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Regeneration of *Acacia* and *Kennedia* from soil stored seed following an autumn fire in jarrah (*Eucalyptus marginata*) forest

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Abstract

Regeneration of species of *Acacia* and *Kennedia* following a fire in autumn was studied in the understorey of jarrah forest near Dwellingup. A total of 4 species of *Acacia* and 2 species of *Kennedia* were recorded in 46 plots assessed prior to burning. Six months after burning all except 1 species (*Acacia pulchella*) were recorded in more plots than before the fire. *Kennedia coccinea* exhibited the greatest increase in distribution following burning. Total seedling numbers did not differ significantly between plots burnt at low intensity ($<300 \text{ kWm}^{-2}$) and plots burnt at greater intensity, including full scorch of the overstorey. Between August 1980 and February 1983 similar changes in plant density were recorded in fenced exclosures and adjacent unfenced areas at 5 sites indicating that grazing had no major impact on populations over this period. A broadscale survey of the 2 200 ha study area 1 year after the fire indicated that about 10% of the area carried dense thickets of *A. pulchella* and *A. celastriifolia* while a further 15% carried thickets of *Acacia drummondii*.

Introduction

Understoreys of native legumes are a distinctive feature of jarrah (*Eucalyptus marginata*) forest throughout the range of this forest type. Most of the common legumes are obligate seed regenerators which re-establish from seed stored in the top few centimetres of the soil profile (Shea *et al* 1979, Monk *et al* 1981). Hardseededness (Gill 1981) is common amongst the legumes with the result that there is little or no regeneration in the absence of fire or mechanical disturbance of the soil.

Germination of soil stored seed following fire is influenced by a number of factors (Gill 1981) including the abundance and viability of seed, the depth of seed burial, the response of different species to heat and the extent of soil heating (Shea *et al* 1979, Monk *et al* 1981, Floyd 1976). The extent of soil heating depends on the physical characteristics and moisture content of the soil (Aston & Gill 1976) and the heating characteristics of the fire, in particular the quantity of fuel consumed (Knight 1981). Fires during summer and early autumn provide ideal conditions for soil heating because soils are dry and litter fuel is entirely consumed (Christensen *et al* 1981).

In jarrah forest, regeneration of dense legume thickets has often been observed following summer fires of moderate to high intensity (Peet 1971, Peet & Van Didden 1973, Shea *et al* 1979, Monk *et al* 1981) but has rarely been associated with the spring fires of low intensity which are periodically used to reduce accumulations of fuel. Manipulation of the season and intensity of prescribed burning has been proposed as a means of promoting

the regeneration of dense thickets of legumes for purposes including the maintenance of animal habitat (Christensen 1980), and the establishment of understoreys resistant to *Phytophthora cinnamomi*, the causal agent of jarrah dieback (Shea *et al* 1979). The factors which determine the regeneration and subsequent growth of native legume species need to be understood if such treatments are to be implemented on an operational scale.

This paper examines the post-fire regeneration of species from 2 genera of native legumes, *Acacia* and *Kennedia*, which are commonly found on a wide range of sites in jarrah forest. Aspects examined are: regeneration in relation to species occurrence prior to burning; comparison of the density of regeneration in forest subject to 2 levels of crown scorch (an index of the intensity of fire); and the effect of grazing exclosures on changes in plant numbers during the 2.5 years following seedling germination.

Study area

The study was undertaken in the 2 200 ha Hakea forest block, 25 km SE of Dwellingup (34° 43'S, 116° 04'E). Six of the vegetation complexes described and mapped for the Darling System by Heddle *et al* (1980) occur within the area, as follows (Fig. 1); Dwellingup complex, medium-high rainfall (1074 ha); Yarragil complex, maximum swamp development (450 ha); Murray-Bindoon complex (211 ha); Pindalup-Yarragil complex (172 ha); and Cooke complex (154 ha).

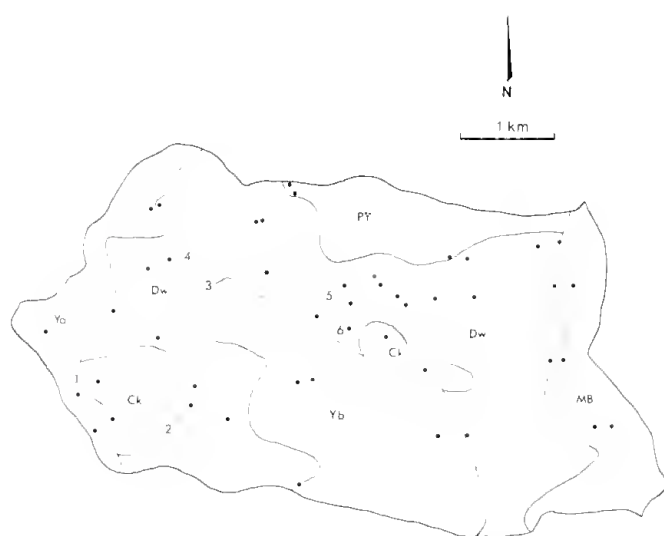


Figure 1 Map of Hakea Block showing location of plots (1-6) and grazing exclosures (1-6). Vegetation complexes (Heddlie *et al.* 1980) represented in the area are Dwellingup (Dw), Yarragil with minimum swamp development (Ya), Yarragil with maximum swamp development (Yb), Murray-Bindoon (MB), Pindalup-Yarragil (PY) and Cooke (Ck).

Vegetation complexes correspond to the major landform units of Churchward & McArthur (1980), and typically combine several of the more specific site vegetation types defined by Havel (1975).

The dominant vegetation on the lateritic uplands that comprise about half the study area (Dwellingup and Cooke complexes) is open forest of jarrah and marri (*Eucalyptus calophylla*), 20-30 m in height, with an understorey of low shrubs. The forests of the other vegetation complexes may also contain jarrah and marri but are generally less than 20 m in height and are distinguished by the presence of other eucalypt species including yarri (*Eucalyptus patens*) and wandoo (*Eucalyptus wandoo*). The area of Yarragil complex in the southern part of the block is dominated by an extensive *Banksia littoralis* swamp.

Fire history records available from 1938 onwards indicate that only small parts of Hakea block have been burnt by wildfires, but that the entire area was subject to fuel reduction burning in spring 1968 and again in spring 1974.

Methods

Pre-fire assessment

The number of plants of *Acacia* and *Kennedia* species was counted in each of 46 permanently marked 20 × 20 m plots during January 1980. These plots were randomly located within the study area (Fig. 1). Contacts with each species were also recorded from 50 point samples following the technique of Levy & Madden (1933). Two legume species common in the area (*Acacia preissiana* and *Bossiaea ornata*) were not included in the study because they commonly regenerate from rootstock after fire and it was considered that this might create difficulty in determining the true extent of regeneration from seed.

Litter fuels samples were collected from four 1 m² quadrats in each plot for determination of oven dry weight. Understorey fuels were not sampled at each plot, but would probably have contributed an additional 1-2 t ha⁻¹ to the total quantity of fuel on upland sites (Sneeuwjagt & Peet 1985).

Samples of litter fuel and the 0-5 cm horizon of the soil were collected at a number of upland sites on the morning immediately prior to burning of the study area. Samples were subsequently oven dried for moisture content determination.

The fire

The study area was burnt on 22 March 1980. The first widespread rain following the summer drought had fallen 2 days previously with 3 mm being recorded in a portable rain gauge located at the eastern end of the study area. On the day of the fire, weather conditions were recorded at the study area and at a nearby fire lookout tower (Table 1).

The area was ignited by an aircraft dropping incendiaries on a grid pattern; ignition commenced at 1500 hrs and continued for 2 hours, after which time fires continued to burn into the evening until about 2100 hrs. Around the perimeter of the area the intensity of fires was generally low (<300 kWm⁻¹) but considerably higher intensities were observed from the aircraft within the centre of the area.

Table 1

Summary of fuel, soil moisture and weather conditions at the Hakea study area on the day of burning (22 March 1980).

Weather	
Maximum temperature (°C)	27
Minimum relative humidity (%)	30
In-forest wind speed at 1600 hr (kmh ⁻¹)	3
Tower wind speed at 1600 hr (kmh ⁻¹)	11
Tower wind direction	ESE
Fuel	
Litter fuel quantity (t/ha) mean	10.5
range	3.2-24.9
SE	0.8
Minimum litter fuel moisture content range (%)	9-10
Soil	
Soil Dryness Index ^A	c 1600
Moisture content of 0.5 cm horizon (%) mean	4
range	3-7

^A Refer to Mount (1972) and Burrows (1987).

Post-fire assessment

Several months after the fire the height of crown scorch was measured on a sample (10-20) of dominant trees in each plot to provide an estimate of the intensity of fire. Based on the relationships reported by Burrows (1984), plots with scorch height ≤ 15 m were estimated to have burnt with an intensity < 300 kWm^{-1} , which is regarded as low (Cheney 1981).

Acacia and *Kennedia* regeneration within the 20×20 m plots was initially assessed in August 1980. The number of seedlings of each species was counted on four 10 m^2 circular quadrats which were located in the corners of each plot. This sampling procedure was adopted because the very high numbers of seedlings in some plots made it impractical to count seedling numbers over the entire plot area. Plant densities before and after burning were expressed in terms of plant/ m^2 . Point sampling was repeated in each plot 2.5 years after the fire.

During early August 1980 grazing exclosures were constructed at 6 sites (Fig. 1) where germination of *A. drummondii* and *A. pulchella* was widespread. At each site an area of about 0.5 ha was fenced with wire mesh to 1.5 m height, and seedling numbers counted on 40 permanently marked 1 m^2 quadrats within the exclosure and on 40 adjacent quadrats outside the exclosure. Quadrats were recounted in February 1983. Mean seedling numbers in 1981, and changes in seedling numbers between 1981 and 1983 were compared between fenced and unfenced quadrats at each site using a *t* test.

The broadscale distribution of *Acacia* and *Kennedia* species was surveyed 12 months after the fire. Survey points were located every 100 m along a series of transects which ran parallel at 400 m intervals across the study area. Plant numbers were counted on a 10 m^2 circular quadrant at each point. The distribution of each species was then plotted at 1:50 000 scale and overlaid onto a map of the vegetation complexes of Heddle *et al* (1980) for tallying of species occurrence by complex. Expected frequencies were calculated according to the hypothesis that species were present in equal proportion in each complex. Observed and expected frequencies were compared using the likelihood ratio (Zar 1974). Several species recorded only at a few points were not subject to this analysis.

Results

Four species of *Acacia* and 2 species of *Kennedia* were recorded in plots prior to burning (Table 2). The most common species, *Acacia drummondii*, occurred in 17 plots while the remainder were found in 1-9 plots.

Six months after the fire all species, except *Acacia pulchella*, occurred in more plots than before the fire; *A. pulchella* was recorded in 9 plots before the fire but only 7 afterwards (Table 2). The *Acacias* typically regenerated within plots where they had been recorded prior to burning and in 1-4 additional plots. Two species which had not been recorded before the fire, *Acacia alata* and *Acacia extensa*, each regenerated in 1 plot following the fire.

Kennedia coccinea was considerably more widespread following the fire being recorded in 26 additional plots, while *Kennedia prostrata* regenerated in 5 additional plots (Table 2).

In a few instances species did not apparently regenerate in all plots where they had been present prior to burning. *A. drummondii*, *Acacia celastrifolia* and *K. coccinea* each disappeared from 1 plot after the fire, while *A. pulchella* disappeared from 3 plots.

The relationship between the number of plants in plots before and after burning varied between species. The density of regeneration of the 2 most common *Acacias* was strongly correlated to the preburn densities of these species within plots (*A. drummondii* $r = 0.756$, $N = 21$, $P < 0.001$; *A. pulchella* $r = 0.718$, $N = 9$, $P < 0.01$). A similar trend was apparent for several other species of *Acacia* although this could not be verified statistically because they occurred in too few plots. On the other hand both species of *Kennedia* mostly regenerated in plots where they had not been recorded prior to burning and no such relationships were apparent.

Numbers of seedlings in plots burnt at low intensity ($< 300 \text{ kWm}^{-1}$) were not significantly different from those observed in plots burnt at higher intensities, including a number subject to complete scorch of the overstorey canopy (Table 3).

Table 2

Occurrence of legume species within plots before and 6 months after burning.

Species	No. of plots in which each species was:			
	Not recorded before or after burning	Recorded before but not after burning	Not recorded before but recorded after burning	Recorded both before and after burning
<i>A. alata</i> R. Br.	45	0	1	0
<i>A. celastrifolia</i> Benth.	39	1	2	4
<i>A. drummondii</i> Lindley	25	1	4	16
<i>A. extensa</i> Lindley	45	0	1	0
<i>A. pulchella</i> R. Br.	36	3	1	6
<i>A. urophylla</i> Benth. ex Lindley	41	0	2	3
<i>K. coccinea</i> Vent.	15	1	26	4
<i>K. prostrata</i> R. Br.	40	0	5	1

Table 3

Comparison of the density of seedling regeneration of all legume species in plots with levels of crown scorch ≤ 15 m (estimated fire intensity $< 300 \text{ kWm}^{-1}$) and > 15 m or fully scorched (estimated fire intensity $> 300 \text{ kWm}^{-1}$).

Variable	Scorch height ≤ 15 m	Scorch height > 15 m
Total no. of plots in class	15	31
No. of plots containing legume seedlings	15	30
No. of seedlings m^{-2} mean	1.32 ¹	0.958 ¹
SD	1.110	1.653
range	0.025-3.725	0-6.500

¹Not significantly different at 0.05 level.

Table 4

Mean frequency (%) of legume species in 46 plots before and 2.5 years after burning determined by Levy point sampling.

Species	Mean frequency (%)	
	Before burning	2.5 years after burning
<i>A. alata</i>	0	0
<i>A. celastrifolia</i>	0.043	0.826
<i>A. drummondii</i>	0.348	3.391
<i>A. extensa</i>	0	0
<i>A. pulchella</i>	2.000	2.860
<i>A. urophylla</i>	0	0.261
<i>K. coccinea</i>	0.043	0.130
<i>K. prostrata</i>	0	0.043

No significant relationship was apparent between the number of seedlings regenerated and the quantity of litter fuel in the plot (Fig. 2).

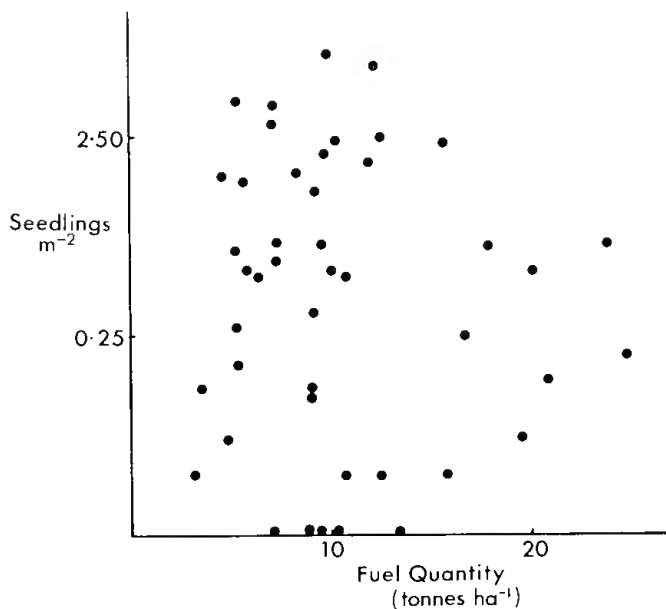


Figure 2 Number of seedlings per m^2 in August 1980 in relation to the quantity of litter fuel in each plot at the time of burning.

Pre- and postfire frequencies were calculated for each species from the Levy point sampling (Table 4). Within 2.5 years the frequency of contacts with each species had returned to prefire levels, and substantial increases were demonstrated for *A. drummondii*, *A. celastrifolia*, *Acacia urophylla* and *K. coccinea*.

At each of the 6 sites where exclosures had been fenced the density of *Acacias* in fenced and unfenced areas did not differ significantly at the time of the initial assessment in August 1981 (Table 5). Between August 1981 and February 1983 the density of plants declined to a similar extent in both fenced and unfenced quadrats at 4 of the sites. At the other 2 sites plant numbers increased over the same period: at site 1 plant numbers in the unfenced quadrats increased; at site 3 plant numbers in the fenced quadrats increased. Only at site 3 did the change in plant numbers differ significantly between fenced and unfenced quadrats. Changes in plant density were of a similar magnitude at each site irrespective of the location within the study area.

All of the species recorded in the plots were also encountered during the broadscale survey conducted 12 months after the fire at generally similar relative levels of frequency (Table 6). A further species (*Acacia divergens*) was also encountered locally in swampy areas where no plots had been established. The hypothesis of uniform relative frequency in all vegetation complexes was sustained for *K. prostrata* and *K. coccinea* but not for any of the common *Acacias* (Table 6).

Data from the broadscale survey were used to estimate the proportion of the study area which had sufficient density of the larger legumes (*A. pulchella* and *A. celastrifolia*) to facilitate development of dense thickets. For the purposes of this estimate it was assumed that a density ≥ 1 plant/ m^2 of either species 1 year after the fire indicated potential for thicket development. On this basis plant densities were estimated to be sufficient for thicket development over about 10% of the study area. Using the same plant density criteria a further 15% of the area carried thickets of *A. drummondii*. Several of the other species grow to sufficient size but do not typically regenerate as thickets in jarrah forest (*A. urophylla*) or are restricted to localized areas, usually in swamps (*A. divergens*, *A. alata*, *A. extensa*).

Table 5

Mean numbers of *A. drummondii* and *A. pulchella* recorded in fenced and unfenced areas at 6 sites (40 1m² permanent quadrats per fencing treatment at each site).
See Fig. 1 for site locations.

Site	Fencing treatment	No. of plants m ⁻² in August 1980	Significance ¹	Change in number m ⁻² between August 1980 and February 1983	Significance ²
1	fenced	16.7	t = 0.095	0.10	t = 1.166
	unfenced	16.3	NS	+1.08	NS
2	fenced	20.9	t = 0.421	0.75	t = 0.540
	unfenced	17.8	NS	1.10	NS
3	fenced	24.3	t = 0.691	+1.48	t = 2.116
	unfenced	29.0	NS	0.56	p < 0.05
4	fenced	20.8	t = 0.585	0.59	t = 1.39
	unfenced	24.3	NS	0.97	NS
5	fenced	11.5	t = 0.850	1.60	t = 0.860
	unfenced	14.2	NS	1.00	NS
6	fenced	13.1	t = 0.700	1.75	t = -0.093
	unfenced	15.6	NS	1.68	NS

¹ Comparison of plant density in fenced and unfenced quadrats at August 1980.

² Comparison of change in plant density in fenced and unfenced quadrats from August 1980 to February 1983.

Table 6

Frequency of legume species within the 6 vegetation complexes represented in the Hakes study area, based on data from 537 sample points. Figures in parentheses indicate the frequency expected if representation was proportional to the area of each complex.

Vegetation complex	Area within study (ha)	Observed and (expected) frequency within each complex for:								
		<i>A. alata</i>	<i>A. celastriifolia</i>	<i>A. divergens</i>	<i>A. drummondii</i>	<i>A. extensa</i>	<i>A. pulchella</i>	<i>A. urophylla</i>	<i>K. coccinea</i>	<i>K. prostrata</i>
Dwellingup med-high rainfall	1074	0	6(13.1)	0	60(73.9)	0	28(30.6)	10(10.2)	49(49.0)	14(16.0)
Yarragil (maximum swamp development)	450	0	12(5.5)	1	44(31.1)	0	7(12.9)	4(4.3)	20(20.7)	5(6.8)
Yarragil (minimum swamp development)	139	0	1(1.7)	0	12(9.6)	5	9(4.0)	5(1.3)	7(6.4)	2(2.1)
Murray-Bindoon	211	1	1(2.6)	0	24(14.7)	0	2(6.1)	2(2.0)	12(9.7)	5(3.2)
Pindalup-Yarragil	172	1	0(2.1)	0	2(11.8)	0	6(4.9)	0(1.6)	7(7.9)	5(2.6)
Cooke	154	0	7(1.9)	0	10(10.8)	0	11(4.5)	0(1.4)	6(7.1)	2(2.3)
Total	2 200	2	27	1	152	5	63	21	101	33
G Statistic		ND	24.54	ND	25.29	ND	18.69	12.49	1.27	3.43
Significance level	—	ND	0.001	ND	< 0.001	ND	< 0.005	< 0.05	> 0.05	> 0.05

ND not determined

Discussion

Six months after burning all of the legume species examined in this study, except *A. pulchella*, were recorded in a greater number of plots than before the fire. There were relatively few examples where species were recorded in plots before, but not after the fire, and these can probably be attributed to the sampling technique adopted for the post-fire assessment. The density of *Acacia* populations has been observed to decline rapidly in the initial 4 years after fire (Monk *et al* 1981). Most, if not all

species would have been less widespread at the time of the pre-fire assessment in 1980 than in the period soon after the 1974 fire.

The most pronounced increase in apparent distribution following burning was displayed by *K. coccinea* and it is likely that this species, being shortlived, had declined to a greater extent in the interfire period than had the longer lived, woody *Acacias*. Species richness and diversity in jarrah forest generally decline when the period between fires exceeds about 6 years due to the senescence of fireweeds and smaller herbaceous species (Bell & Koch 1980).

The intensity of fire, as indicated by crown scorch height, did not appear to influence the extent of germination. Peet (1971) found that the contribution of leguminous species to the understorey, based on projected foliage cover, only varied slightly between areas burnt at a wide range of intensity during a summer wildfire; legumes contributed 38% in defoliated forest, 40% in fully scorched forest and 33% in forest subject to lesser crown damage. Legume contribution was, however, only 20% in similar forest which had been burnt in spring at low intensity. This is consistent with the hypothesis that germination of soil stored seed is governed primarily by fuel and soil moisture at the time of burning, rather than the actual behaviour of the fire (Christensen & Kimber 1975). However where the intensity of fire is sufficient to seriously damage the forest canopy it is likely that understorey thicket development may be enhanced by the temporary reduction in competition. Peet (1971) reported that the total understorey cover (all species including legumes) did in fact increase proportionally with the level of damage to the canopy. Cochrane (1968) also reported that canopy characteristics had a primary regulating role on the regeneration of understorey species following fire in dry sclerophyll forest in Victoria.

No significant influence of fuel quantity on legume germination was established in this study, despite the probable importance of this factor (Christensen and Kimber 1975). Observations following the fire indicated that a large proportion of litter fuel had been consumed, so that differences between the quantity measured prior to burning and the quantity actually consumed by the fire were not great. The most likely explanation for the lack of any clear relationship is that it was obscured by variation between plots in the quantity of seed, depth of burial and heat response characteristics of different species. A further factor potentially influencing germination response was rainfall before the fire. Although the amount of rain (3 mm) was small, it may have been sufficient to dampen the surface layer of soil and restrict penetration of heat to deeper levels (2-4 cm) where much of the seed may be located (Shea *et al* 1979).

The similar changes in numbers of plants in fenced and unfenced areas at 5 sites suggests that grazing did not have a major impact on legume population densities after August 1980. However, the impact of grazing on population densities prior to August, and possible effects on the height or form of individual plants were not determined. Increases in number of plants at 2 sites after August 1980 would have been as a result of later germination. These results contrast with results reported by Shea *et al* (1979) and Christensen (pers. comm.) where heavy grazing of legumes has been observed particularly on small burnt areas and close to unburnt edges. The large size of the area burnt at Hakea and the fact that much of the surrounding forest had been burnt in the previous 12 months may have acted to disperse the potential grazing pressure.

The 2 species of *Kennedia* were ubiquitous throughout the study area but the *Acacias* were not present with equal frequency in all of the mapped vegetation complexes, and several were restricted to a few locations. In some cases this reflects a consistent link between species occurrence and site characteristics. Several of the legumes encountered at Hakea were used as specific indicator species in the site classification scheme developed by Havel (1975); these include *A. alata* (Type C), *A. extensa* (Type W), *A. urophylla* (Types S, T, Q). *A. drummondii* is characteristic of Type O but was not selected as an indicator species. Each of the vegetation complexes mapped by Heddlé *et al* (1980) comprise several of Havel's site vegetation types and so the distribution of individual legume species would be linked to the occurrence of specific types within the complex. The limited presence of *A. urophylla* in the Yarragil (max. swamp development) complex would not be expected on the

basis of known site vegetation occurrence of this species, but may simply reflect the limitations in the method used to combine the maps of species occurrence with those of the vegetation complexes. The 2 most common *Acacias* (*drummondii*, *pulchella*), were recorded in all vegetation complexes but with unequal relative frequencies in each complex; further investigation of species/site relationships would be required to adequately explain this pattern of distribution.

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Calc-alkaline lamprophyres from the Pilbara Block, Western Australia

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Abstract

A suite of calc-alkaline lamprophyre (dominantly spessartite) dykes and plugs forms a belt extending for some 250 km from Balfour Downs to north of Bamboo Creek in the eastern Pilbara. The lamprophyres show characteristic panidiomorphic texture and chemistry (eg. high F, Ba & K), and many are satellite to granitoid plutons. Available data suggest that these lamprophyres, many of which were formerly recorded as "hornblende porphyries", constitute basic members of a Proterozoic (c1700-1800 Ma) calc-alkaline, lamprophyre-porphyrty-granitoid intrusive suite which mirrors younger suites worldwide. Lamprophyres are also known from the Shaw Batholith, in the eastern Pilbara, and from near Roebourne in the western Pilbara. Many other minor intrusions recorded as "hornblende porphyries", "trachyandesites", "diorites", "mafic porphyries" and "diabases" may also be lamprophyres. Lamprophyres form a significant phase of Pilbara magmatism, and thus are important to syntheses of tectonism, magmatism and mineralization.

Introduction

Lamprophyres (notably the lamproite subgroup) are now known to host or be spatially associated with deposits of diamond (at Argyle, in the Kimberley Region of Western Australia: Jaques *et al* 1986) and of gold (at Wood's Point, Victoria: Hills 1952). They can also be associated with carbonatites, which host deposits of phosphate and rare metals (eg. the Bow Hill lamprophyres of the east Kimberleys are contemporaneous with the Cummins Range carbonatite: Jaques *et al* 1985). Active exploration for lamprophyres is consequently being undertaken in Western Australia, and their very widespread distribution in this state (both in time and space) is becoming established: dykes, plugs and diatremes (ranging from Archaean to Miocene in age) have already been discovered or documented in many areas (Jacques *et al* 1985; 1986; Rock *et al* 1987).

This paper aims to reappraise: (1) all previously reported occurrences of "lamprophyres" in the Pilbara Block and (2) a few rocks formerly described under other names, which we also believe to be lamprophyres. It complements an extensive study of lamprophyres in the Yilgarn Block (Rock *et al* 1988). Petrological nomenclature follows Streckeisen (1979) and Rock (1984, 1987, 1988) throughout.

As described in more detail by Rock *et al* (1987), the published literature, together with catalogues and computerized indexes to the rock collections of the Department of Geology of the University of Western Australia (UWA), the Geological Survey of Western Australia (GSWA), CSIRO Division of Minerals and Geochemistry (Floreat Park), and several mining companies, have been searched for specimens described either as "lamprophyres", or under names indicating possible lamprophyric affinities (eg. 'mafic porphyries' or 'hornblende porphyries'). These searches revealed only two previously re-

corded occurrences of "lamprophyres" from the Pilbara. Both of these were summarized by Miles (1945) in the first compilation of lamprophyres throughout Western Australia. Jaques *et al* (1985, 1986) added no information to Miles' account in their otherwise comprehensive reviews of Australian alkaline rocks.

Criteria for reappraising previously described rocks

Streckeisen's (1979) recommended list of lamprophyre field and petrographical characteristics can be expanded, into the following set of criteria, which also consider rock chemistry (Rock 1987). They are listed in approximately decreasing order of significance, although it is the *combination* of as many as possible of these features which is diagnostic of lamprophyres:

- 1) Very high whole-rock K, Ba, Sr, Rb, Th, light rare earth elements (REE), P, F, CO₂, S and SO₃ (1-3 orders of magnitude higher than in basaltic rocks), combined with moderate enrichments in Ti, Zr, Nb, basaltic levels of V, Cr, Co, and Ni, but near to below-basaltic levels of Y and heavy REE.
- 2) Abundance of primary biotite, amphibole, carbonates, zeolites, chlorite, epidote, fluorite, sulphates, etc;
- 3) Certain unusual chemical features of the constituent minerals, including exceptionally high Ti contents in biotite, amphibole and clinopyroxene, and exceptionally high Ba in biotite or K-feldspar;
- 4) Textural features, such as panidiomorphism, battlemented biotites, lack of felsic phenocrysts, or the presence of leucocratic globular structures (ocelli);
- 5) Occurrence as commonly xenolithic minor intrusions (dykes, sills, pipes, diatremes) associated with breccias, tuffs, pyroclastics, etc.; complex to bizarre intrusive forms are common.

The usefulness of characteristic (4) may be reduced in the Pilbara, because most Precambrian rocks have suffered low-grade metamorphism, which readily destroys textural characteristics and makes true meta-lamprophyres petrographically similar to metamorphosed intermediate and basic rocks. Relict lamprophyric textural idiosyncracies, such as "battlemented" biotites, consistently euhedral pseudomorphs after biotite, amphibole or pyroxene, and apatite phenocrysts, are nevertheless observable in the Pilbara rocks described as lamprophyres below.

