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# Vegetation zoning in relation to site and soil properties: A case study in the Darling Range, south-western Australia

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## Abstract

In this paper, we describe, using multivariate analysis, the distribution of plant species at three valley-floor sites in the Northern Jarrah Forest, south-western Australia. At each site, plant species are distributed along a topographic gradient in communities that broadly parallel the valley floor, resulting in a conspicuously zoned vegetation pattern. Soils are arranged in a similar pattern, with a clear distinction between upland sandy soils, sandy loams on the footslope and silty loams on the flat valley floor, as reflected by changes in field texture, gravel content, electrical conductivity (EC) and major element concentrations. We found that the predominant influences on plant distribution were waterlogging and gradient, indicating a direct relationship between vegetation and topography. However, the relationship between vegetation and soil was less pronounced. There were moderate correlations between species distribution and the soil properties Texture, Gravel Content and Electrical Conductivity, and weak correlations with soil concentrations of Fe, C and Mn.

We speculate that soil properties at these sites developed in response to the same seasonal conditions of desiccation and waterlogging that currently control plant distribution, albeit at substantially different timescales. Thus, the relationship between vegetation and soil is an indirect one, reflecting the dominant influence of hydrology on the distributions of both plants and soil.

**Key words:** edaphic controls, jarrah forest, laterite, ordination, soil catena, vegetation mapping, waterlogging.

## Introduction

Relationships between rocks/soils and vegetation have been recognised for centuries and used routinely in mineral prospecting and agriculture (Agricola 1556; Lomonosov 1763, cited in Malyuga 1964; Canon 1960; Ellenberg 1988; Brooks 1998). Some plant communities are consistently associated with particular substrates, such as distinctive 'serpentine flora' in many parts of the world ( *e.g.* Brooks 1987; Proctor & Nagy 1992; Batianoff & Singh 2001), halophytes on saline soils in arid, inland areas (Pan *et al.* 1998) or the calcicole communities of limestone belts (Grime & Curtis 1976; Ström 1997). In Western Australia, following pioneering biogeographical studies by Diels (1906), Gardner (1944) and Beard (1990), edaphic controls on plant distribution are now generally acknowledged at both regional and local scales. In this paper, we explore the possibility that, in at least some situations, the relationship between plants and their substrate might not be a direct one. Instead, the distribution of both plants and soils might be determined by some as-yet-unrecognised factor(s).

In the Northern Jarrah Forest of the Darling Range, south-western Australia, there is a clear demarcation in both soils and vegetation between uplands and valley floors (Havel 1975; Bell & Heddle 1989). Eucalypt open forest (*sensu* Specht *et al.* 1974) occupies the uplands; valley floors are occupied by woody shrubland. There is a distinctive soil catena, from shallow, gravelly sands overlying lateritic duricrust on the uplands, to deep loams overlying saprolitic pallid clay on the valley floors (Siradz 1985; Churchward & Dimmock 1989). Vegetation within most of the forest appears relatively uniform but, on valley floors, there is a conspicuous zonation of species along a micro-topographic gradient, which seems to reflect local differences in water availability and waterlogging. Preliminary observations identified three broad landscape subdivisions from the forest edge to the lowest part of the valley floor – Footslope, Dry Flat and Wet Flat.

In this study, the 'Footslope' includes the downslope edge of jarrah (*Eucalyptus marginata*) forest, which might properly be regarded as the margin of the forested uplands. The uplands are characterised by gravelly (pisolithic) sands, with scattered outcrops of lateritic ferricrete, while the valley floors are dominated by silty or sandy loams. In many situations, the Footslope is a gently concave, transitional geomorphic unit between the upland and the flat valley floor, but its boundaries are not always clearly defined. Vegetation on the Footslope is typically a park-like, low shrubland, often with a sparse overstorey of marri (*Corymbia calophylla*) and yarri (*Eucalyptus patens*).

The 'Dry Flat' includes both the edge of the flat valley floor and permanently dry, slightly elevated parts of the flat. The 'Wet Flat' is that part of the valley floor that is subject to periods of waterlogging in winter. It supports a woody shrubland, which varies throughout the study area from dense *Melaleuca* thickets to meadow-like clearings, where low shrubs are interspersed with sedges and annual herbs. The characteristic high proportion of bare ground surface distinguishes the Wet Flat from the adjacent Dry Flat.

Mäckel (1974) introduced terminology to describe hydrological aspects of zoning in southern African dambos. Our 'Footslope' corresponds to Mäckel's 'upper washbelt' and at least part of his 'lower washbelt', while our 'Wet Flat' is equivalent to his 'seepage zone'. However, our category 'Dry Flat' is not recognised in Mäckel's scheme.

This paper examines the distribution of soils and vegetation at three valley-floor sites in the headwaters of Big Brook and within the Northern Jarrah Forest. The study was part of a larger project investigating hydrological properties of valley floors in the Northern Jarrah Forest, in anticipation of planned bauxite-mining trials. We describe the soil catena in detail at only one of the sites, as catenas at these sites appeared almost identical. We also describe the vegetation at each site. By combining plant and soil observations in a single analysis, we address the question: do plants and soils covary in this area, *i.e.* are they distributed in a similar pattern, possibly indicating a common influence? We discuss management implications of our observations.

## Methods

### Study area

The study area (centred on 32°35'0" S, 116°15'10" E; approximate elevation 270 m) is located in the Darling Range, approximately 70 km SSE of Perth, south-western Australia (Fig. 1). This part of the Darling Range supports jarrah (*Eucalyptus marginata*) forest, as described by Dell *et al.* (1989).

The climate is Mediterranean (Köppen-type *Cs*), with mild, wet winters and hot, dry summers. On average, about 80% of the annual rainfall of approximately 1000 mm falls over the winter rainy season, between May and September (inclusive). Less than 5% falls during the summer months, December – February.

Like other drainage lines in the area, those in the present study are ephemeral streams; surface flow is confined to winter. There is rarely a defined channel. Rather, the flat valley floors are waterlogged during winter across much of their 50–150 m width.

