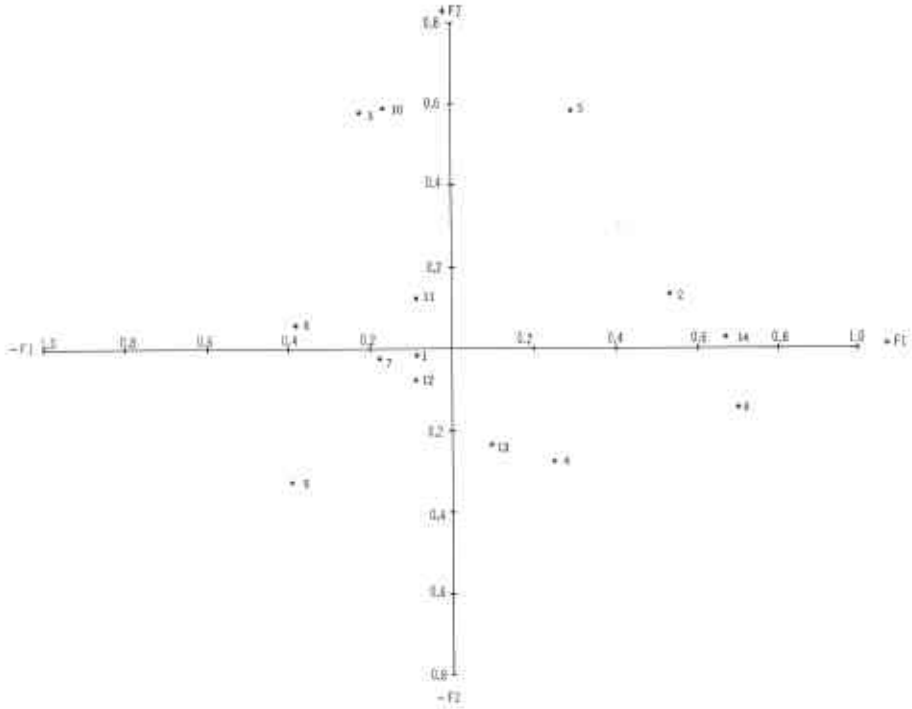


Figure 9

Distribution of tree species within component space—normal loadings, based on 14 tree species, components 1 and 2.

- | | |
|---------------------------------|-----------------------------------|
| 1. <i>Banksia attenuata</i> | 8. <i>Eucalyptus patens</i> |
| 2. <i>Banksia grandis</i> | 9. <i>Eucalyptus wandoo</i> |
| 3. <i>Banksia littoralis</i> | 10. <i>Melaleuca preissiana</i> |
| 4. <i>Casuarina fraseriana</i> | 11. <i>Melaleuca raphiophylla</i> |
| 5. <i>Eucalyptus calophylla</i> | 12. <i>Nuytsia floribunda</i> |
| 6. <i>Eucalyptus marginata</i> | 13. <i>Persoonia elliptica</i> |
| 7. <i>Eucalyptus megacarpa</i> | 14. <i>Persoonia longifolia</i> |

Of the twenty tree species allocated in the data input, only fourteen occurred sufficiently frequently within the plots to be useful in analysis. These were subjected to principal component analysis, and both normal and varimax loadings were derived. Plotting of the loadings indicated that the varimax loadings would be much easier to interpret than the normal loadings (see Figs. 9, 10). The species with the highest positive loading on the first component were *Persoonia longifolia*, *Banksia grandis*, *Eucalyptus marginata* and *Eucalyptus calophylla*. The only species with a high negative loading on the first component was *Eucalyptus wandoo*. The polarity here was essentially due to the difference between lateritic gravels in the high-rainfall zone and loams in the lower-rainfall zone. Three species had a high positive loading on the second component: *Melaleuca raphiophylla*, *Melaleuca preissiana* and *Banksia littoralis*. All are species occurring in excessively wet sites. No species had a high negative loading on the second factor. In essence, there was thus a triangle with the above three groups of species forming its apices with the rest of the tree species near the centre.

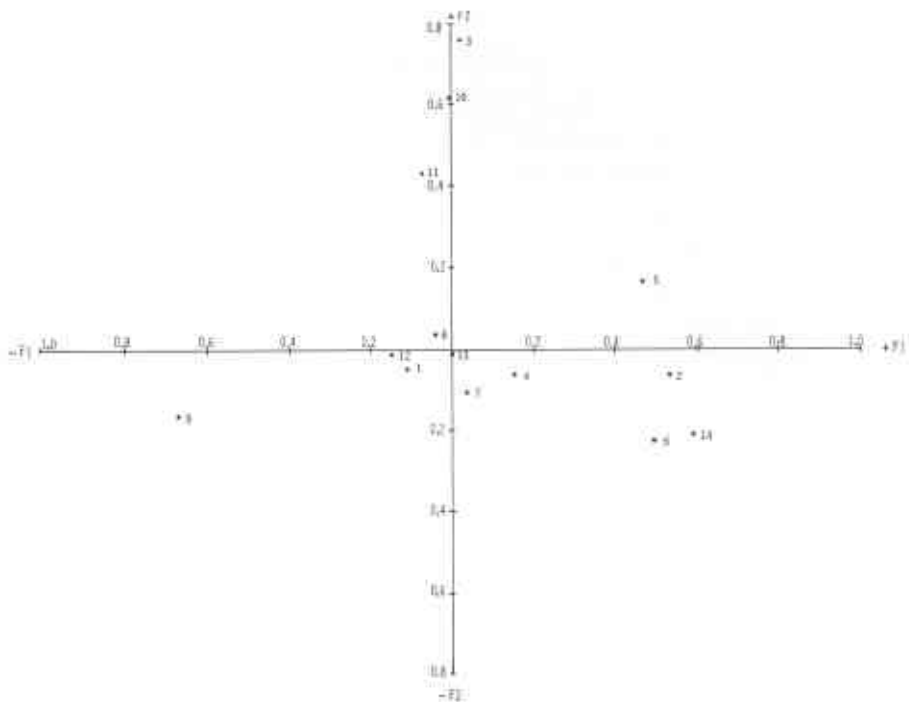


Figure 10

Distribution of tree species within component space—varimax loadings, based on 14 tree species, components 1 and 2. (Species/number sequence is the same as in Figure 9).

The third component appeared to reflect some polarity of soil texture or drainage, the extremes being represented by *E. calophylla* and *Casuarina fraseriana*. This was also true of the fourth factor, where two species occurring on moist alluvial soils, *Eucalyptus patens* and *Eucalyptus megacarpa*, were opposed to *E. marginata*, a species of the gravelly uplands.

The varimax loadings were used to derive component scores and to establish a co-ordinate framework for plots (see Fig. 11). This framework was then used to test the range of occurrence of individual tree species. The ranges varied markedly, from the very broad ranges of occurrence of *E. marginata* and *E. calophylla* to the very narrow ranges of *E. megacarpa* and *M. preissiana*. Certain trends became obvious when some early soil analysis data were fitted into the co-ordinate system derived from the first and second factors. The soil reaction of the topsoil tended towards strongly acid (pH 5.0-5.5) in plots with high positive scores on the second component, that is plots with high proportions of *M. raphiophylla*, *M. preissiana* and *B. littoralis*. By contrast, plots with high negative scores on the first component, that is plots with a high proportion of *E. wandoo*, had only mildly acid soils, with pH ranging from 5.9 to 6.5. The latter group of plots also tended to have higher than average total phosphate, potassium, exchangeable calcium and magnesium, cation exchange capacity and percentage saturation of cation exchange capacity.

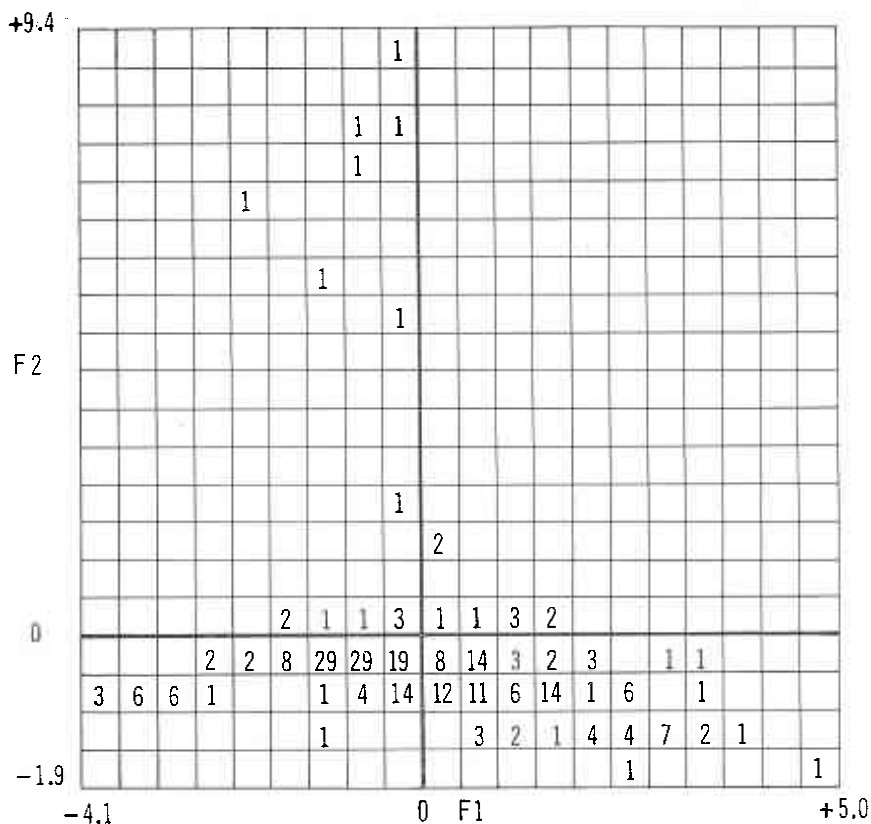


Figure 11

Distribution of ecological sample plots within component framework derived by principal component analysis of 14 tree species—varimax scores, components 1 and 2.

The plot co-ordinate system for the first two components was also used to test the association of trees with understorey species. The understorey species with clear-cut adherence to one of the extremes were:

+F1

Pteridium esculentum
Lasiopetalum floribundum
Leucopogon capitellatus
Leucopogon propinquus
Lomandra sonderii
Acacia strigosa
Acacia urophylla
Adenanthos barbiger
Bossiaea aquifolium
Bossiaea ornata
Macrozamia riedlei

—F1

Hakea lissocarpha
Gastrolobium calycinum
Hakea prostrata
Hibbertia lineata

+ F2

Hakea ceratophylla
Hakea varia
Hypocalymma angustifolium
Leptocarpus scariousus
Leptospermum ellipticum
Mesomelaena tetragona

In some respects, this ordination based on trees only appeared quite promising. However, most of the trends observed in ordination of soil data and cover values of ground storey species referred to extremes, not only of

component space, but of habitat also. They could have been arrived at without complex analysis. A more appropriate test would be the capacity to identify and separate out from the central cluster of plots smaller homogeneous groups of plots. The analysis based on trees alone failed to do this because in the majority of plots the strongest indicators (e.g. *E. wandoo*, *E. patens*, *E. megacarpa*, *M. preissiana* and *B. littoralis*) did not occur at all.

Second approximation on principal component analysis

Choice of species

At this stage, 128 species had been tested for their potential as plant indicators. As the next, and probably final, stage it was decided to re-analyse the data using only species with a proven tendency to reflect environmental conditions. To assess this, the behaviour of all the species within the two co-ordinate systems (based on normal 55 species and varimax 14 tree species respectively) was tabled, enabling fifty-five species to be selected (Appendix 1). The final selection was somewhat influenced by the rather stringent format specifications of the CFAC program. The species had to be chosen from the input arrays in compact blocks rather than individually, so that the whole input format could be specified on one card. An alternative would have been to condense and repunch the semi-processed data used in the testing. This was a formidable task, and, as only very few desirable species were left out, it was not warranted.

It was hoped that the elimination of species with low loadings on most if not all of the components, and of species with a scattered distribution within the co-ordinate framework, would lead to increased clustering of plots, and thus to easier definition, description and separation of groups or continuum segments. This step was considered necessary if the object of the investigation, the definition of site-vegetation types, was to be achieved. The fact that deliberate space distortion is built into many classificatory programmes to encourage clustering was seen as a further justification for this step.

By this time, the number of plots had risen to 295, chiefly by addition of plots from the northern sector. Despite the omission of a number of species considered unsuitable, and their replacement by potentially better indicators, the first four components derived by principal component analysis still accounted for only 22.6% of the total variation within the new set of 55 species.

Ecological trends reflected in component loadings.

Plotting of loadings on component axes for the species indicated that varimax loadings would lend themselves better to relating the components to vegetation than would normal loadings. Plotting on the first two components (Fig 12) once more resulted in a triangular pattern, the apices being as follows:

- F1 *Leptocarpus scariosus*, *Lepidosperma angustatum*, *Dampiera alata*, *Hypocalymma angustifolium*, *Hakea ceratophylla* and *Mesomelaena tetragona*. (Species occurring on wet sites in depressions and on valley floors).

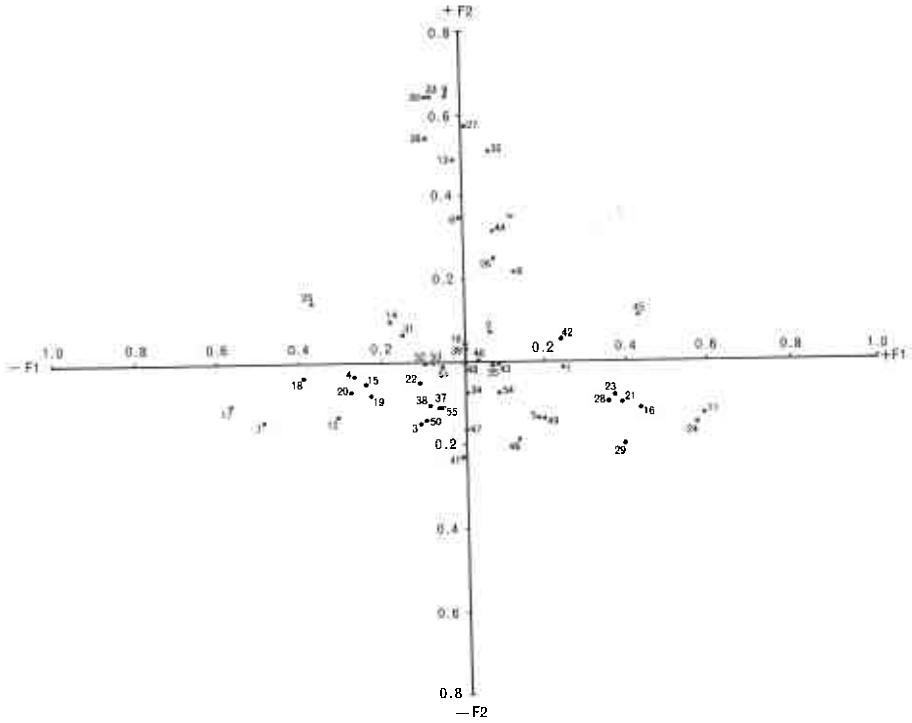


Figure 12

Distribution of indicator species within component space derived by principal component analysis—second approximation, varimax loadings, 55 shrub and tree species, components 1 and 2.

- | | |
|--------------------------------------|------------------------------------|
| 1. <i>Adenanthos barbiger</i> | 29. <i>Pteridium esculentum</i> |
| 2. <i>Adenanthos obovata</i> | 30. <i>Sphaerolobium medium</i> |
| 3. <i>Agonias linearifolia</i> | 31. <i>Stirlingia latifolia</i> |
| 4. <i>Baeckea camphorosmae</i> | 32. <i>Styphelia tenuiflora</i> |
| 5. <i>Bossiaea aquifolium</i> | 33. <i>Synaphea petiolaris</i> |
| 6. <i>Conospermum stoechadis</i> | 34. <i>Trymalium ledifolium</i> |
| 7. <i>Dampiera alata</i> | 35. <i>Trymalium spathulatum</i> |
| 8. <i>Dasyopogon bromeliæifolius</i> | 36. <i>Hakea cyclocarpa</i> |
| 9. <i>Daviesia pectinata</i> | 37. <i>Hakea ceratophylla</i> |
| 10. <i>Daviesia longifolia</i> | 38. <i>Hakea varia</i> |
| 11. <i>Macrozamia riedlei</i> | 39. <i>Hakea lissocarpha</i> |
| 12. <i>Hypocalymma angustifolium</i> | 40. <i>Dillwynia cinerascens</i> |
| 13. <i>Isopogon dubius</i> | 41. <i>Diplolaena drummondii</i> |
| 14. <i>Kingia australis</i> | 42. <i>Leptomeria cunninghamii</i> |
| 15. <i>Kunzea micromera</i> | 43. <i>Hibbertia lineata</i> |
| 16. <i>Lastopetalum floribundum</i> | 44. <i>Hibbertia polystachya</i> |
| 17. <i>Lepidosperma angustatum</i> | 45. <i>Eucalyptus marginata</i> |
| 18. <i>Leptocarpus scariosus</i> | 46. <i>Eucalyptus calophylla</i> |
| 19. <i>Leptospermum ellipticum</i> | 47. <i>Eucalyptus patens</i> |
| 20. <i>Lechenaultia biloba</i> | 48. <i>Eucalyptus wandoo</i> |
| 21. <i>Leucopogon capitellatus</i> | 49. <i>Banksia grandis</i> |
| 22. <i>Leucopogon oxycedrus</i> | 50. <i>Melaleuca preissiana</i> |
| 23. <i>Leucopogon propinquus</i> | 51. <i>Nuytsia floribunda</i> |
| 24. <i>Leucopogon verticillatus</i> | 52. <i>Casuarina fraseriana</i> |
| 25. <i>Mesomelaena tetragona</i> | 53. <i>Banksia attenuata</i> |
| 26. <i>Paterosonia occidentalis</i> | 54. <i>Persoonia elliptica</i> |
| 27. <i>Paterosonia rudis</i> | 55. <i>Banksia littoralis</i> |
| 28. <i>Phyllanthus calycinus</i> | |

- +F1 *Macrozamia riedlei*, *Leucopogon verticillatus*, *Pteridium esculentum*, *Phyllanthus calycinus*, *Lasiopetalum floribundum*, *Leucopogon propinquus*, *Leucopogon capitellatus*, *Eucalyptus marginata*. (Predominantly species occurring on well-drained upper slopes and ridges in the high-rainfall western zone).
- +F2 *Daviesia pectinata*, *Sphaerolobium medium*, *Synaphea petiolaris*, *Hakea cyclocarpa*, *Patersonia rudis*, *Styphelia tenuiflora* and *Isopogon dubius*. (Species occurring on sands and sandy gravels from the dry eastern zone).

There were no species with high negative loadings on the second component.

A similar triangular pattern resulted from plotting on the third and fourth components:

- F3 *Dasyopogon bromeliaefolius*, *Adenanthos obovata*, *Hakea ceratophylla*, *Hakea varia*, *Melaleuca preissiana*, *Mesomelaena tetragona*, *Leptospermum ellipticum*, *Banksia littoralis*, *Hibbertia polystachya*. (Species occurring on moist to wet, leached, acid sands).
- F4 *Diplolaena microcephala* var. *drummondii*, *Trymalium spathulatum*, *Hibbertia lineata*, *Eucalyptus wandoo*, *Eucalyptus patens*, *Hakea lissocarpa*, *Hypocalymma angustifolium*. (Species occurring on fertile, neutral loams, either derived from basic rocks or loamy alluvium, in the main river valleys).
- +F4 *Eucalyptus marginata*, *Adenanthos barbiger*, *Banksia grandis*, *Casuarina fraseriana*, *Lechenaultia biloba*, *Bossiaea aquifolium* and *Lasiopetalum floribundum*. (Species occurring on infertile, phosphate-fixing lateritic gravels on residual plateaus).

There were no species with high positive loadings on the third components.

All of the groupings enumerated above, were, of course, species groupings from extreme habitats and were therefore readily identifiable. However, between them and the species of less extreme habitats they offered an opportunity for an almost unlimited number of combinations. If four levels of each component were considered, the total number of possible combinations would be 256 (4 x 4 x 4 x 4). If only three levels were considered, that is high positive, high negative and intermediate, the number of possible combinations would be 81 (3 x 3 x 3 x 3), which is still excessively high for an applied survey.

Correlation between observed environmental parameters and mathematically-derived component scores based on vegetation.

It is possible to elucidate the relationship between the scores mathematically derived from vegetation parameters and the observed environmental parameters by calculating their mutual correlation. This was carried out by using the stepwise multiple regression program MR 40 T, employing data for 171 plots from the northern sector. It is perhaps worthwhile to stress that the positiveness or negativeness of scores has no environmental significance (e.g. negative score could be either high or low fertility).