In assessing whole-rock chemical data, we recognise that metasomatism (including K-metasomatism) is widespread in the Pilbara Block (eg. Barley 1984, *et al* 1984), and could have induced some of the lamprophyre characteristics in originally non-lamprophyric rocks, or destroyed the original character of true lamprophyres. We have therefore relied less on high K contents than the combination of high Ba, Rb, Sr, La and Ce, with high V, Cr, Co and Ni, while fully taking into account the petrography. Fortunately, sufficient data are also available for associated igneous rock-types (both Archaean and Proterozoic) to allow more objective, comparative assessments. The chemistry of the rocks here claimed as lamprophyres is so distinctly different from all these associated types that their identity is unquestionable. Figure 3 confirms the chemical similarity of the Pilbara lamprophyres to global averages.

A reappraisal of Pilbara lamprophyre occurrences

Old Fortune Copper Mine, Roebourne, Western Pilbara

Miles (1945: 4-5) recorded a "typical mica lamprophyre (kersantite)" with a "rude schistosity", occurring as a dyke in quartz-gabbro. The relevant GSWA sample (12579; section no. 95103) fully confirms Miles' identification, carrying chlorite pseudomorphs after abundant, "battlemented" biotite phenocrysts highly characteristic of mica-lamprophyres (Rock 1984). Unfortunately, this particular rock is too chloritized, silicified and carbonated to be worth analyzing, and we know of no other available material from this locality to follow the identification further.

Shaw Batholith

A suite of ultramafic lamprophyre dykes was discovered during a Department of Geology (UWA) research program on this, one of the major Archaean granitoid batholiths of the Pilbara (Fig. 1; Bettenay *et al* 1981). These dykes, composed predominantly of sodic titanite and alkali to sodic-calcic amphiboles (arfvedsonite, kataphorite, etc.) are detailed in a companion paper (Bettenay *et al* 1988).

Eastern Pilbara

Miles' (1945) only other reported lamprophyre, from Bamboo Creek, is a rock with "scattered clear feldspar phenocrysts up to 2 mm diameter", which is "not typical of the family" but is "in all probability an altered form of original mica lamprophyre—near kersantite". Re-examination of the thin section (GSWA 12545/^s1868) indicates that this rock is a metamorphosed dolerite (epidiorite), and shows no lamprophyric characteristics.

However, some rocks occurring in the same general area, previously described as 'hornblende porphyrites' (Maitland 1905, Finucane 1935, Noldardt & Wyatt 1962), and as 'hornblende porphyries' or 'trachyandesites' (Hickman 1978, Barley 1980, Lewis & Davy 1981, Hickman *et al* 1983), are undoubtedly lamprophyres. Indeed, lamprophyres have now been annotated as such on the Geological Survey of Western Australia's recently published *Balfour Downs* 1:250 000 sheet (Williams 1987). They form part of a suite of dykes and plugs, which extends for some 250 km from Balfour Downs to north of Bamboo Creek (Fig. 1). A suite of lamprophyres, intermediate porphyries and granitoids from near Bamboo Creek has now been dated at c1800 Ma by a Pb-Pb whole-rock isochron (Barley *et al* in prep.).

The most abundant lamprophyres, mapped as "hornblende porphyries" on the GSWA's earlier *Nullagine* and *Yarrle* 1:250 000 sheets (Hickman 1978, Hickman *et al* 1983) contain 15 to 30 per cent of panidiomorphic, dark green-brown hornblende and, more rarely, phlogopitic biotite phenocrysts, in a fine-grained, variably sericitized and carbonated, feldspathic groundmass carrying small apatite and magnetite euhedra. The hornblende may carry clinopyroxene cores, and is rhythmically zoned, chloritized or carbonated (Fig. 2). New data for three lamprophyre plugs—two satellite to the Bridget Adamellite (Hickman 1978), and one part of a composite spessartite-quartz monzonite plug near Bamboo Creek—are compared in Table 1 with analyses of the Bridget Adamellite (from Barley 1980). Other rocks in the eastern Pilbara that have broadly similar chemical composition are Archaean intermediate volcanics (Hickman 1983, Barley *et al* 1984). Although the SiO₂, MgO, Ni, and V contents of these rocks overlap those of the lamprophyres, the lamprophyres have consistently higher Ba (>800 ppm), Rb (>80 ppm) and Sr (>650 ppm) than a suite of relatively unaltered Archaean intermediate volcanics (Barley 1980) with Ba <650 ppm, Rb <50 ppm and Sr <600 ppm.

Lewis and Davy (1981) employed the term 'trachyandesite' as a chemical description of hornblende-phyric dykes and plugs intruding the Mt Edgar Batholith, whilst noting that these rocks had higher K₂O than Le Maitre's (1976) average trachyandesite. The term is now inappropriate in terms of the revised IUGS chemical classification of igneous rocks (Le Bas *et al* 1986), as it implies alkaline affinities for calc-alkaline rocks, and does not recognize their textural, minor or trace element characteristics. The term 'porphyry' is equally inadequate. Instead, the exotic chemistry of these rocks (eg. reported Ba contents of 800-2000 ppm, and F contents of 800-1100 ppm, coupled with moderate Rb, Ce, etc.), their lack of feldspar phenocrysts, and their panidiomorphic mafic phenocrysts, indicate that they should be termed *spessartites* (calc-alkaline lamprophyres dominated by hornblende-plagioclase).

The spessartites commonly appear as plugs and dykes satellite to intermediate hornblende-plagioclase porphyries and hornblende-bearing monzonites to quartz monzonites, such as the Bridget Adamellite (Fig. 1, Hickman 1978, Barley 1980). Similar porphyry plugs and small granitoid intrusions are associated with lamprophyres in the Mt Edgar Batholith (Mt Edgar itself is a small, hornblende-plagioclase porphyry to quartz-monzonite plug) and near Bamboo Creek (Hickman 1978). Petrography and chemical analyses of the Bridget Adamellite (Table 1, Barley 1980) and hornblende-plagioclase porphyries from the Mt Edgar Batholith (Lewis & Davy 1981) indicate that although containing abundant modal quartz (up to 20 per cent by volume; visual estimate) most of these granitoids should be called monzonites or quartz monzonites rather than adamellites (using the terminology of Streckeis 1976).

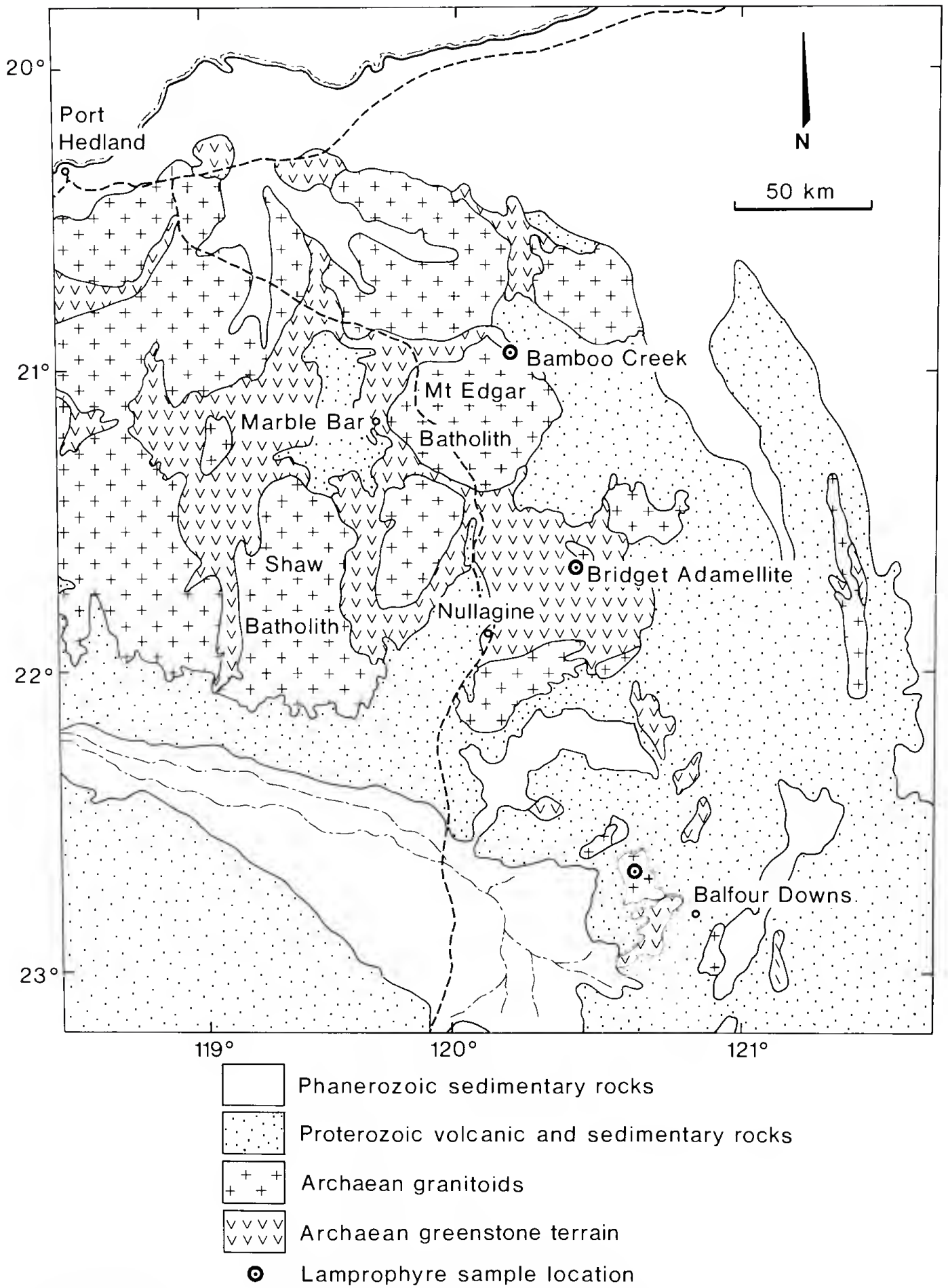


Figure 1 Locality sketch-map of the eastern Pilbara Block, showing general locations of known lamprophyres. Information largely taken from Geological Survey of WA 1:250 000 Series maps.

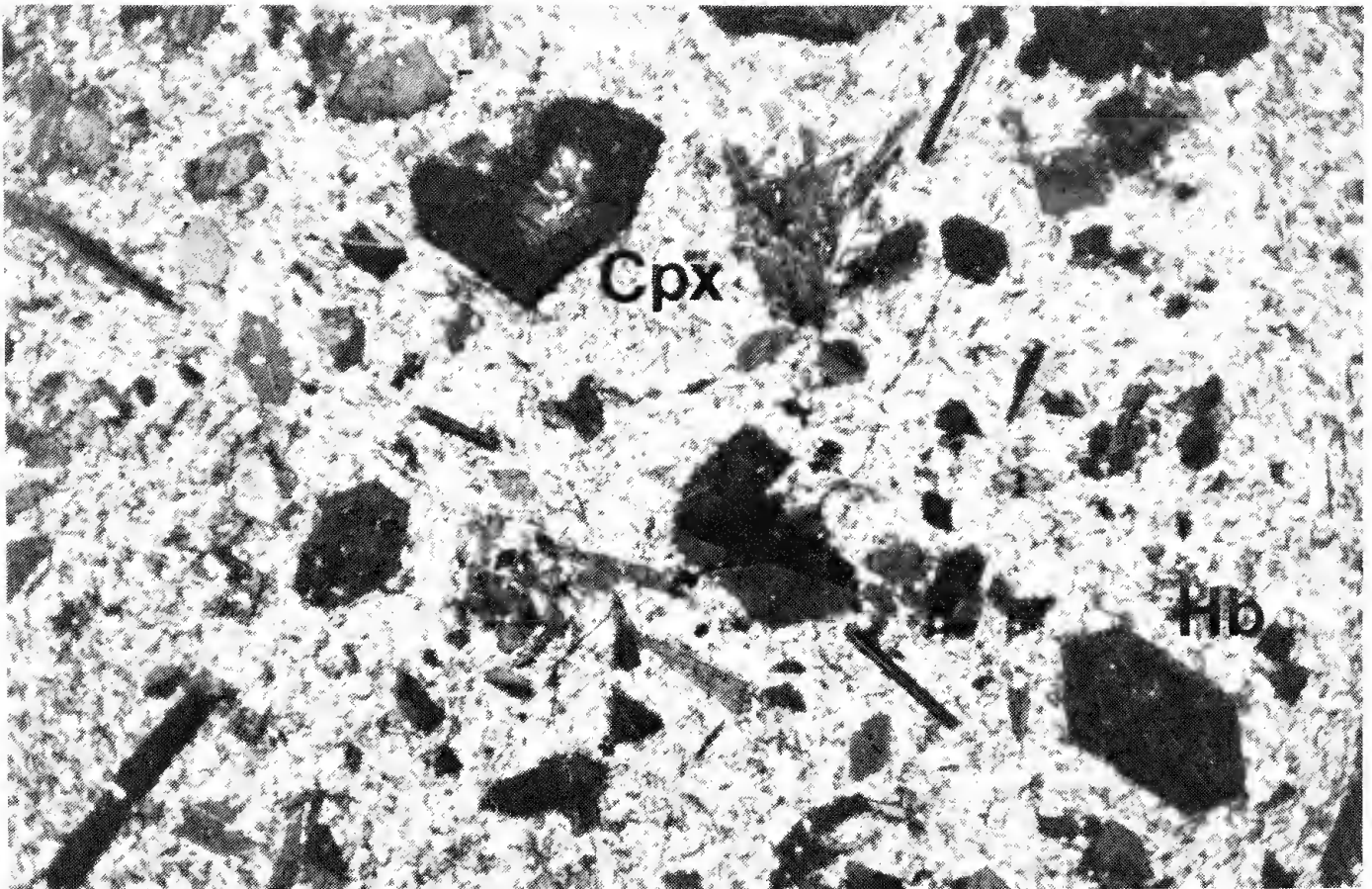


Figure 2 Photomicrograph of spessartite lamprophyre forming a plug satellite to the Bridget Adamellite (sample 86393). Field of view 8 mm; crossed polars. Note twinned, pandiomorphic hornblendes (Hb) one with a core of clinopyroxene (Cpx).

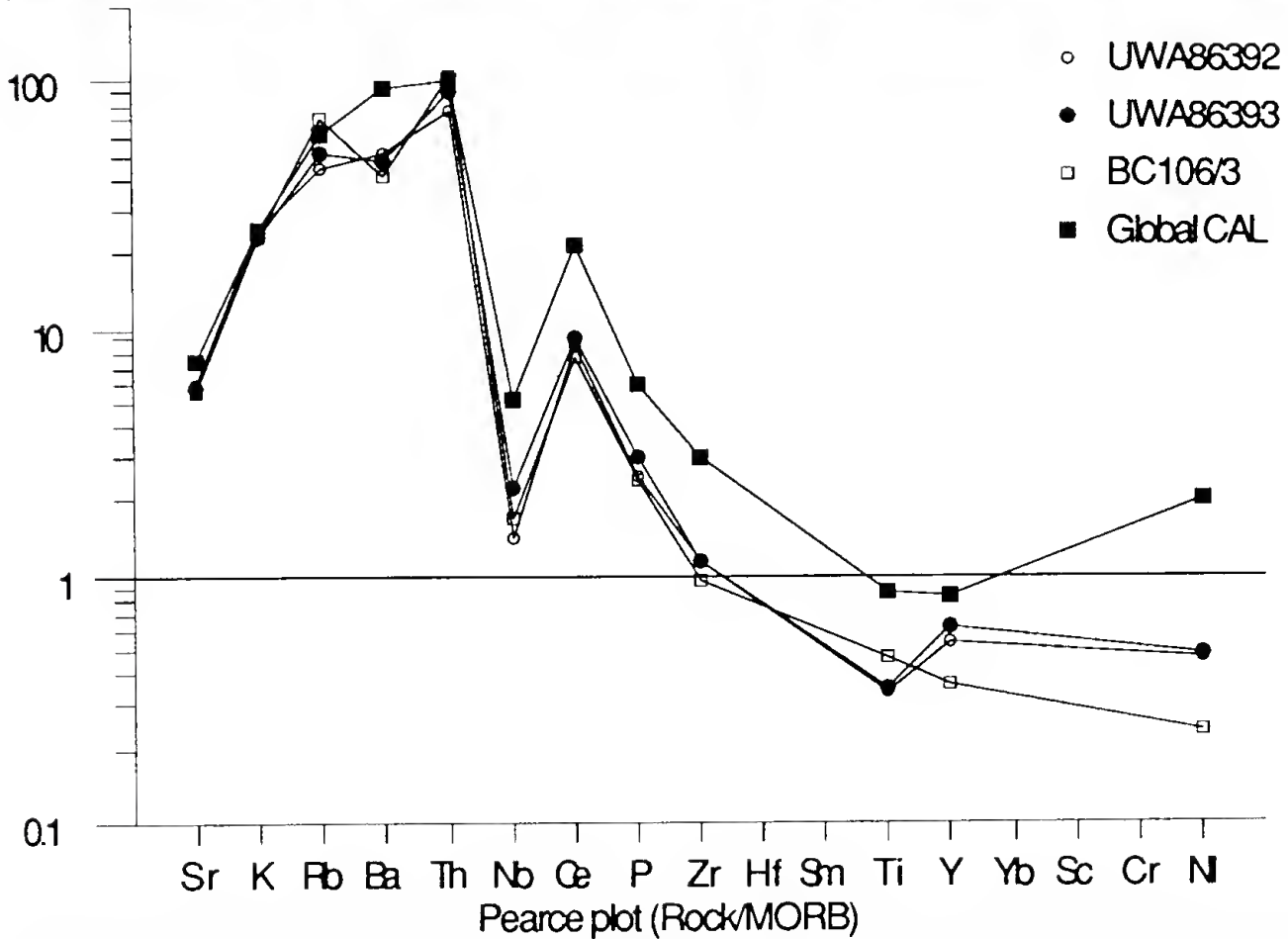


Figure 3 MORB normalized multi-element plots ("spidergrams") of eastern Pilbara suite lamprophyres compared with average global calc-alkaline lamprophyres (pattern labelled "global CAL"). Data from Table 1 and Rock (1987). Elements are arranged such that their incompatibilities and immobilities increase towards the centre of the diagram (Pearce 1983).

Table 1

New analyses of confirmed lamprophyres and associated rocks from the Pilbara

	Lamprophyres			Bridget adamellite		
	Bamboo BC106.3	Area of Bridget adamellite UWA 86392 UWA 86393*		UWA 86389	UWA 86390	UWA 86391
SiO ₂	58.79	58.89	58.44	63.54	63.82	64.76
Al ₂ O ₃	15.24	14.02	14.08	14.67	14.53	14.84
Fe ₂ O ₃	8.16	3.39	3.44	3.67	2.96	2.46
FeO	NA	4.96	4.72	2.54	3.08	2.78
MgO	3.36	4.11	4.41	2.35	2.38	2.33
CaO	5.66	5.97	6.11	4.19	4.22	4.31
Na ₂ O	3.42	3.91	3.02	3.51	3.49	3.51
K ₂ O	3.47	3.70	3.44	4.15	4.11	3.43
H ₂ O+	0.86	0.90	0.73	0.38	0.51	0.81
TiO ₂	0.70	0.50	0.53	0.45	0.44	0.38
P ₂ O ₅	0.29	0.30	0.36	0.23	0.24	0.24
MnO	0.15	0.19	0.12	0.13	0.11	0.08
CO ₂	NA	0.05	0.33	0.19	0.30	0.23
Total	100.10	100.89	99.73	100.00	100.19	100.16
<i>Trace elements (ppm), in order of atomic number</i>						
V	152	197	169	NA	NA	NA
Ni	21	42	44	NA	NA	NA
Cu	8	37	100	26	45	28
Zn	68	84	97	74	74	58
Rb	140	90	104	132	129	123
Sr	675	715	690	670	670	623
Y	11	16	19	20	16	15
Zr	86	102	103	123	125	121
Nb	6	5	8	NA	NA	NA
Sn	2	NA	1	NA	NA	NA
Ba	840	1014	970	900	970	670
La	11	11	22	NA	NA	NA
Ce	76	86	92	NA	NA	NA
Pb	30	92	85	NA	NA	NA
Th	21	15	18	NA	NA	NA
<i>CIPW weight % norms (analyses recalculated to 100% free of H₂O and CO₂)</i>						
qz	8.64	4.38	9.17	14.86	15.57	18.68
ab	29.33	33.11	25.83	29.87	29.66	29.92
or	20.78	21.88	20.55	24.66	24.39	20.42
an	16.20	9.78	14.86	12.08	11.89	14.71
di	8.49	14.41	9.22	5.03	4.66	3.10
hy	10.94	10.81	13.92	8.83	8.96	8.92
mt	3.60	3.88	3.82	2.84	2.79	2.43
il	1.35	0.95	1.02	0.86	0.84	0.73
ap	0.68	0.70	0.84	0.54	0.56	0.56
cc	0.00	0.11	0.76	0.43	0.69	0.53
Total	100.00	100.01	100.00	100.00	100.00	100.00
DI†	58.75	59.37	55.56	69.39	69.62	69.02

†Thornton-Tuttle differentiation index NA=not analysed *see photomicrograph in Fig. 2.

Data from Barley (1980), supplemented with new trace element determinations using conventional XRF techniques (courtesy of Dr R Chang, UWA).

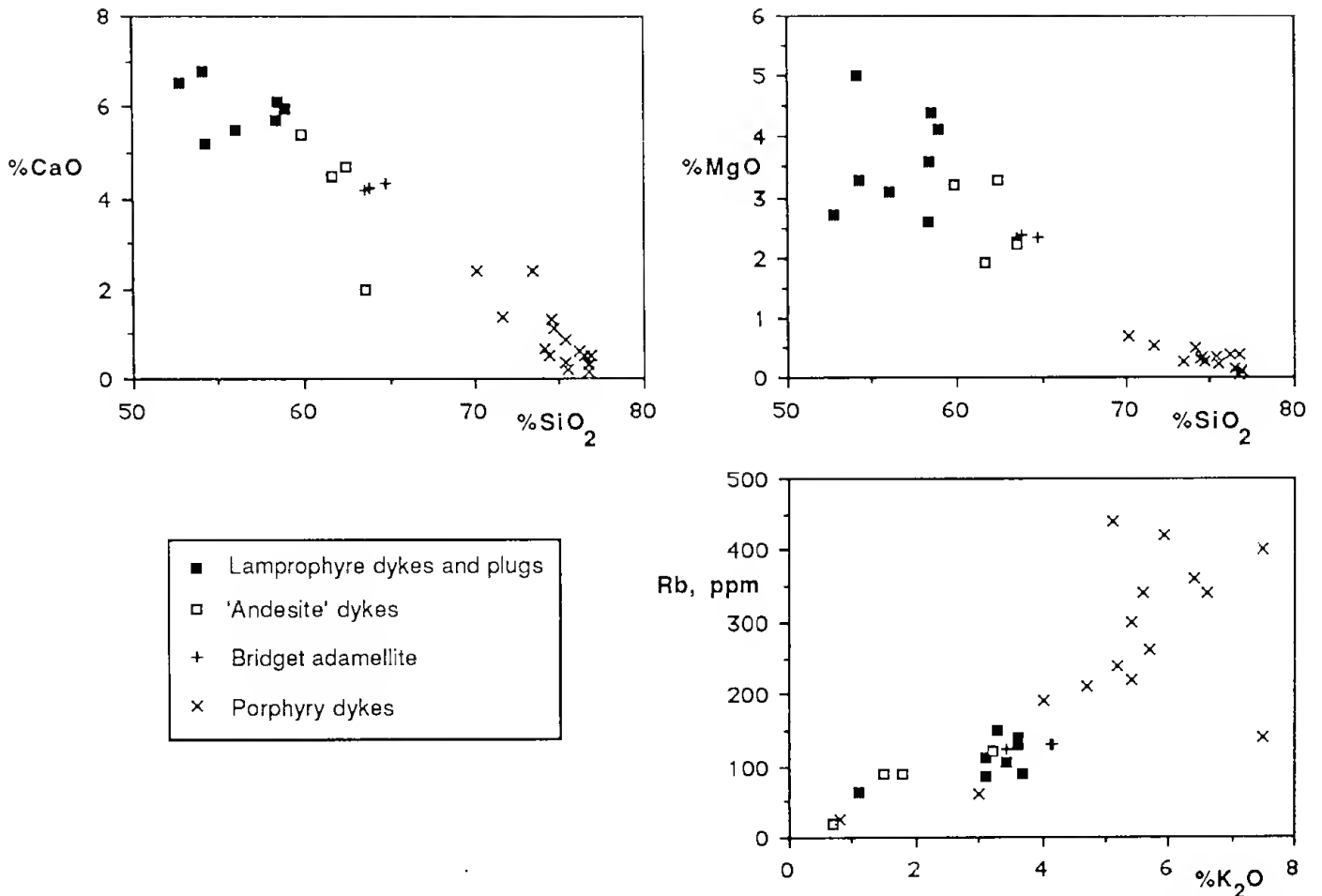


Figure 4 Variation diagrams illustrating coherent trends for geochemically homologous elements in the inferred Proterozoic lamprophyre-porphyry minor intrusive suite of the eastern Pilbara. Data from Table 1, Lewis & Davy (1981) and Barley (1980 unpubl; details available on request). Lamprophyre dykes and plugs are from near Bamboo Creek and the Bridget Adamellite. 'andesite dykes' are hornblende-plagioclase porphyry dykes from the Mt Edgar Batholith, and porphyries are silicic porphyries from the Mt Edgar Batholith.

Limited available data, illustrated in Figure 4, suggest that the spessartites, hornblende-plagioclase porphyries from the Mt Edgar Batholith ('andesite dykes' of Lewis & Davy 1981) and the Bridget Adamellite form a fairly coherent geochemical suite. Note, however, that whilst the hornblende-plagioclase porphyries overlap the granitoids in composition, the spessartites are more basic than any of the known plutonic rocks. Silicic porphyries from the Mt Edgar Batholith are also plotted on Figure 4. Some of these are spatially related to lamprophyre and quartz monzonite intrusions, plot on extensions of the lamprophyre-quartz monzonite trend, and may also be genetically related.

Williams (1987, in press) records plugs of "microcline-biotite trachyte or lamprophyre" from the vicinity of Balfour Downs (Fig. 1), thus extending the belt of presumed Proterozoic lamprophyric magmatism in the eastern Pilbara to at least 250 km. These rocks intrude the Fortescue and Hamersley Groups, and range in composition from trachyte, with phenocrysts of albite and microcline set in a fine-grained feldspathic groundmass (also coarser grained albite-microcline granite), to minette (calc-alkaline lamprophyre dominated by biotite-orthoclase), containing biotite phenocrysts in a variably altered feldspathic groundmass with small apatite and magnetite euhedra. The relationship between the minettes and the spessartites further north is as yet uncertain, although such rocks commonly coexist in regional dyke-swarms, where they may even be heteromorphic (Rock 1984, Rock *et al* 1986b).

Conclusions

The eastern Pilbara spessartites appear to represent mafic end-members of a previously unrecognized lamprophyre-porphyry-minor intrusive suite, typical of examples accompanying other calc-alkaline granitoids of many ages on all six continents (Rock 1984, 1987). Unfortunately, detailed data as yet are few, and some of the available trace element analyses are only semi-quantitative (Lewis & Davy 1981). Features which nevertheless ally these minor intrusions with better-substantiated lamprophyre-porphyry associations elsewhere include the following:

- the chemical gradation in Figure 4 (*cf* Barnes *et al* 1986, Rock *et al* 1986b);
- the occurrence of lamprophyres as plugs satellite to granitoids, notably plugs adjacent to the Bridget Adamellite and similar granitoids near Bamboo Creek (*cf* Rock *et al* 1986a,b);
- the occurrence of plutonic chemical equivalents to the intermediate and felsic but not to the lamprophyric dykes (*cf* Rock *et al* 1988a).

More detailed work is therefore in progress on this minor intrusive suite, to determine the full range of lamprophyres and associated granitoids, their petrogenesis, and their tectonic significance.

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Widespread regeneration failure of *Persoonia elliptica* (Proteaceae) in the northern Jarrah forest of Western Australia

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Abstract

Persoonia elliptica R.Br. is a widely distributed but scattered understorey tree of the northern jarrah forest of Western Australia. Stem diameters (at breast height) of 10-30 cm are common but most populations are deficient in trees <10 cm in diameter. The reason for this was studied.

Fruit production is annual and abundant. Although seed viability is high, none could be induced to germinate in laboratory or forest even after physical and chemical treatment. In the forest, the passage of low intensity fire over leaf litter causes abundant germination of dispersed seeds, but few seedlings survive because of browsing by vertebrates, assumed to be kangaroos and wallabies. Height growth of seedlings and lignotuberous seedlings, and diameter growth of trees is slow: we estimate that diameter (breast height) of 10 cm is attained, on average, in c90 years and that recruitment of *P. elliptica* over much of the northern jarrah forest ceased between 1870 and 1904 (95% confidence limits).

A speculative model relating known changes in fire frequency and plausible changes in the abundance of kangaroos and wallabies since permanent European occupation of south western Australia in 1829 is proposed to account for the present stand structure of *P. elliptica*.

Introduction

The failure of regeneration of trees in forests and woodlands has been frequently recognized. Regeneration failure occurs when seedlings fail to attain the size of saplings, giving rise to a population with discontinuous age classes (Jones 1945). Possible causes of regeneration failure include low seed set, excessive predation of seeds before and after dispersal, low seed viability, poor germination, and high mortality of seedlings. However, a major cause is the palatability of seedlings to animals, eg. insects and molluscs (Watt 1923), rabbits (Watt 1919, 1923; Lange & Graham 1983), rodents (Watt 1923, Wardle 1959, Pigott 1969), sheep (Crisp & Lange 1976, Lange & Willcocks 1980, Pigott 1983), goats (Coblentz 1978, Clark & Clark 1981), and kangaroos (Hall, Specht & Eardley 1964). Other factors including temperature, rainfall, or light, have sometimes been implicated (Wardle 1959, 1963a,b, 1978; Hall *et al* 1964; Pigott 1969).