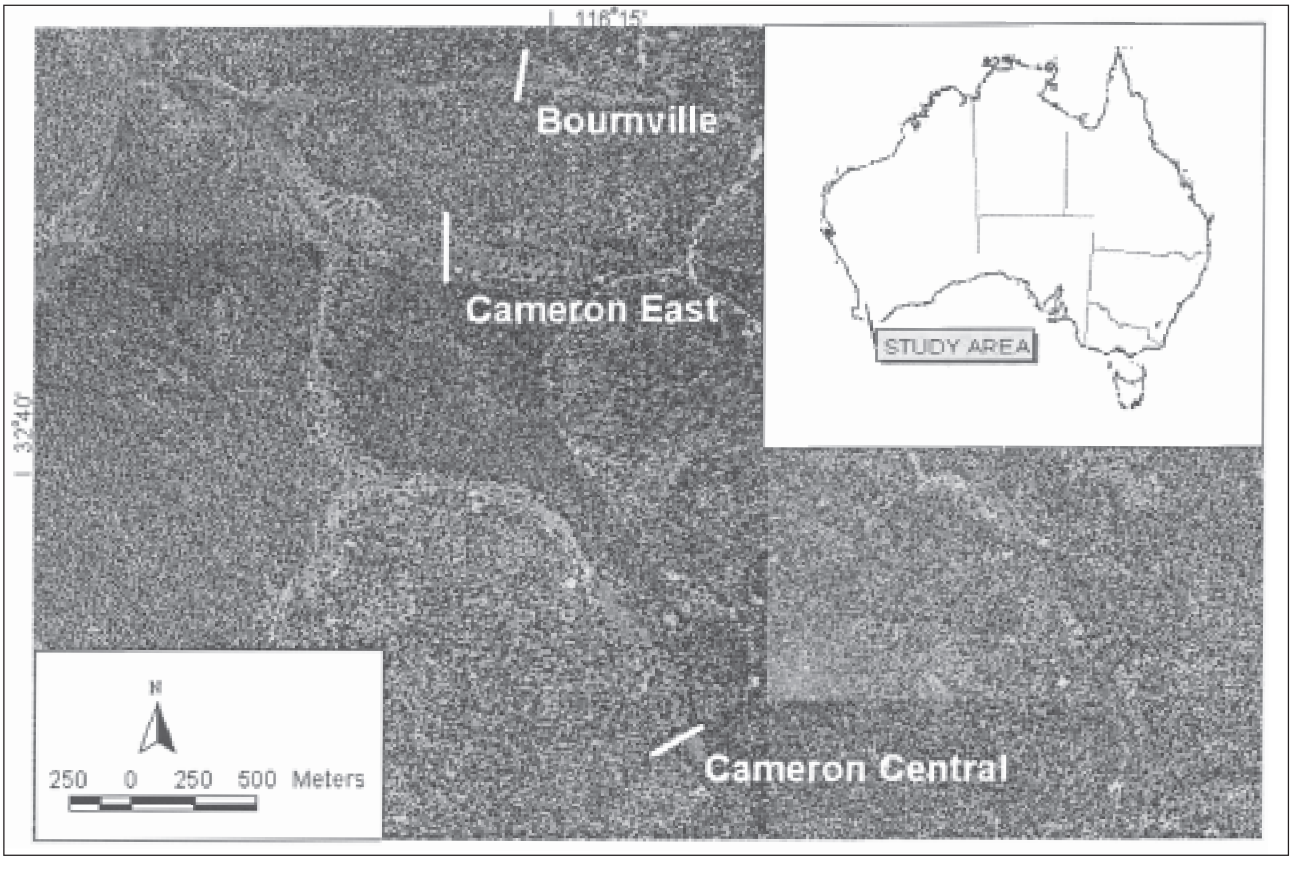

**Figure 1.** Air photographic mosaic of the study area, showing the three valley-floor study sites Cameron Central, Cameron East and Bournville. Note the pale, fine-textured, sinuous valley floors (often flanked by vehicle tracks), which contrast markedly with the dark, coarse-textured uplands.

Vegetation on the flat valley floors is a shrubland, generally 0.3–1.5 m tall, with scattered trees. The dominant shrub species are *Hakea varia, H. prostrata, H. marginata* (Proteaceae) and *Melaleuca incana* (Myrtaceae), with subdominant *Hypocalymma angustifolium* (Myrtaceae), *Astartea fascicularis* (Myrtaceae) and *Baeckea camphorosmae* (Myrtaceae). The main tree species are yarri (*Eucalyptus patens*; Myrtaceae) and paperbark (*Melaleuca preissiana*; Myrtaceae), with minor flooded gum (*Eucalyptus rudis*; Myrtaceae).

### Transect Survey

#### *Site Description*

Three first-order, valley-floor sites in the Big Brook catchment, Cameron Central (CC), Cameron East (CE) and Bournville (BO), were selected for this study (Fig. 1). At CC, a 180 x 60 m grid was established, while at CE and BO single transects, 240 m long, were laid out across the valley floor at right angles to the local creekline, extending a short distance into jarrah forest on either side. Stations were spaced at 20 m intervals. There were 53 stations in total – 13 at each of CE and BO, and 27 at CC. Lines were surveyed with a measuring tape and relative heights were measured to the nearest centimetre using a laser level. Gradients between adjacent stations (expressed in degrees) were calculated from their relative heights using trigonometric relations (sine rule).

Each station was assigned a 'waterlogging index'. This was based on regular observations through the 2000 winter (weekly piezometer readings at Cameron Central and Cameron East, and monthly auger drilling at Bournville). The waterlogging index was assigned as: 0 = dry surface in winter, well drained; 1 = dry surface in winter, but subsurface (perched) water table at < 0.5 m depth for ≥ 2 months; 2 = damp surface in winter, subsurface water table at < 0.2 m depth for ≥ 2 months; 3 = muddy/sticky surface in winter, sodden ground (*i.e.* water table at 0 m) for ≥ 2 months, shallow surface water for a few days after heavy rain; 4 = surface water for ≥ 2 months, occasionally flowing.

#### *Vegetation*

Each station on the CC grid and the CE and BO transects was designated as the centre for a 100 $m^2$ (10 m x 10 m) vegetation-sampling quadrat. In each quadrat, the relative abundance of 66 plant species was scored according to the following scheme: 0 = none; 1 = a few (< 10%); 2= some (10–50%); 3 = many (51–90%); 4 = almost all (> 90%). Abundance was estimated visually as the relative proportion of individuals in the quadrat population, rather than as percentage cover, so that a leafless or diminutive species, such as *Acacia incurva* was not necessarily overwhelmed by a large, leafy species, such as *Acacia saligna*. Thus, the assignment of abundance codes was somewhat subjective. However, for consistency, all estimates were made by the same observer (IRF).

The species were selected as those most frequently occurring in valley-floor situations in the Big Brook area. Fifty-five of these species were recorded from at least two quadrats and were included in the analysis (*i.e.* species recorded from only a single quadrat were excluded from statistical calculations). Species were identified from keys in Marchant *et al.* (1987). Nomenclature follows Paczkowska & Chapman (2000).

We emphasise here that our plant list is not intended as a complete floral audit of the sites. Species were selected from the valley-floor flora, based on their 'commonness' in the Big Brook area and their ease of identification (a particularly relevant consideration for a group whose taxonomic skills varied tremendously). Members of the families Centrolepidaceae, Cyperaceae and Restionaceae, as well as the large genus *Lomandra* were not included in the systematic survey, although their presence was sometimes noted informally. The Wet Flat includes a number of annual species that are widespread in the Big Brook area but rarely abundant in a single quadrat. They are not reported in Table 1 because they were not flowering at the time of the survey; their presence is known, however, from earlier visits. Examples are *Utricularia multifida* (Lentibulariaceae), *Drosera* spp (Droseraceae), *Hypoxis occidentalis* (Hypoxidaceae), *Stylidium spp* (Stylidiaceae) and *Stypandra glauca* (Phormicaceae).

#### *Soil*

Two soil samples were collected from each of the survey stations: (1) a composite sample collected from five shallow (5 cm deep) holes within 1 m of the station; (2) a subsurface sample, collected from the bottom 20 cm of a 1 m auger hole. Field texture was estimated *in situ*, according to the ribbon method described in McDonald & Isbell (1990). The soil textures we encountered varied from sand through loam to medium clay. For computational purposes, we assigned textural codes, as follows: 1 = sand; 2 = loamy sand; 3 = clayey sand; 4 = sandy loam; 5 = loam; 6 = sandy clay loam; 7= clay loam; 8 = sandy clay; 9 = light clay; 10 = medium clay. Thus, the higher the number, the higher the clay content and the heavier the texture of the soil. To ensure consistency, all texture determinations were performed by the same person (SB).

Colour was estimated for moist samples by reference to standard Munsell colour charts (Kollmorgen Corp. 1975). In this paper, 'Soil Colour' is the 'Redness Rating' (RR) of Torrent *et al.* (1980), a single index that combines all three parameters of the Munsell colour sphere, according to the formula

$$RR = [(10-H)C] / V$$

where V and C are numerical values of Munsell value and chroma respectively, and H is the figure preceding YR in Munsell hue. Thus, H = 10 for 10YR, H = 5 for 5YR and H = 0 for 10R. [The hue R (red) is adjacent to YR (yellowish red) on the Munsell sphere and, by convention, 10R is the immediate predecessor of 1YR on colour charts.]

Soil samples were collected from hand-drilled auger holes in each quadrat in the 2000 summer. After air-drying and passing through a 2 mm sieve, both fractions were weighed to determine gravel content, which consisted mostly of ferruginous nodules and pisoliths. Subsequent analyses used the < 2 mm fraction only. Soil pH was determined using a Cyberscan digital meter (Eutech Instruments) for a 1:5 soil:$CaCl_2$ suspension shaken for 1 h at 25°C. Electrical conductivity (EC) was determined for a 1:5 soil:water slurry.

The < 2 mm samples were finely ground, using a mechanical steel mill. Total carbon and nitrogen contents of the soil were determined by combustion, using a CHN-1000 analyser (LECO Corp., Michigan). Plant-available phosphorus and plant-available potassium were estimated by Colwell's (1963) bicarbonate extraction method. The phosphorus present in soil extracts was quantified using a molybdenum-blue colorimetric method (Rayment & Higginson 1992). Potassium was determined for the same soil extract by atomic absorption spectrophotometry (AAS). Total phosphorus, total potassium, sulphur, magnesium, manganese, calcium and iron concentrations of the soil were determined by x-ray fluorescence (XRF), using pressed pellets of finely ground soil with a wax binder.