On the basis of this, component 1 is most closely related to maximum slope ($r = +.536$) and percentage of gravel in the topsoil ($r = +.390$). This indicates that the high positive values of component 1 are associated with

steep (in local sense), gravelly slopes, and high negative values with gravel-free, near-level depressions. It agrees well with field observations reported earlier. There is, however, a second group of edaphic parameters which is also highly significantly correlated with scores on the first component. These include cation exchange capacity of the topsoil (CEC), percentage saturation of the CEC, and levels of calcium, phosphorus and potassium in the soil. This was not anticipated. The multiple correlation coefficient for the regression of component 1 on maximum slope, percentage of gravel, percentage saturation of the cation exchange capacity and level of calcium is 0.633.

Component 2 is highly significantly (in a statistical sense) related to several edaphic parameters, such as the percentage of silt and clay ($r = -.330$) and levels of nitrogen, carbon, phosphorus and calcium ($r = -.333, -.356, -.304$ and $-.305$ respectively). It thus reflects the texture of the soil and the resulting capacity of the soil to hold nutrients. The multiple correlation coefficient for the regression of factor 2 on these five soil parameters is 0.400. The high positive values of component 2 would be expected to be associated with light-textured, sandy soils, a fact well supported by field observations. The relationship between component 2 and climatic parameters, suggested by the easterly occurrence of plots with high scores on $+F_2$, could not be tested by correlation because quantitative climatic data were not available for individual plots.

Component 3 is highly significantly correlated with percentage of gravel ($r = +.402$), maximum slope ($r = +.330$), percentage saturation of the cation exchange capacity ($r = +.347$) and soil reaction expressed as pH ($r = +.324$). The multiple correlation coefficient for the regression of factor 3 on these four parameters is 0.511. High negative values on factor 3 would thus be associated with non-gravelly, acid, strongly-leached soils in level depressions. This agrees well with field observations.

Component 4 is most strongly related to soil fertility: phosphorus ($r = -.383$), nitrogen ($r = -.361$), potassium ($r = -.344$), calcium ($r = -.315$) and cation exchange capacity ($r = -.309$). All of the above correlations are highly significant. The multiple correlation coefficient for the regression of factor 4 on these five soil parameters is 0.411. A second group of edaphic parameters, reflecting moisture-holding capacity of the soils, is also highly significantly correlated with component 4. These include field capacity ($r = -.351$) and available moisture ($r = -.240$). The most likely explanation is that high negative scores on component 4 are associated with heavier-textured, younger soils with a good capacity to hold both nutrients and moisture. This is strongly supported by field observations reported earlier.

There is also a strong mutual correlation between individual environmental parameters. For instance, soil reaction (pH) is highly significantly correlated with percentage saturation of the cation exchange capacity ($r = +.456$), potassium ($r = +.345$) and calcium ($r = +.369$). This could be expected from a basic knowledge of soil chemistry, in that acid soils tend to be more strongly leached than neutral or basic soils. The somewhat weaker, but still significant, relationship of pH to maximum slope ($r = +.348$) presumably reflects a strong geomorphological control of soil formation. All parameters reflecting the fertility of the soil (cation exchange capacity, percentage saturation of CEC, various nutrient levels) are not only mutually strongly

interrelated, they are also highly significantly correlated with the physical properties of the soil, such as the percentage of silt and clay and of coarse sand, field capacity, wilting point and available moisture. All of these parameters are highly significantly correlated with maximum slope, presumably again as a result of a strong geomorphological control of soil formation in an old and stable landscape.

The above correlations between component scores derived mathematically from vegetational parameters and quantitative environmental parameters can be briefly summarized as follows:

- (a) The component scores cannot be simply expressed in terms of individual environmental parameters.
- (b) Environmental parameters explain only a portion of the total variation in component scores. In view of the fact that only a portion of the environmental complex (some aspects of topography and some physical and chemical factors of the topsoil) could be quantified, this too is to be expected.

An alternative approach in relating component scores to environmental parameters is to examine the patterns formed by the environmental parameters within the co-ordinate framework based on vegetation, using the CORD program. As this is merely a substitution of a graphical approach for a mathematical approach, the relationships described earlier (e.g. between component 1 and slope) still hold good. However, in addition the integration of the mathematically-derived principal components becomes much more obvious (Fig. 13).

For instance, the space delineated by negative scores on both component 1 and component 3 is characterized by acid soils (low pH), lowest phosphorus, potassium, calcium and magnesium levels, high exchangeable hydrogen, mild slopes and absence of gravel in topsoil.

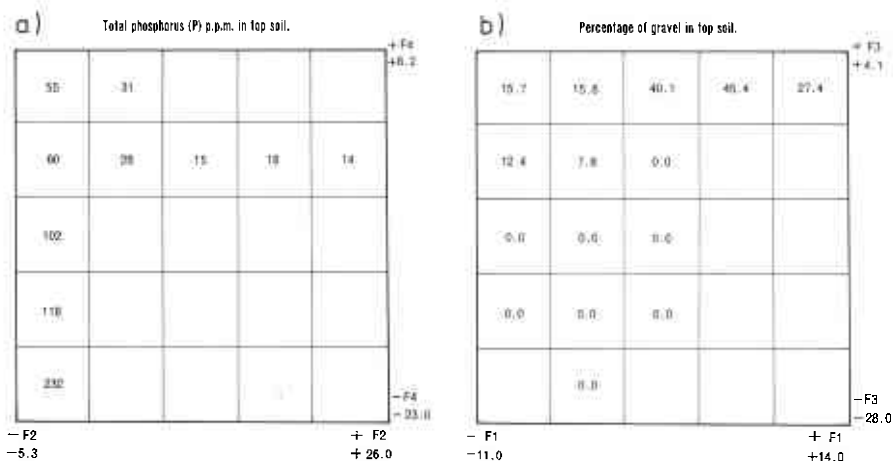


Figure 13

Patterns of environmental parameters within component space calculated on the basis of vegetational data. The values plotted are the mean values for sample plots falling into the particular segments of component space. (Second approximation, varimax scores, 55 shrub and tree species).

The component space delineated by negative scores on components 2 and 4 is characterized by soils with high levels of phosphorus, potassium, calcium and magnesium, high cation exchange capacity, high field capacity and high wilting point. In certain environmental parameters, $-F1 \times -F3$ and $-F2 \times -F4$ combinations appear diametrically opposite to each other, but this is not true of all parameters.

There is also an indication that vegetation responds to the sum total of environmental factors, rather than to precise levels of individual factors. For instance, plot 166 is placed into the $-F2 \times -F4$ segment of component space, despite relatively low levels of calcium and phosphate. This appears to be compensated by higher values of magnesium and high cation exchange capacity.

Both the mathematical and graphical approaches thus point to a relatively complex, highly-interrelated environment-vegetation complex that defies further simplification.

Coping with the complexity of the vegetation model.

It was obvious at this stage that all four components would need to be considered concurrently to arrive at a valid definition of a plot or site. The immediate problem was how to cope with such complexity, inasmuch as there were only three physical space dimensions which could be used in the construction of a model. Colour afforded an opportunity to add yet another dimension. A preliminary run on the CORD program using varimax scores indicated that the scores on the second component were least continuous, and hence easiest to subdivide. The range of scores on this component was therefore broken into four segments, to be represented by blue, green, yellow and red, to give a visual illusion of progression from moist ($-F2$) to dry ($+F2$) sites, which this component appears to reflect. The remaining three components were used as the three dimensions of physical space. A model using perspex plastic as a base plane was constructed in which plot scores on the first component were plotted left to right, scores on the third component from front to back, and scores on the fourth component were represented by the length of coloured plastic rods projecting above and below the base plane (See Plate 1).

Separate models were constructed for the northern and southern sectors. There were two reasons for this. Firstly, by now the number of plots had risen to 320, and any model incorporating all of these would have been too complex. Secondly, the preliminary run on the CORD program indicated that there was a far greater range in the scores for the northern sector, perhaps reflecting a greater environmental range (Fig. 14). To incorporate both sets of data in one co-ordinate framework would therefore have been unwise.

However, subsequent work made it possible to obtain an adequate scheme of classification even for the southern sector. The gravels of the high rainfall zone near Dwellingup have been subjected to detailed sampling and analysis aimed at relating increment rates of jarrah to site factors and understorey vegetation. In addition, an area of 62.2 km² of virgin forest east of Harvey and north of Collie was surveyed during 1972, thus giving an opportunity to sample types inadequately covered in the initial sampling. The survey indicated

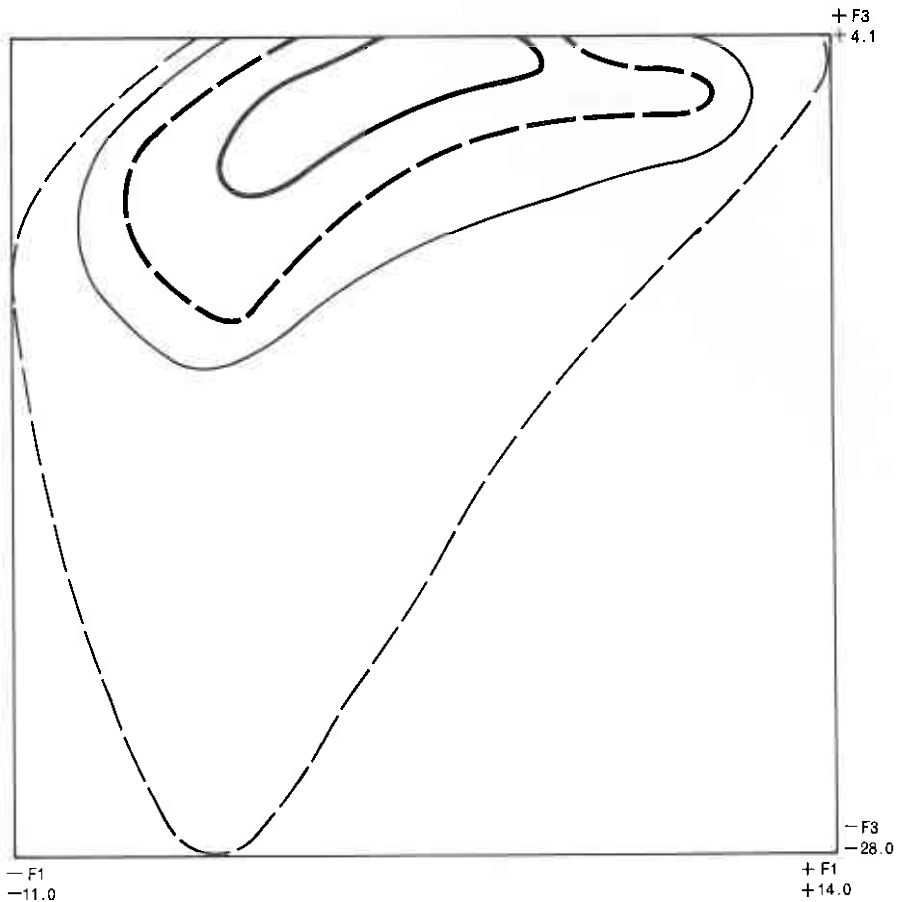


Figure 14

Comparison of component space occupied by ecological sample plots from northern and southern sectors of the study area. Continuous lines delineate areas of high concentration of plots per cell (2^+); discontinuous lines refer to low concentration. Thick lines refer to southern sector, thin lines to northern sector. (Second approximation, varimax scores, 55 shrub and tree species).

that there was no essential difference in site-vegetation types between the north-east and the south-east, there being only a slight shift readily explained by a corresponding shift towards a cooler, moister climate.

Nature of the vegetational continuum as illustrated by the model.

The resulting physical model for the northern sector can only be described as a multi-coloured, three-dimensional crescent, or more simply a multi-coloured banana, fat at the middle and pointed at the two ends (Plate 1). Despite its intriguing appearance, the model makes it possible to relate any plot to any other plot simultaneously in four dimensions, at a glance. It also illustrates the fact that the northern jarrah forest is a highly inter-correlated system in

which the main factors do not act independently. Many potential combinations are missing. There are, for instance, no plots in the combination high +F1 by high —F3, or any of their permutations with F2 and F4. In terms of geomorphology, a residual leached sandplain on an upland, well-drained surface in the high-rainfall zone near the escarpment is a virtual impossibility, as it would have been removed long ago by erosion. Similarly, there are no plots in the combination high —F1 by high +F2 because an excessively-drained droughty swamp is also a physical impossibility. There is no combination of high —F3 with either high +F4 or high —F4. Leached, acid sands can be neither highly fertile nor phosphate fixing.

A similar model, based on component loadings, was also constructed for the 55 species used in the analysis. It not only makes it possible to relate these species to each other, it also helps in visualizing what species contribute to a particular cluster of plots, because the axes and colour scheme, though not the dimensions, of the plot and species models are identical.

A model of plot distribution for the southern sector resembled the model for the northern sector, but with reduced dimensions on all except the first component. There was an overwhelming predominance of blue and green colours, indicating that gravels and sands from the eastern, low-rainfall zone were either not adequately sampled or did not exist. The former is true of the Harvey Division, where they are very remote from the centre of administration, and still largely untouched. The latter is true of the Dwellingup Division, where the eastern region lies largely outside State Forest, and is strongly dissected by the tributaries of the Murray River.

Subdivision of the continuum into segments.

The difficulties in mapping a vegetational continuum have already been briefly referred to in the review of ecological theories and methods. The subdivision of the continuum into segments for the purpose of mapping and description was suggested by Greig-Smith (1964).

This suggestion has already been successfully implemented in an earlier study of a simple two-dimensional continuum on the sands of the coastal plain (Havel, 1968). Its implementation in the present study was made difficult by the fact that here the vegetational continuum has four dimensions. Without the model described earlier it would have been utterly impossible to keep track of four dimensions concurrently. With the help of the model, the impossibility was changed into a refined form of mental self-torture, as the task had some resemblance to dividing up a bowl of soup with the aid of a carving knife. Although some fairly well-defined clusters of plots could be recognized, there were invariably some transitional plots on or near the interface between two segments.

The difficulty of dealing with continua increases rapidly with the increase in dimension. In a uni-dimensional continuum, the division into segments amounts to placing a dividing point on the line representing the continuum. In a two-dimensional continuum, each segment is a plane surface delineated by a minimum of three straight lines. A segment of a three-dimensional continuum is a solid delineated by a minimum of four triangular, or six rectangular, plane surfaces. In a four-dimensional continuum it becomes a multi-coloured three-dimensional mirage.

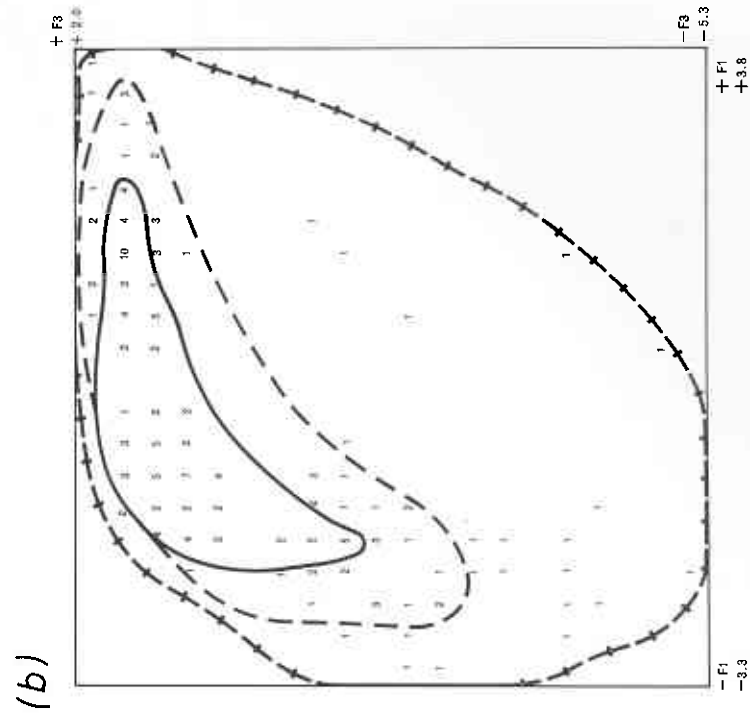


Figure 15
 Comparison of dispersion of ecological sample plots within component space based on the original component scores (a) and their square root transformations (b). Solid lines delineate areas of maximum density of plots per cell; discontinuous lines, moderate density; crossed lines, low density. (Second approximation, varimax scores, 55 tree and shrub species).

The need to consider the ultimate practical application of the study imposed a limit on the number of segments that could be recognized. Experience in earlier site mapping on an ecological basis indicated that not many more than twenty types could be handled by the field staff. Ultimately, nineteen segments were defined for the northern sector. For convenience, they were identified by a letter of the alphabet. At this stage, it was realized that the continuum approach, whilst giving an excellent understanding of relationships between plots and species, also fulfilled every apprehension about difficulties in adopting it for practical use.

Final testing of indicator species.

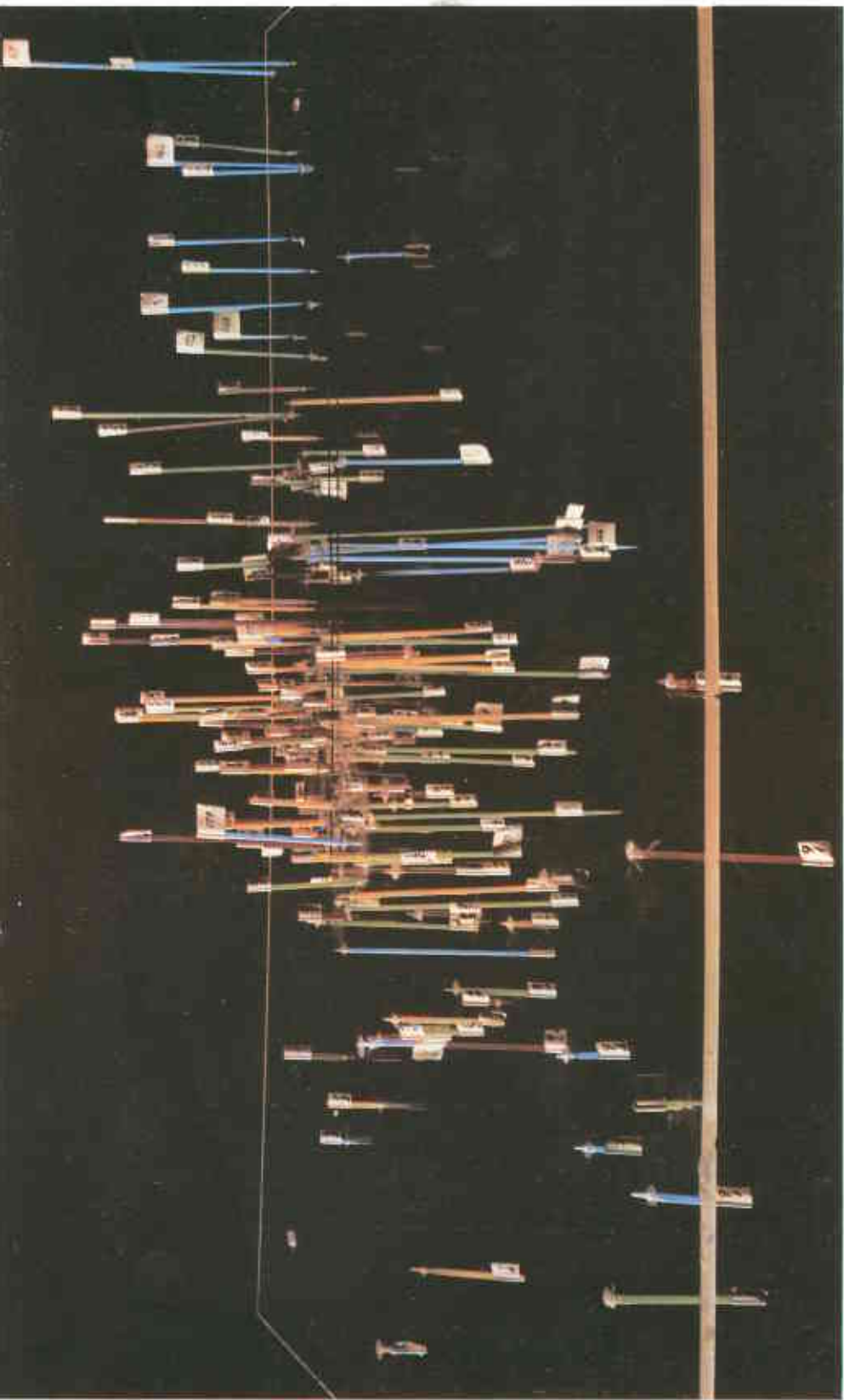
At this stage it was desirable to carry out a final testing of species as to their behaviour within the component framework, so as to determine for which part of the continuum they could be used as indicators, and how narrowly or broadly they reflected it. A preliminary run on the CORD program highlighted the problem encountered earlier, namely that plots of extreme habitats are so distant from the central cluster of more "normal" plots that they cannot be ordinated on the same scale. The separation of these plots was not considered altogether desirable, because the continuum could then not be seen as a whole. To pull in the outside plots, and to separate the inner cluster, the co-ordinates were converted to square roots, and the ordination was based on these. The result was most satisfactory, as can be seen in Figure 15. To obtain a close link between the four-dimensional model and the two-dimensional flat diagrams produced by the CORD program, one diagram was based on the first and third component, and thus matched the horizontal distribution of the plots on the perspex plane. The other diagram incorporated the fourth component as the vertical dimension, corresponding to its vertical representation in the model, and the second component as the horizontal dimension.