Widespread or chronic regeneration failure has not been reported from natural eucalypt forests and woodlands of Australia, although in some years there may be extensive removal of seeds and fruits by ants and mammals or browsing by mammals (Cunningham 1960, Gilbert 1961, Needham 1960, Statham 1983). Despite this, natural regeneration is usually prompt and adequate.

To ensure impartiality, selection of referees and consideration of their reports was undertaken by Dr N G Marchant at the request of the Hon Editor.

Persoonia elliptica R.Br is an understorey tree of the northern jarrah (*Eucalyptus marginata* Donn ex Smith) forest, attaining maximum height of c7 m and maximum diameter at breast height (130 cm, DBH) of c36 cm. It is widely distributed there (Churchill 1959). For convenience, we recognize four stages in the life of *P. elliptica*: seedlings (plants up to one year old), lignotuberous seedlings (plants >1 yr old but <15 cm tall), saplings (plants 15-130 cm tall) and trees (plants >130 cm tall). Our observations since 1979 throughout the northern jarrah forest have shown that saplings and trees with DBH<10 cm are seldom present although seedlings and lignotuberous seedlings occur in most populations.

In this paper we document the present population structure (frequency of differently sized individuals) of *P. elliptica* and examine factors relevant to explaining the observed failure of regeneration. These include supply and viability of seed, success of germination and establishment of seedlings. Measurements of growth of seedlings and trees are used to estimate when the regeneration failure began. Finally, we speculate about ecological changes that may have been responsible for the regeneration failure.

Population Structure

In this Section, we document the diameter structure of nine populations of *P. elliptica* and provide brief notes about the occurrence of seedlings and lignotuberous seedlings.

Methods

Stands of jarrah forest were chosen mainly on the basis of contrasting rainfall zone and fire and logging history (Table 1). Most were of 15 ha, with one 3 ha (No. 9) and another 125 ha (No. 6). Six of the stands were typical of the northern jarrah forest in that they obviously lacked small diameter trees of *P. elliptica*. Three stands (Nos. 7-9) were chosen because of atypically high representation of saplings and small trees of *P. elliptica*. These three stands were the only ones found by us that had this unusual representation of small trees and saplings.

A complete enumeration of diameter was made in populations where there were fewer than 30 trees; in larger populations only the first 30-50 trees were measured. Diameters were measured over bark at 130 cm above ground level (DBH). The diameter of trees which were forked below, or damaged at breast height, was measured 50 cm or 100 cm above ground level and the DBH calculated from a regression equation relating stem diameter to its height of measurement above ground level. The diameter of the largest stem was measured on trees with several stems growing from the same lignotuber. Saplings were specially searched for and the occurrence of seedlings and lignotuberous seedlings was noted.

Results

In the nine populations studied (Fig. 1), the modal DBH classes were 8-10 cm, 12-14 cm, 16-18 cm, 18-20 cm and 24-26 cm (each once), 10-12 cm (twice) and 14-16 cm (thrice). Populations 1-6 had a structure typical of most of the northern jarrah forest, with a deficiency of DBH classes 0-6 cm and limited representation of DBH classes 6-8 and 8-10 cm. Very few trees in any of the populations had DBH values exceeding 30 cm.

In populations for which complete enumerations of trees were made, density was variable: 0.2 individuals ha⁻¹ (No. 6), c3.4 ha⁻¹ (Nos. 1, 2, 4) and c20 ha⁻¹ (No. 9). The spatial pattern of trees in No. 2 is random, with mean distance between trees of 16 m (Abbott 1984a).

Seedlings and lignotuberous seedlings were found in all populations except Nos. 6 and 8 but seemed to be most abundant in populations 1, 2, 5 and 9, where they were found readily. There was no obvious association between the presence of seedlings and fire and logging history of the forest stands (Table 1, Fig. 1). It is important to record that seedlings and lignotuberous seedlings of *P. elliptica* are very rare in comparison to those of other tree species in the jarrah forest. Saplings were found in populations 7 and 9.

Annual Production and Dispersal of Fruits

In this Section we quantify the phenology of fruit production and consider fruit fall and seed dispersal.

Methods

The presence of fruit on the tree or on the ground beneath the canopy was recorded when trees were measured (in Spring) for DBH (as in the previous section). Detailed observations of flowering times were made in population 2 but casual observations were also made elsewhere. In population 2, five easily accessible branches on each of five trees were marked and the numbers of fruits present counted regularly over two years. In this stand and in population 5, the distance of seedlings from the edge of the canopy of the nearest reproductive tree was measured.

Results and Discussion

Flowering took place in December, and fruits (drupes) attained full size (c17 x 10 mm) by the following May. Many of the immature fruits aborted between March and May. Trees with DBH <11 cm were found not to have ever fruited.

There were large annual differences in the numbers of fruits produced, which were greatest in July 1981 and least in July 1983 (Fig. 2). Most fruit had fallen to the ground by August of each year. All fruit fell beneath the canopy because of the large terminal velocity of the fruit (Abbott 1984a).

Table 1
Characteristics of study areas.

Locality	Grid reference*	Rainfall zone (mm)	Features
1 Ashendon	BN 71.2.9	900-1000	State forest. High quality forest. Cut-over 1914, 1930.**
2 Ashendon	BN 71.2.8	900-1000	State Forest. High quality virgin forest. **
3 Chandler	BQ 69.8.2	1100-1200	State Forest. High quality forest. Cut-over 1890, unburnt since 1937.
4 Mundlimup	BT 63.5.6	1200-1300	State Forest. High quality forest. Cut-over 1872, 1928. **
5 Loc. 990	BT 61.9.8	1200-1300	Reserve. High quality virgin forest. **
6 Yarragil	DD 705.7	1100-1200	State Forest. High quality forest. Cut-over 1933. Near southern edge of range of <i>P. elliptica</i> in the jarrah forest. Unburnt since 1973.
7 Sawyers	AP 72.2.3	900-1000	State Forest. High quality forest. Cut-over 1870s. **
8 Loc. 6203	AM 81.3.9	600-700	Reserve. Low quality virgin forest. **
9 Mt Helena	AN 70.6.9	1000-1100	Private property. Low quality forest, last cut-over c1950 and last burnt 1965.

*CALM 1:50 000 maps (publicly available).

**Fire regime of periodic low intensity (~300 kW m⁻¹) fires since the 1950s.

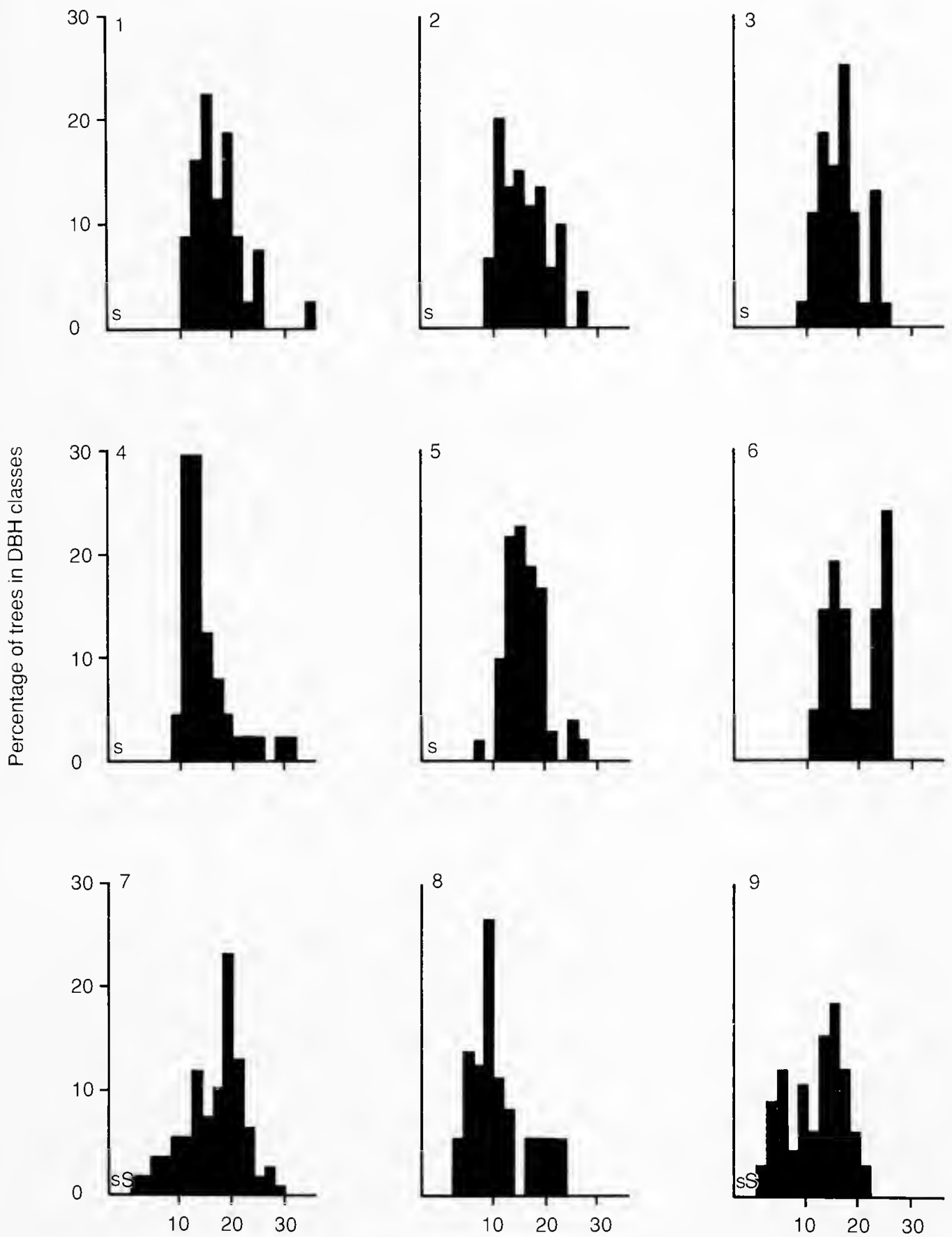


Figure 1 Population structure of *Persoonia elliptica*. Abscissa shows presence of seedlings or lignotuberous seedlings as s, of saplings as S and DBH class, from 0.1-2, 2.1-4 ..., 34.1-36 cm.

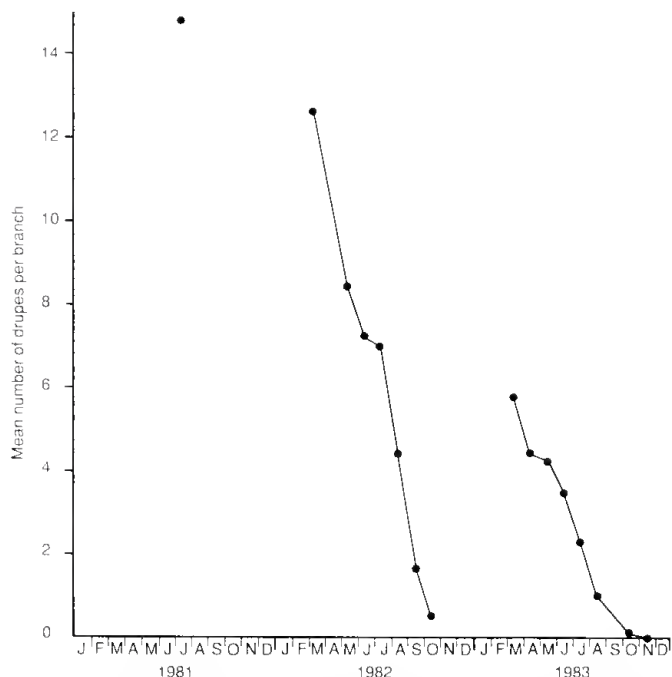


Figure 2 Annual variation in production and shedding of fruit of *Persoonia elliptica* in population 2. One branch of one tree died between October 1982 and March 1983

Although seeds can be found at any time on the ground beneath the canopy of *P. elliptica*, we have seldom observed seedlings there. For example, in population 2, the mean distance of seedlings from the edge of the canopy of the nearest *P. elliptica* tree was 28.6 m (range 2-66 m, $N = 40$). In population 5, the mean distance was 5.5 m ($N = 44$). In this population the average distance between the bole and the edge of the canopy of the same tree was 2.4 m ($N = 24$).

These data indicate that fruits or seeds are removed from the tree, or from the ground under the tree, or both, by some dispersal agent. Vertebrates rather than invertebrates are responsible (Abbott & Van Heurck 1985). Common Brushtail Possums (*Trichosurus vulpecula*) and Western Brush Wallabies (*Macropus irma*) have been observed to take fruits (S. Davies, pers. comm.). We have also found seed in the faeces of Common Brushtail Possums, Western Grey Kangaroos (*M. fuliginosus*) and Emus (*Dromaius novaehollandiae*). Two common frugivorous birds, the Grey Currawong (*Strepera versicolor*) and the Australian Raven (*Corvus coronoides*), may also eat drupes but we have no direct observations. The fruit is also palatable to humans and may have been eaten by Aborigines.

Viability and Germination of Seed

Here we examine whether the deficiency of trees of *P. elliptica* with diameter <10 cm results from most seeds either being inviable or germinating poorly.

Methods

Viability of seeds with endosperm present was checked with tetrazolium chloride (Colburn *et al* 1961).

The following treatments to germinate seeds (collected from beneath the canopies of many trees) were tried:

(a) Seeds were kept at 18°C with full light or 12 hour light/12 hour dark in the laboratory. Part of the sample was then placed on the soil in cages amongst population 2 and kept under observation for two years.

(b) Seeds were soaked in distilled water and then placed in the forest as in (a).

(c) Seeds were kept at 4°C for several weeks and then treated as in (a).

(d) Seeds were filed at both ends to reveal the endosperm and then treated as in (a).

(e) Seeds were boiled in water for 15 minutes and then treated as in (a).

(f) Digestion by birds was simulated by scarifying seeds for 3 hours or treating with acid (as in Glyphis *et al* 1981); seeds were then placed in the forest as in (a).

(g) Seeds were treated with gibberellic acid (method of Bachelard 1967) and then placed in the forest as in (a).

(h) Seeds were placed between hessian sacks (method of Crossland 1981).

(i) Seeds were placed in a small area (1.5 m x 1.5 m) of litter which was then ignited. Seeds were then placed in the forest as in (a).

(j) Seeds from several prolifically fruiting trees in a paddock at Mt Helena were placed in an adjacent fenced enclosure containing a remnant of native vegetation.

(k) Seeds were placed in cages in the forest in various treatments of shading, litter type and depth, and trenching (Abbott 1984b).

(l) Seeds from populations 5 and 9 were placed in cages on the forest floor in population 2.

(m) Fresh drupes were offered to captive emus in order to assess whether passage through the gut facilitated germination.

Results and Discussion

Drupes collected from four populations yielded the following percentage viability: 81% ($N = 52$), 100% ($N = 7$), 73% ($N = 51$) and 48% ($N = 23$). Abbott (1984b) quoted 84% viability for another sample. In all cases there was only one seed per drupe. A sample of 154 seeds collected from under a large *P. elliptica* tree yielded only 7.8% that were obviously damaged by fungi and insects. The presumption is that the remainder were fit for germination.

None of the experimental treatments applied induced seed to germinate, in agreement with Kullman (1981). There is clearly a dormancy mechanism but its precise nature remains unresolved. Our observation (preceding section), that nearly all seedlings are found far from fruiting trees, implicates passage through the gut of vertebrates as the first step in breaking this dormancy.

The emus refused to eat the drupes; it is difficult to introduce new types of food into the diet of captive emus (S. Davies, pers. comm.).

Establishment and Survival of Seedlings

Opportunistic observations made in jarrah forest stands subject to periodic low intensity fire ($<300 \text{ kW m}^{-2}$) in spring showed abundant germination of *P. elliptica* seedlings the following winter. Inspection of these stands more than one year after such fires showed that very few seedlings remained. For example, of 19 seedlings tagged in October 1982 after fire in September 1981 near population 2, only five were alive by February 1983. The other 14 plants had either disappeared or had only their stems remaining, indicating that they had not died because of drought but had died after being browsed. The type of leaf loss was not ascribable to invertebrates but consistent with browsing by vertebrates, probably kangaroos and wallabies. If the seedlings had been killed by drought, their shrivelled remains should have been evident. We therefore designed an experiment to assess the effect of browsing by vertebrates on seedling survival.

Methods

In Chandler Block, 2 km from population 3, a forest stand burnt in spring 1982 was searched in September 1983 for *P. elliptica* seedlings and 49 were located and marked. Twenty were caged (12 mm mesh) and the rest were left as controls. Survival was assessed in November 1983 and March 1984. In August 1981, 14 one year-old seedlings in population 2 were tagged and their survival was checked in August 1982 and August 1983. In September 1981, 41 one year-old seedlings in population 5 were tagged and checked in August of 1982 and 1983.

Results and Discussion

The survival of 6 months-old (November) seedlings differed little between those caged (88.2%) and those uncaged (78.6%). However, after the first summer (March), at 9 months age, there was a significant difference in survival (85% caged, 21% control, $P < 0.05$). Several of the uncaged seedlings showed clear evidence of having been killed by browsing. Because fresh faeces of kangaroos and wallabies (but not of emus) were present, we assume that the first two were responsible. Evidently during the first summer these seedlings are highly palatable to these vertebrates.

After the first year, however, survival of uncaged seedlings is generally high. Of the 14 one year-old seedlings marked in population 2, 13 were still alive one year later and 12 were alive after a further year. Of the 40 one year-old seedlings marked in population 5, 37 were still alive one year later and 35 remained alive after a further year. Hence annual mortality of the seedlings after the first year of life averaged 6.9%. These data suggest that by the second summer the lignotuberous seedling is no longer attractive food for browsing vertebrates.

The apparent contradiction between our observations of abundant germination after fire in the forest and our unsuccessful attempt to germinate seed after an experimental fire ((i), in the previous section) may be explained by assuming that the latter seed had not passed through the gut of a vertebrate. In such a case the seed would still have been dormant. Fire alone is insufficient for germination.

Rate of Growth

Here we examine height growth of seedlings, lignotuberous seedlings and saplings, and diameter growth of trees.

Methods

Rate of growth of seedling, lignotuberous seedlings and saplings was determined from annual measurements of height above ground level. Tree growth was determined from annual measurements of DBH, rather than by counting of growth rings, as these were difficult to discern.

Results and Discussion

Nine months-old seedlings near population 3, caged to prevent browsing, attained a mean height of 5.2 cm (Table 2). Those seedlings 15 months-old (and caged) had achieved a mean height of 6.4 cm (Table 2). Caged plants showed an average annual height increment of 0.2 (range -2 to 1) and 0.6 (range 0-2) cm yr^{-1} in 1981-82 and 1982-83 respectively. Uncaged plants showed an average annual height increment of (-0.4 (range -6 to 4) cm yr^{-1} (Table 2). Thus, as expected, browsing retarded the height growth of those seedlings and lignotuberous seedlings that survived browsing. Uncaged saplings showed an average annual increment in height of 5.9 cm (range 0-14 cm).

Table 2
Growth in height of *Persoonia elliptica*.

Population No. (as in Table 1)	Age (years)	Measured	Height (cm)		N
			Mean	Range	
Seedlings and lignotuberous seedlings					
2	1	Sep 1981*	6.4	3-10	14
2	2	Aug 1982*	6.6	4-11	13
2	3	Aug 1983*	7.2	4-11	12
Near 3	<1	Mar 1984*	5.2	2-7	17
5	2	Aug 1982	6.9	3-10	47
5	3	Aug 1983	6.5	3-10	33
Saplings					
9	?	Sep 1982	62.2	20-120	12
9	?	Sep 1983	68.1	22-130	12

* caged to prevent browsing by vertebrates

Table 3
Growth in diameter at breast height of *Persoonia elliptica*.

Population No (as in Table 1)	Period	DBH range	Mean	DBH increment (cm yr ⁻¹)		95% confidence interval	N
				Range			
1	Feb 1982-Feb 1983	11.7-25.1	0.12	0-0.4		0.03-0.21	10
1	May 1981-May 1982	15.4-34.7	0.20	0-0.4		0.08-0.32	6
1	Apr 1982-May 1983	10.2-22.8	0.11	0-0.2		0.05-0.17	10
2	Feb 1981-Feb 1982	11.6-25.1	0.03	0-0.1		0-0.06	9
4	May 1981-Apr 1982	7.3-21.3	0.11	0-0.4		0.08-0.14	41
4	Apr 1982-May 1983	7.5-31.7	0.10	0-0.4		0.06-0.14	38
9	Sep 1982-Sep 1983	2.5-23.5	0.14	0-0.6		0.06-0.22	17

Diameter increment of trees, averaged over all populations, was 0.11 cm yr⁻¹, with 95% confidence limits of ± 0.02 (Table 3). Values as high as 0.4 or 0.6 cm yr⁻¹ were sometimes recorded but of the 131 increments measured, 40.5% were zero. We calculate that the average *P. elliptica* tree with DBH of 8, 10, 12 or 20 cm should respectively be 73 years (95% confidence interval of 62-89 years), 91 (77-111) years, 109 (92-133) years or 182 (154-222) years old. That is, establishment took place in 1908 (95% confidence interval of 1892-1919), 1890 (1870-1904), 1872 (1848-1889) or 1799 (1759-1827).

Height and diameter growth is much slower than that of *Banksia grandis* Willd., which is also an understorey tree species of the northern jarrah forest (Abbott 1985).

Effect of Fire on Survival and Growth

Because *P. elliptica* develops a lignotuber (woody swelling at the base of the stem) in the second year of life, typical low intensity fires should rarely kill plants two or more years old. We observed that leaves and shoots are killed by these fires but new shoots sprout from the lignotuber within a few weeks.

Mean height of 3-year old lignotuberous seedlings in population 5 in August 1983 was 6.5 cm (Table 2). A patchy low intensity prescribed fire in spring 1983 killed shoots, but by February 1984 mean height was 4.0 cm (N = 36). A sample of lignotuberous seedlings in unburnt patches had a mean height of 7.0 cm (N = 19). Percentage survival from August 1983 to February 1984 was 100% for the unburnt seedlings and 84% for those burnt.

In other stands, several small trees completely scorched by fire recovered quickly by growing new branches. Many of the larger *P. elliptica* trees in the northern jarrah forest carry fire scars on the lower stem, evidence of their ability to recover from even intense fire.

General Discussion

Three distinct hypotheses can be offered to explain failure in regeneration of a tree species:

- 1 No seed is available;
- 2 Seed is available but is not viable;
- 3 Seed is available and viable but
 - (a) The disperser of the seed has become rare or extinct, (eg. Temple 1977);
 - (b) Extreme climatic events or digestion of seed by a vertebrate are needed to break the dormancy of the seed; or
 - (c) Some relevant ecological process has changed in nature or frequency over the period of interest.

Our data allow rejection of the first two hypotheses. Because seedlings and lignotuberous seedlings can occur well away from the nearest reproductive trees, there is obviously no lack of dispersal agents. We therefore reject hypothesis 3a and the part of hypothesis 3b involving vertebrate digestion. The calculated rate of diameter growth implies that the missing diameter classes <8 cm represent a period of 70-80 years. Local weather records show great variability in annual rainfall over the period 1900-1980 with drought years (eg. 1914, 1940, 1959, 1977) and very wet years (1915, 1917, 1926, 1945, 1955, 1964). Most possible combinations of temperature/rainfall should therefore have occurred during this period and at least one of these should have resulted in massive breaking of dormancy at least once (assuming that these factors are indeed causative). Thus hypothesis 3b is not favoured although difficult to reject with certainty.

Because historical records are incomplete or lacking, it is not easy to define ecological changes that may have occurred over the last 70 years (hypothesis 3c). Using the experimental and observational data collected to identify ecological process(es), we constructed a plausible history of events.

Large quantities of fruit are produced annually by larger trees of *P. elliptica*. The seed has a high viability but has a dormancy period broken effectively by passage through the vertebrate gut. Abundant germination is observed in the winter following a low intensity spring fire. Seedlings are highly palatable to browsing (probably by kangaroos and wallabies) during the first summer and few survive. We therefore identify fire (for germination) and herbivory (causing mortality of seedlings) as the relevant ecological processes affecting regeneration of *P. elliptica*.

How have both processes interacted in the past? We have reliable information about fire (Abbott and Loneragan 1983) but only anecdotes about past densities of kangaroos and wallabies in jarrah forest. The main points of our speculative model are summarized in Fig. 3. We now proceed to the detailed argument.

Before the disappearance of Aborigines from the region in the 1850s, the fire regime in the northern jarrah forest was probably one of frequent, low to moderate intensity fires (Abbott & Loneragan 1983). The density of kangaroos and wallabies should have been relatively low because of hunting pressure from Aborigines and the Dingo *Canis familiaris dingo* (Whitehouse 1977, Abbott 1980). We therefore expect that germination occurred regularly and that seedling survival was high, resulting in abundant recruitment of *P. elliptica*.

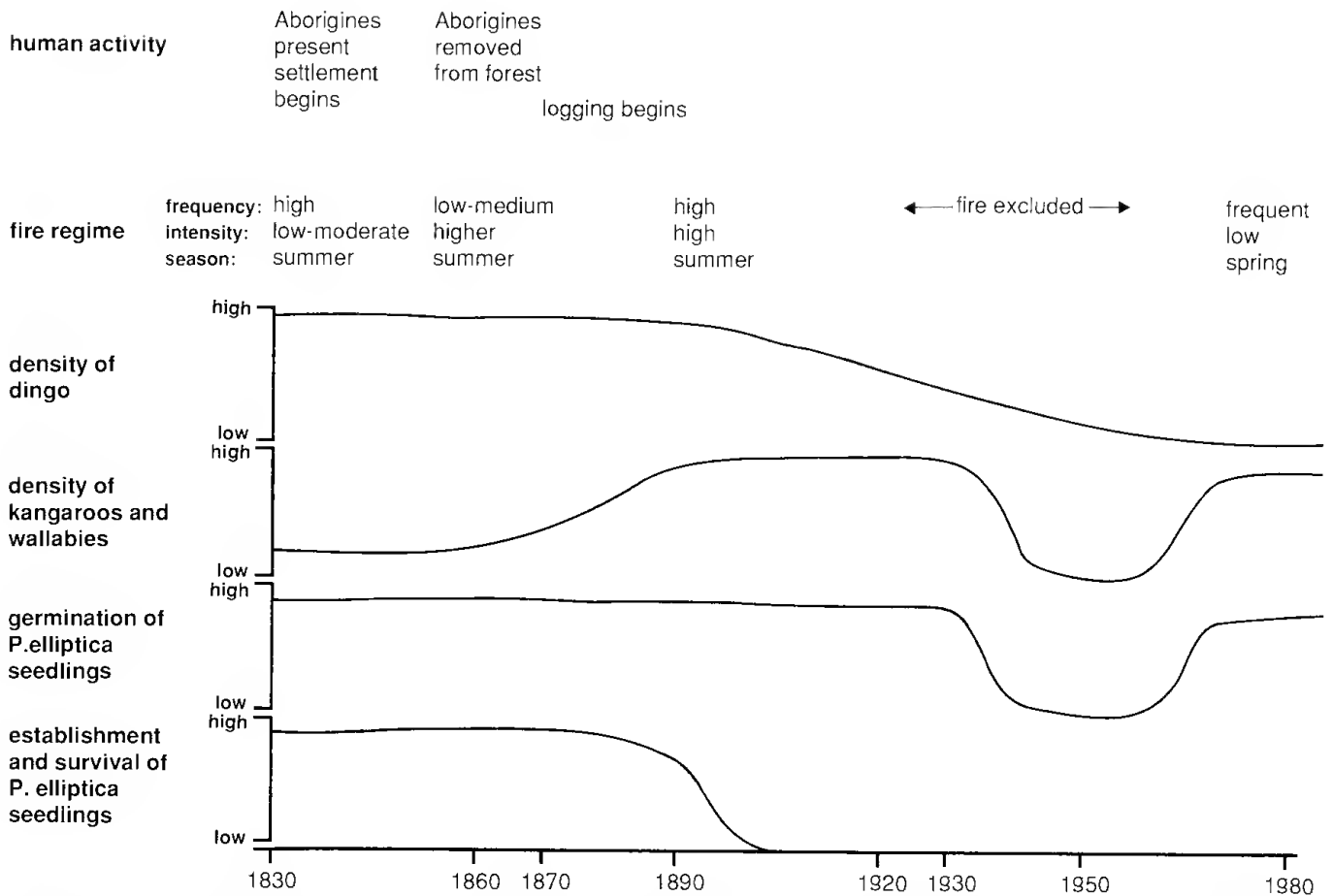


Figure 3 Speculative model relating historical changes in fire regime and hunting pressure by Aborigines to germination and establishment of *Persoonia elliptica*

Following the disappearance of forest-dwelling Aborigines until the beginning of jarrah logging in the 1870s, the frequency of fires probably declined, resulting in an increase in fire intensity. The density of kangaroos and wallabies should have slowly increased, corresponding to the decrease in numbers of Aborigines (but probably no change in density of the Dingo). Both factors should have resulted in declining recruitment of *P. elliptica*. From the 1870s until the introduction of the Forests Act in 1919, fires once again became frequent because of adjacent agricultural clearing and abundant logging debris on the forest floor. Fires probably also increased in intensity for the same reason. Thus, the increasing length of time without Aboriginal occupation and the intensive farming of land adjacent to the forest (and consequent European trapping of the Dingo because it preyed on sheep) should have allowed densities of kangaroos and wallabies to increase to very high levels, effectively suppressing recruitment of *P. elliptica*. Except as noted below, we do not think that hunting of wallabies and kangaroos by Europeans was of great importance because of the large extent of forest, the long distances between settlements and the small population of Europeans present.