### Soil Profiles

After an orientation soil survey over the entire upper Big Brook area, the Cameron Central Site was selected as a representative valley floor. A single pit, approximately 4 m long, 1 m wide and 2 m deep, was excavated by backhoe at each of the three topographic locations described above (Footslope, Dry Flat and Wet Flat). An additional pit was excavated at an upland location, about 30 m uphill of the jarrah forest – shrubland boundary. The soil profile exposed in each of these pits was examined and the horizons described *in situ* with regard to colour, texture and structure (McDonald & Isbell 1990).

### Water Tables

We obtained the depths to a seasonal perched water table and to the permanent, catchment-wide groundwater table at the Cameron Central site from piezometers. These were installed along a transect across the flat valley floor, with an additional nest of piezometers on the Footslope, near the jarrah forest edge. Piezometers more than 1 m deep were drilled using a truck-mounted, 150 mm-diameter, hollow-auger, drilling rig. Slotted-PVC pipes were installed in the open holes and the annulus of each hole was packed with sand. Cement grout was used to seal the borehole at the ground surface. For piezometers less than 1 m in depth, holes were drilled with hand augers.

Water table depths were measured manually with a measuring tape, from April 2000 to April 2001. Measurements were made at weekly intervals throughout the period June – November, and at monthly intervals during the drier months.

### Data analysis

Measured variables were compared between the landscape categories (Footslope, Dry Flat and Wet Flat) by one-way ANOVA, after the data had been appropriately transformed to satisfy requirements for independence of means and variance, as well as for homogeneity of group variances (determined by Cochran's test; Winer 1971) . The following variables required transformation: site gradient, topsoil gravel, topsoil EC, Mn, K, subsoil texture and subsoil EC. Note that the reported means are for untransformed data. Post-hoc comparisons of group means were performed using Spjøtvoll/Stoline tests, which allowed for the unequal sample sizes (Spjøtvoll & Stoline 1973). All univariate and ANOVA calculations were made using Statistica (Version 5.1) software (StatSoft Inc. 1995).

Relationships between the 55 species, 53 quadrats and 26 environmental variables were examined with detrended canonical correspondence analysis (DCCA), using the statistical program CANOCO (Ter Braak 1988). There was no transformation of species, no specification of either species-weights or sample-weights, and no downweighting of rare species. Environmental variables were first range-standardised according to the formula

$$Z_{ij} = (X_{ij} - R_{\min i}) / (R_{\max i} - R_{\min i})$$

where $X_{ij}$ is the i^th^ variable in the j^th^ quadrat, R is the range and Z is the desired range-standardised value. For clarity in presentation, ordination scores for the environmental variables were multiplied by three.

## Results

### Vegetation

As we have already pointed out (see Fig. 1), valley floors, with their characteristic shrubland vegetation, are clearly distinguished from the forested uplands. Within the valley floors themselves, many plant species are confined to particular topographic levels and plant communities are arranged in zones that correspond to the topographic units described above (Table 1). Boundaries between the communities are occasionally sharp, but are more often gradational over several metres. Many of the plant species listed in Table 1 have distributions that include more than one topographic unit. *Eucalyptus patens*, for example, is a common tree in Footslope and Dry Flat locations at all three sites, and even extends to the Wet Flat at Site CC. The woody shrubs *Hakea varia* and *Melaleuca incana*, are moderately to very abundant on the Wet Flat at all three sites; they are less abundant on the Dry Flat and uncommon on the Footslope.

The Footslope supports the highest species diversity because it includes species such as *Eucalyptus marginata* and *Acacia pulchella* that are characteristic of uplands, as well as typical valley-floor species like *Hypocalymma angustifolium*. Comprehensive diversity indices are not reported in this paper however because, as described in the Methods section, the species surveyed are merely a subset of the total flora.

### Soil Profiles

Our detailed soil survey at Cameron Central showed a catena similar to that described for another Darling Range site by Siradz (1985). Typical upland soils beneath the jarrah forest canopy (represented here by Pit 013; Fig. 2A) are gravelly loamy sands, commonly underlain by lateritic duricrust, which is in turn underlain by a considerable thickness of kaolinitic clay (Gilkes *et al.* 1973). Nearby drillholes intersected unweathered bedrock at depths ranging from 20 to 50 m (usually 25–30 m). Valley-floor soils, by contrast, are typically deeper, less gravelly, better structured, more clayey and more brightly coloured. Profiles are well developed, with conspicuous A, B and C horizons. Bright yellowish colours of the hydrated iron oxide goethite near the

## Table 1

Plant species (and number of quadrats they were recorded in) listed in descending order of 'commonness' and grouped according to topographic unit (Footslope, Dry Flat, Wet Flat). Species highlighted in grey are entirely or almost entirely confined to a single topographic unit.

| Topographic Unit | Species | Family | Average Abundance [1] | Percentage of Quadrats [2] | Av. Abundance X Quadrats [3] | No. of Sites [4] |
|---|---|---|---|---|---|---|
| Footslope (*N*=25) | *Eucalyptus marginata (15)* | Myrtaceae | 3.7 | 60 | 220 | 3 |
| | *Corymbia calophylla (16)* | Myrtaceae | 2.4 | 64 | 154 | 2 |
| | *Trymalium ledifolium (15)* | Rhamnaceae | 1.8 | 60 | 105 | 3 |
| | *Pimelea ciliata (13)* | Thymeleaceae | 1.7 | 52 | 88 | 2 |
| | *Hakea lissocarpha (14)* | Proteaceae | 1.2 | 56 | 68 | 3 |
| | *Macrozamia riedleii (11)* | Zamiaceae | 1.0 | 44 | 44 | 3 |
| | *Lechenaultia biloba (8)* | Goodeniaceae | 1.3 | 32 | 40 | 3 |
| | *Pentapeltis peltigera (3)* | Apiaceae | 1.3 | 12 | 16 | 2 |
| | *Tripterococcus brunonis (3)* | Stackhousiaceae | 1.3 | 12 | 16 | 2 |
| | *Phyllanthus calycinus (2)* | Euphorbiaceae | 1.0 | 8 | 8 | 2 |
| | *Pimelea suaveolens (2)* | Thymeleaceae | 1.0 | 8 | 8 | 2 |
| | *Eucalyptus patens (15)* | Myrtaceae | 3.1 | 60 | 189 | 3 |
| | *Dryandra nivea (24)* | Proteaceae | 1.9 | 96 | 184 | 3 |
| | *Xanthorrhoea preissii (19)* | Xanthorrhoeaceae | 1.8 | 76 | 140 | 3 |
| | *Hypocalymma angustifolium (20)* | Myrtaceae | 1.7 | 80 | 136 | 3 |
| | *Baeckea camphorosmae (12)* | Myrtaceae | 1.3 | 48 | 63 | 3 |
| | *Melaleuca incana (5)* | Myrtaceae | 1.6 | 20 | 32 | 1 |
| | *Astroloma ciliatum (7)* | Epacridaceae | 1.0 | 28 | 28 | 3 |
| | *Leucopogon nutans (7)* | Epacridaceae | 1.0 | 28 | 28 | 3 |
| | *Persoonia longifolia (7)* | Proteaceae | 1.0 | 28 | 28 | 2 |
| | *Leptomeria cunninghamii (4)* | Santalaceae | 1.0 | 20 | 20 | 2 |
| | *Ptilotus manglesii (5)* | Amaranthaceae | 1.0 | 20 | 20 | 2 |
| | *Hakea varia (3)* | Proteaceae | 1.0 | 12 | 12 | 2 |
| Dry Flat (*N*=13) | *Hakea prostrata (4)* | Proteaceae | 1.5 | 31 | 47 | 2 |
| | *Hypocalymma angustifolium (13)* | Myrtaceae | 2.4 | 100 | 240 | 3 |
| | *Eucalyptus patens (8)* | Myrtaceae | 3.6 | 53 | 193 | 2 |
| | *Melaleuca incana (9)* | Myrtaceae | 2.1 | 69 | 147 | 3 |
| | *Hakea varia (8)* | Proteaceae | 2.0 | 62 | 124 | 3 |
| | *Xanthorrhoea preisii (7)* | Xanthorrhoeaceae | 1.6 | 54 | 85 | 2 |
| | *Baeckea camphorosmae (5)* | Myrtaceae | 2.0 | 38 | 76 | 2 |
| | *Dryandra nivea (7)* | Proteaceae | 1.2 | 54 | 63 | 3 |
| | *Astroloma ciliatum (5)* | Epacridaceae | 1.6 | 38 | 61 | 2 |
| | *Acacia applanata (7)* | Mimosaceae | 1.0 | 54 | 54 | 3 |
| | *Leucopogon nutans (5)* | Epacridaceae | 1.2 | 38 | 46 | 2 |
| | *Patersonia occidentalis (3)* | Iridaceae | 1.3 | 23 | 31 | 2 |
| | *Persoonia longifolia (2)* | Proteaceae | 1.0 | 15 | 15 | 1 |
| Wet Flat (*N*=15) | *Melaleuca preissiana (4)* | Myrtaceae | 4.0 | 27 | 107 | 2 |
| | *Astartea fascicularis (4)* | Myrtaceae | 2.3 | 27 | 60 | 1 |
| | *Stylidium crassifolium (4)* | Stylidiaceae | 1.8 | 27 | 47 | 1 |
| | *Acacia incurva (6)* | Mimosaceae | 1.0 | 40 | 40 | 2 |
| | *Melaleuca viminea (3)* | Myrtaceae | 1.3 | 20 | 27 | 2 |
| | *Dampiera alata (4)* | Goodeniaceae | 1.0 | 27 | 27 | 1 |
| | *Melaleuca incana (13)* | Myrtaceae | 2.5 | 87 | 220 | 3 |
| | *Hakea varia (14)* | Proteaceae | 2.0 | 93 | 187 | 3 |
| | *Hypocalymma angustifolium (12)* | Myrtaceae | 1.9 | 80 | 153 | 3 |
| | *Eucalyptus patens (5)* | Myrtaceae | 3.5 | 38 | 133 | 3 |
| | *Patersonia occidentalis (8)* | Iridaceae | 1.0 | 53 | 53 | 3 |
| | *Acacia applanata (7)* | Mimosaceae | 1.0 | 47 | 47 | 2 |
| | *Xanthorrhoea preissii (4)* | Xanthorrhoeaceae | 1.5 | 27 | 40 | 2 |
| | *Leptomeria cunninghamii (3)* | Santalaceae | 1.0 | 20 | 20 | 2 |
| | *Dryandra nivea (2)* | Proteaceae | 1.0 | 13 | 13 | 2 |
| | *Persoonia longifolia (2)* | Proteaceae | 1.0 | 13 | 13 | 1 |
| | *Ptilotus manglesii (2)* | Amaranthaceae | 1.0 | 13 | 13 | 1 |