The full set of 128 species was now processed by the program. Similarities appeared between the various species, and were used in substituting a small number of species groups for the large number of individual species. These species groups had an almost identical ecological behaviour, thus presumably reflecting a preference for the same combination of environmental factors.

Formation of indicator groups.

For ease of reference, the groups were given mnemonic code names, compatible with possible future use in FORTRAN programming. The names were abbreviations of habitat characteristics as understood from field observation. Brief descriptions of the groups and their location in the component framework are given in Appendixes 2 and 3.

Species not included in the enumeration are those having too broad or too indefinite ranges, or fitting in groups already amply represented, such as SANLEA. On the other hand, several species which had not been fully tested within the component framework have been added to some of the small species groups because they have been observed to be constantly associated with them.



▲ PLATE 1. Four-dimensional model of ecological relationships in the northern jarrah region. Each coloured stick represents an ecological sample plot. The arrangement of components derived by principal component analysis is as follows.

- (a) Left to right, — F_1 to + F_1
- (b) Front to back, — F_3 to + F_3
- (c) Up + F_4 , down — F_4

- (d) Blue, high — F_2 ; green, low — F_2
- yellow, low + F_2 ; red, high + F_2



PLATE 2:

(a) Site-vegetation Type O.
Overstorey of Jarrah
(*Eucalyptus marginata*) and
tall, open understorey of
Xanthorrhoea preissii on
gravelly slopes in high rainfall
zone.

(b) Site-vegetation Type Q.
Overstorey of yarrri (*Eucalyptus
patens*) on moist, fertile
alluvium in high rainfall zone.





(a) Site-vegetation Type Y. Overstorey of wandoo (*Eucalyptus wandoo*) and low, sparse understorey on seasonally-moist valley floor in low rainfall zone.



(b) Site-vegetation Type C. Overstorey of bullch (*Eucalyptus megacarpa*) and tall, dense understorey of *Agrostis linearifolia* on wet valley floor in high rainfall zone.



▲ PLATE 4.

(a) Site-vegetation Type A. Low, open overstorey of paperbark (*Melaleuca preissiana*) and swamp banksia (*Banksia littoralis*) in a shallow depression in low rainfall zone.

(b) Site-vegetation Type J. Low, open overstorey of *Banksia attenuata* and *Nuytsia floribunda* on deep, leached sands in low rainfall zone. ▼



Delineation of continuum segments.

The division of the vegetational continuum into segments with the help of the four-dimensional model, and the formation of species-groups of comparable ecological ranges through the use of the CORD program, prepared the way for the definition of the segments in terms of their component species. The task had some similarity to the nodal analysis of Lambert and Williams (1962). In view of the large number of species and plots involved, a small program (FORPLOT V) was developed to perform the task speedily, using data cards already available. Inasmuch as the effectiveness of the classification programs DIVINF, DIVINFRE and CLASS could also be best judged on the basis of their ability to form homogeneous groups of plots defined by homogeneous groups of species, it was decided to incorporate this task in the same program. The program could therefore accept either quantitative data and plot and species arrangements based on principal component analysis, or qualitative data and plot and species arrangements based on the various classifications. The processing amounted simply to a two-way reshuffle of plots and species, which could be repeated to optimize the arrangements.

The sequence in which the plots were read in and the sequence of species within plots were matched by arrays specifying the vertical sequence of plots and the horizontal sequence of species to be used in printing a two way table. As the data were read in plot by plot, the table was progressively built up on random access discs, an auxiliary extension of the computer memory, and, when all data were dealt with, the table was output by line printer. For quantitative data the actual cover or basal area value was printed out. For qualitative data, presence of a species was denoted by an asterisk and absence by a blank. A simplified example of such an output is shown later in Figures 18 and 19.

The program was also used to prepare a table giving environmental data for each segment plot by plot. On the basis of these tables it was possible to define each segment in terms of the plots composing it, the species occurring on the plots and the environmental factors associated with them (see Appendix 4).

Definition of continuum segments in terms of their indicator species and underlying environmental conditions.

Northern Sector—In a four-dimensional continuum, it is impossible to enumerate the component segments in a sequence that would adequately illustrate all inter-relationships between them. The enumeration given in Appendix 4 is arranged broadly from high negative scores on components 1 and 3 (sandy swamps) through segments predominantly with high positive scores on components 2 and 4 (infertile, low rainfall) and low \pm on components 1 and 3, to high positive scores on components 1 and 3 (upland, loamy gravels) and then back through segments with high negative scores on components 2 and 4 (high fertility, high rainfall) to segments with negative scores on components 1 and 4 and moderate scores on components 2 and 3 (loamy soils in depressions). The distribution of indicator species along this continuum is shown in Figure 16.

TABLE 1
Chemical properties of soil samples arranged by site-vegetation types

Group	pH		%N x 100		ppm P		K me x 100		Ca ^{ex} me% x 10		M ₁ ^{ex} me% x 100		CEC me% x 10		Saturation%	
	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average
A	5.15-5.50	5.36	2-11	5	8-30	15	2-53	16	7-37	15	42-207	87	65-103	82	22-68	37
B	5.38-5.90	5.78	1-6	3	10-26	16	5-22	10	1-20	10	4-141	61	17-95	63	13-65	35
D	5.45-6.09	5.82	3-16	9	3-97	24	1-40	18	4-34	13	9-314	86	3-138	75	10-68	36
H	4.95-6.45	5.99	2-10	5	2-45	21	5-120	27	4-63	21	15-436	86	32-293	82	11-94	41
E	5.30-6.14	5.83	3-23	7	5-26	17	2-47	18	3-31	17	18-115	63	44-111	74	13-67	36
W	5.49-6.30	5.97	5-34	14	12-66	36	25-86	58	10-64	35	74-540	190	70-230	106	33-67	55
C	4.52-6.00	5.59	4-39	15	19-101	46	5-64	33	9-33	23	29-418	177	61-283	121	25-69	44
F	4.55-6.09	5.52	1-4	2	6-46	19	7-24	15	4-27	15	9-69	36	6-155	52	22-65	40
J	5.65-6.11	5.96	2-4	3	7-14	10	3-15	10	5-19	12	21-142	50	47-80	62	18-57	31
P	5.45-7.12	6.07	1-14	6	12-75	29	5-99	30	5-89	35	38-336	100	22-217	84	11-78	54
Z	5.57-6.15	5.94	3-18	10	3-143	55	5-51	24	7-84	49	20-273	138	43-171	119	15-87	56
S	5.48-6.63	6.12	1-10	6	8-43	25	8-74	35	13-40	29	45-110	84	39-122	69	36-87	59
T	5.80-6.90	6.10	6-30	14	10-188	89	20-104	60	23-147	73	124-528	248	65-259	148	45-80	70
U	6.15-6.31	6.25	22-41	32	103-277	201	32-151	111	60-181	131	581-713	647	161-307	253	78-84	82
R	5.25-6.29	5.91	3-54	19	12-200	80	8-82	42	13-168	73	60-692	281	63-390	185	33-79	60
Q	5.85-7.25	6.30	8-24	14	56-211	114	44-114	82	10-98	47	81-512	221	58-170	104	34-92	67
M	5.55-6.65	6.23	4-29	16	43-262	126	22-124	75	29-141	74	76-299	182	75-188	128	48-95	75
L	5.48-6.52	6.12	27-34	31	64-305	199	79-98	93	70-185	134	274-471	384	209-264	231	49-96	79
Y	5.79-6.29	6.09	6-34	12	14-80	56	17-136	60	23-57	39	105-273	171	72-147	107	44-82	60

To facilitate linkage between the definition of site-vegetation groups and their subsequent field mapping, the latter has been somewhat anticipated here by including a description of topographical position. Some appreciation of the edaphic variation between segments can be obtained from Table 1.

Southern Sector—The scheme suitable for the northern sector did not appear fully suitable for the southern sector. On one hand, many of the drier segments such as Y, M, L, J, F were largely unrepresented in the southern data, though they have been subsequently located in broad-scale surveys. On the other hand, there was an excessively large group of plots falling in or around segments P, S and T, which requires subdivision.

Principal component analysis of plot data collected on upland gravels within the high-rainfall zone near Dwellingup revealed that there is a broad polarity of understorey species, resulting in two main groups of species:

Group 1. *Pteridium esculentum*, *Clematis pubescens*, *Leucopogon verticillatus*, *Leucopogon capitellatus*, *Lasiopetalum floribundum* and partially *Trymalium ledifolium*, *Persoonia longifolia*, *Xanthosia candida*, *Leptomeria cunninghamii*.

Group 2. *Bossiaea ornata*, *Cyathochaete clandestina*, *Conostylis setigera*, *Scaevola striata*, *Lepidosperma angustatum*, *Dampiera linearis* and to a lesser extent *Tetratheca viminea*, *Acacia drummondii* and *Leucopogon propinquus*.

The first group consists essentially of indicators of group T, of high-rainfall lateritic uplands with loamy gravels, and is thus already covered. The second group has affinities with indicators of Group P, but lacks such clear-cut indicators as *Grevillea wilsonii* and *Adenanthos barbiger*. In fact, many of the species present were tested for their indicator value, but were rejected because of their broad range of occurrence. It is therefore necessary to delineate a new category, segment O, which is defined by lack of the more outstanding indicators which define other segments, rather than by any clear-cut indicators of its own. It also differs from P in a somewhat lower score on the second component, and can thus be viewed as the most central, or alternatively the least distinct, of all site-vegetation types. In terms of environment, it again largely corresponds to P, being characteristic of sandy, gravelly colluvium in minor valleys and depressions within the lateritic uplands, but differing from P in moister, possibly slightly cooler, climate. The possibility of edaphic differences cannot, however, be ruled out altogether, as the region within which it occurs is on the whole more strongly dissected than the northern (Kelmscott-Mundaring) region.

Examples of some of the vegetation segments are shown in Plates 2, 3 and 4.

Numerical classification

The option for converting raw plant data to qualitative data for use with classificatory programs was now used. It was reasoned that, in view of the complex nature of the vegetation, the simplistic approach of the classificatory programs to subdivision might be appropriate.

Divisive monothetic classification.

Program DIVINF—Because by this time the Canberra DIVINF program had been adopted for use on the PDP 6 computer at the University of Western Australia Computing Centre, it was used first. The analysis was restricted to 172 plots from the northern sector. On the first run, the full set of 130 species of moderate frequency of occurrence was used. Subsequently, the number was reduced to 55 species, the bulk of which were shared with the second (final) approximation on principal component analysis. In the third and final run, the number was further reduced to 18 species, subjectively chosen as the best indicators on the basis of all work completed up to that stage. The analyses using 55 and 18 species respectively were therefore extensions of the ordination study, without which the same set of species could never have been chosen.

As the local version of the DIVINF program is not coupled to a plotter, the output is entirely numerical, and amounts to a detailed account of the divisive process. At each stage of the normal analysis, the attributes (species) on which the division was made, and the fall of information resulting from the division, are given. The two new groups resulting from the division are described by several features, namely their reference number, their parent group, whether the decision attribute is present or absent, how much information is still held by the group, and what individuals comprise it. On the basis of this description, it is possible to construct a decision tree, which is a graphical representation of the decisions process. In the Canberra Computing Centre, it is prepared by a plotter linked to the computer. For the inverse analysis, the relative positions of plots and species are reversed, in that decisions are based on plots and the groups are composed of species.

The interpretation of the output presented no great problem. The normal analysis of 130 species (Fig. 17) used as the first, and thus implicitly the best, basis of division the sedge *Mesomelaena tetragona*, found by the ordination process to be the best broad indicator of moist, water-gaining sites. The moist group was further subdivided on the basis of *Patersonia rudis*, a species of gravelly sands and gravels. The moist, gravelly plots were further subdivided on the basis of *Casuarina fraseriana*, which is again a species of sandy gravels restricted to medium and high rainfall. The non-gravelly plots were subdivided on the basis of *Lyginia tenax*, a perennial herb occurring on moist to wet, leached sands. The decision sequences on the upland plots from which *Mesomelaena tetragona* was absent could also be interpreted readily. The species on which the divisions were based included *Casuarina fraseriana*, already described; *Eucalyptus wandoo*, characteristic of heavy-textured soils; *Pteridium esculentum* of the western high-rainfall zone; *Leucopogon propinquus* and *Phyllanthus calycinus* of loamy gravels; and *Daviesia pectinata* and *Styphelia tenuiflora* of eastern dry gravels. The subjective impression at this stage is that in some cases the divisive process has been taken too far (e.g. where two species known to occur in similar habitats, such as *Daviesia pectinata* and *Styphelia tenuiflora*, were used for successive divisions). On the other hand, some subdivisions were not taken far enough before the specified number of groups (20) was reached. This was particularly true of the group defined by the presence of *Eucalyptus wandoo*, which is such an important component in the eastern sector.

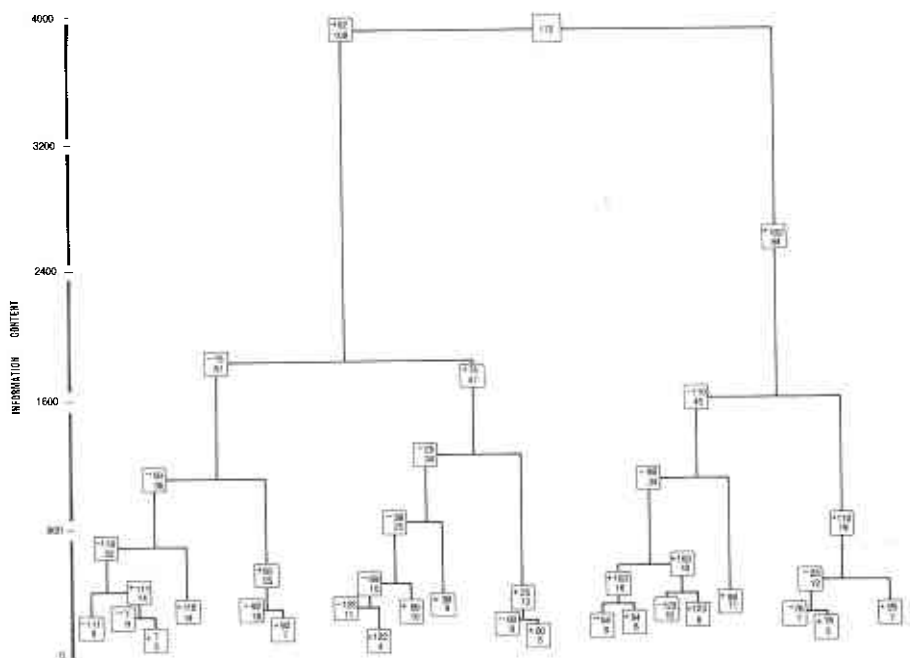


Figure 17

Diagrammatic representation of the subdivision procedure of the normal monothetic divisive classification (program DIVINF, 172 plots, 130 species). The upper number refers to presence or absence of the indicator species on which a particular subdivision was made. Presence is indicated by plus, absence by minus. Lower number refers to number of plots comprising the group. The indicator species used in the subdivision process are:

- 7. *Hibbertia lineata*
- 39. *Daviesia pectinata*
- 60. *Grevillea wilsonii*
- 69. *Hibbertia huegelii*
- 76. *Hovea trisperma*
- 93. *Lyginia tenax*
- 103. *Mesomelaena* sp. nov.
- 111. *Phyllanthus calycinus*
- 122. *Styphelia tenuiflora*

- 25. *Casuarina fraseriana*
- 50. *Eucalyptus wandoo*
- 64. *Hakea lissocarpa*
- 75. *Hovea chorizemifolia*
- 92. *Leucopogon procpinquus*
- 102. *Mesomelaena tetragona*
- 110. *Paterosonia rudis*
- 118. *Pteridium esculentum*
- 123. *Synaphea petiolaris*

The inverse information analysis indicated that, despite the prior elimination of the least common and the most common species, the tendency to separate out the rare and common species persisted. There was a pronounced chaining on the negative side, and the species groups resulting from eight or nine negative answers were strongly heterogeneous. They were composed of species with widely-differing habitat preferences, having nothing in common except their relative rarity. Thus *Banksia attenuata*, typical of deep, dry, leached sands, and *Agonis linearifolia*, typical of moist, alluvial loams, were thrown together. Similarly, at the other extreme, *Hakea lissocarpa* and *Conostylis setigera* were placed in the same group solely because they were the most common of the 130 species used, though they have dissimilar habitat preferences.

The figure is a large, complex two-way table. The vertical axis (rows) represents 172 individual plots, and the horizontal axis (columns) represents 130 individual indicator species. The table is partitioned into several groups by horizontal lines, which are derived from normal analysis. Vertical lines, derived from inverse analysis, partition the species into groups. Each cell in the table contains either a dot (indicating the presence of a species in a plot) or is empty (indicating absence). The species names are listed along the top and left sides of the table, though they are too small to read clearly. The overall layout is a dense grid of data points.

Figure 18

Two-way table of ecological sample plots and indicator species, arranged in groups on the basis of divisive monothetic information analysis (program DIVINF, 172 plots, 130 species). Each column represents an individual indicator species; each row refers to an individual plot. The presence of a species in a particular plot is indicated by a dot. Plot groups derived by normal analysis are delineated by horizontal lines; species groups derived by inverse analysis are delineated by vertical lines.

Nevertheless, several species groups were composed of species with similar habitat preferences:

- (a) Moist, leached sands.
- (b) Fertile loams.
- (c) Dry, sandy gravels of the eastern zone.
- (d) Moist, loamy gravels of the western zone.
- (e) Moist, sandy gravels of the western zone.
- (f) Moist, loamy sands and sandy loams.

Several plot groups were likewise clearly defined, and corresponded well with segments of the continuum based on the principal component analysis. Other plot groups were more loose, and some were completely heterogeneous in terms of the species occurring in them.

On the whole, the groups were looser and less well defined than those derived by principal component analysis, a conclusion shared with Young & Watson (1970). The inter-relationships between groups were difficult to see. On the positive side, twice the number of species were analysed, including some whose value as indicators had been initially overlooked because of their insignificant appearance, such as *Hovea chorizemifolia* and *Gompholobium knightianum*. The speed of processing was very much greater, and the collection of purely qualitative field data would also be much less laborious. The combined normal and inverse analysis for 130 species is shown in Figure 18.

The inverse analysis of 55 species was by far the most promising of all the information analyses (Table 2). With the sole exception of one heterogeneous group of rare species, the remaining groups, usually composed of 2 to 4 species, checked fairly well both with field observations and with ordination on principal component analysis. Normal analysis based on 55 species likewise gave a better grouping of plots.

Shortly afterwards, a visit to Canberra provided an opportunity to classify the same set of 130 species on 172 plots by means of two further programs already described earlier, the modified version of the divisive monothetic information analysis incorporating a provision for revision of groups (DIVINFRE), and polythetic agglomerative analysis (CLASS). Both programs were used with the full set of 130 species and the reduced sets of 55 and 18 species. To minimize cost, the inverse analysis was only carried out for the full set of 130 species on the CLASS program, and not at all on DIVINFRE.

Program DIVINFRE—The sequence of divisions, and the species on which these were based, was the same for normal analysis on DIVINFRE as for DIVINF (e.g. *Mesomelaena tetragona*, *Hovea chorizemifolia*, *Casuarina fraseriana*, *Patersonia rudis*, *Lyginia tenax*, *Eucalyptus wandoo*, *Pteridium esculentum* and others). However, the grouping of plots was markedly altered by two revision cycles. The heterogeneous groups disappeared and there was marked improvement in the homogeneity of the revised groups.

The decrease in the number of species used in the analysis appeared to have led to a loss of some of this homogeneity, presumably because the revision took place on a narrower basis. However, strongly-defined groups, particularly those occurring on loamy gravels in the high-rainfall zone, retained their integrity. The price for the improvement gained by revision was the loss of simplicity in the divisive process.

TABLE 2

Comparison of indicator groups derived by divisive monothetic classification and principal component analysis.

Species groups derived by inverse information analysis based on 55 species, 172 plots from northern sector.

(Ordination groups which have similar distribution patterns are bracketed).