From about 1930 until about 1955, fire was excluded from the northern jarrah forest except for annual burning of 20 m wide firebreaks around 100-200 ha compartments of forest. Such fire exclusion should have reduced the supply of young, nutrient rich plant tissue as food for kangaroos and wallabies, leading to a decline in their numbers. Little recruitment of *P. elliptica* should have occurred in that period. From 1955 to the

present, the northern jarrah forest was again subjected to frequent (5-7 years) low intensity fires. The densities of kangaroos and wallabies were observed to increase following this change in fire policy (J. Havel, pers. comm.) and the density of kangaroos is still relatively high (Short *et al* 1983). Recruitment of *P. elliptica* would have remained low. Although the Dingo in forest areas was replaced by the Fox (*Vulpes vulpes*) by the 1930s, the latter rarely preys on kangaroos and wallabies (Brunner *et al* 1975) and so is not relevant to the ecology of *P. elliptica*.

The ageing of *P. elliptica* on the basis of current diameter growth indicates that, on average, the <10 cm diameter classes represent a period of c90 years, *ie.* regeneration began to fail towards the end of the nineteenth century. The virtual absence of trees of DBH <8 cm (equivalent to c70 years age) suggests that recruitment of *P. elliptica* over most of the northern jarrah forest had ceased by about 1910.

How then do we explain the structure of populations 7-9 (Fig. 1) in which trees with DBH <6 cm are relatively well represented? These three populations occur in the extreme north-eastern sector of the northern jarrah forest and have been close to European settlement (farms, orchards, towns) since the 1870s. We suggest that in and around these stands, hunting pressure from Europeans has been relatively high and consistent during the past 100 years. This depressed the population densities of kangaroos and wallabies and allowed some recruitment of *P. elliptica*.

Although the model outlined above is speculative, particularly when compared to the elegant historical study of Peterken and Tubbs (1965), parts of it are testable. The seedlings of *P. elliptica* that have been caged in population 2 and near population 3 should attain DBH of 8 cm within 70-80 years. An index of the abundance of kangaroos and wallabies, based on counts of faecal pellets in various forest stands (Hill 1981) could be correlated with the density of *P. elliptica* seedlings.

Acknowledgments We thank S. Davies for kindly allowing us to study the *Persoonia* population (No. 9) on his property, and for attempting to feed drupes to his captive emus. P. Christensen, S. Davies, J. Havel, O. Loneragan and R. Underwood provided helpful criticism.

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The Quindalup Dunes: the regional system, physical framework and vegetation habitats

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Abstract

The Quindalup Dunes contain a variety of aeolian landforms developed by regional climatic, geomorphic and sedimentologic factors, as well as local coastal/strandline processes, and vegetative and pedogenic processes. Superimposed on these are factors of distance from the strandline (which determines the degree of wind effects), soil salinity, and height above water table (which is related to height above sealevel). These factors and processes have resulted in a range of geomorphic units, habitats and vegetation responses that can be recognized at various scales of reference.

A consistent terminology for geomorphic units and habitats has been developed in order to compare tracts of Quindalup Dunes along the various sectors of the southern west coast of Western Australia. The large to medium scale geomorphic units include parabolic dunes, chaots (chaotic dune terrain), shore-parallel ridges, blowouts, undulating plain and flats. The small scale geomorphic units, that essentially equate with the basic vegetation habitats, are subdivisions of the larger scale geomorphic units; these include various slope units; crests and depressions of the larger scale units.

Each of the five sectors of the south west coast of Western Australia contains distinct associations of geomorphic units and vegetation habitats that reflect a difference in the regional sedimentological and geomorphic setting, as well as gradients in climate and other edaphic factors. Changes in dominant habitat types from sector to sector, together with the climatic gradient, favour smaller scale heterogeneous distribution in the structure and floristics of the vegetation units along the extent of the Quindalup Dunes. Our analysis of the distribution of reserves for flora and fauna within the Quindalup Dunes indicates that the regional variety of landforms and vegetation habitats is not adequately represented. In particular, there is no reservation of Quindalup landforms and habitats representative of Geographe Bay, the barrier dunes of Leschenault-Preston Sector, and the cusped beachridge plain exemplified by Point Becher.

Introduction

The Holocene coastal dune zone of the Swan Coastal Plain is generally a relatively narrow assemblage of landforms formally termed the Quindalup Dunes (McArthur & Bettenay 1960). The zone extends from Dunsborough in the south to Dongara in the north along the south west coast of Western Australia. Within this zone various authors have described and mapped vegetation, or landforms related to vegetation.

Smith (1973) provided a guide to the flora of the coastal habitats and subdivided the flora of dunes into 4 types: foredune vegetation; mobile dune vegetation; stabilized dune vegetation; and tall closed dune scrub. Smith (1985) later subdivided the dune vegetation into 3 types, apparently excising the tall closed dune scrub from the classification. A number of later authors, particularly in unpublished government reports, adopted the subdivision of Smith (1973) as the basic vegetation units of the Quindalup Dunes. Speck (1952) and Seddon (1972), on the other hand, provided maps of the dune zone, generally treating the vegetation complexes within the Quindalup Dunes as a single unit. Heddle (1979), Heddle et al (1980) and Beard (1976, 1981) similarly mapped the flora of the zone, treating the unit essentially as a homogeneous system although recognizing at least 2 alliances, namely a strand and foredune alliance, and a mobile and stable dune alliance.

McArthur & Bartle (1980a,b) described various stages of Quindalup dune landform evolution (Q1, Q2, Q3 and Q4) and its stabilization by vegetation, and related vegetation assemblages to these landforms. More recently Cresswell & Bridgewater (1985), utilizing a floristic and landform/soil approach, incorporated the Quindalup Dune System into their overall treatment of vegetation of the Swan Coastal Plain. They subdivided the Quindalup Dune vegetation into eight units, which were then related to geomorphic location.

However, the Quindalup Dunes present a much more variable system of habitats than perhaps has been appreciated. The variability in habitat is due to: processes and stages of landform development as determined by regional factors; processes and stages of landform development as determined by local geomorphic history; relative position of landform units with respect to the strandline; relative relief of the various small scale landform units with respect to water table; degree of development of soils and calcrete; and soilwater salinity.

These interacting factors have developed a wide range of small scale geomorphic units each with its own distinct relief, slope, soil cover, and location relative to sea effects. Because geomorphic processes, and the resultant geomorphic units (variable in time, space, intensity of development, and scale), are the

fundamental determinants of habitats, a geomorphic approach should provide a useful framework for vegetation studies. The approach adopted here is to describe the geomorphic units and habitats at various scales of reference in the Quindalup Dunes, and to relate them to coastal and aeolian processes and vegetation. This is a direct application of the coastal sector analysis of Searle & Semeniuk (1985) and landform analysis to vegetation investigations. There is a recurring suite of geomorphic units peculiar to each of the 5 coastal sectors of Searle & Semeniuk (1985) and thus the sector approach provides a framework to identifying and understanding the differences within the Quindalup Dunes along their extent. The approach is useful for analysing the Quindalup Dune vegetation regionally and, in combination with the subcontinental gradient of climate and variability in species pool, helps to explain the complicated pattern of habitats and vegetation assemblage within the Quindalup Dune System. Such information is important for studies in conservation, coastal management or assessment of regional significance of vegetation and landforms within a given sector of the Quindalup Dunes.

This paper reports on the first stage of investigations of the vegetation of the Quindalup Dunes. The objectives of the paper are to describe the regional setting, regional variety and the local variability of the physical features of the Quindalup Dunes throughout their full extent along the Swan Coastal Plain so that the physio-chemical framework, geomorphic units and habitats can be identified. As such this paper provides information on geomorphology and vegetation habitats of the Quindalup Dunes to a level not previously reported and provides the basis for more detailed studies of the habitats and vegetation of the Quindalup Dunes in the future.

Methods

The results of this paper are based on intensive fieldwork, reconnaissance field surveys, aerial photograph studies, low altitude aerial surveys and literature review. Fieldwork involved study of geomorphology, stratigraphy, soils and vegetation by surface mapping, coring/trenching and sample collection. The maps produced in this paper are the result of field work supplemented by ground truthing. Aerial photographs and ground surveys were also used to identify the range of geomorphic units in the region. Sites of intensive fieldwork include (Fig. 1): Geographe Bay area, Leschenault Peninsula-Myalup area, Yalgorup National Park-Mandurah area, Pt Becher-Rockingham Plain area, Trigg Island-Whitfords-Two Rocks area, and areas around Lancelin, Cervantes, Jurien Bay, Green Head-Leeman, and Dongara. Intensive fieldwork was supplemented by reconnaissance surveys and low altitude aerial surveys over the remainder of the southwest coast between Geographe Bay and Dongara. Examination of aerial photographs, utilizing black/white and colour photographs, was also undertaken.

The approach of Semeniuk (1986) was used in mapping and naming of geomorphic/habitat units. This method involves identifying units observable and mappable at a given scale of reference. The scales of reference, slightly modified after Semeniuk (1986), are: **regional scale** (100km x 100km frame of reference); **large scale** (10km x 10km frame of reference); **medium scale** (1km x 1km frame of reference); and **small scale** (100m x 100m frame of reference). The same geomorphic unit may be observable at several scales of reference. For example, parabolic dunes may be mappable at regional and large scales. At medium scale, different types of parabolic dunes such as fretted or attenuated, may be identifiable. At small scale only geomorphic sub-units of the parabolic dune may be mappable, such as the crest or bowl.

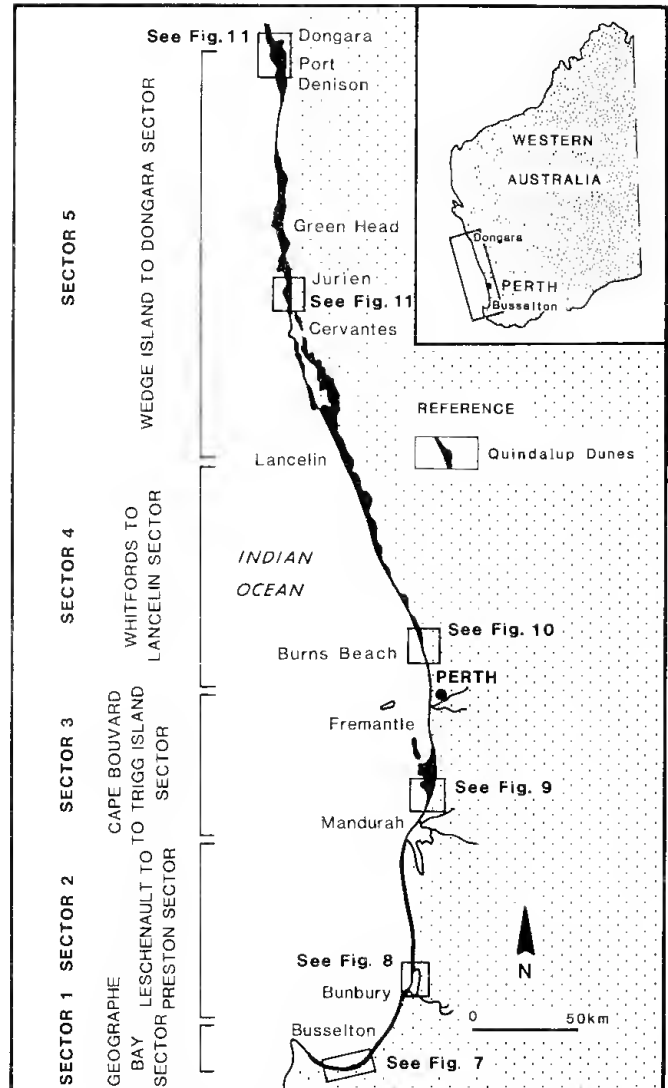


Figure 1 Distribution of Quindalup Dunes and location of study sites in Southwestern Australia.

The stratigraphy of the Quindalup Dune terrain was determined by drilling, trenching and augering, and from information in the literature (Searle 1978, Semeniuk 1983, Woods 1983, Searle & Semeniuk 1985, Semeniuk & Searle 1985a,b 1986). Soil profiles were documented in numerous locations in each of the study sites. The soils were described in terms of humus content, structure, fabric, texture and composition. Soil samples for analyses of salt content were collected along 2-4 transects for each sector. Samples were collected in summer from the shore to the hinterland in transects parallel to the dominant summer wind direction. Sample sites were generally spaced 100m apart for distances 0.5-2.0km along a transect. At each sample site 5 replicate surface soils were collected. In the laboratory soils were dispersed in an aliquot of distilled water to leach out soluble salts and the salinity of the resultant solution was determined by conductivity meter. The salinity results were then converted to mg salt/cm³ of soil. The organic and humus content of soil was determined by heating soils to >450°C to expel carbon as CO₂.

Regional setting**Geomorphology**

The Quindalup Dune System extends along the modern shoreline of the Swan Coastal Plain, spanning a distance from Geographe Bay in the south to Dongara in the north (Gentilli & Fairbridge 1951). It varies from a narrow unit to a locally extensive system up to 10km wide. Topographically the system varies from a low-relief, subdued coastal plain 3-5m above MSL, to steep aeolian highlands with a relative relief of c 30 m. The Quindalup system generally adjoins the older Spearwood Dune system (to landward) but in many locations the Quindalup Dunes are encroaching over the Spearwood Dune terrain.

Climate

The coastal dune belt of the Swan Coastal Plain spans a climate gradient from humid in the south at Geographe Bay to semi-arid at Dongara (Gentilli 1972). Such wide climate variation should influence coastal processes and hence the development of different habitats, dynamics of habitats, availability of water, and consequently the resultant vegetation. The climatic parameters considered most important to development of habitats and to maintenance of vegetation are wind, rainfall, evaporation and temperature. These factors interact to develop a variability in habitat and plant response both regionally and

locally. For instance, onshore wind gradually changes in intensity and direction from Geographe Bay to Dongara (Searle & Semeniuk 1985). As a result, blowouts and parabolic dunes increase in number, and the parabolic dunes extend further inland and become more northerly aligned from south to north along the coast. Rainfall, evaporation and temperature also are critical to dune development and vegetation response, and again from south to north there is an increase in aridity reflected by landforms and vegetation. Rainfall, varying from c 500mm/yr in the north to >800mm/yr in the south, determines the amount of moisture available in the vadose zone and the extent to which the groundwater table is salinized. Climate data for selected locations are summarized in Table 1.

Stratigraphy

The sand of the Quindalup Dunes stratigraphically is referred to as Safety Bay Sand. The unit is juxtaposed against the older more landward Spearwood Dune System or Yoongarillup Plain (MacArthur & Bettenay 1960, MacArthur & Bartle 1980a), the underlying materials of which are stratigraphically referred to as Tamala Limestone (Playford *et al* 1976). The Safety Bay Sand also may adjoin and overlie a Holocene seagrass sedimentary unit, the Becher Sand (Semeniuk & Searle 1985b), or an estuarine sedimentary unit, the Leschenault Formation (Semeniuk

Table 1**Climate data for selected localities along the coast of Southwestern Australia¹**

Climatic Data									
SECTOR	LOCALITY	Annual rain- fall (mm)	Rain days per annum	Annual ² evapo- ration (mm)	Mean daily temperature (°C) in summer (January)	Mean max. temperature (°C) in summer (January)	Mean daily temperature (°C) in winter (July)	Mean min. temperature (°C) in winter (July)	Wind ³ in Summer
1	Busselton	838	137	1200	21.2	28.8	12.4	8.1	landbreeze/seabreeze system mainly 0-20km/hr; emanating mainly from SSE & NW respectively
2	Bunbury	881	122	1300	21.9	27.4	12.9	9.1	landbreeze/seabreeze system mainly 0-20km/hr, but up to 20-40km/hr in the northern areas mainly from SE-NE & SW respectively
&	Mandurah	897	121	1500	23.1	28.7	13.4	9.4	
3	Fremantle	775	128	1900	23.0	27.7	13.9	10.2	
4	Lancelin	627	126	2000	23.0	28.7	14.6	10.1	landbreeze/seabreeze system mainly 20-40km/hr mainly from SE-E & S-SW respectively
&	Jurien Bay	519	100	2200	23.0	29.3	14.5	9.6	
5	Geraldton	477	88	2500	25.1	31.6	14.3	9.2	

¹ Data from Bureau of Meteorology 1975² Estimated from evaporation map (Bureau of Meteorology 1980)³ See Searle & Semeniuk 1985a.

Only summer wind is considered important in developing onshore aeolian landforms. Onshore wind in winter is usually mild, although periodically punctuated by storms accompanied by rain.

1983). The Safety Bay Sand may have one of several types of stratigraphic relationships with the adjoining stratigraphic units (Playford *et al* 1976, Searle 1978, Semeniuk 1983, Semeniuk & Searle 1985b, Searle & Woods 1987). These relationships are (Fig. 2): Type 1, a sheet of Safety Bay Sand overlies seagrass bank sedimentary deposits, but is detached from Tamala Limestone; Type 2, a ribbon to prism of Safety Bay Sand abuts and encroaches upon Tamala Limestone; Type 3, a ribbon or shoestring of Safety Bay Sand is perched upon and overlies Tamala Limestone in a near coastal setting; Type 4, lenses, ribbons and shoestrings of isolated and detached Safety Bay Sand sedimentary deposits are perched upon and overlie Tamala Limestone; and Type 5, a shoestring of Safety Bay Sand overlies estuarine sedimentary deposits but is detached from Tamala limestone.

The significance of these types of large scale stratigraphic contacts is that each provides a separate geomorphic and hydrologic setting for the Quindalup Dunes. A low relief sand

plain situated 2 to 3 to 5m above the water table and overlying a sand aquifer, for instance, provides a different setting to a high relief dune terrain situated 10-30m above the water table and underlain by limestone that has a calcrete capstone. The various stratigraphic types and their distribution with respect to the coastal sectors of Searle & Semeniuk (1985) are illustrated in Figure 2.

There also is a variety of stratigraphic features internal to the Safety Bay Sand; these include: 1) beach/beachridge sheet, overlain by aeolian sand sheets and lenses, which are cross-layered to root structured to homogeneous (Semeniuk & Johnson 1982); and 2) aeolian sand sheets, lenses and wedges, cross-layered to root-structured to homogeneous, with intercalated soil sheets and local development of calcrete sheet (Semeniuk 1983, Semeniuk & Meagher 1981a, Semeniuk & Searle 1985a).

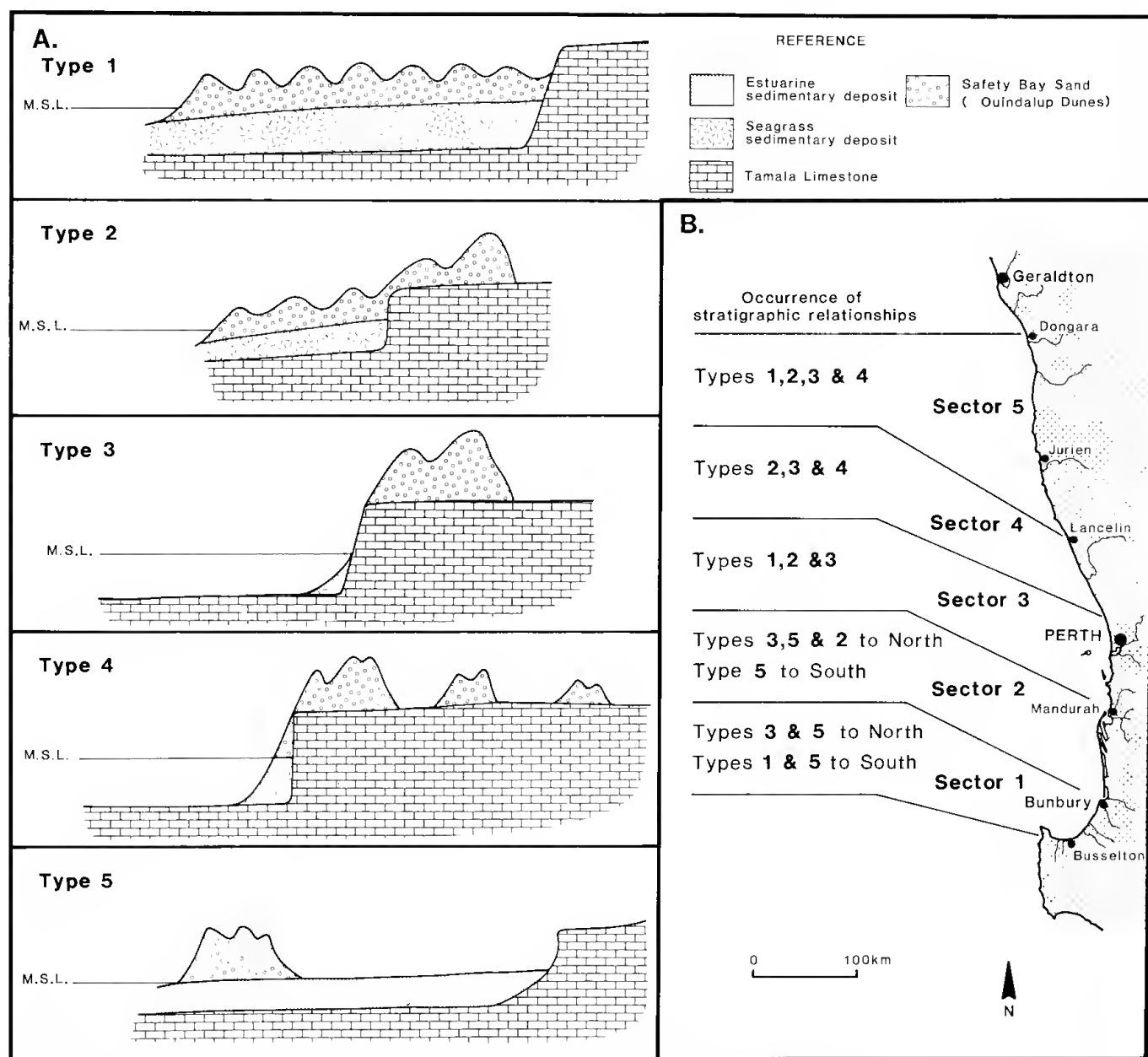


Figure 2 The range of stratigraphic relationships of Safety Bay Sand with adjoining units.

The variety of internal stratigraphic features and lithologies, such as calcretes and buried or intercalated soil sheets, has some relationship to vegetation in that it influences moisture retention and either facilitates or retards vadose water migration. The inter-relationships of calcrete and vegetation have been previously discussed in Semeniuk & Meagher (1981a) and Semeniuk & Searle (1985a).

Soils

The soils of the Quindalup Dunes have been described by McArthur & Bettenay (1960), McArthur & Bartle (1980a,b), Semeniuk & Meagher (1981) and Semeniuk & Searle (1985a). Soils are mostly arenosols (sandy soils) and are developed as pedogenic overprints on a quartzose calcareous, medium to fine grained sand (usually a quartz skeletal lithoclast grainstone, in the terms of Dunham 1962). Degree of soil development is indicated by the amount of humus developed, the degree to which carbonate grains have been leached and the extent of root structuring and bioturbation. The most common soils, listed here in order of developmental maturity and area abundance, are:

- thin (<20cm), weakly humified quartzose calcareous sandy soil;
- thin (<50cm), humic quartzose calcareous sandy soil;
- thick (1-2m), humic quartzose calcareous sandy soil;
- thick (1-2m), humic quartz sandy soil.

The soils generally form sheets over the dune terrain and have their thickest development in swales and lowlands. Subsequent landward migration of aeolian sediments may bury a soil profile. Details of soil profiles and soil features as they relate to habitats and vegetation will be presented in future publications.

The results of soil salinity transects are shown in Fig. 3. Generally soil salinity, although initially highest near the shore, does not gradually increase to landward. However, the occurrence of humic soils increases the capacity of soils to retain salt and results in locally high values of salt content. The mean salt content of the soils increases regionally from south to north in response to more intense (salt bearing) onshore winds, more evaporation and the decreased effect of leaching rainfall. However, at any area locally the salt content of soils also increases due to humus content.

In northern areas where deflation flats have been formed close to a water table, indurated carbonate crusts may also be developed on the aeolian sands. These crusts are wide-spread sheets hundreds of square metres in area and up to 30cm thick. These crusts result in localized limestone-like pavement habitats.

Vegetation

The vegetation of the Quindalup Dunes occurs predominantly as a system parallel to the coast (Beard 1976, 1981). Because the Quindalup Dunes occur over a wide climatic gradient in a north-south direction, and may exhibit an east-west variability in landforms and habitats, it may be expected to exhibit regional variation. A gradient is evident in the structure and floristics of the vegetation from south to north. In the southern sectors low forest, woodlands and scrub are the dominant types with *Agonis flexuosa*, *Eucalyptus gomphocephala* and *Acacia* spp. as the main overstorey species. In the northern sectors the dominant structural units are scrub and heath, with several species of *Acacia* and *Melaleuca* as the main overstorey species.

Although regional changes in vegetation structure and floristics should be gradual, in response to a north-south climatic gradient, this is not strictly the case. The dominant vegetation habitats developed in each of the five sectors identified by Searle & Semeniuk (1985) are distinct from adjoining sectors,

and therefore there is not a simple recurring pattern of similar habitats along the entire length of the southwestern coast. Thus the changes in dominant habitat types between the sectors and the climatic gradient along the length of the coast interact to develop a heterogeneous distribution in the structure and floristics of the vegetation units at regional and large scales. At the local scale vegetation also is strongly related to habitat features. Therefore as the habitat types change so does vegetation structure and floristics. Within any given area there will be vegetation response due to factors such as distance from ocean, soil development, position in the landscape and fire history. Furthermore, soil and landscape factors are also related to climate, and altogether produce distinct regional and local patterns in the vegetation of the Quindalup Dune System.

Terminology for geomorphic/habitat units

It is important to compare *similar* geomorphic units or habitats if patterns of vegetation distribution are to be understood at the regional scale through to the local scale. Accordingly, it is necessary to apply a consistent set of geomorphic/habitat terms throughout the Quindalup Dunes.

In terms of vegetation habitats it is necessary only to note the resulting shape of the land surface, and apply a non-genetic term to describe it. This approach is the basis for our choice of non-genetic terminology. Criteria adopted in this paper to describe and name dune landforms are: dune geometry (eg parabolic); relief (eg high, medium, low, undulating, flat); continuity (continuous vs disrupted); and alignment relative to shore (parallel, oblique, transverse)

Geomorphology

A number of authors have described and classified dune landforms (Goldsmith 1985, Cooper 1967, McKee 1979, 1982, Breed & Grow 1979, Davies 1980, Mainguet 1984, Hesp 1984a, Tinley 1985, etc). Most of the terms in these works are non-genetic and based on geometric criteria and, as such, are adopted here. However some terms have been coined in this paper because there were inadequate terms in the literature for the type of landform encountered in this study, or because the only terms available were genetic.

The new terms for dune landforms coined in this paper are *chaots*, *conical hill residuals*, and *shore-transverse ridges*. Definitions of terms used are provided in Table 2. Parabolic dunes also have been subdivided into *crescentic*, *attenuated* and *fretted* types. The fretted category is a new form described in this paper. Some of the subdivisions of parabolic dune systems into components of arms, inner face, advancing face and bowl, for purposes of distinguishing habitats for vegetation, also are new. The other terms used are established in the literature but are modified by descriptors to denote features such as relief, continuity and alignment in relationship to the shore. Illustrations of large and medium scale units are provided in Fig. 4.