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[1] Abundance index (0-4) described in text

[2] Percentage of quadrats in which the species is present

[3] This is the property referred to in the text as 'commonness'

[4] Number of sites (Cameron Central, Cameron East, Bournville) at which this species is present

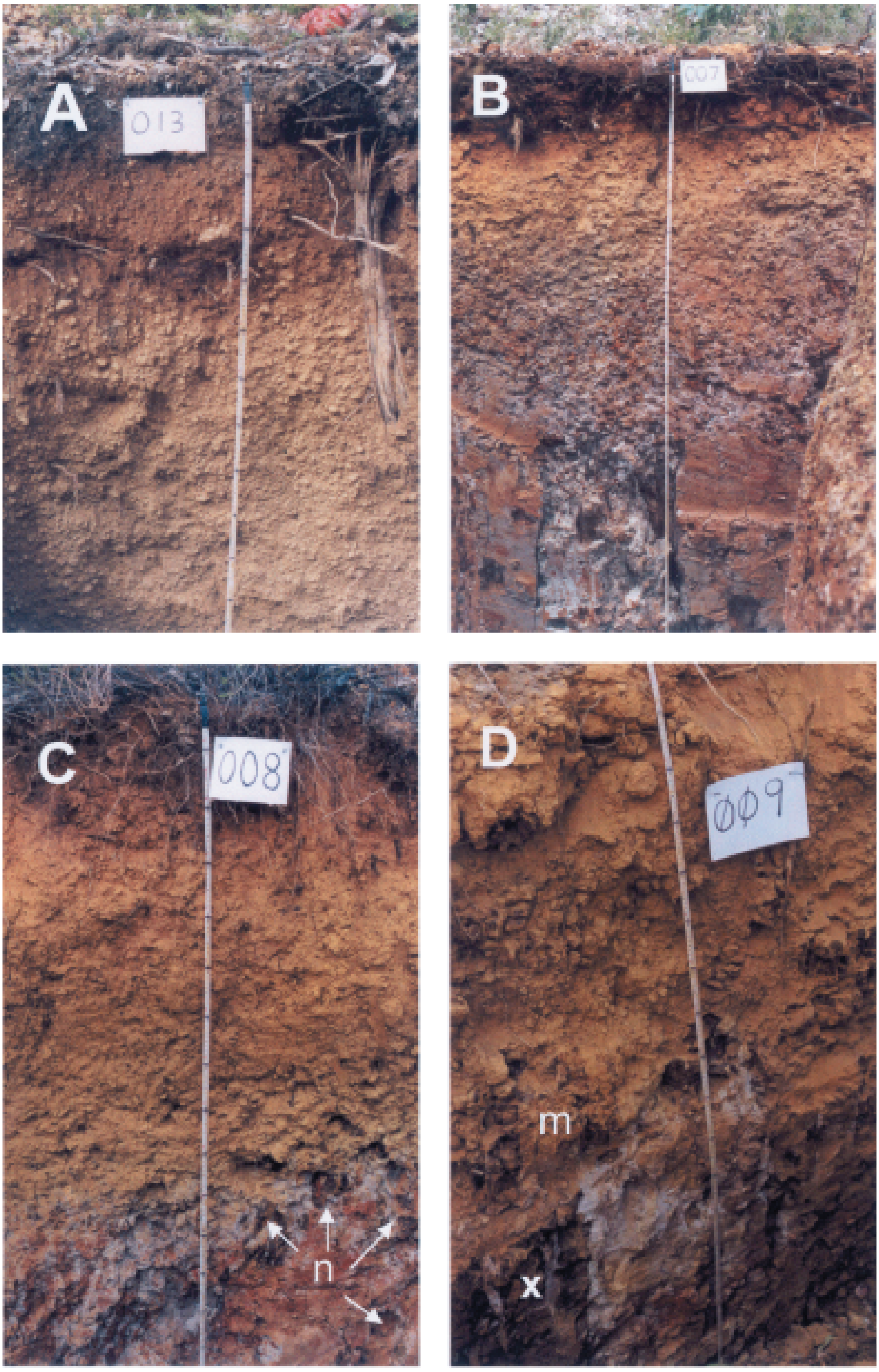

**Figure 2. A.** Soil profile on an upland forested hillslope adjacent to Site CC (Pit 013). Dull yellowish brown, very gravelly loamy sand. Note rudimentary pedological development and very weak colluvial sorting. The pit floor (not shown) is massive lateritic duricrust. **B.** Soil profile on the Footslope at Site CC (Pit 007). Bright orange sandy loam, passing gradually into dull yellowish brown and reddish brown clay loam, and underlain at about 1.35 m by grey clay. **C.** Soil profile on the Wet Flat at Site CC (Pit 008). Bright yellowish orange silty loam, underlain at about 1.0 m by grey clay. Note irregular nodules (n) of bog iron ore at clay-loam boundary. **D.** Soil profile on the Dry Flat at Site CC (Pit 009). Bright yellowish orange gravelly clay loam and silty loam, underlain by massive (m), becoming columnar (x), bog iron ore. There is an indistinct boundary with grey clay at about 1.55 m.

surface contrast with the dark reds and purples of hematite at depth.

Within the valley-floor environment, footslope soils are readily distinguished from soils of the valley-floor flat. Footslope soils (represented here by Pit 007; Fig. 2B) are sandy loams or clay loams, with abundant pisoliths (presumably derived from eroding duricrust uphill). The flat part of the valley floor, on the other hand, is underlain by silty loam, which has a characteristic brightly coloured, spongy surface. Gravel content is less than 5% at the surface, increasing to 20–50% at depth (Pit 008; Fig. 2C). This increase in the proportion of > 2 mm material (gravel) is due mostly to the *in situ* growth of ferruginous micro-nodules, rather than to the presence of colluvial pisoliths.