Group No.	Sequence of Decisions	Component Species	Corresponding Ordination Groups
32	+++	<i>Eucalyptus wandoo</i> , <i>Loxocarya flexuosa</i>	Wandoo Brofer Drygra
33	+ + -	<i>Hakea lissocarpa</i>	
22	+ - +	<i>Patersonia rudis</i> , <i>Styphelia tenuiflora</i>	
23	+ - -	<i>Leptomeria cunninghamii</i> , <i>Leucopogon capitellatus</i> , <i>Leucopogon propinquus</i>	Fregra
18	- + +	<i>Eucalyptus patens</i> , <i>Leptospermum ellipticum</i> , <i>Synaphea petiolaris</i>	Fermo Browet Bromo
19	- + -	<i>Dampiera alata</i> , <i>Leptocarpus scariosus</i> , <i>Mesomelaena tetragona</i>	Brofem Browet Bromo
24	- + +	<i>Adenanthos barbigera</i> , <i>Persoonia elliptica</i> , <i>Phyllanthus calycinus</i>	Gramed Fregra
28	- - + +	<i>Daviesia pectinata</i>	Dryslag
36	- - + - +	<i>Casuarina fraseriana</i> , <i>Trymalium ledifolium</i>	Fregra Sangra
37	- - + - -	<i>Grevillea wilsonii</i> , <i>Hakea ruscifolia</i>	Sangra Dryslag
10	- - - - +	<i>Petrophile striata</i> , <i>Pimelea suaveolens</i> , <i>Hakea cyclocarpa</i> , <i>Baeckea camphorosmae</i>	Drygra Eagsan Brofem
30	- - - - - + +	<i>Sphaerolobium medium</i>	Eagsan
38	- - - - - + - +	<i>Lyginia tenax</i> , <i>Patersonia occidentalis</i>	Sanlea
39	- - - - - + - -	<i>Conospermum stoechadis</i> , <i>Hibbertia polystachya</i> , <i>Petrophile linearis</i> , <i>Isopogon dubius</i> , <i>Dasygogon brcmeliaefolius</i>	Sanlea Eagsan Samorg
16	- - - - - - +	<i>Adenanthos obovata</i> , <i>Banksia littoralis</i> , <i>Melaleuca preissiana</i> , <i>Hakea ceratophylla</i>	Samorg Verwet
20	- - - - - - +	<i>Diplolaena microcephala</i> var. <i>drummondii</i> , <i>Hibbertia lineata</i> , <i>Trymalium spathulatum</i>	Dryfer Fehira
26	- - - - - - - +	<i>Banksia attenuata</i> , <i>Nuytsia floribunda</i> , <i>Stirlingia latifolia</i>	Sanlea Eagsan
34	- - - - - - - +	<i>Dillwynia cinerascens</i> , <i>Gastrolobium calycinum</i>	Dryfer Drinf
35	- - - - - - - -	<i>Agonis linearifolia</i> , <i>Bossiaea aquifolium</i> , <i>Kingia australis</i> , <i>Leucopogon oxycedrus</i> , <i>Lysinema ciliatum</i>	Wetal Grahir Bromo Sanlea

Agglomerative polythetic classification.

Program CLASS—The CLASS program, being polythetic and agglomerative, operates on a markedly different principle to DIVINF and DIVINFRE, and consequently its output is also quite different. The numerical printout traces the progress of fusion from single individuals (plots) to progressively larger and larger groups, until the number of groups is reduced to the number specified, which in this case was again twenty. At this point, the groups are defined by their identification number and by enumeration of

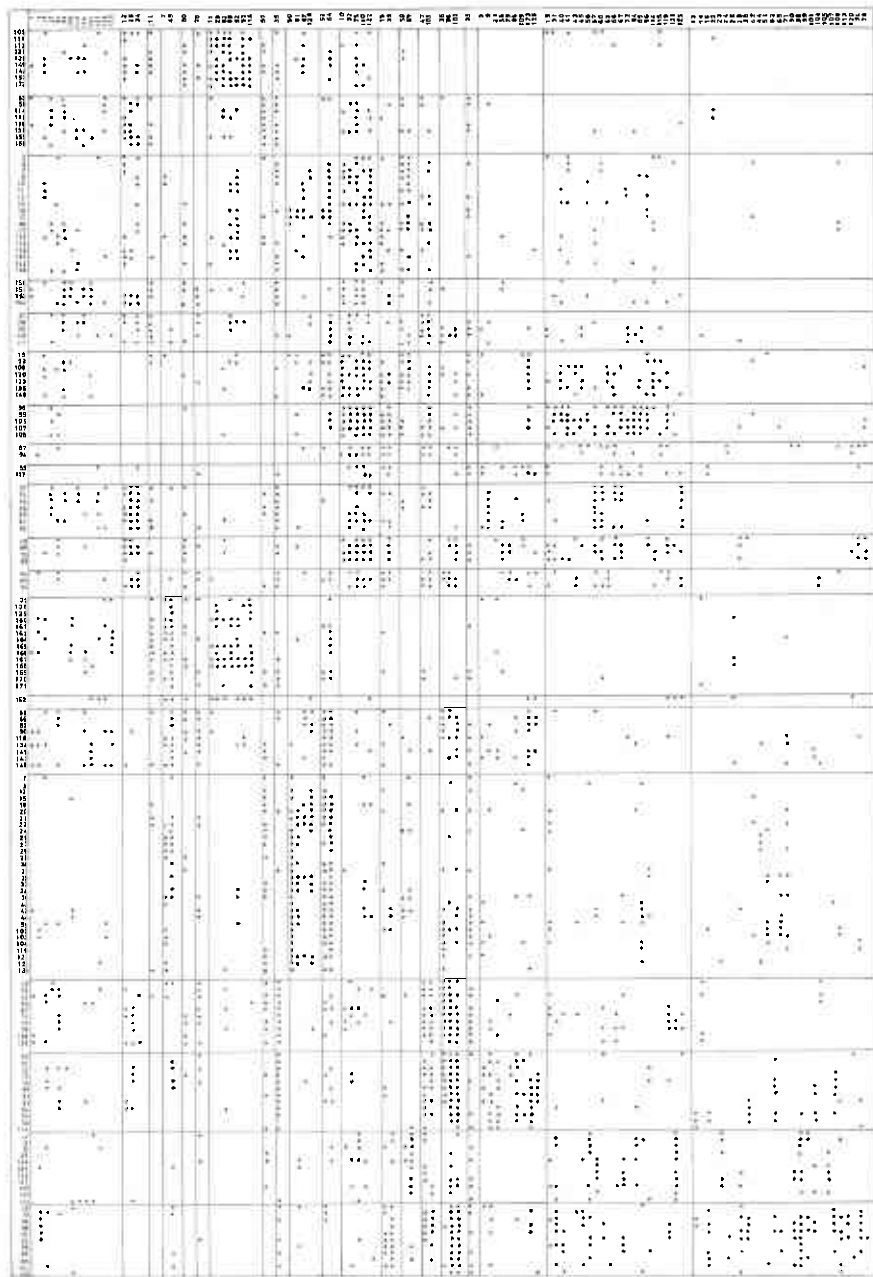


Figure 19

Two-way table of ecological sample plots and indicator species, arranged in groups on the basis of agglomerative polythetic information analysis (program CLASS, 172 plots, 130 species). Each column represents an individual indicator species; each row refers to an individual plot. The presence of a species in a particular plot is indicated by a dot. Plot groups derived by normal analysis are delineated by horizontal lines; species groups derived by inverse analysis are delineated by vertical lines.

their components. The graphical output comes in at this point and traces the subsequent stages of fusion until all groups coalesce into one. Because the process of fusion is not based on one but on all the species, it is virtually impossible to trace, short of complete plot/species enumeration prior to each fusion. For the inverse analysis, the fusion of species into groups is based on all plots, and its logic is again virtually impossible to trace. The final result of the analyses is shown in Figure 19.

The plot groups resulting from the normal analysis of 130 species appeared to be very tightly defined by the species found on them. For instance, Group No. 299, containing five plots, is defined by five occurrences of *Acacia strigosa*, *Hovea chorizemifolia*, *Styphelia tenuiflora*, *Patersonia rudis*, *Daviesia pectinata*, *Mesomelaena sp. nov.*, *Conostylis setigera*, *Daviesia rhombifolia*, *Lepidosperma scabrum* and *Lomandra purpurea*. The first five of these came very close to each other on principal component analysis, and all are common on dry, infertile gravels in the eastern zone. All five plots occur near the eastern boundary of the survey area. All but one of these plots occur together in a group resulting from the analysis based on 55 species, and three of them are still placed in the same group in the analysis based on only 18 species.

Similarly, Group No. 314, containing nine plots, is tightly defined by nine occurrences of *Leucopogon capitellatus* and *Lasiopetalum floribundum*, seven of *Acacia urophylla* and *Clematis pubescens* and six of *Adenanthos barbiger*, *Kennedia coccinea*, *Pteridium esculentum* and *Hovea chorizemifolia*. These species come again close together on principal component analysis, and are found together in the field on gravels close to the western margin of the Plateau, where the rainfall is high; they are indicators of continuum segment T. Most of the plot groups recur in analyses based on 55 and 18 species respectively.

The disintegration of homogeneous plot groups with the reduction of the number of species used appears to be much less serious than in the case of DIVINF, and the overall level of clustering is also increased. Surprisingly, the grouping of species by inverse analysis is not as good, consisting chiefly of either very large unmanageable groups or small groups of one or two species.

Comparison of classification methods.

An overall comparison of the various outputs is thus possible. The agglomerative polythetic approach appears superior to the monothetic divisive approach in grouping of plots which apparently are part of a continuum. It is much more robust. The groups defined by it correspond well to segments of the continuum derived by principal component analysis, and can be readily referred to known habitats.

The chief limitation of the agglomerative polythetic approach is that the decisions, being made on a very broad basis, are difficult to trace. The defect is aggravated in this particular case by the relatively poor results of the inverse analysis. The original simplicity of the divisive process in DIVINF is lost in the revision of initial allocations in DIVINFRE. The dilemma of the classificatory programs is that two of them (DIVINFRE and CLASS) arrive at good groupings by complex processes, whereas the third (DIVINF) uses a very simple and direct approach, but produces groupings which are poor. This limits the usefulness of classificatory programs in developing a simple but reliable method for allocating new observations to an existing framework.

3. ALLOCATION OF NEW OBSERVATIONS TO SEGMENTS OF THE CONTINUUM DEFINED BY PRINCIPAL COMPONENT ANALYSIS

Nature of data collected on broad-scale surveys

The precision data collection for the initial study of the vegetation (total enumeration of all trees by diameter, and cover estimate of all undergrowth species averaged over 16, one-square-metre quadrats) could not be maintained in any broad-scale survey. For this purpose, all that could be done at any one observation point would be some quantitative estimate of the occurrence of selected species with proven indicator value. Furthermore, for ease of booking of observations in the field, and for subsequent processing, all information for one observation point should not occupy more than one line.

To satisfy these restraints, a field booking sheet was designed on which the observation point was identified by six co-ordinates. As any data entered in the last two spaces of a punch card caused difficulties in processing on the local computer, the last three spaces were left blank. On the remaining 71 spaces (80-6-3), the indicator species were arranged in their alphabetical order, one space per species. Their occurrence was rated on a scale 0 to 5, defined separately for trees, shrubs and perennial herbs.

Rating of trees was based on an area of 40 metre radius from the observation point, and took the following form:

- 0 — Absent.
- 1 — One or two trees.
- 2 — Three to five trees.
- 3 — More than five trees, but contributing less than one third of total stand.
- 4 — Between one third and one half of total stand.
- 5 — More than one half of total stand.

Rating of undergrowth species was based on an area of 20 metre radius from the observation point, and took the following form:

- 0 — Absent.
- 1 — Very rare—seen only after careful search.
- 2 — Present, observable, but in small numbers only.
- 3 — Common locally, but not uniformly over the whole area.
- 4 — Common over the whole area.
- 5 — Completely dominating undergrowth.

The ratings do not conform to any standard vegetation parameter, such as cover density, frequency or abundance. They may approximate Curtis and McIntosh's (1951) importance value, but were not derived by detailed combining of relative frequency, relative density and relative dominance. They were devised to give rapid estimates of the relative importance of all 71 species at an observation point. In practice, an experienced observer was able to carry out 15 to 25 such observations per day, spread along a three to five kilometre traverse. Allowing for travel to the survey area, location of traverse and other ancillary tasks, each observation averages 15 minutes.

Given these basic data, the main task was the allocation of any observation to an appropriate segment of the continuum. There was quite a considerable range of alternatives. The difference between the survey data and the data

used in the basic study precluded the use of the most obvious solution, that is the calculation of the component scores for each observation spot. This could then have been used to plot a separate map for each component, and the segment would then be defined by combination of the four components on an overlay. Alternatively, the segments could have been defined directly by specifying the approximate lower and upper limits on each component. Neither method would be free of inherent problems. However, as the survey data were of a much lower standard, some alternative method was needed. The simplest approach would have been to parallel the monothetic divisive classification:

decision 1 — if species A is present, go to decision 2, if absent go to decision 3;

decision 2 — if species B is present, place in category I, if absent, place in category II etc.

The choice would have gone against all past experience with this classification, which appears least suited to dealing with a continuum.

In view of the better performance of the polythetic agglomerative classification, this appeared to be a more suitable alternative, in particular as far as the use of a number of species rather than a single species is concerned.

The next point requiring decision was how the full spectrum of species was to be used in allocating the plots.

Allocation by matching

Two alternatives were considered. One was the matching, species by species, of the "normal" expected ratings for the various segments, with actual ratings at the particular observation spot. The observation would be placed into that segment with which it scored the greatest number of similarities or coincidences.

The chief limitation of the matching approach is the definition of the "normal" composition of a segment. These do not approach even distantly the precisely-defined, narrow associations of the Southern European School. Some of them are the main type of undergrowth vegetation over tens of thousands of hectares. As segments of a continuum they must be expected to vary greatly about the central nodum, to the point where they could be equally placed in either of two neighbouring segments.

Yet another problem is the value that should be placed on the individual species matches. A match involving a species which is a precise indicator of a narrow range of environmental conditions, such as *Diplolaena microcephala* var. *drummondii*, is obviously more significant than a match involving a mediocre indicator of a broad range of environmental conditions, such as *Lepidosperma angustatum*. This is further aggravated by the fact that some of the best indicators are never very prominent visually and thus would receive low ranking (e.g. *Chorizema ilicifolium*), whereas others, less precise indicators, tend to dominate the picture (e.g. *Macrozamia riedlei*). Some of the species (e.g. *Eucalyptus marginata*) can only be considered indicators in the negative sense, in that their absence indicates a major departure from average conditions.

Despite all these possible contra-indications, the approach has been successfully applied to two batches of survey data. In one of the cases, junior technical staff used a set of strips showing "normal" composition patterns for the segments (Fig. 20). The matches were classed in three categories:

- (a) No match—the species should be absent.
- (b) Low match—the species should be present, but its absence is not critical. Its presence is indicative and confirmatory, but requires collaboration by stronger indicators.
- (c) Key match—the species should be present. Its absence is a contra-indication, unless outweighed by a strong occurrence of other species from the same group. Its presence is significant, and can only be ignored if outweighed by the absence of other species from the same group.

The operation was quite mechanical, to a set of visual specifications. The results were quite satisfactory, though the progress was slow. Difficult transitional plots, or plots with abnormal occurrences of one indicator species, were referred to senior staff for final allocation. The matching of the second batch was done by a senior technical assistant thoroughly acquainted with the significance of the various species. In this case, the visual specification was used chiefly as a check on the more rapid mental decision making.

Some consideration was given to converting the visual matching to computer matching, in which the comparison would be quantified (e.g. the score of -2 for failure of a key match, -1 for failure of a low match and $+1$ for low match and $+2$ for key match) and the scores summed up. The new observation would be placed into that segment in which it had the highest positive matching score. Although not particularly difficult, the programming of this approach appeared likely to be time consuming. In addition, the problem of disparity in the level of occurrence of broad and precise indicators would have to be dealt with because the tendency is for the greatest noise to come from those species which have least information to give.

Allocation by computer

As an aid to the construction of a complex decision program, the use of decision tables has been advocated by several workers. Cipra *et al* (1969) used the decision tables in allocating soils to their appropriate category in the Seventh Approximation of the Soil Classification. Although the number of samples and the range of soil types studied by them were relatively small, they encountered many problems. The earlier discussions of the technique by King (1967) and Dixon (1964) dealt with even smaller problems. The use of special computer languages, such as DETAB-X, LOGTAB and FORTAB, was considered desirable by King. The decision table is essentially a logical aid, a bridge between the specification of categories and the flow-chart of the decision program. In this particular case, it was felt that the logic of the program for allotting new observations to appropriate segments of the continuum could be better derived from the model of the continuum itself. This is then the second major alternative.

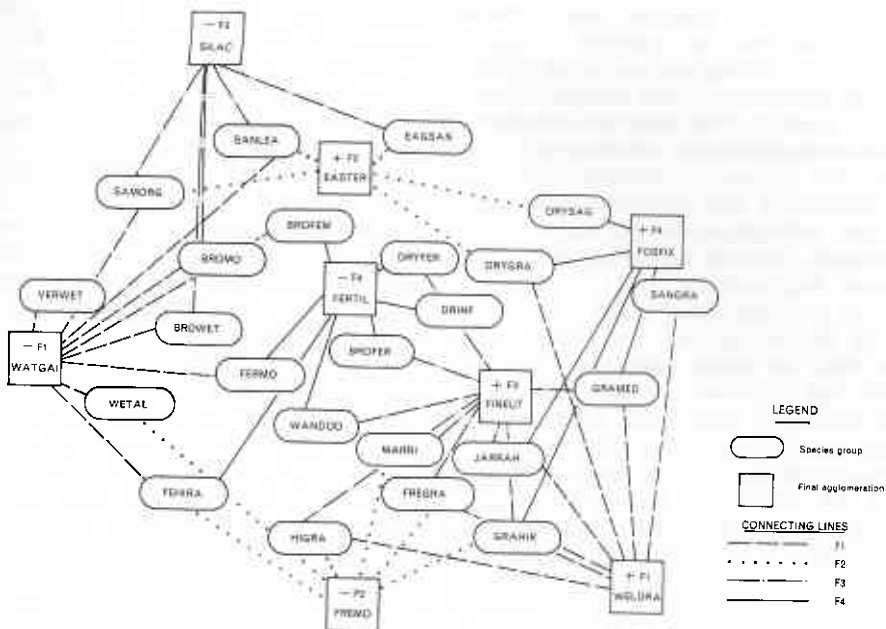


Figure 22

Diagram illustrating the second stage of allocation of new observations to site-vegetation types by the use of computer program ALLOT.

When the agglomeration was completed, the decision process commenced. At first, the shortest route was taken, that is progressive division into smaller and smaller segments of the continuum. The first decision was on the basis of a trend towards waterlogging and low topographical position ($-F1$) or towards adequate or excessive drainage and high topographic position ($+F1$). It became immediately obvious that the first, and therefore the most critical, decision was separating the least-clearly defined groups on the basis of broad trends. Admittedly, provision could have been made for revision within each sub-group, but that would have virtually amounted to a duplication of each decision. The obvious alternative was to separate the most distinctive and extreme groups first, and progressively extend the process towards the centre of the multi-dimensional continuum. The decisions would thus become progressively more difficult, but the impact of any misallocation would be less serious. It can be best visualised as the difference between slicing an onion into halves, then quarters, sixteenths and so forth, or taking it apart by progressively removing the outer layers. The number of necessary decisions would depend on the distance from the centre. An observation from an extreme habitat, consisting of clear-cut indicators, would be allotted to its appropriate segment by only three or four decisions. An observation from a site average in all aspects would require two or three times that number of decisions.

Testing and optimization of the program.

The development of the program took much longer than was anticipated. The first version was tested against a portion (approximately one-sixth) of the batch of survey data which it was meant to classify. The

output of the program was so designed that the logic of all successive decisions could be retraced in the case of a misallocation, and the error corrected. Misallocations were detected by comparing the actual species array with the species array appropriate to the segment into which the observation was placed. The amended program was then used for the next run, and any misallocations detected by it were once more corrected. There were several sources of misallocation. The first decision sought overwhelming tendency in one direction or another, for example overwhelmingly (4 to 1) more indicators of well drained than of waterlogged sites. The subsequent decision allowed for progressively less overwhelming trends, and the ratios were decreased to 2 to 1. Ultimately, the decision was merely more of one than the other, that is any departure from the 1 to 1 ratio. It was found that this assumption was too glib, and the ratios had to be repeatedly adjusted. It was also found necessary to base some decisions solely on the presence of the key indicators, in that some of the best indicators tended to be swamped if compared with their more common antagonist from the opposite end of the continuum. The fact that the segments were not precisely defined categories also created many difficulties. As the process approached the centre of the continuum, it was increasingly necessary to allow for the possibility that the earlier decision did not exactly coincide with the interface between two segments, so that, although the bulk of the plots had been placed in the correct segments, the remainder would need to be allowed for in subsequent decisions. Thus, with successive runs the precision of allocation increased, but so also did the complexity of the program. At times, the corrections created more misallocations than they avoided, and had to be toned down. The development of the program came nearer to the human-computer interaction advocated by Williams (1966) and Gibbons *et al* (1968) than any other part of this study.