Some of the new terms in this paper are equivalent, either fully or in part, to those in the literature. This applies to the terms shore-transverse ridges, bowls, and conical hill residuals. Shore-transverse ridge is equivalent to longitudinal dune of Thom (1965), and may be partly equivalent to wind rift dune of Hack (1941) and Mabbut (1977). However, shore-transverse ridge is preferred because the term does not carry a genetic connotation, as wind rift does, and does not imply an orientation with respect to wind direction and origin that is associated with the term longitudinal. The term bowl incorporates the term dune slack of Ranwell (1972), but the former term is preferred because it does not carry implication of wind deflation down to a non-erodable surface such as rock, shingle or wet sand. The

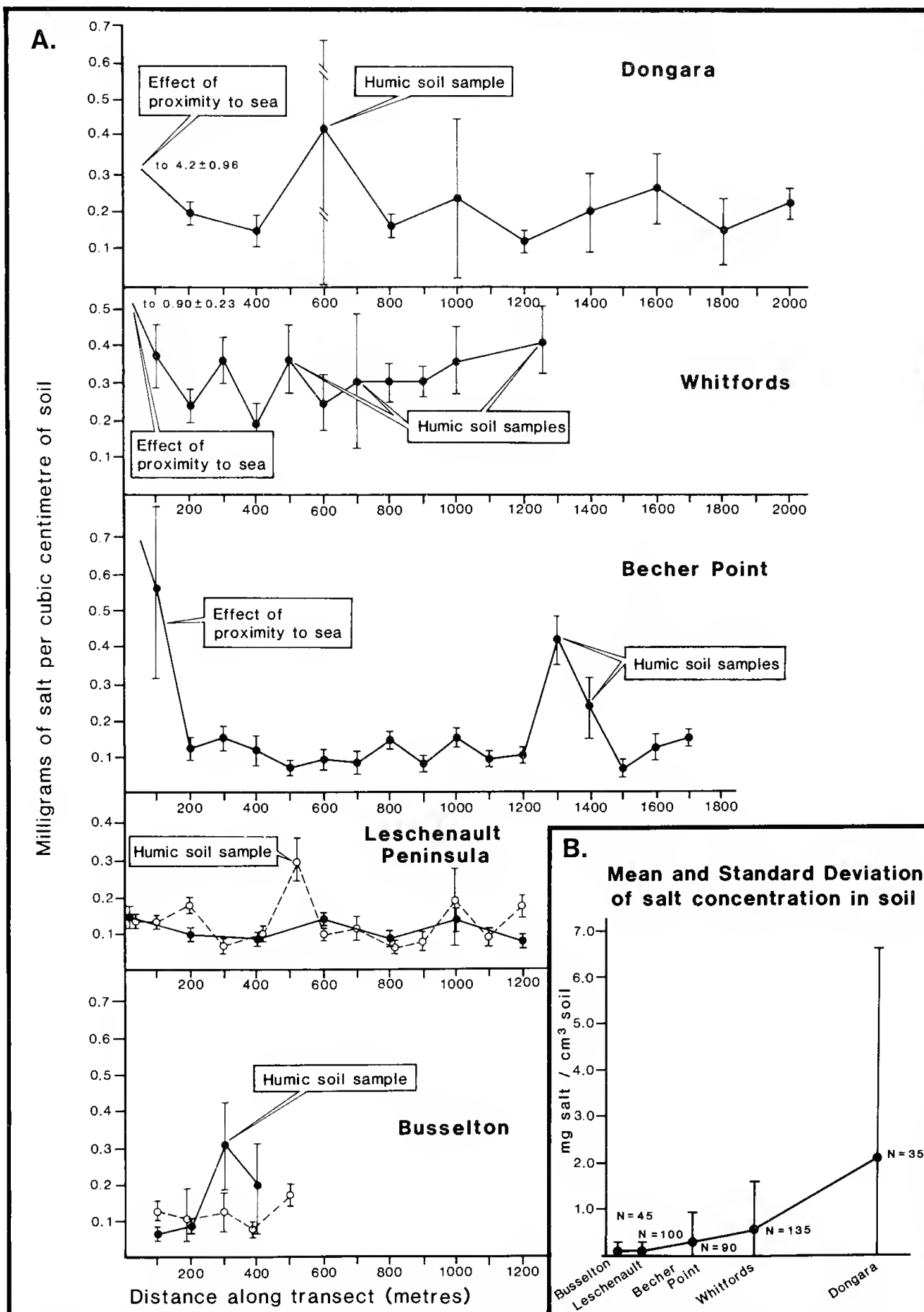


Figure 3 A Salt concentration in soils along transects from shore to hinterland, parallel to dominant wind direction, for each sector (replicate sample $n = 5$).

B Bulk mean salt concentration of coastal dune soils in a subcontinental perspective from Busselton to Dongara.

Table 2
Definition of terms

Geomorphic term	Definition*	Comments
Shoreline dune ribbon	shore-parallel, low relief dune complex with ribbon-shaped plan and cross-sectional geometry; the complex abuts/adjoins the hinterland	a regional to large scale feature
Barrier dunes	shore-parallel, low or high relief, narrow dune complex forming a barrier to lagoon or estuary	a regional to large scale feature
Cusate beachridge plain	low relief accretionary plain of parallel sand ridges; coastal margin of plain is cusate; plain is result of coalescence of adjoining cusps	a regional to large scale feature
Cusate foreland, or cusp	isolated, accretionary sediment body; triangular in plan; composed of low relief to high relief dune complex	a regional to large scale feature; the term cusate foreland refers to the largest type of cusp (see Bates & Jackson 1980); the term cusp in the literature usually refers to small beach cusps but there is no scale restriction to the term; in this paper there also is no size implication in the use of the term
Perched dunes	shoreward encroaching dune complex of parabolic dunes and sand sheets perched upon and transgressing the upland hinterland limestone terrain; irregular plan and cross-sectional geometry	a regional to large scale feature
Foredunes	shoestring deposit of sand developed by aeolian processes usually as a low ridge immediately landward of beach and seaward of the first high relief-medium relief dune complexes further to landward; may comprise a narrow belt on the sheltered coast of cusate forelands	subdivision of foredune morphology is provided by Hesp (1984a)
Parabolic dunes	sand dune, u-shaped to spatulate in plan, convex in downwind direction. Three types are recognized based on plan geometry: <i>crescentic</i> , which is a short to elongate u-shape; <i>attenuated</i> which is markedly elongate to the extent that the dune form consists mostly of parallel arms; and <i>fretted</i> , where the arms of the dune have developed subsidiary smaller blow-outs and parabolic dunes. Parabolic dunes are subdivided into components of arms, bowl, advancing face, inner face, conical hill residuals	attenuated parabolic dunes are termed hairpin (Bates & Jackson 1980) and fretted parabolic dunes are <i>in part</i> synonymous with compound imbricated parabolic dunes of Tinley (1985)
Chaots	a <i>chaotic</i> system of sand hills, mostly conical in shape and of <i>various sizes and relief</i> , and associated, mostly circular depressions. The entire chaot system may be low relief, medium relief or high relief. The chaot system itself may be sheet-form or ridge form	this geomorphic term is new as defined in this paper; however the term incorporates erosional as well as accretionary dune forms and is intended to be descriptive not genetic

Table 2
Definition of terms (continued)

Geomorphic term	Definition*	Comments
Shore-parallel ridges	a system of linear parallel sand ridges usually of similar relief (ie low or high) with intervening linear depressions. The ridges may be subdivided into continuous and discontinuous (disrupted) types	these low ridges are also termed "beachridges" in this paper and by others (Woods & Searle 1983)
Shore-transverse ridges	a system of high relief ridges developed transverse to the shore; in specific areas there may be a system of adjacent parallel transverse ridges	the term may be in part synonymous with wind rift dunes of Hack 1941 & Mabbut 1977; these dune forms are not longitudinal dunes
Blowout	small to large trough shaped depression or scour formed by wind erosion. Blowouts are subdivided into the components of floor, walls, and, where vestiges of the original terrain remain, conical hill residuals. The transported sand may form local conical hills or parabolic dunes	Bates & Jackson 1980 use the term "blowout" to refer to the eroded terrain and to the adjoining accumulation of sand, where recognizable, derived from the depression. However in this paper if the derived sand assumes a recognizable parabolic form it is termed a parabolic dune
Undulating plain	low relief plain with broad, gentle undulations	A large to medium to small scale feature
Flat	medium to small scale geomorphic feature comprised of flat terrain	the flat is not obviously linked to any parabolic dune, in which case it would be a bowl; see bowl
Conical hill residual	small to medium scale conical hill left as an erosional residual as the surrounding terrain is scoured away, either in a blowout or within a migrating parabolic dune	the conical hill residual usually has a capping of tenacious vegetation which has determined why the landform remains as a residual
Bowl	flat or slightly concave floor of the inner portion of a parabolic dune; the bowl is contained by the arms and inner face of the parabolic dune	bowls and flats are similar except that bowls are confined by parabolic dune arms; the term is partly synonymous with dune slack, Ranwell 1972
Coppice dune	a conical mound or hummock of sand accumulated around vegetation (Cooper 1967)	these dunes are not common in the study area
Barchans and Barchanoid ridges	intergradational spectrum from small isolated crescentic dunes oriented transverse to wind direction, with a gently convex windward face, concave leeward face and horns pointing downwind (barchans), to ridges, transverse to wind direction, with incipient barchan geometry	these dunes are not common in the study area and usually occur as small-medium scale units on crests and margins of active parabolic dunes
Transverse dunes	linear, strongly asymmetric dune ridge oriented transverse to wind direction with gently sloping windward face and steep leeward face (Bates & Jackson 1980); grades into barchanoid ridge	these dunes are not common in the study area and usually occur as small-medium scale units on crests and margins of active parabolic dunes
Wetland	Wet, waterlogged or inundated flats within the dune terrain	the wetland types are not discussed further in this paper

* of dune geometry regardless of whether dune is mobile, bare, or fixed

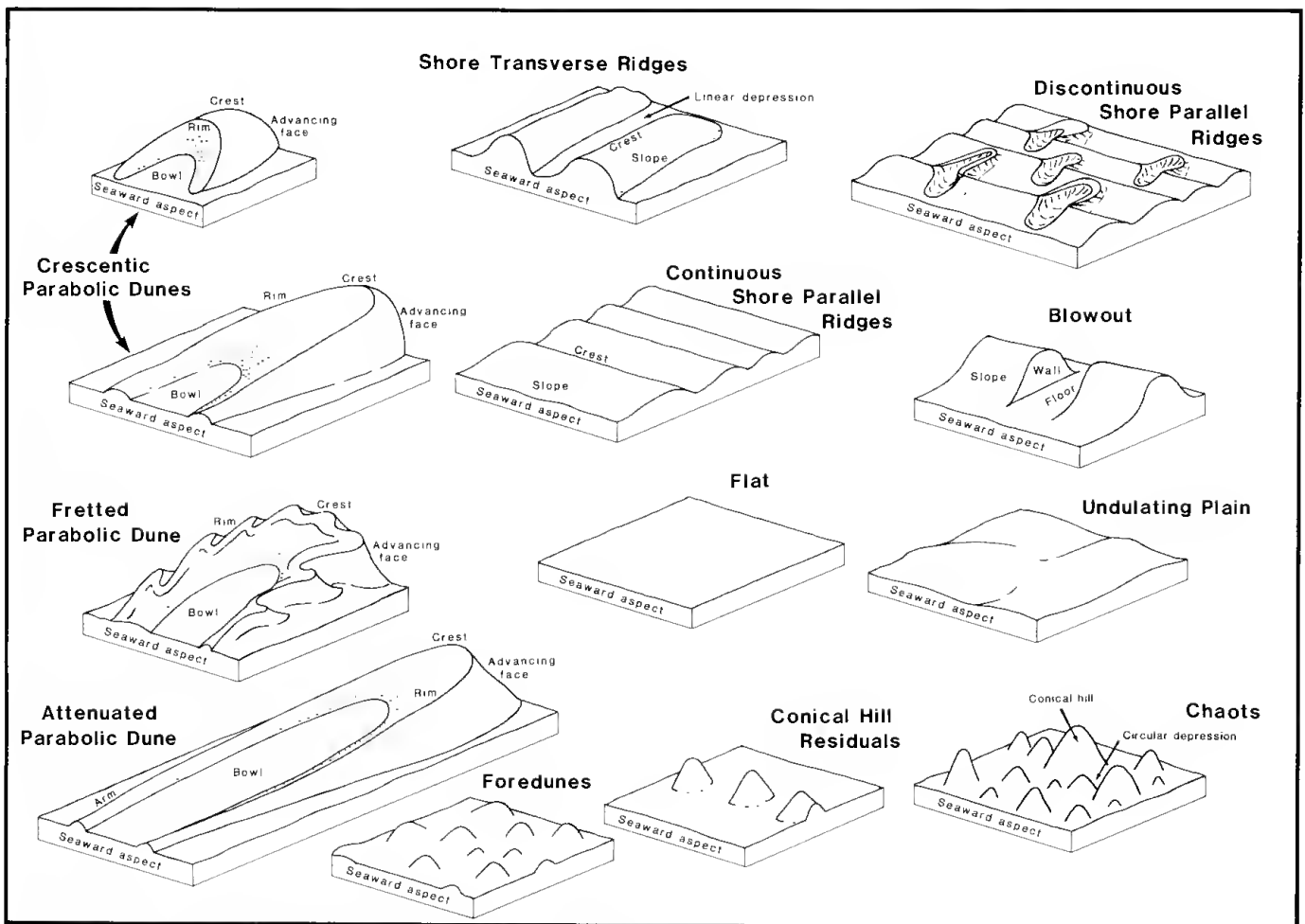


Figure 4 Diagram illustrating the range and geometric features of the most common coastal-dune landforms.

term bowl is intended to describe the geometric form of the concave centre of a parabolic dune system regardless of whether or not its floor lies at a distinct stratigraphic or hydrologic interface. The term flat thus also is partly equivalent to dune slack. The term conical hill residual is preferred to remnant dune of Davies (1980) because it conveys description of a conical shaped remnant.

The descriptive term chaot is applied to a system of dunes whose surface is a chaotic system of conical landforms. The chaotic terrain may be the result of erosion producing conical hill residuals, or the result of erosion and accretion, where accretion has resulted in acute coppice dunes, parabolic dune fronts, and sand sheets. In these terrains with the chaotic system composed of a closely related aggregate of landforms of various origins it is difficult to separate accretionary and erosional components for classification. The term chaot thus is intended to address this situation descriptively.

The use of terminology such as "vegetated dune" or "fixed dune" as a geomorphic unit as distinct from "bare and mobile dunes" or "non-vegetated dunes" is widespread in the literature (Goldsmith 1985) and in the past also has been applied to the coastal dunes of Western Australia (Semeniuk & Meagher 1981b). This terminology for geomorphic units based on absence or presence of vegetation has been rejected in this paper. Dune landforms are described and termed according to their geometry, relief and configuration, and the presence of vegetation

should have no part in primary terminology of geomorphology and habitats. Accordingly, dunes such as parabolics that vary from actively-mobile bare forms, to recently-fixed vegetated forms, through to older, fixed vegetated forms, may comprise similar components and geometry, and as such are simply termed parabolic dunes. The absence, presence, or range of vegetation cover is viewed as varying stages of plant colonization on a dune habitat. The description and nomenclature of the various stages of plant colonization through time is viewed as the realm of plant ecology and not geomorphology.

Habitats

Vegetation responds to variability in landform and edaphic features at the small scale, and it is the small scale geomorphic unit that forms the basic habitat unit. Thus the range of small scale features of the various large to medium scale geomorphic units are treated as the habitat types of the Quindalup Dunes. However, geomorphology alone does not determine whether a given terrain is a suitable habitat for the various species of vegetation. Other features of the habitat, such as seaward aspect, landward aspect, north (sun-facing) aspect, height relative to the water table, salinity of vadose and phreatic water, and extent of soil development also need to be considered. The smallest scale of geomorphic features provides the basis upon which to overlay the other edaphic features.

The amount of detail required to describe habitats for vegetation necessitated subdividing the landforms of the coastal dunes into smaller and smaller units to arrive at the scale at which the vegetation responds. Accordingly, there is a range of geomorphic terminology applicable at the various scalar frames of reference (Table 3). The range of smaller scale variability in geomorphology can result in a mosaic of small scale vegetation responses. Thus shore-parallel, low, continuous ridges provide one type of habitat distribution, and shore-parallel, low, disrupted ridges provides a more complex habitat system.

In this paper, the term habitat is used interchangeably with small scale geomorphic unit and differentiation of habitats beyond this scale was not undertaken. The basic geomorphic and

habitat unit, however, will be differentiated on other edaphic criteria in future habitat and vegetation studies.

Geomorphic processes and the development of coastal dune morphology

Whereas the approach adopted here to describe and name geomorphic units of the coastal dunes in the first instance has been based on non-genetic precepts, it is nonetheless worthwhile to describe briefly the origin and genetic interrelationships of aeolian landforms to provide an understanding of their temporal and spatial relationships. The importance of recognizing the genetic category to which a geomorphic unit belongs is that habitats can be broadly viewed in terms of their

Table 3
Geomorphic units present at each scale of mapping

Regional scale	Large scale	Medium scale	Small scale
• Shoreline dune ribbon	• Foredunes	• Foredunes	• Hill or ridge slope
• Barrier dunes	• Parabolic dunes crescentic attenuated fretted	• Parabolic dunes crescentic attenuated fretted	• Linear depression
• Cuspate beachridge plains			• Circular depression
• Cuspate forelands, or cusps	• Chaots low relief medium relief high relief	• Components of parabolic dunes arms bowl inner face advancing face conical hill residual	• Conical slope
• Perched dunes	• Shore parallel ridges		• Crests
	• Shore transverse ridges	• Chaots low relief medium relief high relief	
	• Blowout	• Shore parallel ridges continuous low relief continuous high relief disrupted low relief disrupted high relief	
	• Undulating plain	• Shore transverse ridge ridge slope swale crest	
		• Barchans	
		• Barchanoid ridges	
		• Transverse dune	
		• Coppice dune	
		• Flat	
		• Blowout	
		• Undulating plain	

longevity, stability and dynamics which then can be related to interpretations about the stage of succession that a vegetation complex has achieved, recognizing that other processes such as fire also might influence vegetation succession.

The variety of coastal dune landforms can be categorized into 4 genetic/process-related types: accretionary; erosional; mobile; and degraded. These types may be expressed at the large, medium or small scales. In addition the various types may be related in time and space (eg an eroding dune supplies sand to a mobile dune which, once mobilized, uses the store of sand in its migration. There also may be smaller scale overprinting of one dune form on another. For example, a medium scale system of shore-parallel, continuous, low ridges (accretionary dune) may be overprinted by small scale blowouts (erosional form) to develop small scale shore-transverse parabolic dunes (mobile dune). Thus the original shore-parallel system of continuous low ridges is transformed into a system of shore-parallel disrupted low ridges. This sequence has been described previously, in part, by Ranwell (1972).

The main large to medium scale geomorphic units occurring within the four genetic coastal dune landform categories are:

- *accretionary types*: foredunes; coppice dunes; shore-parallel ridges (beachridges); chaots;
- *erosional types*: blowouts; flats;
- *mobile types*: parabolic dunes; barchans; barchanoid ridges; transverse dunes;
- *degraded types*: chaots; undulating plain; shore-transverse ridges.

Further accretion, erosion, degradation, or migration of these basic landform types results in the proliferation of medium and small scale geomorphic units. The relationships and evolution of one landform into another are diagrammatically illustrated and described in Fig. 5.

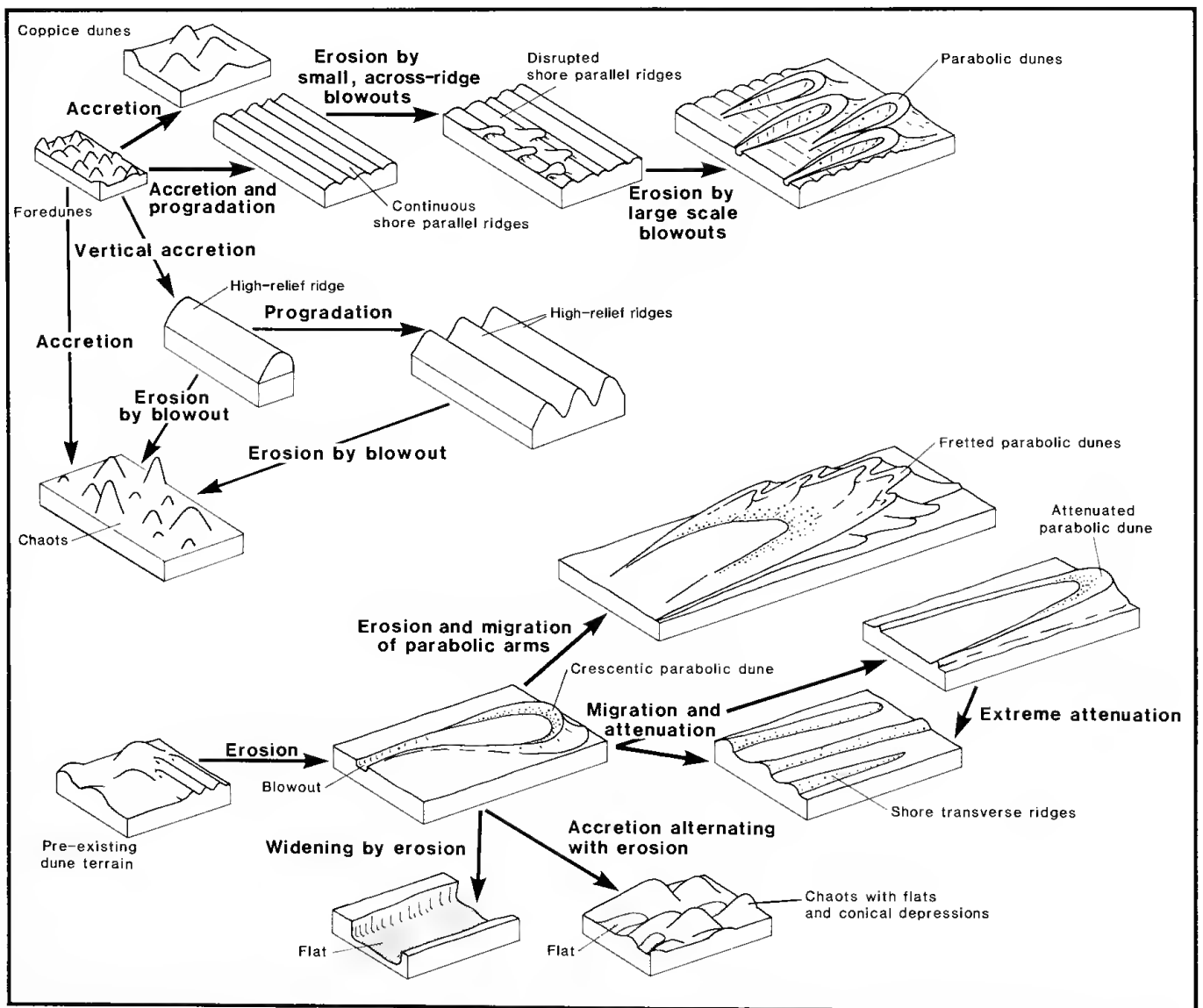


Figure 5 Inter-relationships between the various geomorphic units of the Quindalup Dunes, and the process by which one landform develops into another.

Geomorphology and habitats of the Quindalup Dunes

The coast adjoining the Swan Coastal Plain has been divided into five sectors by Searle & Semeniuk (1985). Each is distinguished by a unique combination of modern onshore and off-shore geomorphology, coastal processes and Holocene sediment accumulations. The sectors from south to north are: Geographe Bay Sector; Leschenault-Preston Sector; Cape Bouvard-Trigg Island Sector; Whitfords-Lancelin Sector; and Wedge Island-Dongara Sector.

Each sector has a distinct array of Quindalup Dunes based on the criteria of: 1) total external geometry (eg beachridge plains, cusped forelands or cusps, using the definition in Bates and Jackson (1980) that a cusped foreland is the largest type of "cusp"); 2) internal array of landforms (linear depressions

(swales) and ridges, parabolic dunes, blowouts); 3) dynamics of landform (prograding strandline, actively migrating parabolic dunes, vertically degrading ridges); and 4) relative relief.

The Quindalup Dunes within each sector are described below in terms of both geomorphology and vegetation habitats. At the regional scale the different shapes of the Quindalup Dune terrain can be recognized as 1) shoreline dune ribbon, 2) barrier dune, 3) cusped beachridge plains, 4) cusped forelands, or cusps, 5) perched dunes. Representative maps showing distribution of typical landforms/habitats within each sector are provided in Figs 6-11. A summary of the essential geomorphic features of the Quindalup Dunes in each sector is provided in Fig. 12. A summary of the main habitats encountered in each sector is provided in Table 4.

Table 4
Dominant habitats occurring in each of the sectors

Sector	Dominant regional scale units	Dominant medium scale geomorphic units	Dominant habitat types
1	E-W oriented, low, linear barrier of, and a N-E oriented shoreline ribbon of parabolic dune	undulating plain shore-parallel ridges	<ul style="list-style-type: none"> • undulating plain • linear depressions • ridge slopes, seaward and landward aspect • ridge crests
2	N-S oriented linear high barrier dune and northern section of shoreline ribbon of parabolic dunes	attenuated parabolic dunes blowouts shore-transverse ridges	<ul style="list-style-type: none"> • bowl • inner face • advancing face • crest • conical hill residuals • blowout floor • blowout wall • ridge slopes, north and south aspect • ridge crests • linear depressions
3	extensive cusped low beach ridge plain	attenuated parabolic dunes chaots	<ul style="list-style-type: none"> • bowl • inner face • advancing face • crest • conical hill residuals • crests of chaots • slopes of chaots • circular depressions
4	large scale cusped forelands (or cusps) and perched parabolic dunes	fretted parabolic dunes	<ul style="list-style-type: none"> • bowls • inner face • advancing face • crest • conical hill residuals
5	large scale cusped forelands (or cusps) and perched parabolic dunes	attenuated parabolic dunes fretted parabolic dunes shore-parallel ridge systems	<ul style="list-style-type: none"> • bowl • inner face • advancing face • crest • conical hill residuals • bowls • inner face • advancing face • crest • conical hill residuals • linear depressions • ridge slopes, seaward & landward aspects • ridge crests

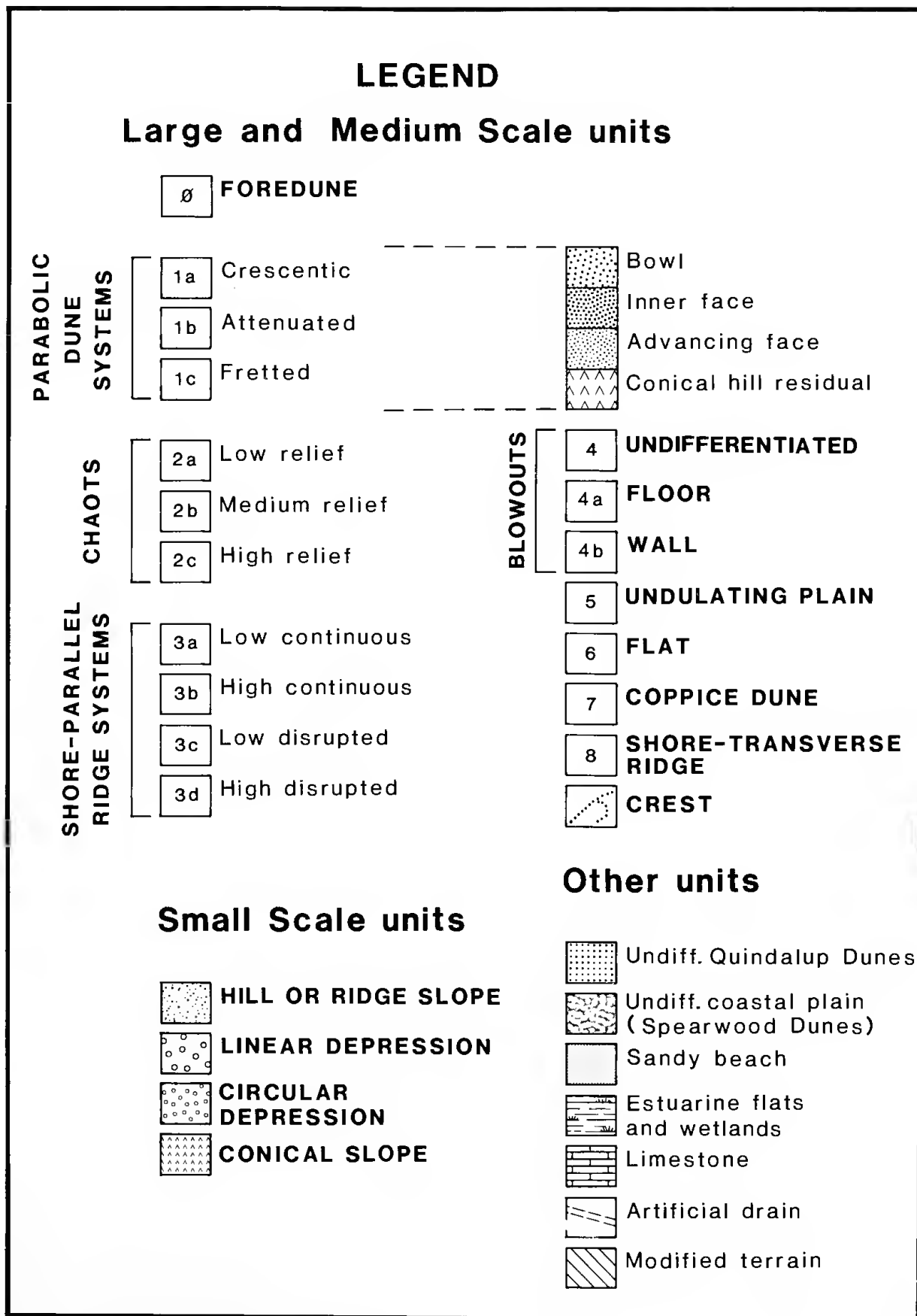


Figure 6 Legend to be read in conjunction with Figures 7-11.

Geographe Bay Sector

Regional and Large Scale Geomorphology

Geographe Bay is a broad, 100km wide, north-facing embayment at the southern end of the Rottnest Shelf. The Quindalup Dune zone is simple and consists, in the central portion of the sector, of a low barrier dune plain which forms a narrow band (average 500m wide), and in the northeast portion, of a shoreline ribbon comprised of parabolic dunes. Along the seaward edge there are beaches, beachridges and low foredunes. Long term Holocene sediment accretion has resulted in progradation of the shoreface along a broad front, generally maintaining the arcuate bay form and developing a beachridge ribbon peripheral to the bay (Searle 1978, Searle & Semeniuk 1985). The development of successive beachridges during coastal progradation has impeded the natural drainage from the hinterland, resulting in the development of elongate fresh to brackish lagoons and inlets in and behind the ridges. In the short term, geologically, the coast has undergone local realignment with development of small to medium scale accretionary cusped shoreline and erosional scallops that alternate in time and space along a net progradational shore (Paul & Searle 1978).

Medium and small scale geomorphology

An undulating plain dominates the Quindalup Dunes in this sector, but there are also multiple sand ridges, each usually less than 1m high, but up to 5-6m high, and 50m wide, and corresponding linear depressions (swales) and wetlands. There are no blowouts and parabolic dunes in the central portion of the sector, and the Quindalup Dune morphology is essentially similar throughout this portion of the sector. Toward the northeast parabolic dunes and blowouts are present and increase in number as the coast swings to a northerly alignment.