At CC and at many other valley-floor sites in the study area, irregular lumps or columns of bog iron ore have developed at the soil-clay interface or in the horizon above it. Within the Dry Flat portion of the CC grid area, massive bog iron ore forms a more-or-less continuous pan across the valley floor flat (Pit 009; Fig. 2D).

Figure 3 is a schematic cross-section across the valley floor at Site CC, illustrating the general relationship between vegetation, soil and topography. A similar catenary situation exists at the other sites. Whereas vegetation is clearly zoned at each of the three sites (CC, CE and BO) and there is a consistent relationship between vegetation and topography, there is no unique (one-to-one) relationship between either soil and topography or soil and vegetation. Furthermore, boundaries between soil units are generally gradational.

This diagram illustrates an important point – valley-floor soils in the Darling Range are not all derived from identical parent materials. Even at the same site, as shown here, some parts of the Footslope are developed on lateritic duricrust, while other parts are underlain by pallid sandy clay. On the flat portion of the valley floor, soils are developed on various parts of the pre-existing laterite profile (usually, but not always, the pallid sandy clay), and include varying proportions of alluvial and colluvial material. In addition, there are authigenic minerals that have crystallised relatively recently, in response to the repeated wetting/drying conditions (Dixon & Weed 1977).

### Soil Transects

Analysis of variance showed that there were significant differences in site and soil properties between topographic units (Table 2). Only one property, waterlogging index, was significantly different for all topographic units. The remainder showed similarities between two or all three of the units, which was consistent with our observation that soil changes were often gradual between units. For example, at CC, the typical upland soil encountered in Pit 013 encroached at least 10 m downhill onto the valley-floor Footslope unit.

**Table 2**

Mean values and standard error (S.E.) of site and soil properties for the three topographic units (Footslope, Dry Flat, Wet Flat). Numbers in each row followed by the same superscript letter are not significantly different.

| | **Property** | **Units** | **Mean Footslope (*N*=25)** | **S.E.** | **Mean Dry Flat (*N*=13)** | **S.E.** | **Mean Wet Flat (*N*=15)** | **S.E.** |
|---|---|---|---|---|---|---|---|---|
| Site: | Gradient | degrees | 3.3 | 0.3 | 0.71$^{a}$ | 0.1 | 0.34$^{a}$ | 0.08 |
| | Waterlogging Index [1] | code (0-4) | 0.32 | 0.09 | 1.8 | 0.1 | 3.0 | 0.1 |
| Topsoil: | Field texture [1] | code (0-10) | 3.6$^{a}$ | 0.3 | 4.5$^{ab}$ | 0.1 | 4.7$^{b}$ | 0.2 |
| | Colour [1] | | 2.5$^{a}$ | 0.1 | 0.5 | 0.04 | 2.6$^{a}$ | 0.2 |
| | Gravel (wt) | % | 46 | 4 | 9.5$^{a}$ | 2 | 14$^{a}$ | 3 |
| | pH (in $CaCl_2$) | | 4.8$^{a}$ | 0.1 | 4.4$^{b}$ | 0.05 | 4.6$^{ab}$ | 0.1 |
| | Electrical Conductivity | µmS cm$^{-1}$ | 54$^{a}$ | 4 | 59$^{a}$ | 6 | 83 | 9 |
| | C | % | 5.9$^{a}$ | 0.4 | 5.6$^{a}$ | 1.0 | 7.4$^{a}$ | 0.8 |
| | N | % | 0.29$^{a}$ | 0.04 | 0.40$^{a}$ | 0.08 | 0.38$^{a}$ | 0.05 |
| | Available P | ppm | 7.3$^{a}$ | 1.1 | 5.4$^{a}$ | 1.5 | 5.6$^{a}$ | 0.9 |
| | Available K | ppm | 91$^{a}$ | 11 | 85$^{a}$ | 17 | 114$^{a}$ | 15 |
| | Fe | % | 5.8$^{a}$ | 0.7 | 4.6$^{a}$ | 1.1 | 6.5$^{a}$ | 0.9 |
| | Mn | % | 0.060$^{ab}$ | 0.010 | 0.022$^{a}$ | 0.004 | 0.087$^{b}$ | 0.026 |
| | Ca | % | 0.31 | 0.03 | 0.16$^{a}$ | 0.03 | 0.20$^{a}$ | 0.02 |
| | K | % | 0.14 | 0.01 | 0.23$^{a}$ | 0.03 | 0.28$^{a}$ | 0.03 |
| | S | % | 0.058$^{a}$ | 0.008 | 0.08$^{ab}$ | 0.01 | 0.11$^{b}$ | 0.01 |
| | P | % | 0.028$^{a}$ | 0.002 | 0.021$^{a}$ | 0.003 | 0.024$^{a}$ | 0.003 |
| | Si | % | 19$^{a}$ | 1 | 24$^{a}$ | 3 | 21$^{a}$ | 2 |
| | Al | % | 8.4$^{a}$ | 0.5 | 6.6$^{a}$ | 0.6 | 6.7$^{a}$ | 0.5 |
| | Mg | % | 0.098$^{a}$ | 0.005 | 0.09$^{a}$ | 0.01 | 0.11$^{a}$ | 0.01 |
| Subsoil: | Field texture [1] | code (0-10) | 4.2$^{a}$ | 0.3 | 6.2$^{ab}$ | 0.7 | 6.4$^{b}$ | 0.7 |
| | Water | % | 12$^{a}$ | 1 | 13$^{ab}$ | 1 | 15$^{b}$ | 1 |
| | Colour | | 5.5$^{a}$ | 0.2 | 1.4 | 0.1 | 4.2$^{a}$ | 0.3 |
| | Gravel (wt) | % | 68$^{a}$ | 3 | 41$^{b}$ | 6 | 54$^{ab}$ | 5 |
| | pH (in $CaCl_2$) | | 4.8$^{a}$ | 0.1 | 4.4$^{a}$ | 0.1 | 4.6$^{a}$ | 0.2 |
| | Electrical Conductivity | µmS cm$^{-1}$ | 35$^{a}$ | 3 | 58$^{a}$ | 6 | 193 | 61 |