Evaluation of the program.

Finally, when the misallocations appeared to have reached a virtually irreducible level, the remaining five-sixths of the survey data were processed, and the results entered on the survey framework. It resulted in a very satisfactory representation of the vegetation distribution, as will be discussed in the section dealing with site-vegetation mapping (Havel, 1975). To that extent the program was successful, but the expenditure of time involved in converting human judgement into a precise set of decision sequences was excessive. It could only be justified if subsequently the program could be used for a very large batch of data. For a limited batch of data, the allocation could be carried out more rapidly by experienced technical personnel without the added expense of computer time. It supports the claims of Williams and Gibbons *et al* that human judgement will be hardest to replace by computers.

SECTION VII

CONCLUSIONS

The feasibility of using plant indicators to define sites in the northern jarrah region has been demonstrated. The task has not been without problems, in that the vegetation and the associated environmental factors form a complex continuum which does not lend itself to easy manipulation. It is difficult to delineate any clearly defined groups or types, with the result that typing and mapping of vegetation cannot be reduced to a simple mechanical process. On the positive side, the nature of the continuum ensures that the effect of any misallocation is minimal.

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APPENDIX 1

Table of potential indicator species with respect to their performance in first approximation on principal component analysis and principal component analysis based on trees only.

(= strong, — weak bias towards negative component scores; ++ strong, + weak bias towards positive component scores).

No.	Species (Name)	Card on which it occurs	Distribution Patterns in component space						New numbers for second approximation
			On 55 species normal				On 14 trees varimax		
			F1	F2	F3	F4	F1	F2	
1	<i>Acacia alata</i>	1	—	+					
2	<i>Acacia extensa</i>	1		+		—			
3	<i>Acacia strigosa</i>	1	+						
4	<i>Acacia urophylla</i>	1	+	+					
5	<i>Acacia</i> sp.	1							
6	<i>Adenanthos barbiger</i>	1	++	=	+	+	++	=	1
7	<i>Adenanthos obovata</i>	1	=	+	+				2
8	<i>Agonis linearifolia</i>	1		+	=	=		++	3
9	<i>Baeckea camphorosmae</i>	1	=	+	=		—		4
10	<i>Bossiaea aquifolium</i>	1	++	++	++		+	—	5
11	<i>Bossiaea ornata</i>	1						+	
12	<i>Bossiaea pulchella</i>	1							
13	<i>Casuarina humilis</i>	1							
14	<i>Conospermum stoechadis</i>	1	=	—					6
15	<i>Dampiera alata</i>	1	—		=	—	—	+	7
16	<i>Dasyopogon bromeliaefolius</i>	1	=					+	8
17	<i>Daviesia pectinata</i>	1	—	=					9
18	<i>Daviesia longifolia</i>	1							10
19	<i>Macrozamia riedlei</i>	1	+	++		—		=	11
20	<i>Melaleuca scabra</i>	1							
21	<i>Hypocalymma angustifolium</i>	2		+	=	—		+	12
22	<i>Isopogon dubius</i>	2	—	—		+			13
23	<i>Kingia australis</i>	2	—		=				14
24	<i>Kunzea micromera</i>	2			—				15
25	<i>Lasiopetalum floribundum</i>	2	++		+	++	++	=	16
26	<i>Lepidosperma angustatum</i>	2	=		—		+		17
27	<i>Leptocarpus scariosus</i>	2	=					++	18
28	<i>Leptospermum ellipticum</i>	2	=	++	—	+	—	+	19
29	<i>Lechenaultia biloba</i>	2							20
30	<i>Leucopogon capitellatus</i>	2	+	++	+		++		21
31	<i>Leucopogon oxycedrus</i>	2					+	—	22
32	<i>Leucopogon propinquus</i>	2	+	++					23
33	<i>Leucopogon verticillatus</i>	2	++	++	+	+	+	=	24
34	<i>Leucopogon cordatus</i>	2	=						
35	<i>Lomandra sonderi</i>	2	+				+	—	
36	<i>Lomandra caespitosa</i>	2							
37	<i>Loxocarya fasciculata</i>	2	—						
38	<i>Loxocarya cinerea</i>	2		+					
39	<i>Lyginia tenax</i>	2	—	+	++	=			
40	<i>Lysinema ciliatum</i>	2	—		+	—			
41	<i>Mesomelaena tetragona</i>	3	=		—				25
42	<i>Patersonia occidentalis</i>	3	—			=			26
43	<i>Patersonia rudis</i>	3		—		+			27
44	<i>Phyllanthus calycinus</i>	3			+				28
45	<i>Petrophile linearis</i>	3	=						

No.	Species (Name)	Card on which it occurs	Distribution Patterns in component space						New numbers for second approximation
			On 55 species normal				On 14 trees varimax		
			F1	F2	F3	F4	F1	F2	
46	<i>Petrophile striata</i>	3							
47	<i>Pimelea suaveolens</i>	3							
48	<i>Pteridium esculentum</i>	3	++	++	++				29
49	<i>Sphaerolobium medium</i>	3			—				30
50	<i>Stirlingia latifolia</i>	3			—				31
51	<i>Styphelia tenuiflora</i>	3	++	—		++			32
52	<i>Synaphea petiolaris</i>	3	—	+					33
53	<i>Trymalium ledifolium</i>	3	+	+					34
54	<i>Trymalium spathulatum</i>	3	—	+	—	—			35
55	<i>Conostylis aculeata</i>	3							
56	<i>Xanthorrhoea preissii</i>	3							
57	<i>Dryandra sessilis</i>	3	+			—			
58	<i>Gastrolobium calycinum</i>	3		—					
59	<i>Grevillea wilsonii</i>	3	+	—		++	+		
60	<i>Grevillea pulchella</i>	3		—	—	+	+		
61	<i>Hakea cyclocarpa</i>	4		—	—	+		—	36
62	<i>Hakea ceratophylla</i>	4	=	++		+		++	37
63	<i>Hakea varia</i>	4	=	++				++	38
64	<i>Hakea lissocarpha</i>	4		+	—	—		=	39
65	<i>Hakea ruscifolia</i>	4		—					
66	<i>Hakea undulata</i>	4							
67	<i>Hemigenia pritzelii</i>	4							
68	<i>Hibbertia montana</i>	4	+						
69	<i>Hibbertia huegelii</i>	4							
70	<i>Hibbertia lineata</i>	4	++			—			
71	<i>Hibbertia subvaginata</i>	4			+				
72	<i>Hovea chorizemifolia</i>	4					+		
73	<i>Astroloma ciliatum</i>	5	++						
74	<i>Astroloma pallidum</i>	5							
75	<i>Scaevola striata</i>	5							
76	<i>Xanthosia candida</i>	5	++						
77	<i>Gompholobium marginatum</i>	5			—				
78	<i>Dryandra nivea</i>	5							
79	<i>Tetrariopsis octandra</i>	5							
80	<i>Kennedia prostrata</i>	5	+						
81	<i>Hibbertia amplexicaulis</i>	5	+		=				
82	<i>Xanthorrhoea gracilis</i>	5	+						
83	<i>Caustis dioica</i>	5	—						
84	<i>Cyathochaete clandestina</i>	5							
85	<i>Grevillea synapheae</i>	5	+						
86	<i>Lepidosperma tenue</i>	5							
87	<i>Dilwynia cinerascens</i>	5			—	+			40
88	<i>Diplolaena microcephala</i>	5	++						
	var. <i>drummondii</i>	5	++	++	=	=			41
89	<i>Leptomeria cunninghamii</i>	5	+						42
90	<i>Hibbertia lineata</i> *	5	++			—			43
91	<i>Hibbertia polystachya</i>	5	=		+	—			44
92	<i>Petrophile macrostachya</i>	5							
93	<i>Jacksonia sternbergiana</i>	6							
94	<i>Boronia spathulata</i>	6	++	+				+	
95	<i>Acacia pulchella</i>	6							
96	<i>Hibbertia lasiopus</i>	6	+				+	—	

No.	Species (Name)	Card on which it occurs	Distribution Patterns in component space						New numbers for second approximation	
			On 55 species normal				On 14 trees varimax			
			F1	F2	F3	F4	F1	F2		
97	<i>Isopogon sphaerocephalus</i>	6	+					+	-	
98	<i>Hibbertia amplexicaulis*</i>	6	+					+	-	
99	<i>Gompholobium polymorphum</i>	6								
100	<i>Lomandra endlicheri</i>	6	++							
101	<i>Calytrix flavescens</i>	6							-	
102	<i>Xanthosia ciliata</i>	6							-	
103	<i>Opercularia hispidula</i>	6								
104	<i>Conostylis setigera</i>	6								
105	<i>Persoonia saccata</i>	6								
106	<i>Grevillea bipinnatifida</i>	6	+						-	
107	<i>Petrophile seminuda</i>	6								
108	<i>Mesomelaena sp. nov.</i>	6								
109	<i>Hakea prostrata</i>	6	=							
110	<i>Dryandra bipinnatifida</i>	6	-					-	-	
111	<i>Cavistis dioica*</i>	6	-						-	
112	<i>Trymalium ledifolium*</i>	6								
113	<i>Eucalyptus marginata</i>	7						+		45
114	<i>Eucalyptus calophylla</i>	7								46
115	<i>Eucalyptus patens</i>	7						-		47
116	<i>Eucalyptus wandoo</i>	7						=	-	48
117	<i>Banksia grandis</i>	7						++		49
118	<i>Melaleuca preissiana</i>	7						-	++	50
119	<i>Nuytsia floribunda</i>	7						-		51
120	<i>Casuarina fraseriana</i>	7						++	=	52
121	<i>Banksia attenuata</i>	7						-	-	53
122	<i>Persoonia elliptica</i>	7								54
123	<i>Banksia littoralis</i>	7							++	55
124	<i>Eucalyptus accedens</i>	7								
125	<i>Eucalyptus megacarpa</i>	7							-	
126	<i>Eucalyptus rudis</i>	7								
127	<i>Persoonia longifolia</i>	7						++	=	
128	<i>Melaleuca rhapsiophylla</i>	7						-	+	
129	<i>Casuarina huegeliana</i>	7								
130	<i>Banksia littoralis</i> var. <i>seminuda</i>	7								
		7								
131	<i>Banksia menziesii</i>	7								
132	<i>Banksia ilicifolia</i>	7								

* Erroneously duplicated. Already dealt with on earlier cards.

APPENDIX 2

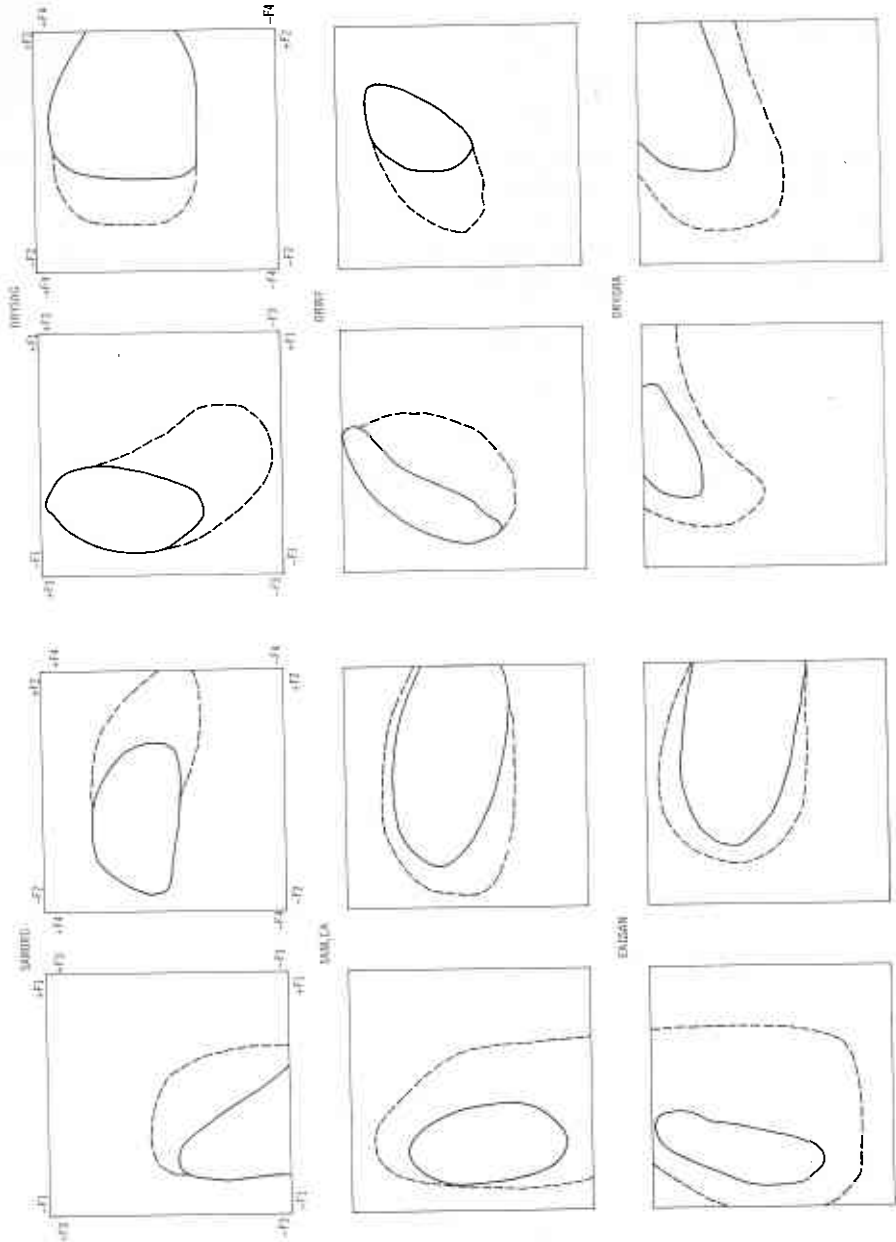
Enumeration of indicator groups

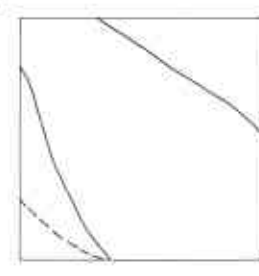
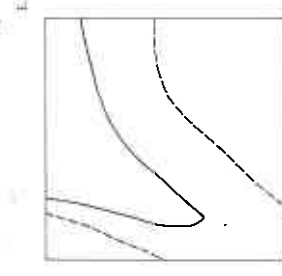
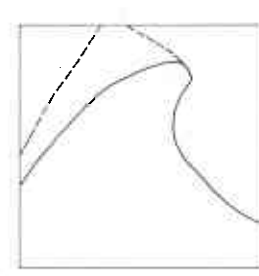
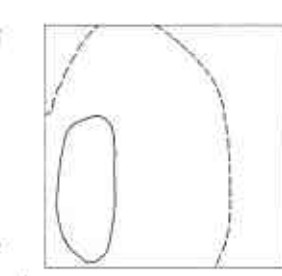
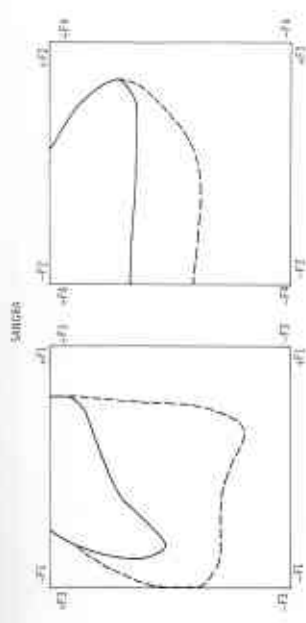
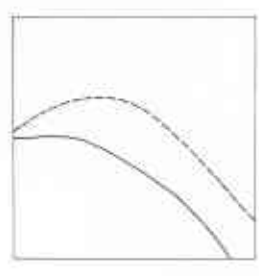
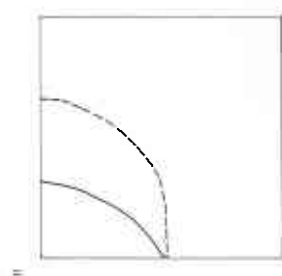
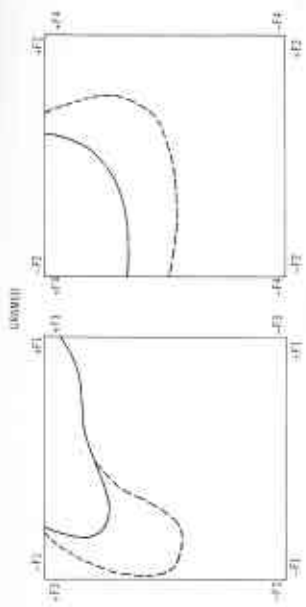
- (1) *Dasyogon bromeliaefolius*, *Adenanthos obovata*. SANDs, Moist, heavy ORGANIC matter incorporation in topsoil—SAMORG.
- (2) *Banksia attenuata*, *Caustis dioica*, *Conospermum stoechadis*, *Hibbertia polystachya*, *Leucopogon cordatus*, *Nuytsia floribunda*, *Patersonia occidentalis*. SANDs, strongly LEAched—SANLEA.
- (3) *Hakea cyclocarpa*, *Isopogon dubius*, *Sphaerolobium medium*, *Stirlingia latifolia*. EASTern Gravelly SANDs—EAGSAN.
Stirlingia latifolia had a somewhat narrower range on the second component, not occurring on plots with high +F2. It was included here to avoid creating too many groups.
- (4) *Daviesia pectinata*, *Hakea ruscifolia*. DRY SANDy GravelS—DRYSAG.
- (5) *Casuarina humilis*, *Dillwynia cinerascens*. DRY soils of INTERmediate Fertility—DRINF.
- (6) *Acacia strigosa*, *Patersonia rudis*, *Pimelea suavolens*, *Styphelia tenuiflora*. DRY GRAvels—DRYGRA.
- (7) *Casuarina fraseriana*, *Grevillea wilsonii*. SANDy GRAvels, medium rainfall zone—SANGRA.
- (8) Jarrah (*Eucalyptus marginata*) has, in view of its importance, been retained as a group, though its wide range of occurrence makes it of limited use as an indicator. There are several understorey species, such as *Hibbertia montana* and *Xanthorrhoea gracillis*, whose range is very similar.
- (9) Marri (*Eucalyptus calophylla*) has been retained for the same reasons as *E. marginata*. Understorey species with a comparable range of occurrence are *Bossiaea ornata*, *Dryandra nivea* and *Xanthorrhoea preissii*.
- (10) *Adenanthos barbiger*, *Banksia grandis*, *Hovea chorizemifolia*, *Persoonia longifolia*. GRAvels in MEDium rainfall zone—GRAMED.
- (11) *Acacia urophylla*, *Bossiaea aquifolium*, *Lasiopetalum floribundum*. GRAvels in HIGH Rainfall zone—GRAHIR.
- (12) *Leucopogon capitellatus*, *Leucopogon propinquus*, *Macrozamia riedlei*, *Phyllanthus calycinus*, *Trymatium ledifolium*. FRESH GRAvels (maximum development on admixture of lateritic gravels and fresh soils developed from underlying rocks)—FREGRA.
- (13) *Leucopogon verticillatus*, *Pteridium esculentum*. HIGH rainfall, predominantly GRAvelly soils—HIGRA. *Pteridium* differs slightly from *Leucopogon* in that it has a broader edaphic range, extending further on to fertile soils (high-F4).
- (14) *Hakea lissocarpha*. (*Kennedia coccinea* appears to have a comparable range, but has not been fully tested). BROad tendency towards higher FERTility—BROFER.
- (15) Wandoo (*Eucalyptus wandoo*) retained as a separate group because of its overall importance; closely resembles BROFER.
- (16) *Diplolaena drummondii*, *Hibbertia lineata*, *Gastrolobium calycinum*. DRY FERTile soils—DRYFER. *Gastrolobium calycinum* has a broader range than the other two species, and is intermediate between groups DRINF, BROFER and DRYFER.

- (17) *Trymalium spathulatum*. (*Chorizema ilicifolium* has a comparable, though somewhat narrower, range and is less common). FERTile loams in HIgh RAInfall zone—FEHIRA.
- (18) *Acacia extensa*, *Eucalyptus patens*, *Hypocalymma angustifolium*. FERtile MOist soils—FERMO.
- (19) *Agonis linearifolia*, *Eucalyptus megacarpa*. (*Lepidosperma tetraquetrum* and *Grevillea diversifolia* have comparable ranges, but have not been fully tested). *Eucalyptus megacarpa* occasionally extends on to drier ground. WET ALLuvium—WETAL.
- (20) *Baeckea camphorosmae*, *Dampiera alata*. BROad tendency towards FERtile Moist soils.—BROFEM.
- (21) *Kingia australis*, *Mesomelaena tetragona*, *Synaphea petiolaris*, *Lepidosperma angustatum*. BROad tendency towards MOist sites—BROMO. *Kingia australis* differs from the rest in having a narrower range on the second component, being absent from plots with high +F2.
- (22) *Leptocarpus scariosus*, *Leptospermum ellipticum*. BROad tendency towards WET sites—BROWET. The range of *Leptospermum* is slightly narrower than that of *Leptocarpus*.
- (23) *Banksia littoralis*, *Hakea ceratophylla*, *Hakea varia*, *Melaleuca preissiana*. (*Astartea fascicularis* has a comparable range, but has not been fully tested). VERy WET sites—VERWET.