Habitats

The main habitats within the Quindalup Dunes are undulating plains with low and relict ridges, comprised of crests and slopes and depressions. All habitats are of relatively low relief and consequently depth to the water table is usually less than 3-5m. Humic soils are commonly developed on the aeolian landforms throughout this sector.

Leschenault-Preston Sector

Regional and Large Scale Geomorphology

The Leschenault-Preston Sector extends about 80km in a northerly alignment. The Quindalup Dune zone is characterized by an extensive linear, narrow, barrier dune system (some 20-30m high and 0.5-2.0km wide) with its accompanying lagoons (Semeniuk & Meagher 1981b). The barrier is actively retrograding to the east by parabolic dunes and encroaching onto the lagoon environments, and its seaward face is generally undergoing net erosion (Semeniuk 1985). Staggered dune advances in the past several thousand years to the present has resulted in an irregular encroachment of the barrier into the barred lagoon. The current coastal landforms of barrier dunes, segmented lagoons and inlets reflect this history.

Medium and small scale geomorphology

The barrier is dominated by blowouts and eastward migrating attenuated parabolic dunes with their accompanying arms and bowls. These are in various stages of geomorphic degradation and fixing by vegetation. There also are undulating plains (geomorphically degraded dunes), and shore-transverse ridges (= arms of former parabolic dunes). Along the seaward edge of this barrier there are beachridges, foredunes and cliffed dunes.

Habitats

The main habitats are those associated with parabolic dunes, blowouts and undulating plains. Much of the terrain is of high relief, situated well above the water table. Crests and slopes, depending on aspect, type of vegetation cover and stage of vegetation succession, are covered either with minimal humic soil or with moderately developed humic soil. The undulating plains are situated within 1-3m of the water table and are underlain by thick humic soil and a calcrete sheet. The dune landforms are of various ages and in various stages of geomorphic degradation, and accordingly support vegetation at different stages of succession.

Cape Bouvard-Trigg Island Sector

Regional and Large scale geomorphology

The Cape Bouvard to Trigg Island Sector extends over 100km in a north to northwesterly alignment. This sector is characterized by complex nearshore bathymetry and discrete cells of Holocene sediment accretion reflecting net, long term, coastal progradation (Searle 1984, Woods & Searle 1983). The Quindalup Dunes mainly form an extensive low cusped beachridge plain up to 10km wide. They are developed as a beachridge/dune cover to a Holocene sequence of seagrass sedimentary deposits that have extended from the hinterland towards an offshore limestone barrier. The beachridge/dune plain also has extended seaward, linking with emergent remnants of an offshore limestone ridge to form tombolos and cusped forelands. The resultant Quindalup Dune morphology is well marked by beachridge accretion lines showing successive shorelines. Intermittent erosion, or cessation in progradation, has developed localized blowouts and parabolic dunes which may appear along a specific former shoreline trend. At present, the five major bank and cusped foreland structures within the sector represent various stages of an evolutionary process from a submarine lobe to fully-emergent cusped plain stage (Searle 1984, Searle & Semeniuk 1985).

Medium and small scale geomorphology

Multiple parallel sand ridges, 1-3m high and up to 50m wide, and associated depressions dominate the terrain. However, there also are local areas of blowouts and associated parabolic dunes (up to 20-30m high), bowls, wetlands, and residual conical sand hills. The seaward zone contains low foredunes to steep foredunes, beachridges, coppice dunes and locally, cliffed dunes.

Habitats

The linear crests, slopes and depressions associated with the low parallel sand ridges (or beachridges) are the dominant habitats in this sector. These habitats are situated within 3-5m of the watertable. Humic soils are developed over the terrain to a moderate extent, and more particularly in depressions between the ridges. The occasional parabolic dunes in this area are habitats of high relief and the crests and slopes of these geomorphic units are situated >5m above the watertable, while flats and bowls have been developed to within 1m of the watertable.

Whitfords-Lancelin Sector

Regional and Large scale geomorphology

The Whitfords-Lancelin Sector extends 100km in a north-northwestly alignment. The coast consists largely of eroding rocky shores and pocket beaches interspersed with straight, beached coasts backed by high and perched dunes. Locally, isolated large scale dune-topped sandy promontories extend up to 800m seawards (cf Semeniuk & Searle 1986). These cusped forelands in the long term are either accretionary or slowly eroding. The Quindalup Dunes are restricted to 1) a thin ribbon

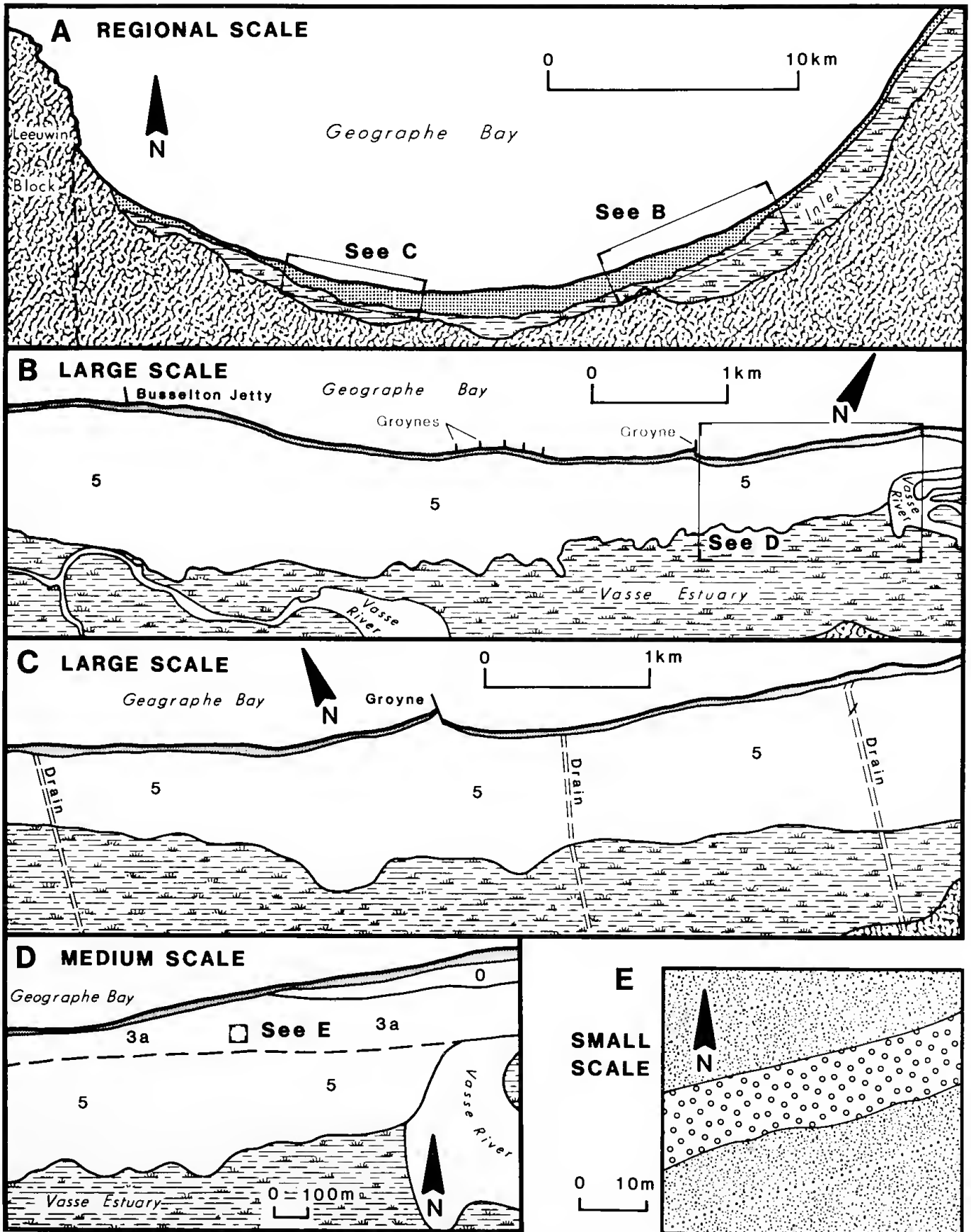


Figure 7 Geomorphic features of the Quindalup Dunes typical of Sector 1. Location of area shown in Fig. 1.

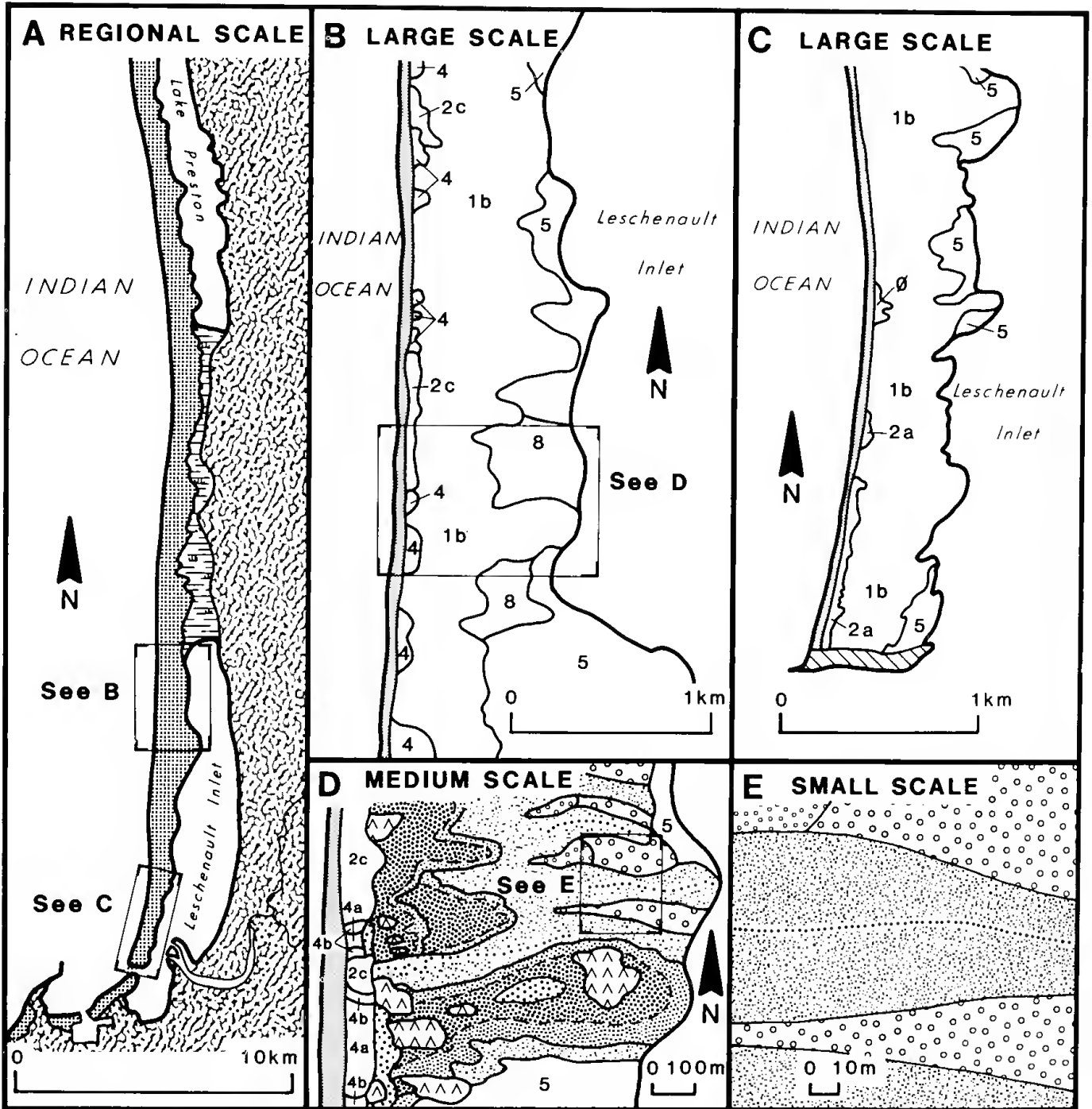


Figure 8 Geomorphic features of the Quindalup Dunes typical of Sector 2. Location of area shown in Fig. 1. Note that some units listed as small scale in the legend (Fig. 6) are also evident in the medium scale maps.

along the rocky shore, 2) small systems of perched dunes (landward advancing parabolic dunes encroaching over the Spearwood Dune terrain) at sites of the large pocket beaches and 3) terrains of the large scale cusped forelands wherein blowouts and parabolic dunes are dominant, or beachridge plains are present.

Medium and small scale geomorphology

The strandline is dominated by rocky shores, but pocket beaches have beach ridges, low foredunes and (locally) cliffed

dunes. Dunes perched on the limestone hinterland tend to be linear chaots or high relief ridges; they are parallel to the shore and tend to be high relief and well-vegetated. Inland, the perched dunes are either chaots or parabolic dunes. The parabolic dunes are the stabilized forms emanating from large blowouts, and they are uniformly oriented to the prevailing onshore winds. Locally, on the discrete large-scale cusped forelands there is a complex system of overlapping and detached dunes with beachridges and swales, parabolic dunes, conical residual hills and wetlands.

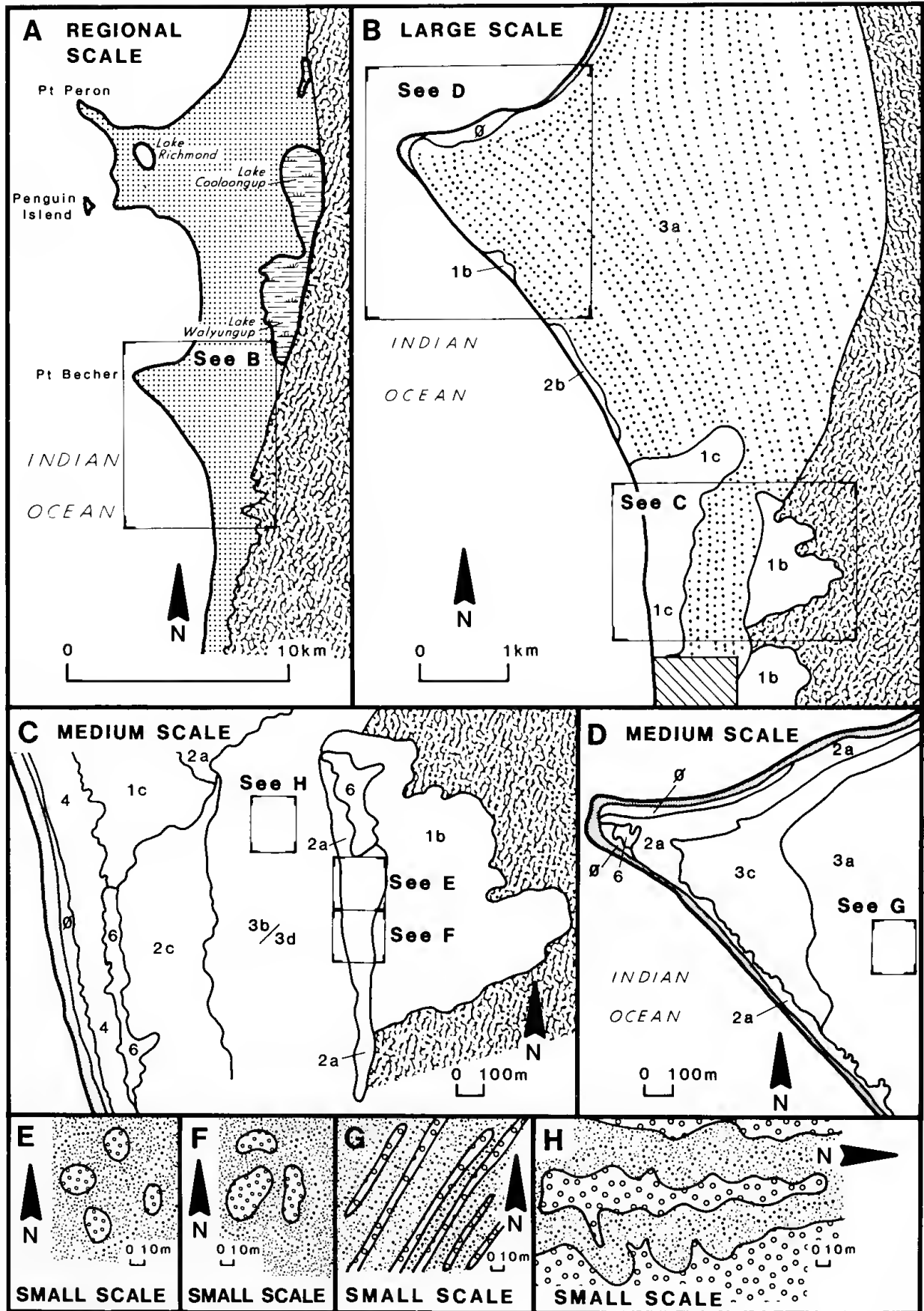


Figure 9 Geomorphic features of the Quindalup Dunes typical of Sector 3. Location of area shown in Fig. 1.

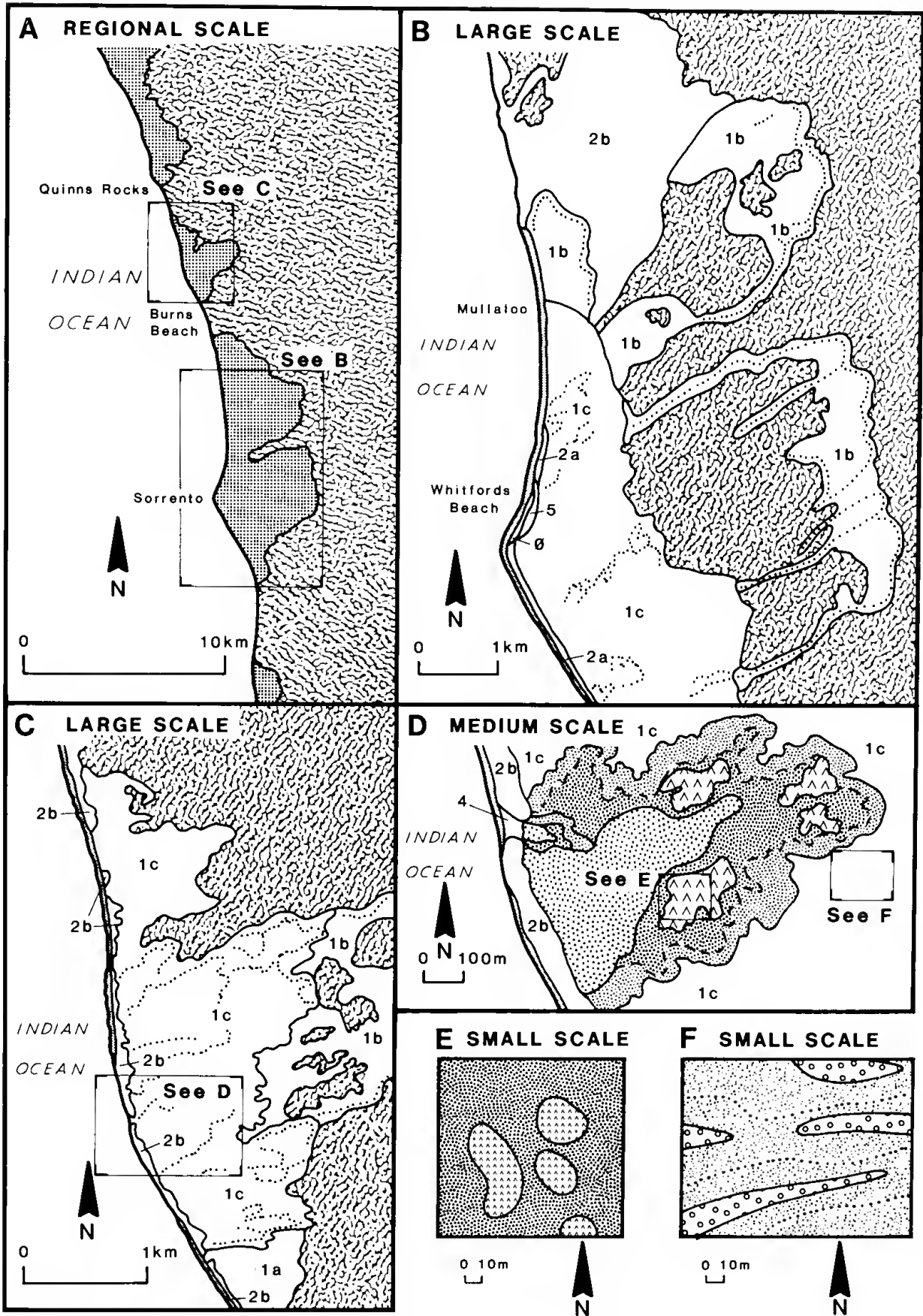


Figure 10 Geomorphic features of the Quindalup Dunes typical of Sector 4. Location of area shown in Fig. 1

Habitats

Parabolic dunes, chaots and blowouts dominate this sector, and the associated habitats of crests and slopes (with varying development of humic soils) are situated high above the water table and may overlie limestone with calcrete capstone. The wind-excavated bowl or flat areas are relatively closer to the watertable but are still elevated. In some places these deflation zones expose underlying limestone such that a limestone pavement habitat becomes exposed as an inlier within the parabolic dune system.

The habitats of the large scale cusped forelands are slopes, crests and swales of the beachridge plains, and are all situated low in relationship to the watertable. The slopes, crests and flats/swales/bowls associated with parabolic dunes and chaots, are all high relief structures situated >5m above the watertable.

Wedge Island-Dongara Sector

Regional and Large scale geomorphology

The sector from Wedge Island to Dongara extends 180km in an approximately northerly alignment. The coastal geomorphology consists mainly of large erosional scallops into the Pleistocene limestone as well as discrete, accretionary, cusped forelands which are net-progradational forms (Woods 1983, Hesp 1984b). The rocky coastline is slowly eroding and contains numerous small pocket beaches, and is interspersed with straight to gently arcuate beached coasts. The dune terrains adjacent to the coast are perched dunes and form a discontinuous and irregular high relief ridge, or system of chaots. Markedly attenuated mobile dunes (oriented NNE) and old vegetated parabolic dunes exhibit an alignment between about 010° and 030°. Elongate, roughly shore-parallel wetlands (lagoons or saline marshes) may be developed in the coastal dune terrain.

The coastal morphology of this sector reflects the decline in shelter afforded by the offshore bathymetry and the increase in onshore development of NNE migrating dunes. In the northern parts of the sector, the coast is devoid of prominent cusped forelands, which reflects the lack of offshore bathymetric features for protection.

Medium and small scale geomorphology

Markedly attenuated parabolic dunes dominate the terrain. Thus there are successive parabolic dune arms oriented N to NNE. The bowl areas are vegetated or have developed into wetlands. On the accretionary cusped forelands there are multiple beachridges 3-5m high and up to 50-100m wide, with associated swales. Interspersed through the beachridge plain there are blowouts and parabolic dune systems aligned along specific former shorelines. These contain parabolic dunes and bowls. The strandline has beaches, beachridges and low foredunes.

Habitats

Parabolic dunes and blowouts dominate this sector with the concomitant development of the habitats of crests, slopes and bowls. These habitats are situated 5-10m above the watertable with varying development of weakly humic soils. Also present are low beachridge plains with development of crests, slopes and swales situated within 5m of the water table. In local areas there are habitats of extensive limestone-like crust pavements.

Discussion

The regional variability of geomorphology of the Quindalup Dunes, its use in comparative vegetation studies, and its significance to conservation of landforms and habitats are discussed below.

Regional variability of geomorphology

Small scale habitats are determined by the geomorphic processes that are now operating or have operated in the region. Each sector is identifiable because of its distinct suite of coastal landforms and its location in the climate gradient, and it is axiomatic that habitats for vegetation will have developed as a result of those processes peculiar to a given sector.

It is apparent, for instance, that the coastal evolutionary processes of Sectors 2,3 and 4 are markedly different. Sector 2 contains a retrograding barrier dune system and the entire terrain has developed by long term retrogradational dynamics. Sector 3 contains a progradational plain formed by long term net accretion of shoreline sediments to develop a successive series of parallel low beachridges. Sector 4 contains slowly eroding limestone shores and associated pocket beaches, together with the local sedimentary cusped accumulations in the energy shadow of offshore islands/ reefs, and presents yet another suite of coastal landforms determined by the processes operating in that sector.

Clearly, a variety of landforms exist across and along, the extent of the Quindalup Dunes, and that each sector to some degree contains a suite of coastal landforms unique to that sector. Thus while there is a common thread in the occurrence of some landforms (eg beachridges, and foredunes), other specific landforms may occur exclusively or mainly only in a given sector. However, even if a given landform may occur in several sectors, its dynamic morphology may vary regionally. For instance parabolic dunes appear virtually in every sector, but they are most abundant in Sectors 2, 4 and 5 and are most active only in Sectors 2 and 5. Sector 4 contains a predominance of fixed parabolic forms; Sector 5 contains a proportion of active and relict parabolic dunes, but they are incomparable to those in Sector 2 because they are highly attenuated and are associated with much more extensive bowls.

In terms of landform complexity and heterogeneity, the Quindalup Dunes of Sectors 4 and 5 exhibit most variability. There are cusps, perched dunes, parabolics, blowouts, beachridge plains, chaots etc. Sector 1 exhibits least variability probably as a result of the relatively low energy progradational setting, as well as the less intense wind system (resulting in little or no aeolian remobilisation), and higher rainfall (resulting in more marked geomorphic degradation). Sector 3 with its beachridge plain and occasional lines of blowouts and parabolic dunes also exhibits minimal heterogeneity. Sector 4 exhibits moderate landform complexity with its ranges of blowouts, parabolic dunes, plains, shore- transverse ridges etc.

Comparative vegetation studies

The geomorphic framework presented above provides a reference base for future studies of vegetation of the Quindalup Dunes. This framework should enable future workers to allocate vegetation associations (or vegetation complexes) to more specific geomorphic or habitat settings; the framework should also provide for more realistic comparisons between vegetation complexes of widely dispersed localities, and should enable trends in the variation of species distribution in the region, as reflecting variation in the species pool, to be determined. The absence/presence of a given species can then be related either to the absence/presence of an appropriate habitat or to external factors such as climate.

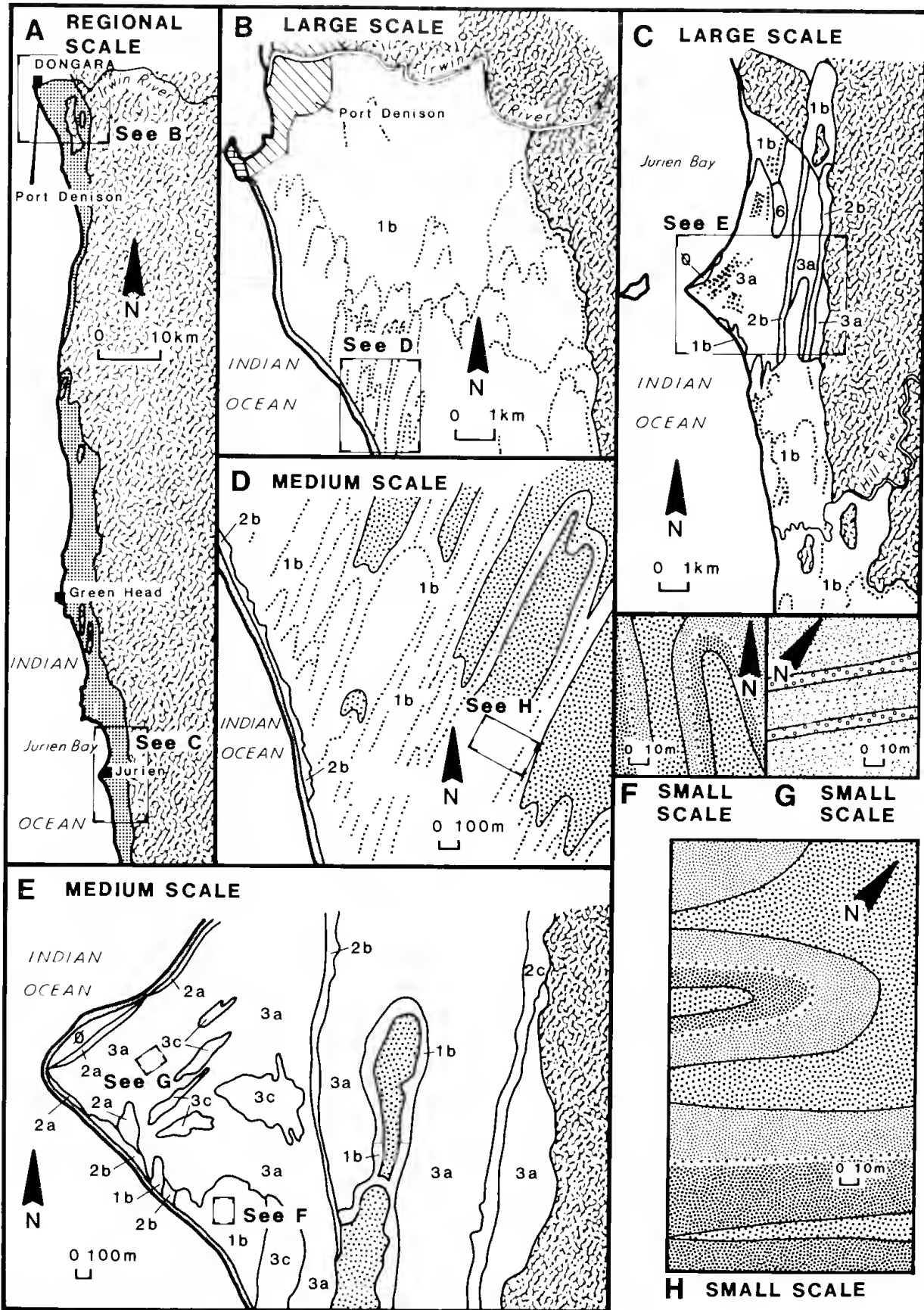


Figure 11 Geomorphic features of the Quindalup Dunes typical of Sector 5. Location of area shown in Fig. 1.