[1] See text for description

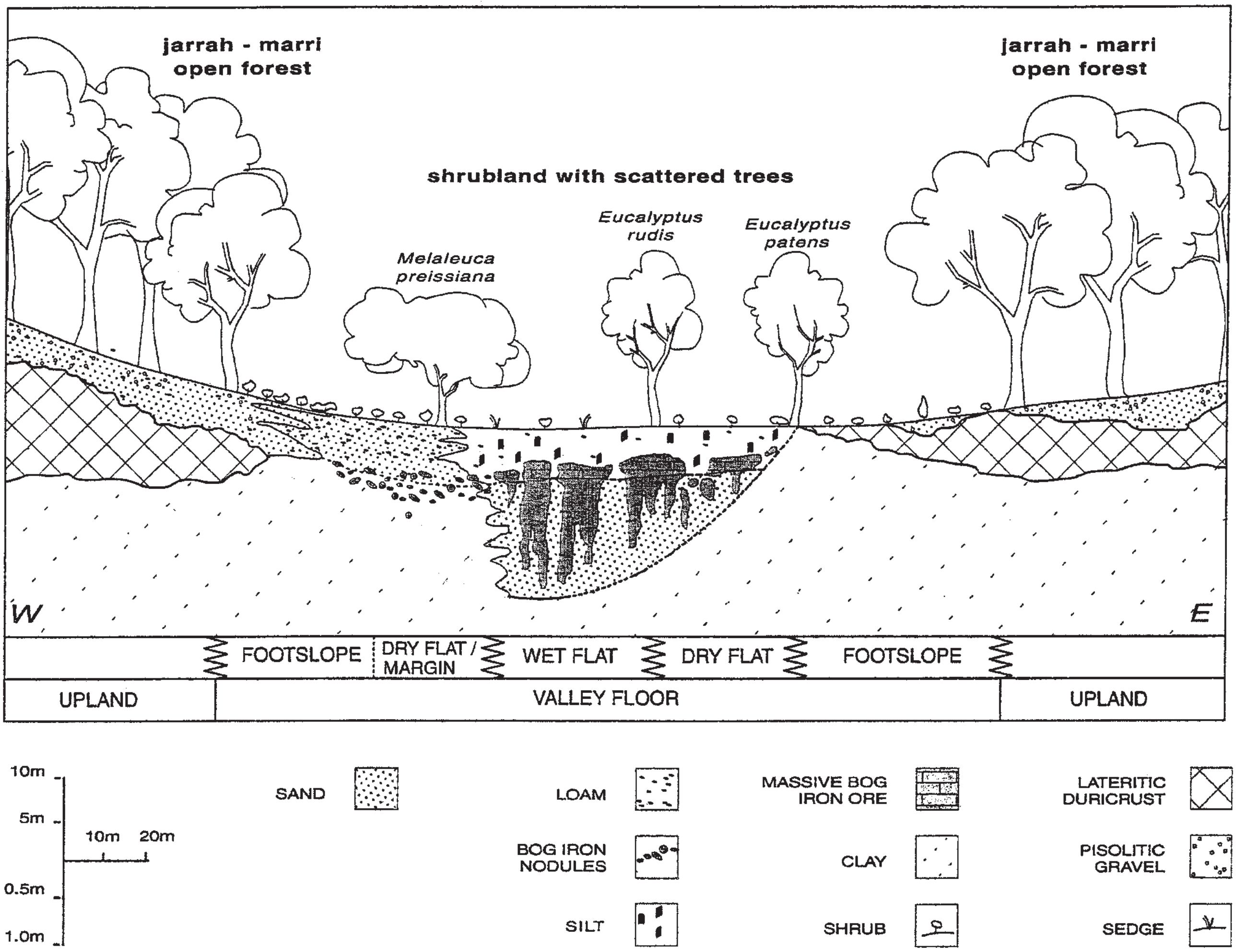

**Figure 3.** Schematic cross-section across the valley floor of the Cameron Central site, showing relationships between vegetation zoning, soil and topography. Note the vertical exaggeration and the difference in vertical scales between above-ground and below-ground features.

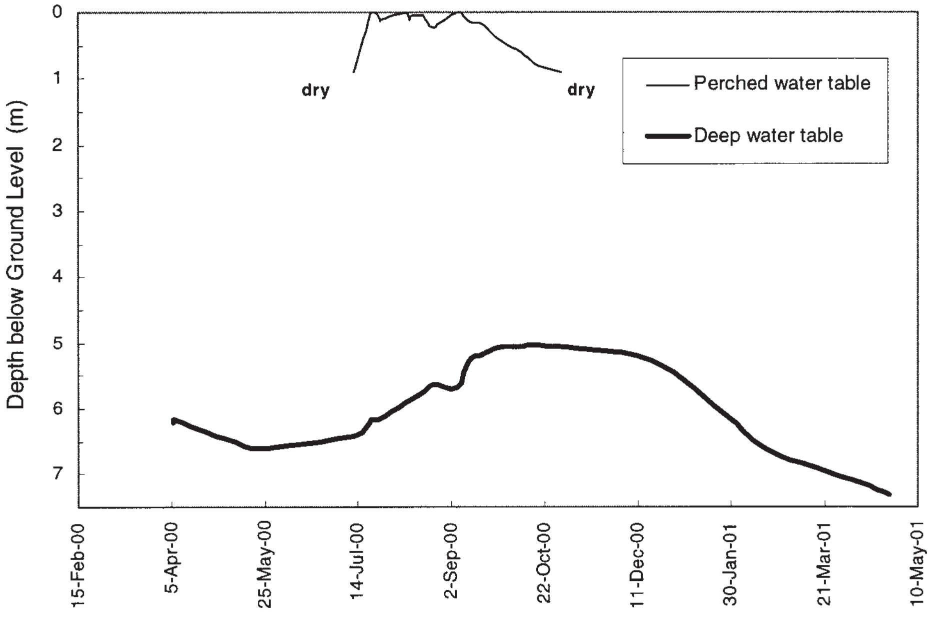

**Figure 4.** Depths of perched water and groundwater tables at Site CC.

### Water Tables

Water levels in two of the CC piezometers (both located on the Wet Flat, near the southern edge of the grid) are shown in Fig. 4. The local catchment groundwater table fluctuated during the study period between 7.1 m and 5.1 m, maintaining its peak level (*i.e.* its shallowest depth) through spring and early summer. This groundwater table was identified in numerous drillholes throughout the Cameron Central catchment, and water tables at similar depths and with similar seasonal fluctuations were recorded in neighbouring catchments throughout the Big Brook area (Ken McIntosh, Alcoa hydrologist, pers. comm.).

The perched water table was confined to winter months on the flat part of the valley floor. At Site CC, this perched water table did not extend across the entire flat, but was confined to the western sector. We observed similar, localised, perched water tables on all drainage lines in the Big Brook area, and believe that these are characteristic features of valley floors throughout this part of the Northern Jarrah Forest.

### Ordination

Detrended canonical correspondence analysis clearly separated both quadrats and species of the Footslope from those of the Wet Flat (Figs 5 and 6). This separation was most pronounced on the first ordination axis. Quadrats and species of the Dry Flat occupied a transitional position on the primary axis; their separation was most pronounced along Axis 2. Figure 7A shows the position in the same ordination space occupied by environmental variables. Table 3 lists correlation

**Table 3**

Correlation constants (Pearson's product moments) between environmental variables and DCCA axes.

| | Property | DCCA Axis 1 | DCCA Axis 2 |
|---|---|---|---|
| Site: | Gradient | -0.72 | -0.02 |
| | Waterlogging Index | 0.85 | -0.05 |
| Topsoil: | Field Texture | 0.48 | 0.07 |
| | Colour 0.00 | -0.35 | |
| | Gravel (wt) | -0.74 | -0.06 |
| | pH (in $CaCl_2$) | -0.42 | -0.42 |
| | Electrical Conductivity | 0.34 | -0.38 |
| | C | 0.09 | -0.44 |
| | N | 0.27 | -0.36 |
| | Available P | -0.11 | -0.26 |
| | Available K | 0.10 | -0.17 |
| | Fe | 0.03 | -0.44 |
| | Mn | 0.03 | -0.31 |
| | Ca | -0.50 | -0.32 |
| | K | 0.55 | 0.47 |
| | S | 0.42 | -0.40 |
| | P | -0.25 | -0.47 |
| | Si | 0.22 | 0.26 |
| | Al | -0.40 | 0.00 |
| | Mg | 0.09 | 0.23 |
| Subsoil: | Field Texture | 0.46 | 0.36 |
| | Water | 0.33 | -0.09 |
| | Colour | -0.18 | -0.12 |
| | Gravel (wt) | -0.32 | -0.20 |
| | pH (in $CaCl_2$) | -0.32 | -0.06 |
| | Electrical Conductivity | 0.56 | -0.01 |

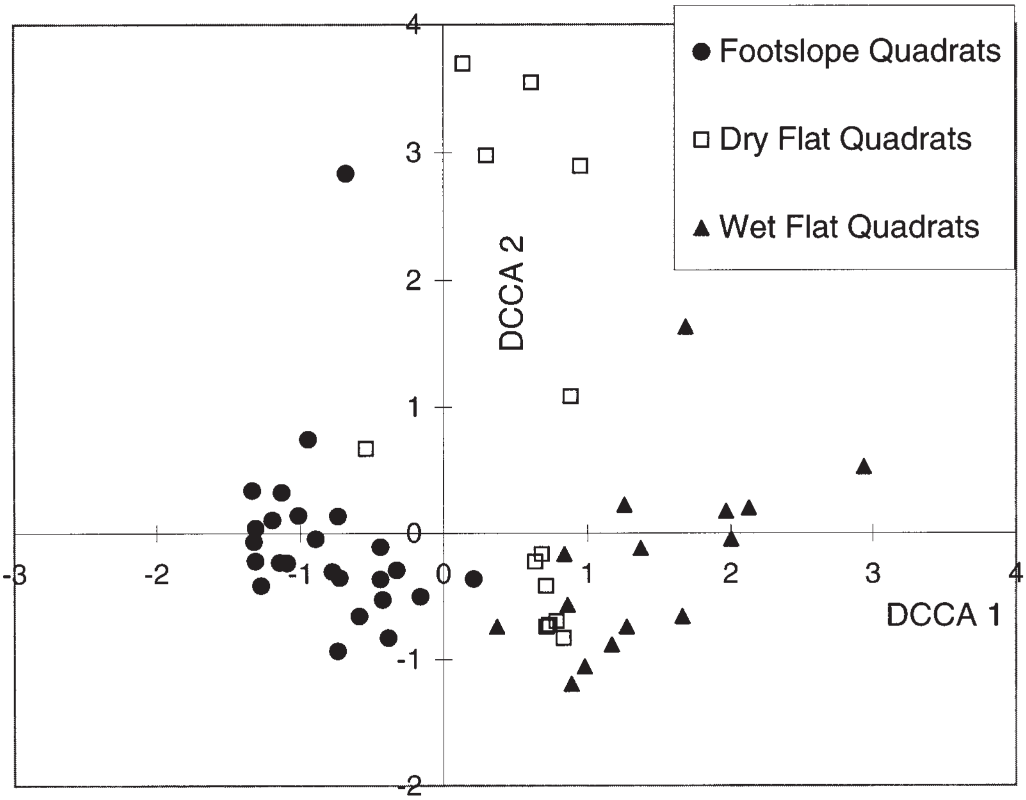

**Figure 5.** Detrended canonical correspondence analysis ordination of all 53 quadrats at all three study sites combined. Eigenvalues: axis 1 = 0.486; axis 2 = 0.330.