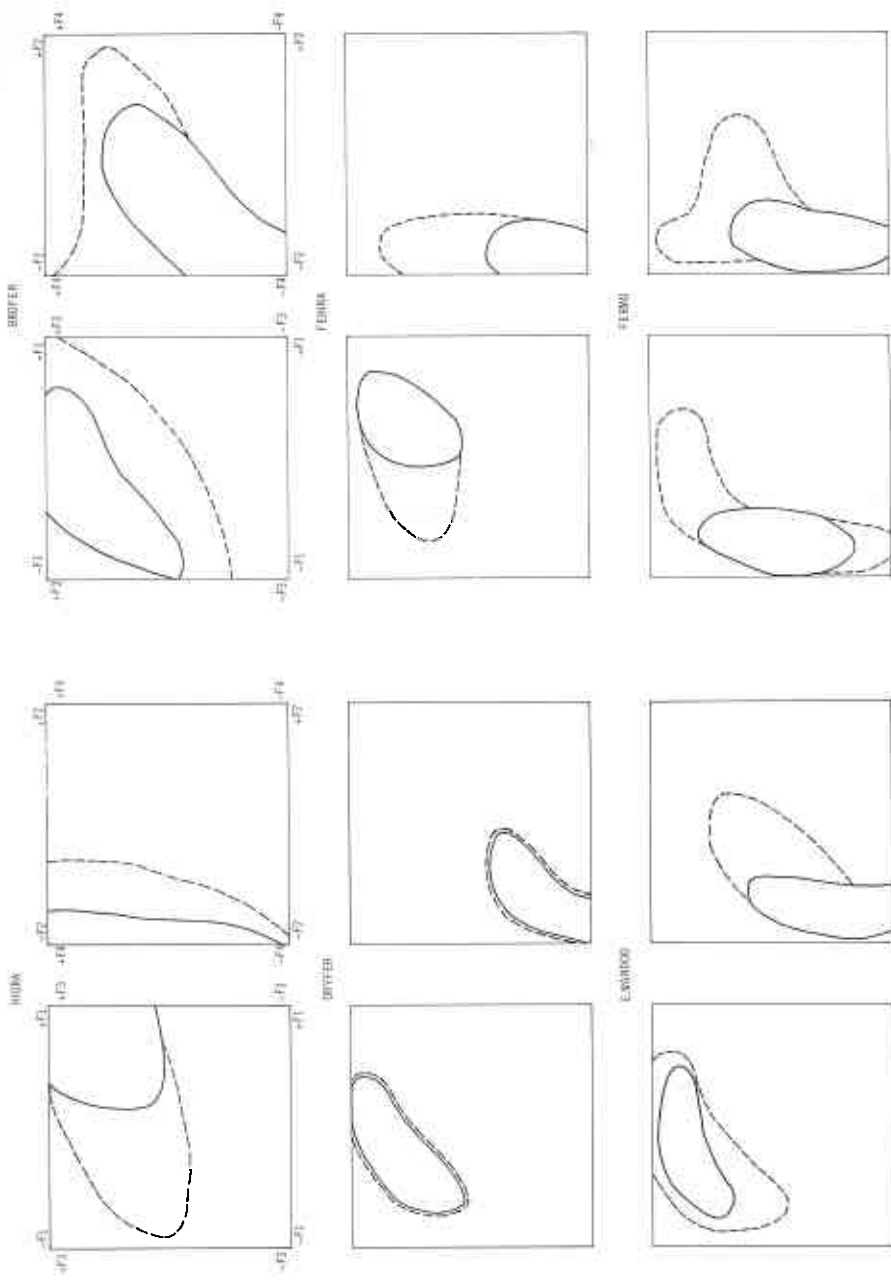
APPENDIX 3

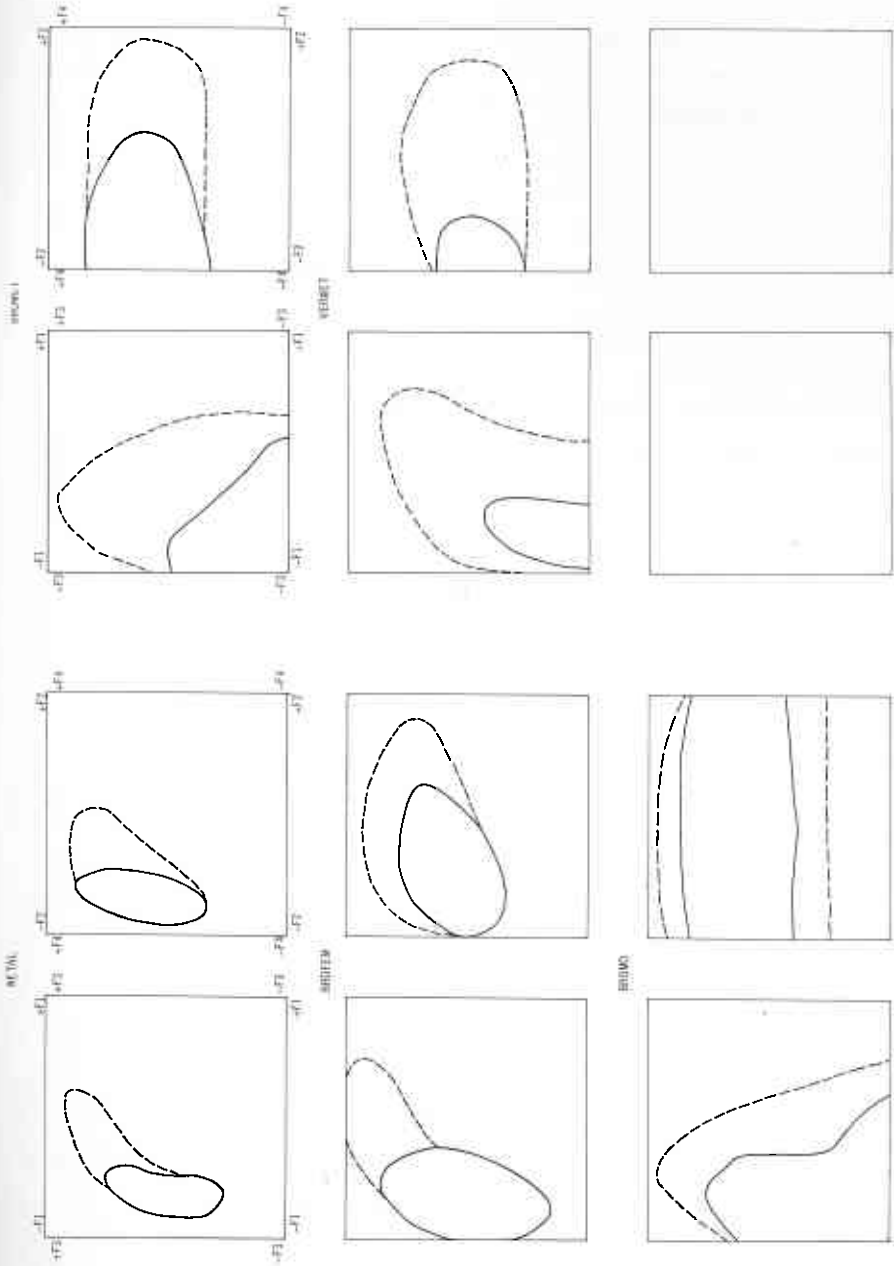
Diagrammatic representation of indicator groups within component space.





FIGURA





APPENDIX 4

Enumeration of continuum segments (site-vegetation types) in terms of composition, structure and environmental features.

SEGMENT A CO-ORDINATES high — F1, low — F2, high — F3, low ± F4.

PLOTS (147) (81, 85, 71, 93)

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
VERWET <i>Melaleuca preissiana</i> , <i>Banksia littoralis</i> , <i>Hakea ceratophylla</i> , <i>Hakea varia</i> .
BROWET <i>Leptocarpus scariosus</i> , <i>Leptospermum ellipticum</i> .
BROMO <i>Mesomelaena tetragona</i> , <i>Synaphea petiolaris</i> , <i>Lepidosperma angustatum</i> .

Less consistently :

SAMORG <i>Adenanthos obovata</i> , <i>Dasyopogon bromeliaefolius</i> .
FERMO <i>Hypocalymma angustifolium</i> , <i>Eucalyptus patens</i> , <i>Acacia extensa</i>
SANLEA <i>Lyginia tenax</i>

(b) TREE STRATUM

	RANGE	MEAN
GENERAL: Sparse, low stand	BASAL AREA (m ² /ha) 7-20	13
	HEIGHT (m) 16-23	19
COMPOSITION: <i>Melaleuca preissiana</i> , <i>Banksia littoralis</i> , <i>Eucalyptus calophylla</i> , <i>Eucalyptus patens</i> .		

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

	RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees) 0-3	2
GENERAL: Broad heads of valleys in eastern zone	ROCK OUTCROPS: Nil	

(d) SOIL

GENERAL: Grey sand over pale yellow or pale brown sand, often clay or organic-iron hardpan at depth. Plot 147 differs markedly in having much heavier texture and is not included in following figures.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	Nil		FIELD CAPACITY (%)	3-7	5
SILT + CLAY (%)	2-13	7	WILTING POINT (%)	1-3	2
DEPTH TO WATER TABLE (cm)	0-15		AVAIL. MOISTURE (%)	2-4	3

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.1-5.5	5.4	EXCH. Ca(me%)	0.7-3.7	1.5
N%	0.02-0.11	0.05	EXCH. Mg(me%)	0.4-2.1	0.9
P (ppm)	8-30	15	C.E.C. (me%)	6.5-10.3	8.2
K (me%)	0.02-0.53	0.16	SATURATION (%)	22-68	37

(e) BROAD DESCRIPTION

Wet, leached acid sands, waterlogged in winter, underlain by impermeable horizon. Plot 147 differs from the remainder both in soils and in vegetation, and is included solely to minimize the number of groups. It shares with them the very wet site conditions.

SEGMENT B CO-ORDINATES low \pm F1, medium to high + F2, high — F3, low \pm F4.
 PLOTS (144, 88, 86, 91, 92) (69) (83, 48, 84)

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
BROWET	<i>Leptocarpus scariosus</i> , less <i>Leptospermum ellipticum</i> .
BROMO	<i>Mesomelaena tetragona</i> , <i>Synaphea petiolaris</i> , <i>Lepidosperma angustatum</i> .
SAMORG	<i>Adenanthos obovata</i> , <i>Dasyogon bromeliaefolius</i> , <i>Petrophile linearis</i> .
SANLEA	<i>Conospermum stoechadis</i> , <i>Patersonia occidentalis</i> , <i>Hibbertia polystachya</i> , <i>Lyginia tenax</i>

Less consistently :

FERMO	<i>Hypocalymma angustifolium</i> , <i>Acacia extensa</i>
EAGSAN	<i>Sphaerobolium medium</i> , <i>Isopogon dubius</i>
BROFEM	<i>Baeckea camphorosmae</i> , <i>Dampiera alata</i>

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Very open forest to wood land	BASAL AREA (m ² /ha) 14-41	24
	HEIGHT (m) 13-28	21
COMPOSITION: <i>Eucalyptus marginata</i> , <i>Eucalyptus calophylla</i> , scattered understorey of <i>Banksia grandis</i>			

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees) 1-3	2
GENERAL: Upland depressions and broad valley heads, mainly in eastern zone	ROCK OUTCROPS: Nil		

(d) SOIL

GENERAL: Light grey sand over grey to pale yellow sand, somewhat heavier texture and compaction in subsoil. Plots 83, 48 and 84 approach loamy sand.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL % 0-26	3	FIELD CAPACITY (%)	2-12	5
SILT + CLAY (%) 3-22	7	WILTING POINT (%)	1-6	2
DEPTH TO WATER TABLE (cm)	2-90	AVAIL. MOISTURE (%)	2-5	3

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH 5.4-5.9	5.8	EXCH. Ca(me%) 0.1-2.0	1.0
N% 0.01-0.06	0.03	EXCH. Mg(me%) 0.1-1.4	0.6
P (ppm) 10-26	16	C.E.C. (me%) 1.7-9.5	6.2
K (me%) 0.05-0.22	0.10	SATURATION (%) 13-65	35

(e) BROAD DESCRIPTION

Leached infertile acid grey sands, moist to wet in winter, rapidly drying out in summer. Plot 69, with group WETAL, forms transition to segment D. Plots 83, 84, 48, with groups DRYGRA, SANGRA and GRAMED, form transition to segment E, and have slightly heavier texture.

SEGMENT D CO-ORDINATES high — F1, low ± F2, F3, F4.

PLOTS 80, 57, 50, 76, 72, 63, 73, 158, 82, 77, 66, 102.

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
BROWET	<i>Leptocarpus scariosus</i> , <i>Leptospermum ellipticum</i> .
BROMO	<i>Mesomelaena tetragona</i> , <i>Synaphea petiolaris</i> , <i>Lepidosperma angustatum</i> , <i>Kingia australis</i> .
BROFEM	<i>Dampiera alata</i> , to lesser degree <i>Baeckea camphorosmae</i> .
FERMO	<i>Hypocalymma angustifolium</i> , <i>Acacia extensa</i> , some <i>Eucalyptus patens</i> .

Less consistently :

BROFER	<i>Hakea lissocarpa</i> .
DRYSAG	<i>Daviesia pectinata</i>
WETAL	<i>Agonis linearifolia</i>

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Variable, frequently affected by dieback	BASAL AREA (m ² /ha)	11-38	21
	HEIGHT (m)	16-33	24
COMPOSITION: <i>Eucalyptus marginata</i> , <i>Eucalyptus calophylla</i> , slight admixture of <i>Eucalyptus patens</i>			

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees)	1-3	2
GENERAL: Lower slopes and floors of valleys	ROCK OUTCROPS: Isolated outcrops of secondary lateritic ironstone		

(d) SOIL

GENERAL: Orange-brown loamy sands and sandy loams over sandy clay or secondary lateritic ironstone.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	0-26	11	FIELD CAPACITY (%)	2-33	15
SILT + CLAY (%)	4-23	14	WILTING POINT (%)	1-12	6
DEPTH TO WATER TABLE (cm)	2-80	AVAIL. MOISTURE (%)	2-23	9

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.4-6.4	6.0	EXCH. Ca(me%)	0.4-3.4	1.3
N%	0.03-0.16	0.09	EXCH. Mg(me%)	0.1-3.1	0.9
P (ppm)	5-97	24	C.E.C. (me%)	0.1-1.4	0.7
K (me%)	0.01-0.40	0.18	SATURATION (%)	10-68	36

(e) BROAD DESCRIPTION

Orange-brown loamy sands or sandy loams, over impermeable horizon, on lower slopes and valley floors, seasonally waterlogged.

SEGMENT E. CO-ORDINATES low — F1, high + F2, low ± F3, low ± F4.

PLOTS 79, 67, 96, 101, 64, 39, 59, 120, 74, 75, 78, 52, 55.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
BROMO	<i>Mesomelaena tetragona, Synaphea petiolaris, Lepidosperma angustatum.</i>
BROFEM	<i>Baeckea camphorosmae, Dampiera alata, Kingia australis</i>
FERMO	<i>Hypocalymma angustifolium.</i>

Less consistently :

EAGSAN	<i>Sphaerolobium medium, Hakea cyclocarpa.</i>
DRYSAG	<i>Daviesia pectinata.</i>
BROWET	<i>Leptocarpus scariosus, Leptospermum ellipticum.</i>
GRAMED	<i>Adenanthos barbiger, Banksia grandis.</i>
SANLEA	<i>Patersonia occidentalis, Hibbertia polystachya.</i>

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Variable	BASAL AREA (m ² /ha) 0.5-43	20
	HEIGHT (m) 14-30	23
COMPOSITION: Chiefly <i>Eucalyptus marginata</i> , light admixture of <i>Eucalyptus calophylla</i> , few <i>Banksia grandis</i>			

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees) 1-5	3
GENERAL: Lower slopes and depressions	ROCK OUTCROPS: Mostly nil.		

(d) SOIL

GENERAL: Grey, yellow or brown sands and loamy sands with admixture of lateritic gravel which tends to increase with depth; orange mottling in subsoil.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL % 0-65	21	FIELD CAPACITY (%)	7-14	8
SILT + CLAY (%) 5-15	10	WILTING POINT (%)	1-5	3
DEPTH TO WATER TABLE (cm)	27-90+	AVAIL. MOISTURE (%)	3-9	5

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH 5.3-6.1	5.8	EXCH. Ca(me%) 0.3-3.1	1.7
N% 0.03-0.23	0.07	EXCH. Mg(me%) 0.2-1.1	0.6
P (ppm) 5-26	17	C.E.C. (me%) 4.4-11.1	7.4
K (me%) 0.02-0.47	0.18	SATURATION (%) 13-67	36

(e) BROAD DESCRIPTION

Gravelly sands, moist to wet in winter, dry in summer, of medium fertility. This is a broad transitional segment between swamps and gravelly slopes, held together by species groups BROMO, BROFEM, FERMO.

SEGMENT W CO-ORDINATES low — F1, low — F2, low ± F3, low — F4.

PLOTS 65, 45, 36, 118, 170, 149, 90.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
BROMO	<i>Lepidosperma angustatum</i> , <i>Mesomelaena tetragona</i> , <i>Synaphea petiolaris</i> .
BROFER	<i>Hakea lissocarpha</i> .
FERMO	<i>Hypocalymma angustifolium</i> , <i>Eucalyptus patens</i> , <i>Acacia extensa</i> .
Less consistently :		
BROWET	<i>Leptocarpus scariosus</i> , <i>Leptospermum ellipticum</i> .
BROFEM	<i>Dampiera alata</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Moderately dense, of medium height	BASAL AREA (m ² /ha)	24-54	33
	HEIGHT (m)	18-32	27
COMPOSITION: Equal admixture of <i>Eucalyptus marginata</i> , <i>Eucalyptus calophylla</i> and <i>Eucalyptus patens</i> .			

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees)	1-4	3
GENERAL: Lower slopes and valley floors	ROCK OUTCROPS: Rare, occasionally granite floors		

(d) SOIL

GENERAL: Yellow-brown or orange-brown sandy loams to loams occasionally with lateritic gravel, especially in the subsoil.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	0-26	14	FIELD CAPACITY (%)	3-35	16
SILT + CLAY (%)	13-20	12	WILTING POINT (%)	1-12	6
DEPTH TO WATER TABLE (cm)	27-90	AVAIL. MOISTURE (%)	1-22	9

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.5-6.3	6.0	EXCH. Ca(me%)	1.0-6.4	3.5
N%	0.05-0.34	0.14	EXCH. Mg(me%)	0.7-5.4	1.9
P (ppm)	12-66	36	C.E.C. (me%)	7.0-23.0	10.6
K (me%)	0.25-0.86	0.58	SATURATION (%)	33-67	55

(e) BROAD DESCRIPTION

Moist sandy loams on lower slopes and valley floors, with tendency to excessive wetness in winter.

SEGMENT C. CO-ORDINATES low — F1, med to high + F2, low ± F3, low to med ± F4
 PLOTS 40, 49, 159, 171.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
BROWET	<i>Leptocarpus scariosus</i> .
BROMO	<i>Mesomelaena tetragona</i> , <i>Lepidosperma angustatum</i> .
WETAL	<i>Agonis linearifolia</i> , <i>Eucalyptus megacarpa</i> .
FERMO	<i>Hypocalymma angustifolium</i> , <i>Eucalyptus patens</i> .

Less consistently :

BROFEM *Dampiera alata*, *Baeckea camphorosmae*.

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Low to medium density and height	BASAL AREA (m ² /ha)	15-24	19
	HEIGHT (m)	20-27	24

COMPOSITION: Chiefly *Eucalyptus patens* with admixture of *Eucalyptus megacarpa*, *Eucalyptus calophylla*, *Eucalyptus marginata*. Occasionally also *Eucalyptus rudis*, *Banksia littoralis*.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees)	1-2	1
GENERAL: Valley floor	ROCK OUTCROPS: Occasional outcropping of secondary (valley) laterite in form of sills.		