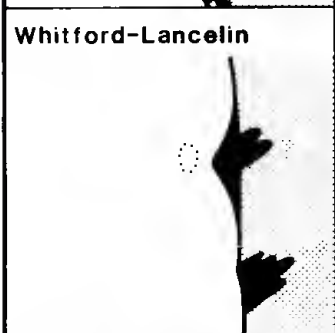





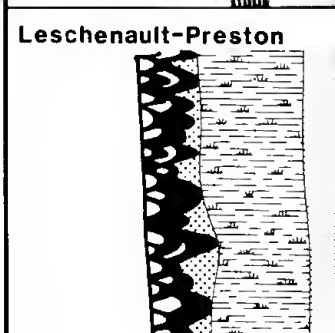



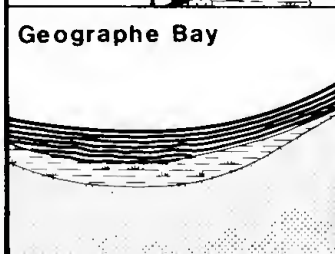


Sector	Dominant Coastal Process	Continuity of Coastal Dunes	Dominant Land Form (plan)
Wedge Island-Dongara 	Limestone coast retreat and landward dune encroachment alternating with areas of coastal progradation in cusps	Discontinuous in discrete accumulations connected by thin ribbons	Attenuated parabolic dunes  Bowls  Shore parallel ridges 
Whitford-Lancelin 	Limestone coast retreat and landward dune encroachment alternating with areas of coastal progradation in cusps	Discontinuous in discrete accumulations connected by thin ribbons	Parabolic dunes  Chaots 
Cape Bouvard-Trigg Island 	Shoreline progradation and development of beachridge plain	Continuous extensive cusplate plain	Shore parallel ridges  Parabolic dunes 
Leschenault-Preston 	Barrier retreat and development of blowouts and parabolic dunes	Continuous linear high-relief ridge	Parabolic dunes  Blowouts  Undulating plain 
Geographe Bay 	Shoreline progradation	Continuous arcuate low-relief ribbon	Undulating plain  Shore parallel ridges 

Figure 12 Summary of key features of the Quindalup Dunes in each sector. In this figure the term cusp refers to the large scale coastal cusps (- cusplate forelands).

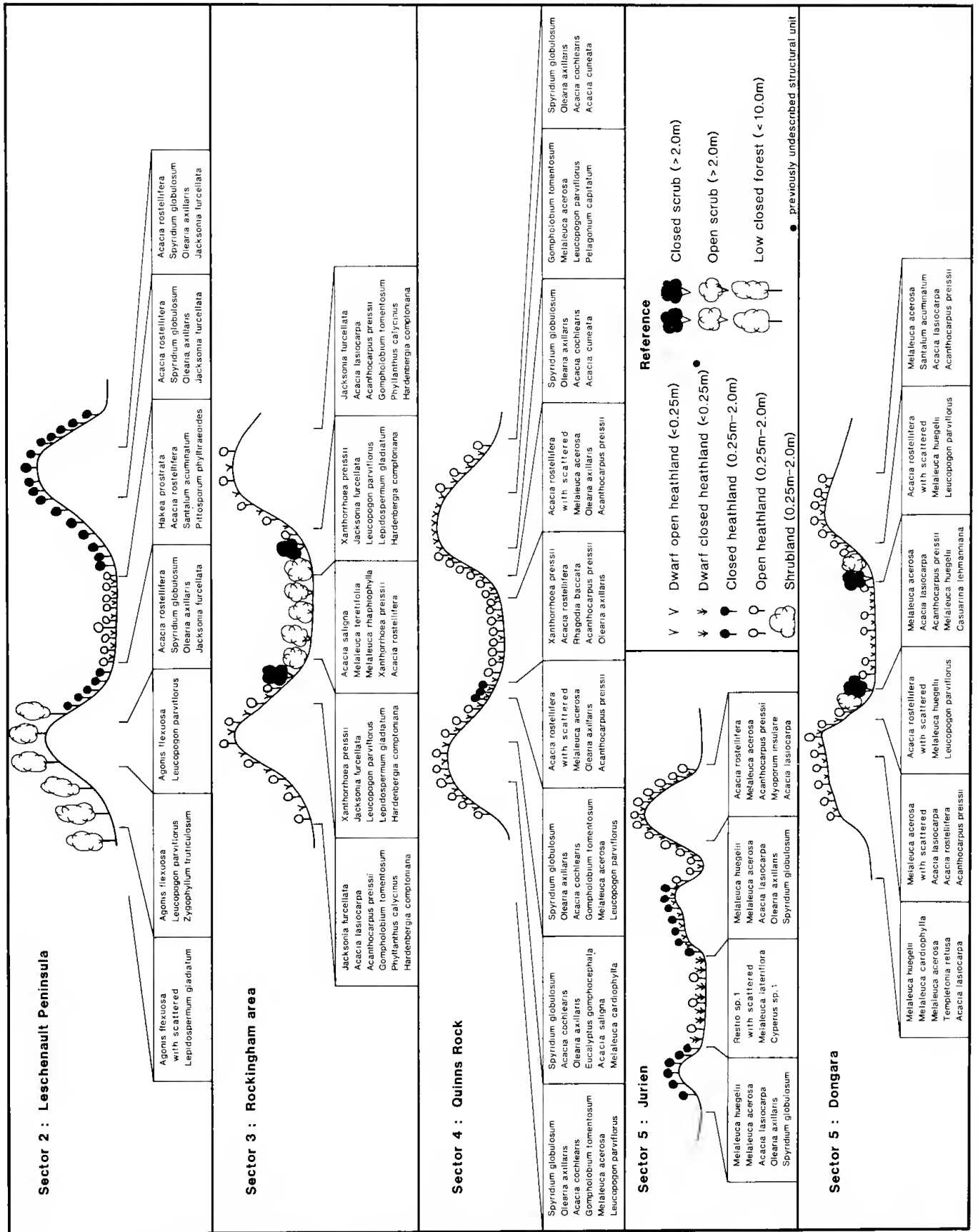


Figure 13 Cross section and vegetation transects through parabolic dunes in sectors 2-5 to illustrate habitats and vegetation structure and floristics. The species noted for each dune habitat represent the dominant species in terms of numerical and/or structural dominance. Vegetation structure terminology modified after Specht 1981.

An example of a vegetation study in a specific geomorphic unit/habitat is provided here to illustrate the suggested manner in which comparative vegetation studies may be undertaken in a regional to subcontinental system. Large scale to medium scale geomorphic units such as parabolic dunes that are common to a majority of coastal sectors were chosen as a basic unit. The vegetated parabolic dunes of Sectors 2, 3, 4 and 5 were studied. The parabolic dunes were subdivided into habitats of crest, slope, toe (= interface between slope and bowl/flat), bowl/flat, and the vegetation was described in terms of structurally or numerically dominant species and vegetation structure for each habitat. The results are presented in Fig. 13.

These results are only preliminary but serve to illustrate that there are significant changes in structure and/or floristics of the Quindalup Dunes between a similar habitat setting within the same sector and from sector to sector. The conclusion underscores the need to compare vegetation from similar geomorphic settings and habitats, when assessing the regional significance of flora. Conversely, it is also obvious that if adjoining sectors have markedly different suites of geomorphic units and habitats then the vegetation complexes of those adjoining sectors may be incomparable, even if there are a number of species in common between the complexes. As a result some sectors may contain unique associations or assemblages of flora. This is not to imply that the components of the flora are rare or endangered but rather that the vegetation associations or complexes may be linked to a specific habitat which is not regionally widespread. This conclusion has implications for allocations of vegetation reserves and in assessment of regional significance of flora in environmental studies.

Adequacy of reserves in the Quindalup Dunes

Reserves for purposes of conservation are intended to preserve occurrences of rare and endangered flora and fauna, examples of vegetation assemblages, examples of landscape ecology, areas of scientific interest such as geological features, areas for research and education purposes, or to provide sanctuaries and security for a range of fauna and flora (Frith 1973, Lunney & Recher 1979, Messer & Mosley 1980, McMichael 1980, Ovington 1980, Dept of Conservation & Environment 1983a,b, Anon 1982, Leigh *et al* 1984). Indeed the various reserves in southwestern Australia have been established for a range of the above reasons. However, there is inadequate conservation of the variety of geomorphic, habitat and vegetation systems in the Quindalup Dunes. Where reserves are present in the Quindalup Dunes in the Perth metropolitan area there has been a tendency for undue emphasis in preserving the more seaward assemblages at the expense of the more landward assemblages.

It is also clear that the regional array of landforms and vegetation represents a wide spectrum of types and that a few reserves, as presently distributed, cannot adequately cover and secure sufficient representation of this variability. It would be preferable to preserve examples of each of the vegetation formations, and associated geomorphology and geological features within the Quindalup Dunes.

The distribution of existing reserves in the Quindalup Dunes between Geographe Bay and Dongara is shown in Fig. 14. There are a number of other reserves in the Quindalup Dunes but these are for a range of purposes other than conservation of flora and fauna (such as recreation, camping, government requirements, explosive reserves).

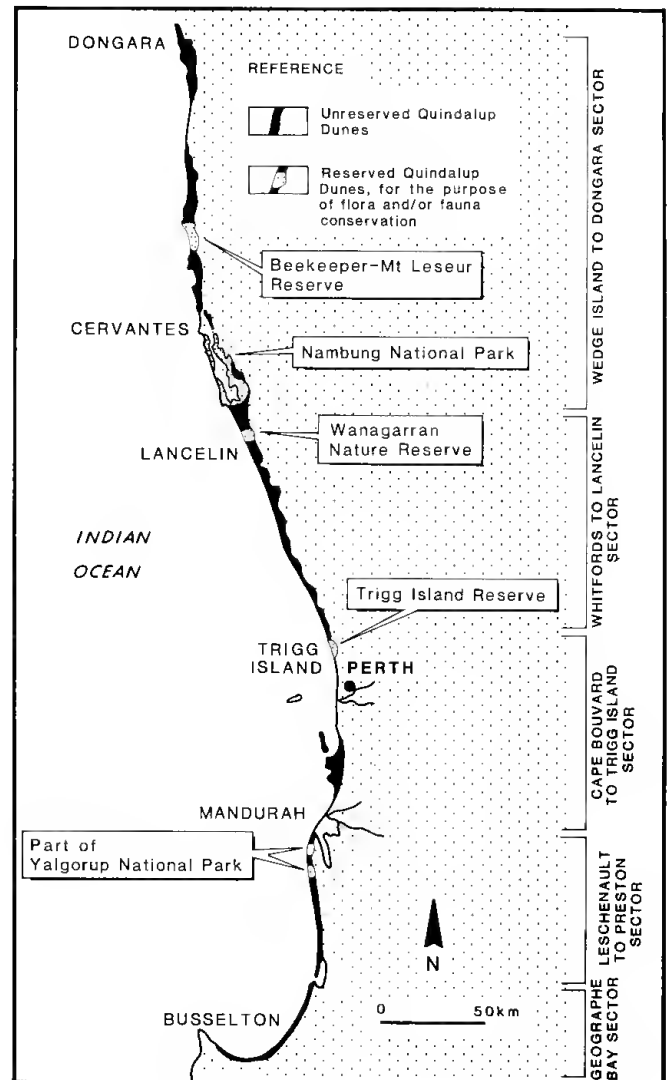


Figure 14 Location of reserves and national parks in the Quindalup Dunes.

Only five reserves cover areas of Quindalup Dunes, viz Beekeepers-Mt Lesueur Reserve, Nambung National Park, Wanagarran Nature Reserve, the Trigg Island Reserve and Yalgorup National Park. Three of these are located in Sector 5, but of these only one, Nambung National Park, adequately covers a significant area of the Quindalup Dunes, but even here the park does not extend to incorporate the major accretionary beachridge plain cusp in the area. The Wanagarran Nature Reserve covers a terrain of perched dunes and an accretionary cusp with blowouts and parabolic dunes. The Beekeepers-Mt Lesueur Reserve covers a portion of perched Quindalup Dunes in Sector 5. The Trigg Island Reserve covers a relatively small part of the perched dune system of Sector 4. Most of the Yalgorup National Park is located on the geomorphic unit, underlain by limestone and wetland deposits, termed by McArthur & Bartle (1980b) the Yoongarillup Plain, and the Quindalup Dunes comprise only some 5 km² of the National Park.

The essential features of the Quindalup Dunes that warrant conservation for each coastal sector throughout the southwestern coastal zone are listed in Table 5.

Table 5

Main natural features within each coastal sector and their conservation status

Coastal sector	Main natural features particular to a given sector	Conservation status¹
Geographe Bay	barrier dune and shoreline dune ribbon with plains and parabolic dunes, respectively	none of the significant examples of this sector are conserved
Leschenault-Preston	barrier dune terrain composed predominantly of mobile and fixed parabolic dune systems	main significant portion not conserved ² ; Yalgorup National Park covers a small area of northern part which is not typical of this sector
Cape Bouvard-Trigg Island	cusate beachridge plain composed of low relief shore-parallel sand ridges and intervening swales	no features of this sector conserved
Whitfords-Lancelin	perched dunes and accretionary cusps composed of (fretted, crescentic, attenuated) parabolic dunes and chaots	no examples of perched dunes and accretionary cusps are conserved
Wedge Island-Dongara	perched dunes composed of attenuated and fretted parabolic dunes, and accretionary cusate forelands composed of low-relief shore-parallel sand ridges and intervening swales	perched dunes secured in Nambung National Park; examples of cusate forelands not conserved

¹ Conservation status as at January 1987

² Although there are plans to reserve the Leschenault Peninsula as an example of this sector these plans have yet to be formalized.

This list of features illustrates the largely inadequate preservation of the variable Quindalup Dune systems. In many areas the major attributes that are specific or typical of a given sector are not reserved:

- the shoreline ribbon of the Geographe Bay Sector
- the barrier dune of the Leschenault-Preston Sector
- the cusate beachridge plain centred on Becher Point and Rockingham, of the Cape Bouvard-Trigg Island Sector
- the perched dunes and accretionary cusps of the Whitford-Lancelin Sector
- the beachridge plain cusps of the Wedge Island-Dongara Sector

Hence there still is a need for conservation of areas of Quindalup Dunes and this should be based on their landform, scientific interest, representativeness, vegetation and relative lack of disturbance. It should be noted that there are still significant portions of the Quindalup Dunes that are listed as vacant crown land, land for government purposes or reserves for recreation etc., which could be reverted or reallocated to become reserves for conservation of flora and fauna.

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A field guide to the dung beetles (Scarabaeidae:Scarabaeinae and Aphodiinae) common in pastures in South-western Australia

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Abstract

A key to 4 native and 7 introduced species of dung beetles (Scarabaeidae:Scarabaeinae and Aphodiinae) common in pastures in south-western Australia is provided, together with notes on their distribution and biology. Scanning electron micrographs are given to assist in the separation of the species and distribution maps are provided.

Introduction

The species considered here are dung feeding beetles of the family Scarabaeidae (subfamilies Scarabaeinae and Aphodiinae). There are 19 species of Scarabaeinae and 7 species of Aphodiinae which are endemic to the south-western region of Australia, many of which are described by Matthews (1972, 1974), with new records by Ridsdill-Smith *et al* (1983 and unpubl data). The adults of all these endemic species are trapped in undisturbed vegetation (Ridsdill-Smith *et al* 1983), during the cool humid period of the year from May to September (Ridsdill-Smith & Hall 1984a). Four of the endemic Scarabaeinae are also trapped in pastures, but only *Onthophagus ferox* Harold is common (Ridsdill-Smith & Hall 1984b). Six species of cosmopolitan Aphodiinae are present in pastures, of which *Aphodius pseudolividus* Balthasar is most common (Snowball 1942, Ridsdill-Smith & Hall 1984b).

To increase breakdown of cattle dung in pastures throughout Australia, CSIRO has been introducing species of Scarabaeinae from Africa and Europe. Over 500 releases of beetles of 14 species have been made in south-western Australia between 1972 and 1986, of which 9 species are known to be established by 1987. Seven species are common. Since 1978 these introduced species have become dominant members of the dung beetle fauna in pastures in south-western Australia.

Because introduced dung beetles are now abundant in pastures, there is considerable interest in which species are present, their biology and seasonal abundance. In this field guide we summarize data we have collected over the past 10 years on the biology and distribution of species common in pastures. We have omitted both introduced and endemic species which are not commonly encountered. The distribution of some of these species may change in the future, and further introduced species may become abundant. A key is provided to separate the 4 native and 7 introduced species which are common in pastures in south-western Australia. Only adults are described and data on occurrence and abundance refer to the adult stage.

Identification of species

Description of characters

Males and females of all species except *A. pseudolividus* can be distinguished by examining the ventral abdominal segments (Figs 1B and C). In the males the segment before the pygidium is constricted in the mid-line, whereas in the female it is of even width. Horn size in horned beetles varies and some specimens may be worn or damaged, and thus a combination of characters should be used for identification.

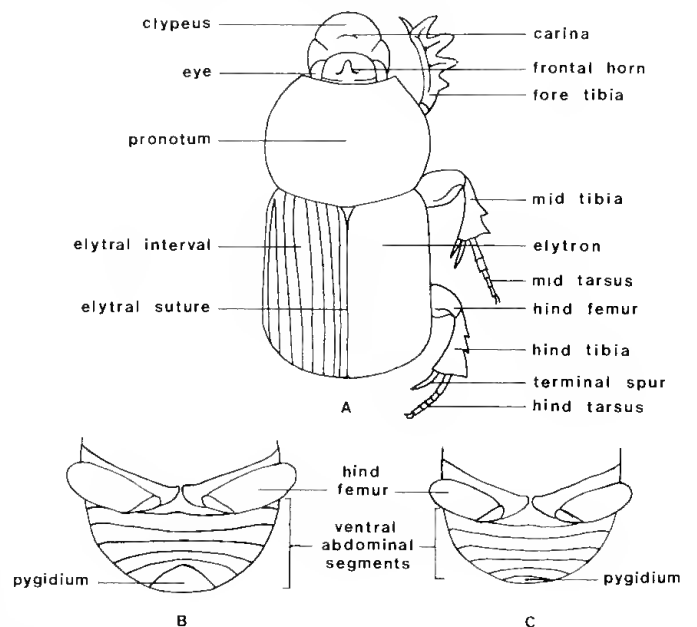


Figure 1 A Stylized dung beetle showing parts referred to in key. Underneath of abdomen showing method of sexing scarabaeine **B** males and **C** females.

Glossary

bidentate—with 2 teeth, or teeth-like processes (eg-clypeal margin in Fig 6H)
 bifid—forked, opening with a medial cleft (eg-horn in Fig 6D)
 carina—keel-like ridge (Fig 1A)
 clypeus—the antero-median part of the head (Fig 1A)
 elytral interval—space between lines (striae) on elytra (Fig 1A)
 lamina—a plate-like projection (eg-Figs 6E,F)
 pubescent—covered with hair (eg-Fig 6C)
 pygidium—the terminal abdominal segment (Fig 1B)
 rugose—with wrinkles and ridges (eg-clypeus in Fig 3E)

Key to species

1 Pronotum green, brown or coppery; elytra brown
 Pronotum black or with a bronze sheen; elytra black
 2(1) Small, shining beetles, total length <5mm; pronotum blackish-brown medially with pale margins; elytra totally covering the pygidium; hind tibia with two terminal spurs (Figs 2A,C)-*Aphodius pseudolividus* Balthasar
 Larger, less shining beetles, total length >7mm; pronotum variously coloured; elytra not covering the pygidium (Fig 2B); hind tibia with one terminal spur
 3(2) Total length >12mm; fore tarsi absent; dorsal part of eyes wide (Figs 3E,F); males with 1 or 2 spines on the hind femora (Figs 3G,H) and fore tibiae elongate (Fig 3A); females with a carina on the clypeus (Figs 3E,F)
 Total length <12mm; fore tarsi present; dorsal part of eyes narrow (Figs 2D-H); males without spines on hind femora, fore tibiae not elongate (Fig 3B); females without a carina on the clypeus (Figs 2F,H,3D)
 4(3) Male with 1 outwardly facing spine on the posterior edge of the hind femora (Fig 3G); female with a squarish clypeus which has a carina equidistant between the eyes and the anterior edge (Fig 3E) -*Onitis alexis* Klug
 Male with 2 inwardly facing spines on the posterior edge of the hind femora (Fig 3H); female with a rounded clypeus which has a carina nearer to the anterior edge than to the eyes (Fig 3F) -*Onitis aygulus* Fabricius
 5(3) Fringe of long hairs on apex of elytra restricted to area near suture; head of male with two carinae (Fig 2G); head of female lacking carinae (Fig 2H); pronotum lacking distinct "speckled" markings
 -*Euoniticellus fulvus* (Goeze)
 Fringe of long hairs on apex of elytra extending along whole apical edge; head of male either with a single horn (Fig 3C) or with 3 carinae (2 in some small males) (Figs 2D,E); head of female with a carina level with front of eyes and another carina at the back of the head (Fig 3D); pronotum with distinct "speckled" markings
 6(5) Head of male with a single horn (Fig 3C); head of female with clypeus smooth and frontal carina of even height (Fig 3D); pronotal "speckling" appearing light-brown
 -*Euoniticellus intermedius* (Reiche)
 Head of male with 3 carinae (2 in some small males) (Figs 2D,E); head of female with clypeus rugose or heavily punctured, not smooth and frontal carina raised in the centre (Fig 2F); pronotal "speckling" dark-brown to black
 -*Euoniticellus pallipes* (Fabricius)

7(1) Male and female with similar head and pronotal armament; head with single horn, entire at apex; pronotum with two forward-projecting horns. Total length >10mm (Figs 5A-D)
 -*Onthophagus ferox* Harold
 Head and pronotal armament different to above; male head with either single horn bifid at apex, a lamina, two horns at the back of the head, or no horns; pronotum with projections or not. Total length <10mm - 8
 8(7) Elytral intervals with a median row of prominent, shiny, raised lines or beads (Figs 6B,E) -9
 Elytral intervals flat, without sculpturing (Figs 4A,E) -10
 9(8) Dorsal surface bronzed; pronotum without prominent projections, pubescent; head with some scattered hairs and clypeal margin feebly bidentate (Fig 6G); total length <8mm (Figs 6A,B,C)
 -*Onthophagus vermiculatus* Frey
 Entirely black; pronotum with projections in both sexes, not pubescent; head with hairs only along front margin and clypeal margin medially more strongly bidentate (Fig 6H); male with either high bifid horn or two-pointed lamina on head; total length >8mm (Figs 6D,E,F)
 -*Onthophagus haagi* Harold
 10(8) Pronotum without lobes in both sexes; head of male either with a pair of curved horns arising between the eyes and extending back along sides of pronotum or with horns much reduced or replaced by a carina; head of female with a carina between the eyes (Figs 4A,B,C)
 -*Onthophagus taurus* (Schreber)
 Front of pronotum with a prominent median lobe, subquadrate or rounded; head of both male and female without horns, with a carina between the eyes (Figs 4D-H)
 -*Onthophagus binodis* Thunberg

Notes on the species

Locations mentioned in the text are shown in Fig 8F.
 a) *Aphodius pseudolividus* Balthasar. (Figs 2A,C)
 A small shining beetle (4.5 mm long) which is elongate and brown. This accidentally-introduced species occurs widely in Australia and in other countries (P Hammond, pers comm).
 There are two patterns of seasonal abundance in south-western Australia. At sites north of Perth, beetles are common in all seasons and fly during the day. At sites south of Perth they are most common in summer and autumn (December to May) and fly at dusk. Some individuals are found throughout the year at all sites.
 Distribution: (Fig 7A) Widespread throughout the region, where it is common in pastures, but rare in undisturbed vegetation.
 b) *Euoniticellus fulvus* (Goeze). (Figs 2B,G,H)
 Brownish-yellow beetle (7-11mm long) with a plain brown pronotum. An introduced beetle from Europe. The strain released is from France.
 This species is abundant in summer and autumn. It breeds during summer and flies during the day.
 Distribution: (Fig 7B) Current records are from Bridgetown and near Bunbury.

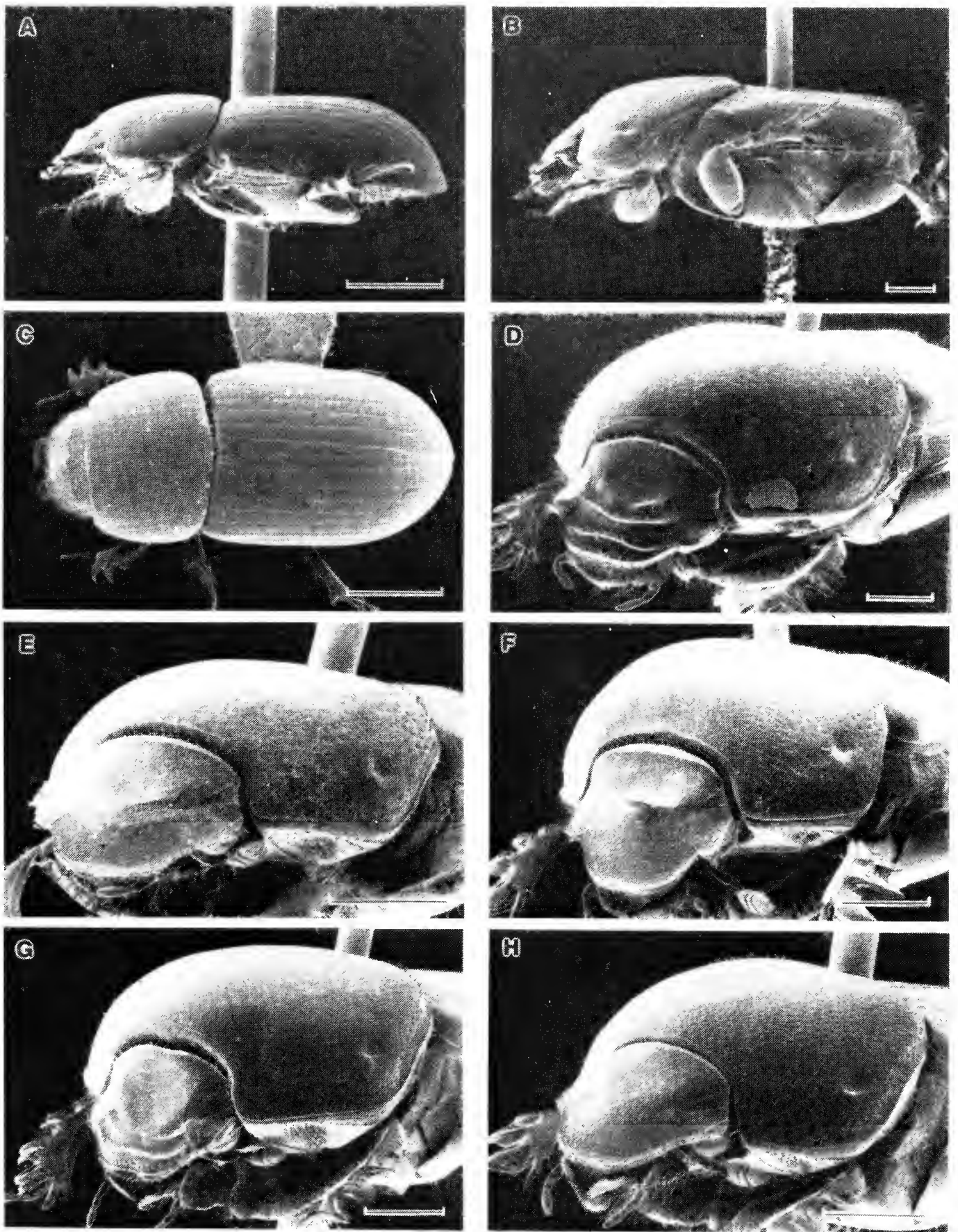


Figure 2 Dung beetles. Elytra covers pygidium in **A**. *A. pseudolivoidus*, but not in **B** *E. fulvus*. **C** *A. pseudolivoidus*; **D** & **E** *E. pallipes* males; **F** *E. pallipes* female; **G** *E. fulvus* male; **H** *E. fulvus* female. Scale lines: 1 mm.