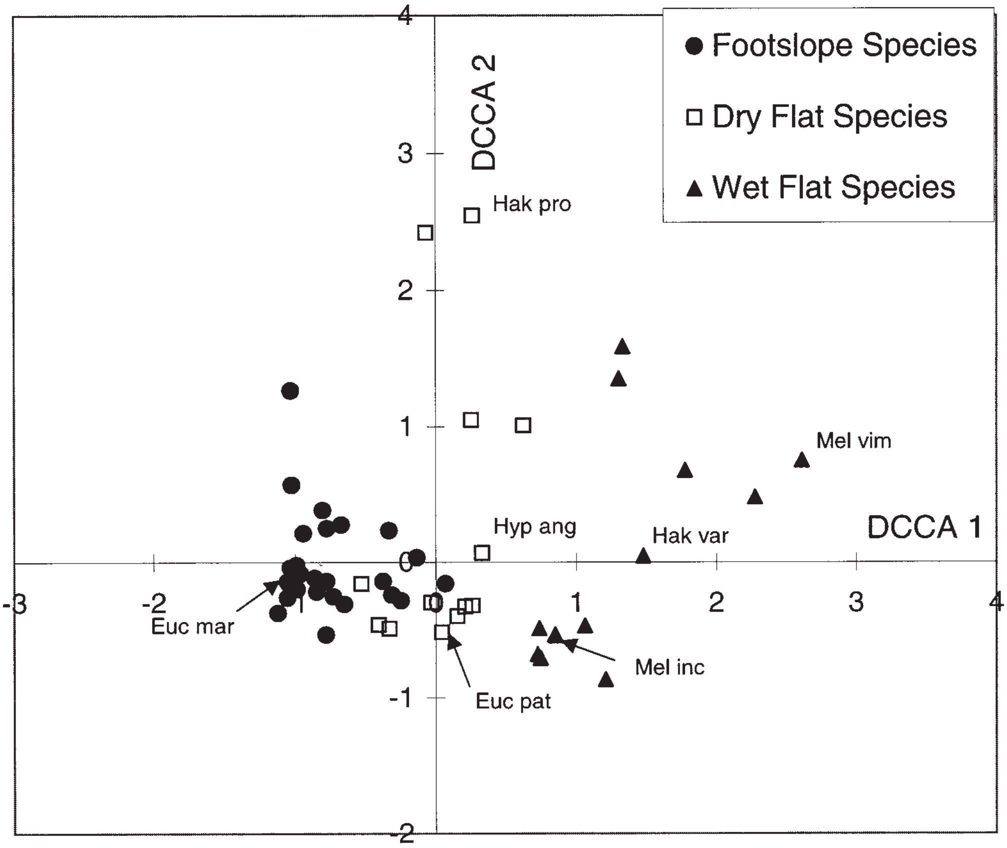

**Figure 6.** Detrended canonical correspondence analysis ordination of all 55 species. Eigenvalues: axis 1 = 0.486; axis 2 = 0.330. Note that species were assigned to the topographic unit in which they were most commonly recorded. Euc mar = *Eucalyptus marginata* (jarrah); Euc pat = *Eucalyptus patens*; Hak pro = *Hakea prostrata*; Hak var = *Hakea varia*; Hyp ang = *Hypocalymma angustifolium*; Mel inc = *Melaleuca incana*; Mel vim = *Melaleuca viminea*

constants for relationships between environmental variables and the first two DCCA axes. There were strong correlations between several environmental variables and the first axis ($r_{max}$ = 0.85), but the second axis produced correlations of only moderate strength ($r_{max}$ = 0.47).

As summarised in Figure 7B, Axis 1 is associated with variation in the site properties Gradient and Waterlogging Index, as well as the soil physical properties of Field Texture, Topsoil Gravel and Subsoil Water Content. Secondary variation on Axis 2 is associated with the soil chemical properties Iron, Carbon and Manganese, and the related entity Colour (Redness Rating).

Much of the variation on DCCA Axis 2 was associated with Site CE, particularly with Dry Flat quadrats containing the shrub species *Hakea prostrata* (Proteaceae). The association of DCCA Axis 1 with waterlogging owes much of its strength to the winter-wet valley floor at Site BO, which supports a number of species rarely seen at other sites, *e.g. Acacia incurva* (Mimosaceae), *Astartea fascicularis* (Myrtaceae) and *Melaleuca viminea* (Myrtaceae).

## Discussion

The ordination described here confirmed our preliminary hypothesis that the distribution of both vegetation and soils on Darling Range valley floors is correlated with topography and waterlogging. On the basis of both vegetation and site/soil properties, valley floors could be subdivided into the three units informally identified before the survey — Footslope, Dry Flat and Wet Flat. This same pattern was reproduced at sites on at least three neighbouring drainage lines — Cameron Central, Cameron East and Bournville — despite the fact that the three sites had slightly different soils and supported some different plant species.

This Wet Flat – Dry Flat dichotomy is a general feature of valley floors in the Big Brook region. In fact, we observed localised winter-waterlogging on drainage lines throughout the Darling Range. Waterlogged areas support a distinctive vegetation of swamp-loving woody shrubs and winter-flowering annual herbs. By contrast, few species are confined to (or even most abundant on) the Dry Flat (see Table 1).

Although sharp boundaries between topographic units can be observed at some localities, there is considerable overlap in most situations in both vegetation and environmental properties. This is reflected in the imprecise borders between units in the quadrat/species ordination (Figs 5 and 6), the many plant species shared between adjoining units (Table 1), and the absence of significant differences between units for many soil properties (Table 2).