(d) SOIL

GENERAL: Sandy loam to sandy clay topsoil, sandy clay subsoil, colour yellow-grey to brown.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	0-78	23	FIELD CAPACITY (%)	6-13	9
SILT + CLAY (%)	7-33	18	WILTING POINT (%)	3-7	5
DEPTH TO WATER TABLE (cm)	10-70	AVAIL. MOISTURE (%)	3-6	5

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	4.5-6.0	5.6	EXCH. Ca(me%)	0.9-3.3	2.3
N%	0.04-0.39	0.15	EXCH. Mg(me%)	0.3-4.2	1.8
P (ppm)	19-101	46	C.E.C. (me%)	6.1-28.3	12.1
K (me%)	0.05-0.64	0.33	SATURATION (%)	25-69	44

(e) BROAD DESCRIPTION

Moist to wet sandy loams along creeks and on margins of swamps.

Plot 40 differs from the rest in several aspects, such as heavier occurrence of group BROFEM and heavier soil texture. It shares with them the occurrence of key group WETAL and shallow depth to ground-water table.

SEGMENT F CO-ORDINATES low ± F1, low + F2, low ± F3, low ± F4.

PLOTS 4, 5, 8, 25, 127, 129.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
EAGSAN	<i>Stirlingia latifolia.</i>
BROWET	<i>Leptocarpus scariosus.</i>
SANLEA	<i>Nuytsia floribunda, Caustis dioica,</i>
Less consistently :		
BROMO	<i>Mesomelaena tetragona.</i>
DRYSAG	<i>Daviesia pectinata.</i>

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Low, medium density	BASAL AREA (m ² /ha)	7-48	21
	HEIGHT (m)	15-27	20

COMPOSITION: *Eucalyptus marginata* almost without admixture or second storey.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform to concave	SLOPE (degrees)	1-2	1
GENERAL: Lower slopes and broad upland depressions	ROCK OUTCROPS: Nil		

(d) SOIL

GENERAL: Coarse grey sand over yellow sand.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN	RANGE	MEAN
GRAVEL %	Nil		FIELD CAPACITY (%)	2-5 3
SILT + CLAY (%)	2-6	3	WILTING POINT (%)	1 1
DEPTH TO WATER TABLE (cm)	>150	AVAIL. MOISTURE (%)	1-3 2

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	4.5-6.1	5.5	EXCH. Ca(me%)	0.4-2.7	1.5
N%	0.01-0.04	0.02	EXCH. Mg(me%)	0.1-0.7	0.4
P (ppm)	6-46	19	C.E.C. (me%)	0.6-15.5	5.2
K (me%)	0.07-0.24	0.15	SATURATION (%)	22-65	40

(e) BROAD DESCRIPTION

Mildly sloping sand plains, generally on lower slopes of broad eastern valleys.

Additional indicators not fully tested, but found quite consistently are *Lysinema ciliatum*, *Gompholobium tomentosum*, *Bossiaea eriocarpa*, *Calytrix flavescens*.

SEGMENT J. CO-ORDINATES low—F1, high + F2, low ± F3, low ± F4.

PLOTS 126, 128, 43, 45, 97, 68, 89, 107.

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
SANLEA	<i>Conospermum stoechadis</i> , <i>Hibbertia polystachya</i> , <i>Nuytsia floribunda</i> , <i>Lyginia tenax</i> .
BROMO	<i>Mesomelaena tetragona</i> , <i>Lepidosperma angustatum</i> .
BROWET	<i>Leptocarpus scariosus</i> .
DRYGRA	<i>Patersonia rudis</i> , <i>Styphelia tenuiflora</i> .
Less consistently :	
EAGSAN	<i>Stirlingia latifolia</i> , <i>Isopogon dubius</i> , <i>Sphaerolobium medium</i> .
BROFEM	<i>Baeckea camphorosmae</i> , <i>Dampiera alata</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Medium density and height	BASAL AREA (m ² /ha)	5-28	14
	HEIGHT (m)	10-28	21

COMPOSITION: *Eucalyptus marginata*, *Eucalyptus calophylla*, *Eucalyptus patens* at the moist and *Banksia attenuata* at the dry end of the range.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform to concave	SLOPE (degrees)	1-3	2
GENERAL: Lower slopes and broad upland depressions	ROCK OUTCROPS: Nil		

(d) SOIL

GENERAL: Deep, pale yellow-grey sand, frequently underlain by lateritic gravel in sandy clay matrix at depth.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	2-18	4	FIELD CAPACITY (%)	2-8	4
SILT + CLAY (%)	1-8	5	WILTING POINT (%)	1-3	2
DEPTH TO WATER TABLE (cm)	>90	AVAIL. MOISTURE (%)	2-4	3

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.6-6.1	6.0	EXCH. Ca(me%)	0.5-1.9	1.2
N%	0.02-0.04	0.03	EXCH. Mg(me%)	0.2-1.4	0.5
P (ppm)	7-14	10	C.E.C. (me%)	4.7-8.0	6.2
K (me%)	0.03-0.15	0.10	SATURATION (%)	18-57	31

(e) BROAD DESCRIPTION

Leached sands in medium to low-rainfall zone.

SEGMENT H. CO-ORDINATES low \pm F1, high + F2, low \pm F3, low \pm F4.

PLOTS (124, 99, 108, 153) (123, 70, 62, 94, 44, 117, 100, 87) (105, 14, 6, 135, 106, 41, 56, 58, 98)

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
BROMO	<i>Mesomelaena tetragona</i> , <i>Synaphea petiolaris</i> , <i>Lepidosperma angustatum</i> .
EAGSAN	<i>Stirlingia latifolia</i> , <i>Sphaerolobium medium</i> , <i>Hakea cyclocarpa</i> , <i>Isopogon dubius</i>
DRYSAG	<i>Daviesia pectinata</i> , <i>Hakea ruscifolia</i> .
DRYGRA	<i>Styphelia tenuiflora</i> , <i>Patersonia rudis</i> , <i>Acacia strigosa</i> .
Less consistently :	
BROFER	<i>Hakea lissocarpa</i>
BROFEM	<i>Baeckea camphorosmae</i> .
SANGRA	<i>Casuarina fraseriana</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Variable	BASAL AREA (m ² /ha)	2-57	25
	HEIGHT (m)	19-33	25

COMPOSITION: Overwhelmingly *Eucalyptus marginata*, little *Eucalyptus calophylla*, some second storey of *Casuarina fraseriana* and *Banksia grandis*.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform to concave	SLOPE (degrees)	1-16	3
GENERAL: Lower and middle slope in mildly undulating landscape, eastern zone	ROCK OUTCROPS: Occasional low outcropping of lateritic ironstone.		

(d) SOIL

GENERAL: Yellow-grey sand or loamy sand merging into lateritic gravel at depth.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	0-71	24	FIELD CAPACITY (%)	2-15	12
SILT + CLAY (%)	2-15	9	WILTING POINT (%)	1-9	8
DEPTH TO WATER TABLE (cm)	>90	AVAIL. MOISTURE (%)	1-6	4

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	4.9-6.4	6.0	EXCH. Ca(me%)	0.4-6.3	2.1
N%	0.02-0.10	0.05	EXCH. Mg(me%)	0.1-4.4	0.9
P (ppm)	3-100	28	C.E.C. (me%)	3.2-29.3	8.2
K (me%)	0.05-1.20	0.27	SATURATION (%)	11-94	41

(e) BROAD DESCRIPTION

Gravelly sands in low-rainfall zone.

This large group of plots could be further subdivided into three subgroups, as indicated by brackets above. The first of these, characterized by *Stirlingia latifolia*, tends toward segment F; the second, characterized by *Mesomelaena tetragona*, tends toward segment E. The third has no definite trend.

SEGMENT P CO-ORDINATES low \pm F1, mod. to high + F2, high + F3, high + F4.

PLOTS 154, 61, 2, 143, 130, 47, 114, 51, 54, 116, 141, 60, 113, 156.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
BROMO	<i>Lepidosperma angustatum</i> , <i>Lechenaultia biloba</i> .
SANGRA	<i>Casuarina fraseriana</i> , <i>Grevillea wilsonii</i>
DRYGRA	<i>Styphelia tenuiflora</i> , <i>Patersonia rudis</i> , <i>Acacia strigosa</i> .
GRAMED	<i>Banksia grandis</i> , <i>Adenanthos barbigera</i> , <i>Hovea chorizemifolia</i> , <i>Persoonia longifolia</i> .

Less consistently :

DRYSAG	<i>Daviesia pectinata</i> , <i>Hakea ruscifolia</i> .
GRAHIR	<i>Lasiopetalum floribundum</i> .
FREGRA	<i>Phyllanthus calycinus</i> , <i>Trymalium ledifolium</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Moderately tall, dense stand	BASAL AREA (m ² /ha)	18-78	40
	HEIGHT (m)	24-35	29

COMPOSITION: Overwhelmingly *Eucalyptus marginata* with occasional *Eucalyptus calophylla*; strong development of second storey of *Casuarina fraseriana* and *Banksia grandis*.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Mostly uniform	SLOPE (degrees)	0-12	4
GENERAL: Mild, lower and middle slopes	ROCK OUTCROPS: Moderately frequent occurrence of isolated lateritic ironstone outcrops.		

(d) SOIL

GENERAL: Lateritic gravel with sand or loamy sand matrix, or sand with heavy gravel.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	15-73	55	FIELD CAPACITY (%)	5-11	7
SILT + CLAY (%)	4-18	8	WILTING POINT (%)	2-6	3
DEPTH TO WATER TABLE (cm)	Not detected		AVAIL. MOISTURE (%)	2-5	3

Much greater than 90

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.4-7.1	6.1	EXCH. Ca(me%)	0.5-8.9	3.5
N%	0.01-0.14	0.06	EXCH. Mg(me%)	0.4-3.4	1.0
P(ppm)	12-100	35	C.E.C. (me%)	2.2-21.7	8.4
K (me%)	0.05-0.90	0.30	SATURATION (%)	11-78	54

(e) BROAD DESCRIPTION

Gravelly sands and sandy gravels, occurring on mid and lower slopes in medium and high-rainfall zone.

SEGMENT Z CO-ORDINATES low + F1, low + F2, low + F3, low + F4.

PLOTS (151) (37, 19, 11, 46, 13, 9, 23, 18).

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
FREGRA <i>Phyllanthus calycinus</i> , <i>Macrozamia riedlei</i> , <i>Leocopogon capitellatus</i> , <i>Leucopogon propinquus</i> .
BROFER <i>Hakea lissocarpa</i> .
DRYGRA <i>Styphelia tenuiflora</i> , <i>Patersonia rudis</i> , <i>Acacia strigosa</i> .

Less consistently :

BROMO *Lepidosperma angustatum*, *Lechenaultia biloba*, *Synaphea petiolaris*

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Open forest	BASAL AREA (m ² /ha) 11-62	29
	HEIGHT (m) 20-32	24

COMPOSITION: Chiefly *Eucalyptus marginata* with admixture of *Eucalyptus calophylla*. Second storey largely missing.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Mainly uniform	SLOPE (degrees) 2-8	5
GENERAL: Mainly valley slopes	ROCK OUTCROPS: Variable with none to heavy ironstone and occasional granite.		

(d) SOIL

GENERAL: Grey-brown loamy sands to sandy loams with moderate to heavy admixture of lateritic gravel, frequently over base of gravel in clay matrix.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL % 30-75	50	FIELD CAPACITY (%)	6-18	12
SILT + CLAY (%) 7-13	10	WILTING POINT (%)	2-7	4
DEPTH TO WATER TABLE (cm)	>90	AVAIL. MOISTURE (%)	4-10	6

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH 5.6-6.1	5.9	EXCH. Ca(me%) 0.7-8.4	4.9
N% 0.03-0.18	0.10	EXCH. Mg(me%) 0.2-2.7	1.4
P (ppm) 3-143	58	C.E.C. (me%) 4.3-17.1	11.9
K (me%) 0.05-0.99	0.24	SATURATION (%) 15-87	56

(e) BROAD DESCRIPTION

This segment is representative of upper slopes and uplands in medium to low-rainfall zone. The composition of the soil and the combination of the indicator groups indicates that it is a drier equivalent of segment S.

Plot 151, which virtually doubles the basal area range for this segment, has been placed here although it has a very poor development of the key group, DRYGRA, simply because it would be too small a group on its own or even in combination with plot 150 from segment S, which resembles it in many respects.

SEGMENT S CO-ORDINATES low to med. + F1, medium — F2, high + F3, high + F4.
 PLOTS 150, 109, 112, 152, 115, 155, 133, 137, 38.

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
GRAMED <i>Banksia grandis</i> , <i>Persoonia longifolia</i> , <i>Hovea chorizemifolia</i> , <i>Adenanthos barbiger</i> .
FREGRA <i>Macrozamia riedlei</i> , <i>Phyllanthus calycinus</i> , <i>Leucopogon capitellatus</i> , <i>Leucopogon propinquus</i> .
DRYGRA <i>Acacia strigosa</i> , <i>Styphelia tenuiflora</i> , <i>Patersonia rudis</i> .
Less consistently :	
BROMO <i>Lepidosperma angustatum</i> , <i>Lechenaultia biloba</i> .
SANGRA <i>Casuarina fraseriana</i> .
GRAHIR <i>Bossiaea aquifolium</i> , <i>Lasiopetalum floribundum</i> , <i>Acacia urophylla</i> .
HIGRA <i>Leucopogon verticillatus</i> .
DRYSAG <i>Daviesia pectinata</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Moderately tall, dense stand	BASAL AREA (m ² /ha)	27-64	39
	HEIGHT (m)	23-35	30
COMPOSITION: Predominantly <i>Eucalyptus marginata</i> with some <i>Eucalyptus calophylla</i> and second storey of <i>Banksia grandis</i> , <i>Persoonia longifolia</i> and <i>Casuarina fraseriana</i>			

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform or convex.	SLOPE (degrees)	2-9	5
GENERAL: Mid and upper slopes, plateaus and ridges in medium to high-rainfall zone.	ROCK OUTCROPS: Frequent massive lateritic ironstone.		

(d) SOIL

GENERAL: Yellow to orange heavy lateritic gravel with loamy sand matrix.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	21-76	51	FIELD CAPACITY (%)	8-15	10
SILT + CLAY (%)	8-12	10	WILTING POINT (%)	3-6	4
DEPTH TO WATER TABLE (cm)	Much greater than 90	AVAIL. MOISTURE (%)	4-8	6

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.5-6.6	6.1	EXCH. Ca(me%)	1.3-4.0	2.9
N%	0.08-0.43	0.25	EXCH. Mg(me%)	0.4-1.1	0.8
p (ppm)	8-43	25	C.E.C. (me%)	3.9-12.2	6.9
K (me%)	0.08-0.74	0.35	SATURATION (%)	36-87	59

(e) BROAD DESCRIPTION

Heavy gravels with sandy loam matrix, occurring on slopes, ridges and plateaus in medium to high-rainfall zones.

SEGMENT T CO-ORDINATES high + F1, high + F2, high + F3, medium to high + F4.
 PLOTS (172, 168, 162, 167) (157, 140, 142, 132, 111).

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
HIGRA	<i>Leucopogon verticillatus</i> , <i>Pteridium esculentum</i> , <i>Clematis pubescens</i> .
FREGRA	<i>Macrozamia riedlei</i> , <i>Leucopogon capitellatus</i> , <i>Leucopogon propinquus</i> , <i>Phyllanthus calycinus</i>
GRAHIR	<i>Acacia urophylla</i> , <i>Lasiopetalum floribundum</i> , <i>Bossiaea aquifolium</i> .
Less consistently :		
FEHIRA	<i>Chorizema ilicifolium</i> .
GRAMED	<i>Banksia grandis</i> , <i>Adenanthos barbiger</i> .
FERMO	<i>Eucalyptus patens</i> .
DRYGRA	<i>Styphelia tenuiflora</i> , <i>Acacia strigosa</i> , <i>Patersonia rudis</i> .
BROFER	<i>Hakea lissocarpha</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Tall, dense stand	BASAL AREA (m ² /ha)	26-44	35
	HEIGHT (m)	29-39	33
COMPOSITION: <i>Eucalyptus marginata</i> with moderate admixture of <i>Eucalyptus calophylla</i> , in few plots also <i>Eucalyptus patens</i> , second storey of <i>Banksia grandis</i> , <i>Persoonia longifolia</i> .			

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Mainly convex	SLOPE (degrees)	2-15	7
GENERAL: Upper slopes and ridges in strongly dissected, high-rainfall western zone.	ROCK OUTCROPS: Heavy massive lateritic ironstone, occasional granite and epidiorite.		

(d) SOIL

GENERAL: Orange to brown gravel with sandy loam to loam matrix, in a few marginal cases loam with medium gravel.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	3-84	44	FIELD CAPACITY (%)	11-23	16
SILT + CLAY (%)	9-46	25	WILTING POINT (%)	5-14	8
DEPTH TO WATER TABLE (cm)	Much greater than 90	AVAIL. MOISTURE (%)	5-11	8

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.8-6.9	6.1	EXCH. Ca(me%)	2.3-14.7	7.3
N%	0.06-0.30	0.14	EXCH. Mg(me%)	1.2-5.8	2.5
P (ppm)	10-188	89	C.E.C. (me%)	6.5-25.9	14.8
K (me%)	0.20-1.04	0.60	SATURATION (%)	45-80	70

(e) BROAD DESCRIPTION

In the northern portion of the jarrah forest, this segment is very much restricted to the slopes of the strongly dissected high-rainfall western zone. By contrast, it is more broadly distributed in the southern portion.

The segment can be subdivided into two groups, one characterized by the presence of *Adenanthos barbiger* and *Leptomeria cunninghamii*, having a lower silt and clay fraction.

The other is characterized by the absence of *Adenanthos* and some occurrence of *Eucalyptus patens*, and *Chorizema ilicifolium* having a markedly higher silt and clay fraction and higher fertility. It has a strong affinity to Segment U.

SEGMENT U CO-ORDINATES high + F1, high + F2, low ± F3, low — F4.

PLOTS, 138, 139, 35.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
FERMO	<i>Eucalyptus patens</i> .
FREGRA	<i>Macrozamia riedlei</i> , some <i>Leucopogon capitellatus</i> , <i>Phyllanthus calycinus</i> .
HIGRA	<i>Pteridium esculentum</i> , <i>Clematis pubescens</i> , some <i>Leucopogon verticillatus</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Moderately tall, dense stand	BASAL AREA (m ² /ha)	34-59	49
	HEIGHT (m)	26-31	29

COMPOSITION: Mixture of *Eucalyptus patens* and *Eucalyptus calophylla*.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform	SLOPE (degrees)	1-5	3
GENERAL: Uniform slope in dissected high-rainfall western zone	ROCK OUTCROPS: Nil		

(d) SOIL

GENERAL: Brown sandy loam over clay loam at 40 cm.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	0-36	14	FIELD CAPACITY (%)	33-40	36
SILT + CLAY (%)	15-23	20	WILTING POINT (%)	13-15	14
DEPTH TO WATER TABLE (cm)	30 for plot 35 only		AVAIL. MOISTURE (%)	20-24	22

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	6.1-6.3	6.2	EXCH. Ca(me%)	6.0-18.1	13.1
N%	0.22-0.41	0.32	EXCH. Mg(me%)	5.8-7.1	6.5
P (ppm)	105-277	201	C.E.C. (me%)	16.1-30.7	25.6
K (me%)	0.32-1.54	1.11	SATURATION (%)	78-84	82

(e) BROAD DESCRIPTION

Fertile loams on slopes of main river valleys in high rainfall zone.

The members of this group all occur on the peripheries of former agricultural clearings, and although heavily wooded, may have been subject to considerable disturbance in the past. If this is so, plots 138 and 139 should be combined with the fertile subgroup of segment T, and plot 35 with segment Q, with which they have much in common. The former group would be retained as Segment U. This would result in a narrower, clearer definition of Segment T.

SEGMENT R CO-ORDINATES medium + F1, low — F2, high + F3, low — F4.

PLOTS 17, 95, 131, 110, 10, 53, 16.

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
FREGRA <i>Trymalium ledifolium</i> , <i>Phyllanthus calycinus</i> , <i>Macrozamia riedlei</i> , <i>Leucopogon capitellatus</i> , <i>Leucopogon propinquus</i>
BROFER <i>Hakea lissocarpa</i>

Common species of broad distribution

patterns : *Hibbertia hypericoides*, *Hibbertia montana*, *Dryandra nivea*, *Grevillea synapheae*.

Less consistently :

BROMO <i>Lepidosperma angustatum</i> , <i>Lechenaultia biloba</i> .
DRYGRA <i>Styphelia tenuiflora</i> , <i>Patersonia rudis</i> , <i>Acacia strigosa</i> .
GRAMED <i>Adenanthos barbiger</i> , <i>Leptomeria cunninghamii</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Open forest, irregular stocking	BASAL AREA (m ² /ha)	10-38	21
	HEIGHT (m)	16-30	26

COMPOSITION: Mainly *Eucalyptus marginata* with admixture of *Eucalyptus calophylla*.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform or concave	SLOPE: (degrees)	1-9	5
GENERAL: Valley slopes, frequently in proximity to granite outcrops	ROCK OUTCROPS: Variable, from none to heavy.		

(d) SOIL

GENERAL: Grey to brown sandy loam to sandy clay with admixture of lateritic gravel.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	32-66	58	FIELD CAPACITY (%)	20-37	28
SILT + CLAY (%)	9-20	15	WILTING POINT (%)	8-21	15
DEPTH TO WATER TABLE (cm)	90	AVAIL. MOISTURE (%)	11-15	13

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.2-6.3	5.9	EXCH. Ca(me%)	1.3-16.8	7.3
N%	0.03-0.54	0.19	EXCH. Mg(me%)	0.6-6.9	2.8
P (ppm)	12-209	80	C.E.C. (me%)	6.3-39.0	18.5
K (me%)	0.08-0.82	0.40	SATURATION(%)	33-79	60

(e) BROAD DESCRIPTION

Gravels with loamy to clayey matrix, occurring chiefly on lower and middle slopes of valleys, probably representing admixture of the ironstone gravel and kaolinitic clay from the old lateritic profile.

SEGMENT Q. CO-ORDINATES + low F1, + high F2, + medium F3, — high F4.

PLOTS 148, 163, 161, 164, 166, 169, 22, 160, 165.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
FERMO	<i>Hypocalymma angustifolium</i> , <i>Eucalyptus patens</i> , <i>Acacia extensa</i> .
FEHIRA	<i>Trymalium spathulatum</i> , <i>Chorizema ilicifolium</i> .
FREGRA	<i>Macrozamia riedlei</i> , <i>Phyllanthus calycinus</i> , <i>Trymalium ledifolium</i> , <i>Leucopogon capitellatus</i> , <i>Leucopogon propinquus</i> .
DRYFER....	<i>Hakea tissocarpa</i> .

Less consistently :

DRYFER....	<i>Hibbertia lineata</i> .
HIGRA	<i>Pteridium esculentum</i> .
BROMO	<i>Lepidosperma angustatum</i>
GRAHIR	<i>Lasiopetalum floribundum</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Moderately tall and dense stand	BASAL AREA (m ² /ha)	17-46	29
	HEIGHT (m)	24-38	31

COMPOSITION: Mainly *Eucalyptus patens* with admixture of *Eucalyptus calophylla* and some *Eucalyptus marginata*.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform or Convex	SLOPE (degrees)	2-6	4
GENERAL: Lower and middle slopes, high-rainfall zone	ROCK OUTCROPS: Occasional lateritic or epidioritic boulders.		

(d) SOIL

GENERAL: Dark brown sandy or silty loam over red-brown clay loam.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN	RANGE	MEAN
GRAVEL %	0-44	18	FIELD CAPACITY (%)	14-30 20
SILT + CLAY (%)	15-34	18	WILTING POINT (%)	4-11 9
DEPTH TO WATER TABLE (cm)	120 and above	AVAIL. MOISTURE (%)	8-16 11

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.8-7.2	6.3	EXCH. Ca (me%)	1.0-9.8	4.7
N%	0.08-0.24	0.14	EXCH. Mg(me%)	0.8-5.1	2.2
P (ppm)	56-211	114	C.E.C. (me%)	5.8-17.0	10.4
K (me%)	0.44-1.14	0.82	SATURATION (%)	34-92	67

(e) BROAD DESCRIPTION

One of the best sites from the point of view of fertility and moisture, occurring chiefly on slopes of major valleys in western high-rainfall zone.

SEGMENT M CO-ORDINATES low + F1, low + F2, low + F3, medium + F4.

PLOTS (30, 24, 42) (1, 29, 12) (33, 121, 32) (15, 136, 34, 21)

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
		<i>Eucalyptus wandoo</i> .
BROFER	<i>Hakea lissocarpa</i> .
FREGRA	<i>Macrozamia riedlei</i> .

Other common species, not tested fully by CORD program, include :

Acacia pulchella, *Loxocarya flexuosa*, *Kennedia prostrata*, *Ptilotus manglesii*.

Less consistently :

DRYFER	<i>Gastrolobium calycinum</i> .
FERMO	<i>Hypocalymma angustifolium</i> , <i>Eucalyptus patens</i> .
BROFEM	<i>Baeckea camphorosmae</i> , <i>Dampiera alata</i> .
DRYGRA	<i>Patersonia rudis</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Open stand of medium height	BASAL AREA (m ² /ha) 5-19	12
	HEIGHT (m) 21-37	27
COMPOSITION: Largely <i>Eucalyptus wandoo</i> with occasional <i>Eucalyptus patens</i> at lower and <i>Eucalyptus marginata</i> at upper range of occurrence. Second storey missing.			

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Uniform to concave.	SLOPE (degrees) 2-9	4
GENERAL: Valley slopes in middle and upper reaches of valley in dry eastern zone.	ROCK OUTCROPS: Either none or scattered iron-stone floaters.		

(d) SOIL

GENERAL: Brown sandy loam to loam over yellow or red-brown clay loam.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL % 6-73	44	FIELD CAPACITY (%)	7-27	19
SILT + CLAY (%) 12-27	18	WILTING POINT (%)	2-11	7
DEPTH TO WATER TABLE (cm)	With one exception >90		AVAIL. MOISTURE(%)	4-16	11

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH 5.5-6.6	6.3	EXCH. Ca(me%) 2.9-14.1	7.4
N% 0.04-0.29	0.16	EXCH. Mg(me%) 0.8-3.0	1.8
P (ppm) 43-262	126	C.E.C. (me%) 7.5-18.8	12.8
K (me%) 0.22-1.24	0.75	SATURATION (%) 48-95	75

(e) BROAD DESCRIPTION

Loams with medium to heavy admixture of lateritic gravel, occurring chiefly on valley slopes in dry eastern zone.

On both edaphic and topographic characteristics and in terms of vegetation it represents a drier equivalent of R. This large segment could be subdivided on the occurrence of *Macrozamia riedlei* and *Hypocalymma angustifolium*, but the advantage of this is difficult to assess.

SEGMENT L CO-ORDINATES low — F1, low — F2, low + F3, high + F4.

PLOTS 26, 27, 28, 134

(a) INDICATOR SPECIES

GROUPS	INDIVIDUAL SPECIES
BROFER	<i>Eucalyptus wandoo</i> .
 <i>Hakea lissocarpa</i> .
FERMO <i>Eucalyptus patens</i> , <i>Hypocalymma angustifolium</i> .
DRYFER <i>Diplolaena drummondii</i> , <i>Hibbertia lineata</i> .

The following species, not otherwise used as indicators, also occur consistently :

Acacia pulchella,
Hibbertia montana.

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Open stand of medium height	BASAL AREA (m ² /ha)	2-19	14
	HEIGHT (m)	24-31	28

COMPOSITION: Mainly *Eucalyptus wandoo* with admixture of *Eucalyptus patens*. On one occasion, away from the plots, *Acacia acuminata* has been observed in this type.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees)	2-5	4
GENERAL: Lower slopes, dry eastern zone.	ROCK OUTCROPS: Few ironstone floaters		

(d) SOIL

GENERAL: Brown silty loam over red-brown clay loam.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	0-50	12	FIELD CAPACITY (%)	23-33	28
SILT + CLAY (%)	14-31	24	WILTING POINT (%)	7-11	9
DEPTH TO WATER TABLE (cm)	30 in one plot > 90 in others		AVAIL. MOISTURE(%)	15-21	18

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.5-6.5	6.1	EXCH. Ca(me%)	7.0-18.5	13.4
N%	0.27-0.34	0.31	EXCH. Mg(me%)	2.7-4.7	3.8
P (ppm)	64-306	199	C.E.C. (me%)	20.9-26.4	23.1
K (me%)	0.79-0.98	0.93	SATURATION (%)	49-96	79

(e) BROAD DESCRIPTION

Fertile loams on lower slopes in low-rainfall zone. The paucity of perennial species in three of the plots may reflect grazing disturbance in the area half-a-century ago. In both edaphic topographic features and in some species-groups, this segment is a drier equivalent of segment Q. This is particularly true of plot 134.

SEGMENT Y CO-ORDINATES low — F1, low ± F2, low ± F3, low — F4.

PLOTS 103, 104, 119, 31, 20, 122.

(a) INDICATOR SPECIES

GROUPS		INDIVIDUAL SPECIES
		<i>Eucalyptus wandoo</i> .
BROFER	<i>Hakea lissocarpa</i> .
FERMO	<i>Hypocalymma angustifolium</i> .
BROFEM	<i>Baeckea camphorosmae</i> , <i>Dampiera alata</i> .
DRYFER	<i>Hibbertia lineata</i> , <i>Gastrobium calycinum</i> .
BROMO	<i>Mesomelaena tetragona</i> , <i>Lepidosperma angustatum</i> .
Occasionally	
SANLEA	<i>Hibbertia polystachya</i> .

(b) TREE STRATUM

		RANGE	MEAN
GENERAL: Open stand of medium height	BASAL AREA (m ² /ha)	7-20	13
	HEIGHT (m)	20-31	27

COMPOSITION: *Eucalyptus wandoo* virtually without any associates or second storey.

(c) TOPOGRAPHICAL AND GEOGRAPHICAL POSITION

		RANGE	MEAN
CURVATURE: Concave	SLOPE (degrees)	1-5	3
GENERAL: Valley floors and lower slopes	ROCK OUTCROPS: Nil		

(d) SOIL

GENERAL: Yellow-grey sandy loam to sandy clay over pale yellow or grey sandy clay at varying depth.

PHYSICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
GRAVEL %	0-27	10	FIELD CAPACITY (%)	7-33	14
SILT + CLAY (%)	12-25	19	WILTING POINT (%)	2-9	4
DEPTH TO WATER TABLE (cm)	15 and above		AVAIL. MOISTURE (%)	4-23	9

CHEMICAL PROPERTIES (TOPSOIL)

	RANGE	MEAN		RANGE	MEAN
pH	5.8-6.3	6.1	EXCH. Ca(me%)	2.3-5.7	3.9
N%	0.06-0.34	0.12	EXCH. Mg(me%)	1.0-2.7	1.7
P (ppm)	14-85	56	C.E.C. (me%)	7.2-14.7	10.7
K (me%)	0.17-1.36	0.60	SATURATION (%)	44-82	60

(e) BROAD DESCRIPTION

Pale loamy soils which become hard and crusted in summer and waterlogged in winter, occurring in broad valleys in eastern dry zone.

APPENDIX 5

List of plant species referred to in Bulletins 86 and 87.

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| <p><i>Acacia acuminata</i> Benth.
 <i>Acacia aneura</i> F. Muell. ex Benth.
 <i>Acacia alata</i> R.Br.
 <i>Acacia cyanophylla</i> Lindl.
 <i>Acacia drummondii</i> Lindl.
 <i>Acacia extensa</i> Lindl.
 <i>Acacia microbotrya</i> Benth.
 <i>Acacia nigricans</i> R.Br.
 <i>Acacia pulchella</i> R.Br.
 <i>Acacia sibirica</i> S.Moore
 <i>Acacia strigosa</i> Link. *
 <i>Acacia urophylla</i> Benth.
 <i>Actinostrobos pyramidalis</i> Miq.
 <i>Adenanthos barbiger</i> Lindl.
 <i>Adenanthos cygnorum</i> Diels.
 <i>Adenanthos meissneri</i> Lehm.
 <i>Adenanthos obovata</i> Labill.
 <i>Adiantum aethiopicum</i> L.
 <i>Agonis flexuosa</i> (Spreng.) Schau.
 <i>Agonis juniperina</i> Schau.
 <i>Agonis linearifolia</i> (DC.) Schau.
 <i>Agonis parviceps</i> Schau.
 <i>Albizzia lophantha</i> (Willd.) Benth.
 <i>Astartea fascicularis</i> (Labill.) DC.
 <i>Astroloma ciliatum</i> (Lindl.) Druce
 <i>Astroloma pallidum</i> R.Br.
 <i>Baeckea camphorosmae</i> Endl.
 <i>Banksia attenuata</i> R.Br.
 <i>Banksia grandis</i> Willd.
 <i>Banksia ilicifolia</i> R.Br.
 <i>Banksia littoralis</i> R.Br.
 <i>Banksia littoralis</i> R.Br. var. <i>seminuda</i>
 A. S. George
 <i>Banksia menziesii</i> R.Br.
 <i>Banksia prionotes</i> Lindl.
 <i>Boronia spathulata</i> Lindl.
 <i>Borya nitida</i> Labill.
 <i>Bossiaea aquifolium</i> Benth.</p> | <p><i>Bossiaea linophylla</i> R.Br.
 <i>Bossiaea ornata</i> (Lindl.) Benth.
 <i>Bossiaea pulchella</i> Meissn.
 <i>Brachychiton gregorii</i> F. Muell.
 <i>Callitris preissii</i> Miq.
 <i>Calytrix flavescens</i> A. Cunn.
 <i>Casuarina decussata</i> Benth.
 <i>Casuarina fraseriana</i> Miq. **
 <i>Casuarina huegeliana</i> Miq.
 <i>Casuarina humilis</i> Otto & Dietr.
 <i>Casuarina obesa</i> Miq.
 <i>Caustis dioica</i> R.Br.
 <i>Chorilaena quercifolia</i> Endl.
 <i>Chorizema ilicifolium</i> Labill.
 <i>Clematis pubescens</i> Hueg.
 <i>Codonocarpus cotinifolius</i> (Desf.)
 F. Muell.
 <i>Conospermum stoechadis</i> Endl.
 <i>Conospermum triplinervium</i> R.Br.
 <i>Conostylis aculeata</i> R.Br.
 <i>Conostylis setigera</i> R.Br.
 <i>Cyathochaete clandestina</i> R.Br.
 <i>Dampiera alata</i> Lindl.
 <i>Dampiera linearis</i> R.Br.
 <i>Dasypogon bromeliaefolius</i> R.Br.
 <i>Daviesia longifolia</i> Benth.
 <i>Daviesia pectinata</i> Lindl.
 <i>Daviesia polyphylla</i> Benth. ex Lindl.
 <i>Daviesia preissii</i> Meissn.
 <i>Daviesia rhombifolia</i> Meissn.
 <i>Dillwynia cinerascens</i> R.Br.
 <i>Diplolaena microcephala</i> Bartl. var.
 <i>drummondii</i> Benth.
 <i>Dryandra bipinnatifida</i> R.Br.
 <i>Dryandra nivea</i> R.Br.
 <i>Dryandra sessilis</i> (Knight) Domin
 <i>Eucalyptus accedens</i> W.V. Fitzg.
 <i>Eucalyptus astringens</i> Maiden</p> |
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* Since the completion of the field work, taxonomic revision has resulted in the subdivision of *Acacia strigosa* Link. into *Acacia preissiana* (Meissn.) B. R. Maslin and *Acacia lateriticola* B. R. Maslin. Where uncertainty exists as to which of the two new species is involved, the old name has been retained.

** The rectification of an old spelling error has resulted in the recent changing of *Casuarina fraseriana* to *Casuarina fraserana*. This announcement came too late for the amendment to be made in this Bulletin, and the incorrect spelling therefore remains.

- Eucalyptus camaldulensis* Dehn.
Eucalyptus calophylla R.Br.
Eucalyptus decipiens Endl.
Eucalyptus decurva F. Muell.
Eucalyptus diversicolor F. Muell.
Eucalyptus drummondii Benth.
Eucalyptus haematoxylon Maiden
Eucalyptus kingsmillii Maiden and
 Blakely
Eucalyptus laeliae Podger and
 Chippendale
Eucalyptus lane-poolei Maiden
Eucalyptus longicornis F. Muell.
Eucalyptus loxophleba Benth.
Eucalyptus macrocarpa Hook.
Eucalyptus marginata Sm.
Eucalyptus megacarpa F. Muell.
Eucalyptus occidentalis Endl.
Eucalyptus patens Benth.
Eucalyptus platypus Hook.
Eucalyptus radis Endl.
Eucalyptus salmonophloia F.Muell.
Eucalyptus salubris F.Muell.
Eucalyptus tetragona (R.Br.) F.Muell.
Eucalyptus wandoo Blakely
Gastrolobium calycinum Benth.
Gompholobium knightianum Lindl.
Gompholobium marginatum R.Br.
Gompholobium polymorphum R.Br.
Grevillea bipinnatifida R.Br.
Grevillea diversifolia Meissn.
Grevillea pulchella Meissn.
Grevillea synaphaea R.Br.
Grevillea wilsonii A.Cunn.
Hakea amplexicaulis R.Br.
Hakea ceratophylla (Sm.) R.Br.
Hakea corymbosa R.Br.
Hakea cyclocarpa Lindl.
Hakea elliptica (Sm.) R.Br.
Hakea lasiantha R.Br.
Hakea lissocarpa R.Br.
Hakea marginata R.Br.
Hakea prostrata R.Br.
Hakea trifurcata (Sm.) R.Br.
Hakea undulata R.Br.
Hakea varia R.Br.
Helipterum cotula (Benth.) DC.
Helipterum manglesii (Lindl.) Benth.
- Hemigenia pritzelii* S.Moore
Hibbertia amplexicaulis Steud.
Hibbertia hypericoides (DC.) Benth.
Hibbertia huegelii (Endl.) F.Muell.
Hibbertia lasiopus Benth.
Hibbertia lineata Steud.
Hibbertia montana Steud.
Hibbertia polystachya Benth.
Hibbertia subvaginata (Steud.) F.Muell.
Hovea chorizemifolia (Sweet) DC.
Hovea trisperma Benth.
Hypocalymma angustifolium Endl.
Hypocalymma cordifolium (Lehm.)
 Schau.
Isopogon dubius (R.Br.) Druce
Isopogon sphaerocephalus Lindl.
Jacksonia stenbergiana Hueg.
Kennedia coccinea Vent.
Kennedia prostrata R.Br.
Kingia australis R.Br.
Kunzea micromera Schau.
Lasiopetalum floribundum Benth. ***
Lechenaultia biloba Lindl.
Lepidosperma angustatum R.Br.
Lepidosperma scabrum Nees
Lepidosperma tenue Benth.
Lepidosperma tetraquetrum Nees
Leptocarpus scariosus R.Br.
Leptomeria cunninghamii Miq.
Leptospermum ellipticum Endl.
Leucopogon capitellatus DC.
Leucopogon cordatus Sond.
Leucopogon oxycedrus Sond.
Leucopogon propinquus R.Br.
Leucopogon verticillatus R.Br.
Lomandra caespitosa (Benth.) Ewart
Lomandra endlicherii (F.Muell.)
 Ewart
Lomandra purpurea (Endl.) Ewart
Lomandra sonderii (F.Muell.) Ewart
Loxocarya cinerea R.Br.
Loxocarya fasciculata (R.Br.) Benth.
Loxocarya flexuosa (R.Br.) Benth.
Lyginia tenax R.Br.
Lysinema ciliatum R.Br.
Macrozamia riedlei (Gaud.)
 C.A. Gardn.
Melaleuca preissiana Schau.

*** As in the case of * (previous page) *Lasiopetalum floribundum* Benth. has been subdivided into *Lasiopetalum floribundum* Benth. and *Lasiopetalum glabratum* S. Panst.

- Melaleuca raphiophylla* Schau.
Melaleuca scabra R.Br.
Melaleuca uncinata R.Br.
Mesomelaena tetragona (R.Br.)
 F.Muell.
Mesomelaena sp. nov.
Millotia tenuifolia Cass.
Mirbelia spinosa Benth.
Nuytsia floribunda (Labill.) R.Br.
Opercularia hispidula Endl.
Patersonia occidentalis R.Br.
Patersonia rudis Endl.
Petrophile linearis R.Br.
Petrophile macrostachya R.Br.
Petrophile seminuda Lindl.
Petrophile striata R.Br.
Persoonia elliptica R.Br.
Persoonia longifolia R.Br.
Persoonia saccata R.Br.
Phyllanthus calycinus Labill.
Pimelia suaveolens (Endl.) Meissn.
Pinus pinaster Ait.
Pinus radiata D.Don
Podocarpus drouyniana F.Muell.
Pteridium esculentum (Forst.F.)
 Nakai
Ptilotus manglesii (Lindl.) F. Muell.
Santalum acuminatum (R.Br.) Druce
Scaevola striata R.Br.
Sphaerolobium medium R.Br.
Stirlingia latifolia (R.Br.) Steud.
Synaphea petiolaris R.Br.
Styphelia tenuiflora Lindl.
Tetradthea viminea Lindl.
Tetrariopsis octandra (Nees)
 C.B. Clarke
Triodia basedowii E. Pritzel
Trymalium ledifolium Fenzl.
Trymalium spathulatum (Labill.) Ostf.
Waitzia acuminata Steetz.
Xanthorrhoea gracilis Endl.
Xanthorrhoea preissii Endl.
Xanthosia candida (Benth.) Steud. ex
 Bunge
Xanthosia ciliata Hook.
Xylomelum occidentale R.Br.