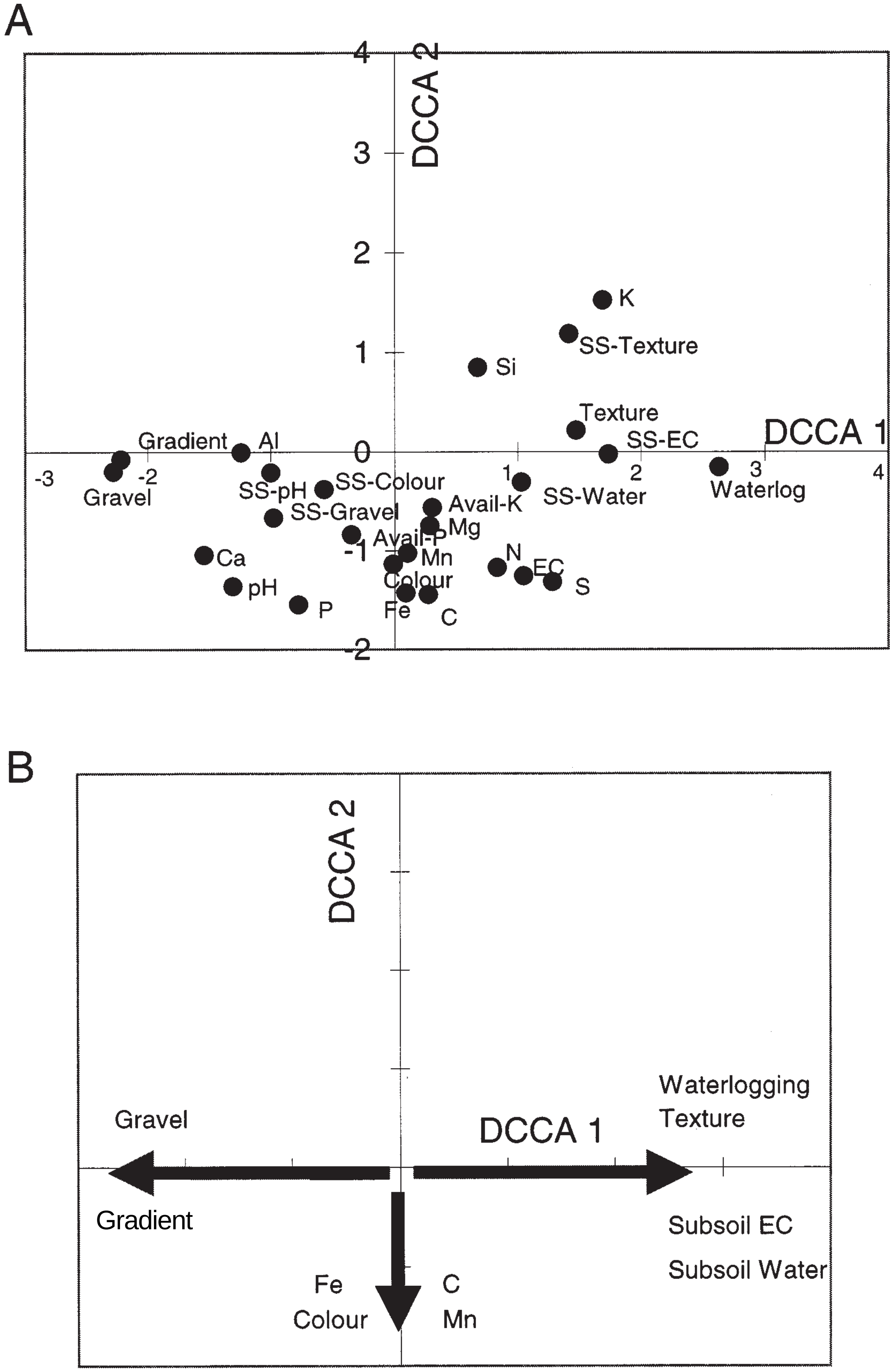

**Figure 7. A.** Detrended canonical correspondence analysis ordination of all 26 environmental variables. Eigenvalues: axis 1 = 0.486; axis 2 = 0.330. The prefix 'SS' denotes subsoil. Texture = field texture (an approximation of clay content). Waterlog = waterlogging index (see text). **B.** Summary of DCCA ordination in Fig. 7A, showing the main relationships between the ordination axes and environmental variables. Axis 1 is associated with variation in the site properties Gradient and Waterlogging Index, as well as the soil physical properties Field Texture, Subsoil Water Content and Subsoil EC. Axis 2 is associated with the soil chemical properties Fe, Mn, C, and Colour (Redness Rating).

We note that the variables Gravel and Gradient are close together in the Footslope region of the ordination space. High contents of gravel (> 2 mm material) on the slopes can be attributed almost entirely to lateritic pisoliths (see Fig. 2A). Although ironstone is also present on the flat part of valley floors (as bog iron ore), its contribution to the gravel fraction is substantial only in the subsoil. It is interesting that total Al (aluminium) in the soil lies near *Eucalyptus marginata* (jarrah) in the ordination diagram (both plot near –1,0 on Figs 6 and 7(a)). This is not inconsistent with the anecdotal observation that the richest bauxite deposits are found in high-quality jarrah forest.

Levels of plant-available (*i.e.* bicarbonate-extractable) P and K are very low. This has an important influence on the floristic composition of valley floors. Only those species (such as members of the family Proteaceae, with their characteristic proteoid roots; Jeschke & Pate 1995) that are able to tolerate a low P-K environment, are present.

The environmental variable which probably has the strongest influence on plant and soil distribution on valley floors is waterlogging. The waterlogging index used in this paper, a relative measure of the duration of waterlogging, identifies those parts of the valley floor with a perched water table in winter. Adaptations to waterlogging in wetland plants have been reviewed by Armstrong *et al.* (1995) and Crawford (1996), and some Australian examples have been described by Jolly & Walker (1996), Akeroyd *et al.* (1998) and Denton *et al.* (1999). Our observations in Darling Range plants have not been detailed enough to allow us to contribute to the discussion on waterlogging tolerance. However, some general features of the valley-floor vegetation can be identified: (1) there are many woody shrub species and few trees, (2) the dominant vegetation is shrubland, and (3) valley floors appear as gaps in the jarrah-dominated regional forest cover. The sensitivity of jarrah roots to even intermittent waterlogging has been described by Davison (1988).

The first two ordination axes account for only 31.4% of the variance in the species-quadrat-environmental variable relationship. Okland (1999) found that canonical correspondence analysis regularly underestimates this percentage. Nevertheless, it seems likely that other factors, not measured in our survey, were influencing plant distribution on Darling Range valley floors. Possible influences include fire, *Phytophthora* dieback and increased sedimentation associated with logging and road construction in adjacent uplands (Abbott & Loneragan 1983; Dawson *et al.* 1985; Borg *et al.* 1987; Stoneman *et al.* 1987; Bell *et al.* 1989). Historical records (Western Australian Department of Conservation and Land Management, Dwellingup, pers. comm.) indicate that Site CC had indeed burned (albeit patchily) three years before the survey (*i.e.* 1997). Air photos suggest that much of the CE and BO valley floors had been burnt at least once in the early-mid 1990s. However, in the three-year period that we visited these sites, we noted no consistent changes in the vegetation that might be interpreted as a recovery trend from disturbance.

The relationship between vegetation and topography is essentially related to differences in water availability, whereas soils are related not just to topography but also to parent materials. The relative sharpness of the relationship between vegetation and topography, compared with the fuzziness of relationships between both soil-and-topography and soil-and-vegetation, can probably be attributed to difference in timescales between the establishment of a plant community and the formation of a soil. Plants arrange themselves into communities over hundreds of years or decades, whereas the pedological processes that take place during soil formation may require thousands of years or longer to achieve an equilibrium state. The present laterised landscape of the Darling Range is thought to have existed since at least mid-Tertiary times (20–30 million years ago; Anand & Paine 2001). However, there have been major changes in the climate and vegetation of southwestern Australia during that interval (Frakes 1999; Frakes & Barron 2001). By comparing the distribution of fossil pollen of South-West forest trees with their present rainfall requirements, Churchill (1968) identified shifts in the hydrological regime over the past six thousand years. Such very recent hydrological changes would not necessarily be reflected in the soil.

By analogy with other areas in the Darling Range and from the results of in-house, hydrological modeling (Croton & Bari 2001; Croton & Barry 2001), it is anticipated that bauxite mining, with its attendant forest clearing, could result in increased levels of runoff and drainage. This, in turn, would lead to increases in the extent and/or duration of waterlogging on valley floors, an increase in the proportion of Wet Flat over Dry Flat environments, and changes in the floristic composition of valley-floor vegetation. Although bauxite ore is generally absent from valley floors and there is no intention to mine valley floors themselves, some transient 'collateral damage' (*e.g.* haulage roads, turnaround areas) will inevitably take place. Our work shows that species selection for the rehabilitation of such damaged areas should be informed, not by maps of soil distribution or pre-mining vegetation, but by post-mining waterlogging patterns.

An additional feature of valley floors in the Darling Range, which has not been explicitly examined in the present study, but which may nevertheless have a prominent role in determining plant distribution, is the summer insolation. Because valley floors are often treeless and canopy cover tends to be lower than in adjacent forest, they are exposed to full summer sun and drying winds. Claypans are commonly characterised by cracking surfaces and patches of bare ground. The vegetation inhabiting such places must be capable of tolerating periodic desiccation as well as seasonal waterlogging.

## Conclusion

We conclude, from the transect data, that the predominant influences on plant distribution across valley floors in the Big Brook area of the Darling Range are the site properties Waterlogging and Gradient. There were also strong correlations between vegetation and the soil properties Field Texture, Gravel Content, Electrical Conductivity (EC) and some major element concentrations. Our data are insufficient to imply causal relationships; however, we speculate that these soil properties have developed in response to the same seasonal conditions of desiccation and waterlogging that currently control plant distribution on these valley floors. Pedogenesis takes place over a timescale of many thousands (possibly millions) of years, rather than the hundreds of years or decades required to establish plant communities. It is suggested that any proposed developments on these valley floors should consider changes in the local hydrology.

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