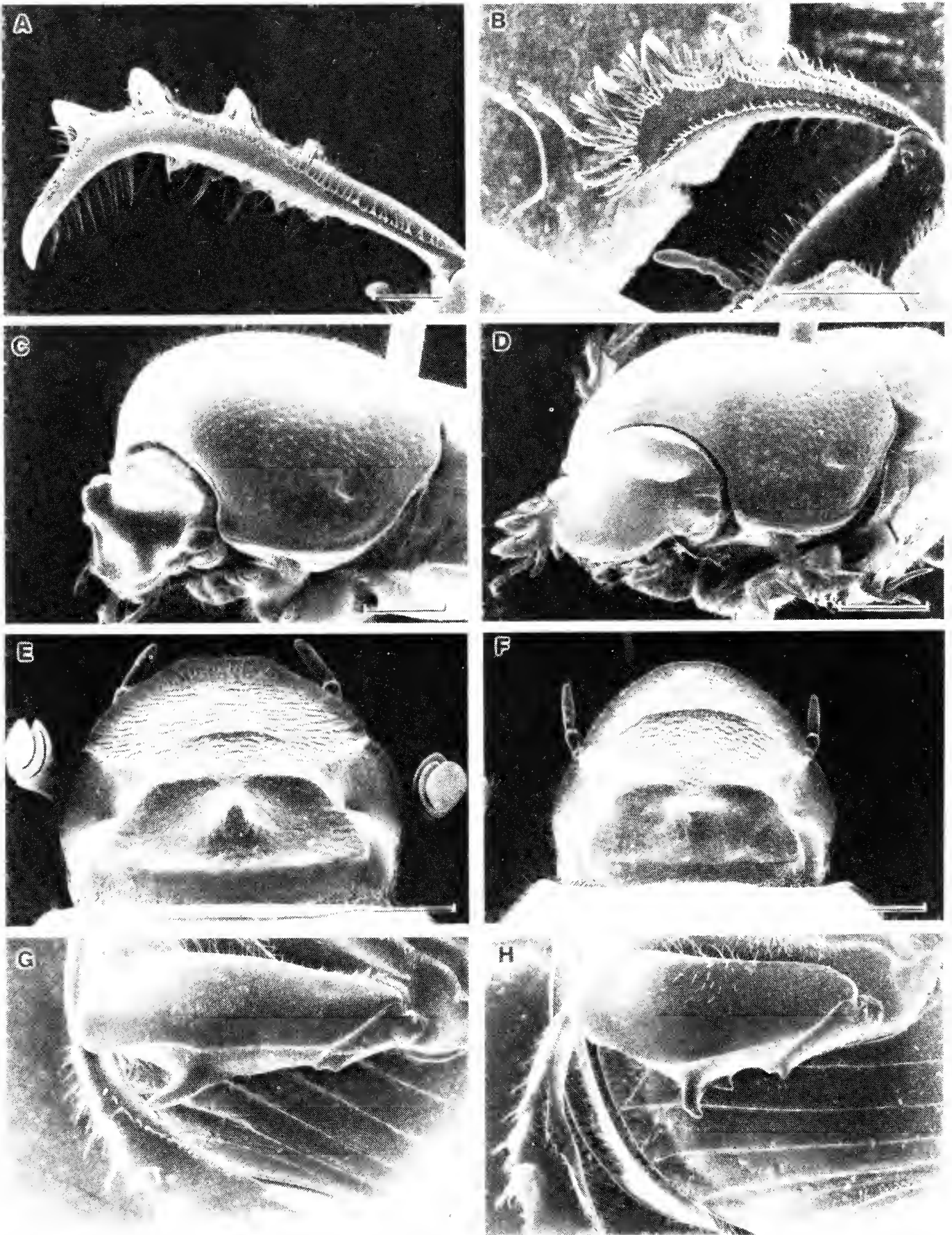


Figure 3 Dung beetles. Foreleg of **A** *Onitis* sp. and **B** *Euoniticellus* sp.; **C** *E. intermedius* male; **D** *E. intermedius* female; **E** Head of *O. alexis* female; **F** Head of *O. aygulus* female; **G** Hind femur of *O. alexis* male; **H** Hind femur of *O. aygulus* male. Scale lines:1 mm.

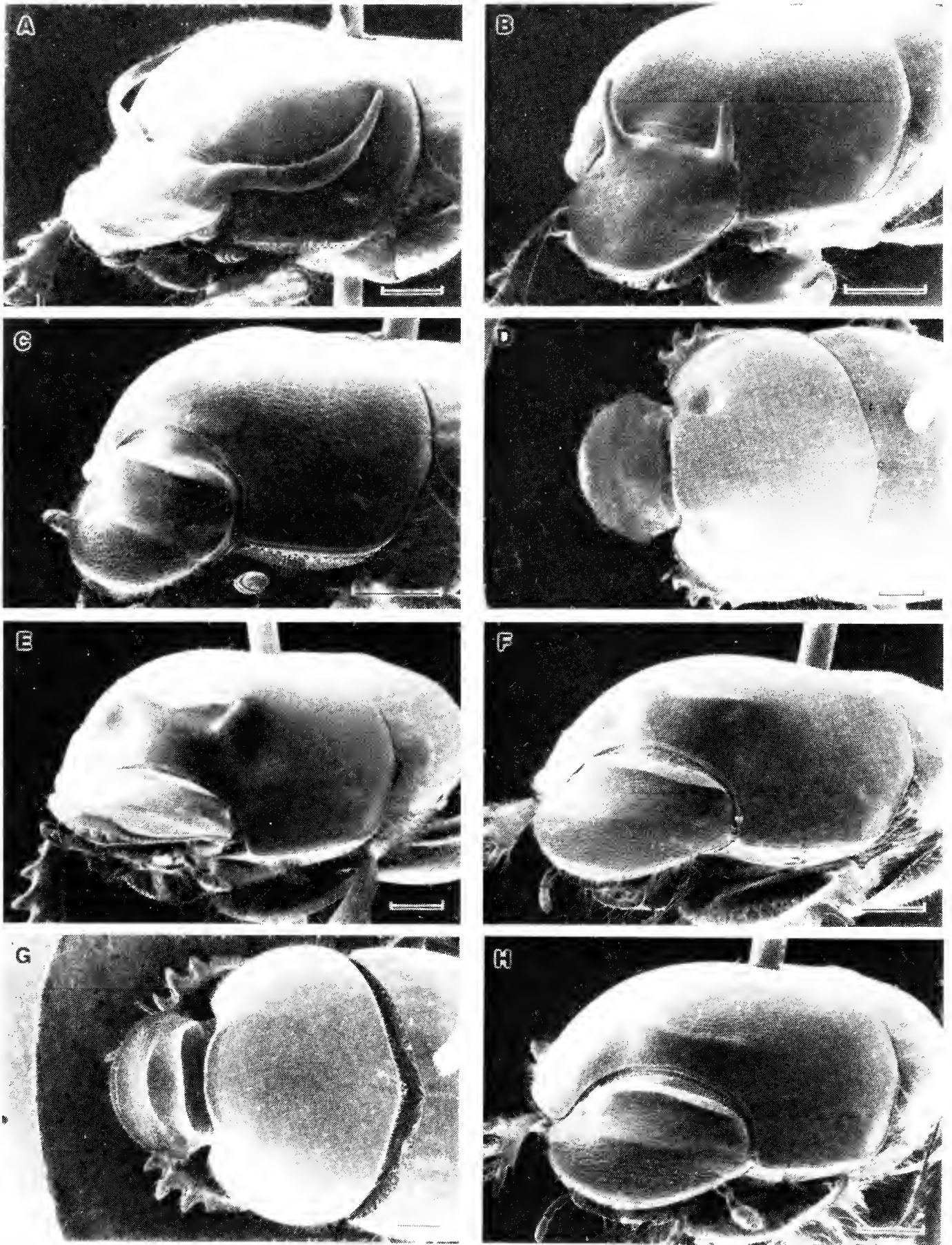


Figure 4 Dung beetles. **A & B** *O. taurus* males; **C** *O. taurus* female; **D, E & F** *O. binodis* males; **G & H** *O. binodis* females. Scale lines: 1 mm.

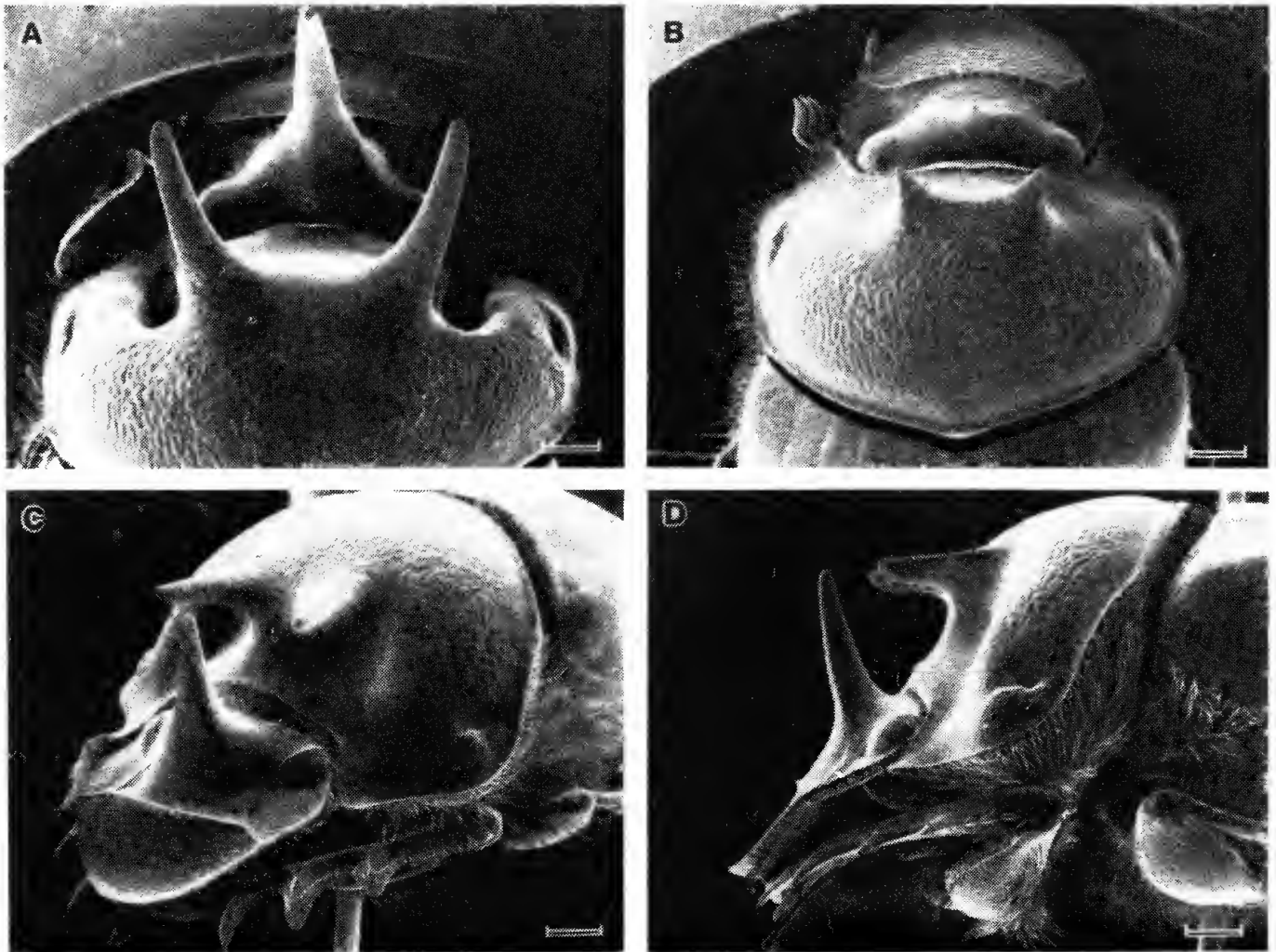


Figure 5 Dung beetles. **A & B** *O. ferox* males; **C & D** *O. ferox* females. Scale lines:1 mm.

c) *Euoniticellus intermedius* (Reiche). (Figs 3C,D)

A brownish-yellow speckled beetle (7-10mm long) with a small horn on the head of the male. An introduced species from southern Africa. One of the first species to be released in the region in 1972.

Adults are present all year round with peaks of abundance in winter and in summer, and breeds mainly at these times. Beetles fly during the day. *E. intermedius* is common in pastures near Moora, adjacent to sites of dung beetle studies in undisturbed vegetation (Ridsdill-Smith & Hall 1984a). Out of 19109 scarabaeine and aphodiine dung beetles trapped during 1982-1984 only 8 are *E. intermedius*. There is no evidence that they are competing with endemic beetles.

Distribution:(Fig 7C) Mainly in the hotter parts of the region from Geraldton to Perth and eastward to Bruce Rock. This species is adapted to dry conditions. Adults can breed in very dry, sandy soil (Barkhouse & Ridsdill-Smith 1986).

d) *Euoniticellus pallipes* (Fabricius). (Figs 2D,E,F)

A brownish-yellow beetle (6-11mm long) with dark-brown to black speckling. An introduced species native to Europe and Asia. The strains released are from Iran and Turkey.

Adults are most abundant in summer and autumn, and breed mainly from January to March. Low numbers are also seen in spring. Beetles fly during the day.

Distribution: (Fig 7D) Southern half of the region, from Perth to Bruce Rock, but not present along the south coast.

e) *Onitis alexis* Klug. (Figs 3E,G)

A robust large beetle (12-19mm long) with greenish pronotum and brown elytra. An introduced species from southern Africa. The strain released is the cold-adapted strain from summer rainfall regions.

This species emerges in November and is abundant for a month; the second generation emerges in March. The species spends the winter as larvae in brood masses in the soil. Beetles fly at dusk.

Distribution:(Fig 7E) Mainly in the warmer drier parts of the region from Geraldton to Pinjarra, and Perth to Cunderdin.

f) *Onitis aygulus* Fabricius. (Figs 3F,H)

The largest of the dung beetles present in pastures (18-23mm long). A coloured beetle with greenish pronotum and brown elytra. An introduced species from southern Africa. The strain released is a winter-rainfall strain.

The biology of this species is very similar to that of *Onitis alexis*. Beetles fly at dusk.

Distribution:(Fig 7F) Mainly in drier areas between Cunderdin and Williams, and from Pinjarra to Hyden. The distribution of this species tends to be more southerly than that of *Onitis alexis*.

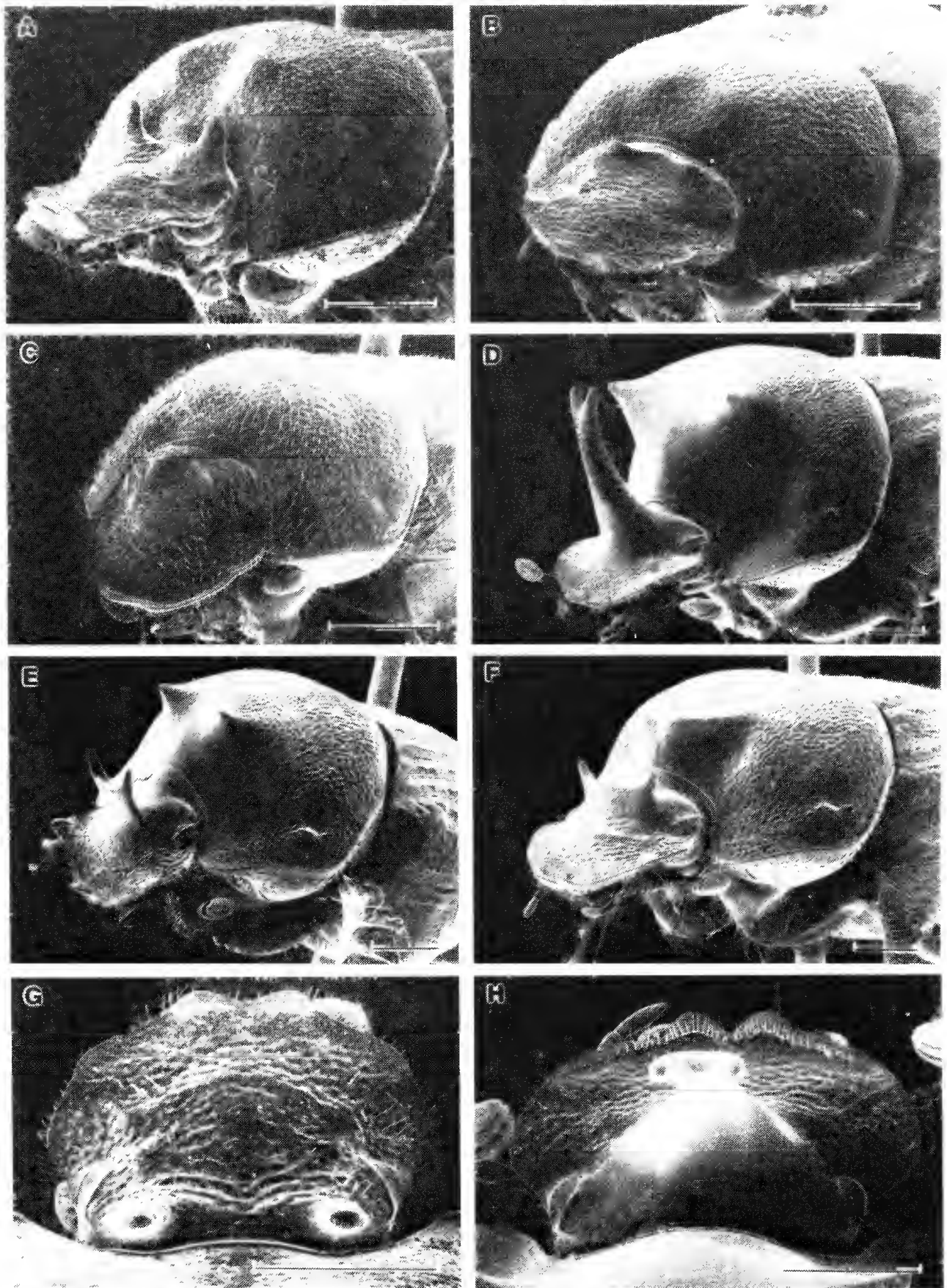


Figure 6 Dung beetles. **A & B** *O. vermiculatus* males; **C** *O. vermiculatus* female; **D & E** *O. haagi* males; **F** *O. haagi* female; **G** Head of *O. vermiculatus* male; **H** Head of *O. haagi* male. Scale lines: 1 mm.

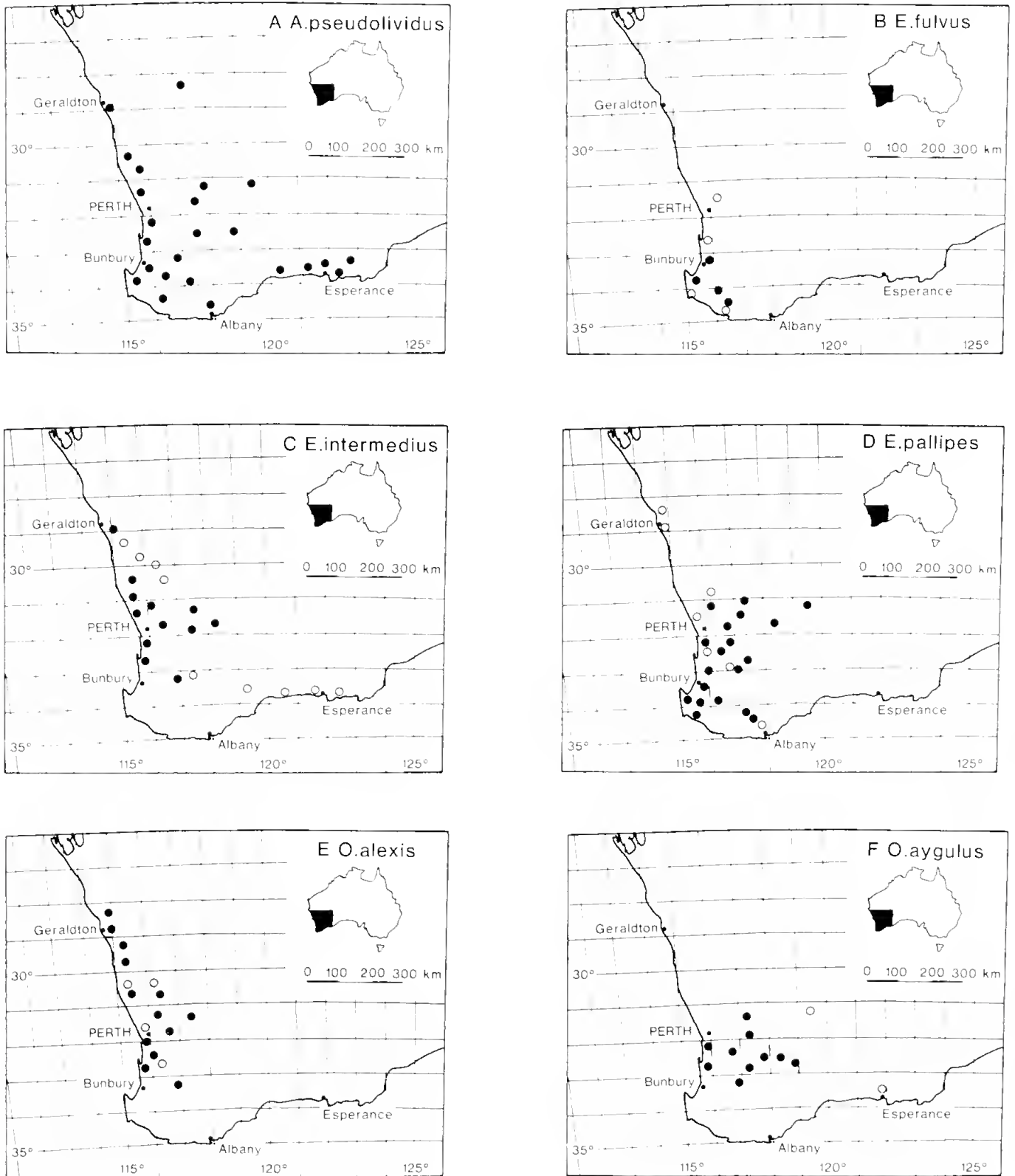


Figure 7 A - F Distribution maps for *Aphodius*, *Euoniticellus* and *Onitis* spp. Full circles represent establishment and open circles represent releases where the species has not yet been recovered.

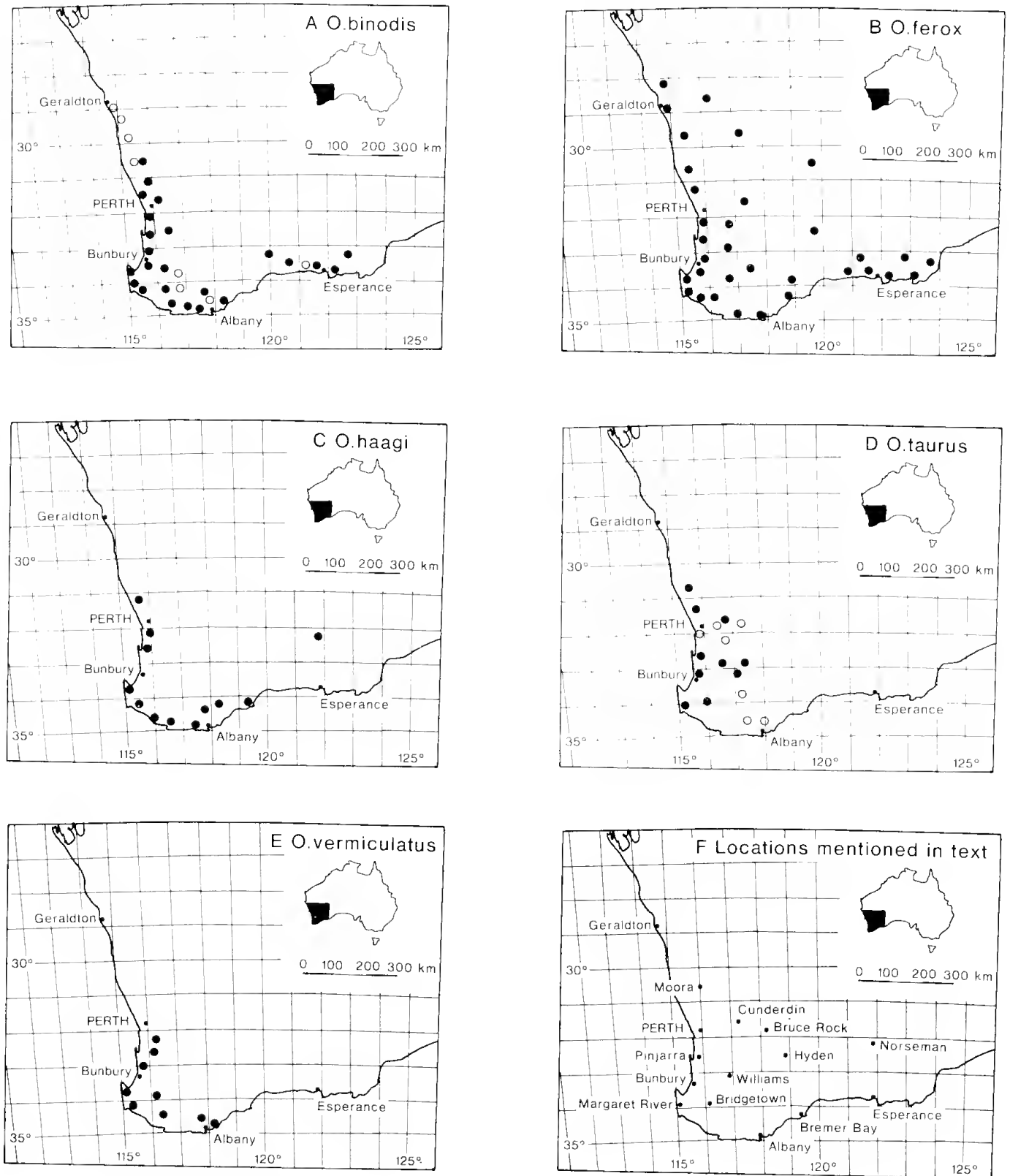


Figure 8 A - E Distribution maps for *Onthophagus* spp. Full circles represent establishment and open circles represent releases where the species has not yet been recovered. **F** Locations mentioned in text.

g) *Onthophagus binodis* Thunberg. (Figs 4D-H)

A matt black beetle (7-12mm long) with a lobe on the pronotum. An introduced beetle from southern Africa. Nearly all releases are of the winter rainfall strain.

This species is very abundant in summer and autumn, and in lower numbers in winter. Mainly breed in spring but some breeding also occurs during the summer. Flies during the day. Out of 19109 scarabaeine and aphodiine dung beetles trapped in undisturbed vegetation over two years at six sites (Ridsdill-Smith & Hall 1984a) there are 12 *O. binodis*. There is no evidence that they are competing with endemic beetles.

Distribution:(Fig 8A) Mainly in the higher rainfall areas along the coast from Moora to Esperance. Does not persist in drier areas. More abundant at sites with some summer moisture or irrigation. Adults cannot not breed in dry, sandy soil (Barkhouse & Ridsdill-Smith 1986).

h) *Onthophagus ferox* Harold. (Fig 5)

A large robust shining black beetle (12-20mm long) with one horn on its head and two on the pronotum. This is a native species.

Adults are active during the cool humid period of the year (Ridsdill-Smith & Hall 1984a,b). To the north of Perth this is from May to September and to the south from May to December. It is most abundant in May and June and breeds in the spring. Adults fly at night and are commonly found at lights. It is rarely seen during the summer, although a few individuals are found at this time along the south coast, and some emerge after summer thunderstorms at Cunderdin.

Distribution:(Fig 8B) Widespread throughout the south-west region. There are two unconfirmed records from Alice Springs. It is also found in undisturbed vegetation, where it is more common at jarrah forest and heath sites than in karri forest (Ridsdill-Smith *et al* 1983).

i) *Onthophagus haagi* Harold. (Figs 6D,E,F,H)

A black, shining beetle (8-10mm long) with a single horn or a lamina with two points on the head. This is a native species.

Adults are active during the cool humid period from May to September. It is most abundant in May, June, August and September and breeds in the spring. Adults fly during the day. Adults are rarely found during the summer, except along the south coast.

Distribution: (Fig 8C) Mainly in the higher rainfall areas along the coast from Perth to Bremer Bay. There is one unconfirmed record from Norseman. It is present also in undisturbed vegetation, where it occurs in jarrah forest and heath. It appears to be more common near swamps.

j) *Onthophagus taurus* (Schreber). (Figs 4A,B,C)

A shining black beetle (7-10mm long) with two long curving horns on the head of the male. This is an introduced species, and the strains released are from Greece, Spain, Italy and Turkey.

It is most abundant in the summer and breeds in the spring. Adults fly during the day. Beetles are more abundant at sites with summer moisture or irrigation and breeding continues at these sites during the summer.

Distribution: (Fig 8D) Moora to Margaret River, and from Pinjarra to Williams.

k) *Onthophagus vermiculatus* Frey. (Figs 6A,B,C,G)

A small black beetle (5-8mm long) with bronze reflections. This is a native species.

Adults are present mainly during the cool humid period from March till November.

Distribution:(Fig 8E) Perth to Albany in undisturbed vegetation including karri forest, jarrah forest and heath. It appears in pastures near the south coast at Albany.

Acknowledgements We thank Alec Mahon, John Matthiessen, Lynne Hayles and officers of the WA Department of Agriculture for help in releasing beetles, and members of the CSIRO Dung Beetle Groups for collecting and rearing the beetles. The Electron Microscopy Unit, CSIRO Division of Entomology, Canberra took the scanning electron micrographs and prepared the plates.

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The early evolution of the plant life of South-western Australia*

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Abstract

A general review is given of the evolution of plant life in Australia, with special reference to south-western Australia where the evidence permits, from the beginning of life on Earth to the end of the Cretaceous, at which time recognizably modern floras had come into existence. Western Australia comprises the whole span of life as it has fossil stromatolites of the earliest known, 3 500 million years old, and living colonies of stromatolites at the present day. Only very primitive forms of life existed until the Cambrian, 570 my ago; land plants first appeared in the Upper Silurian (400 my) and became well established in the Devonian (395-345 my). An accurate impression of the plant life in Western Australia in the Lower Permian (270 my) can be formed due to the abundant remains in coal deposits when the *Glossopteris* flora of seed ferns was dominant.

Development of higher forms of life continued into the Mesozoic Era (225-65 my) with rising temperatures and climates at first arid and then humid tropical. Cycads and cycad-like plants, and gymnosperms ancestral to modern southern conifers — kauri pines, podocarps and Araucarians — became dominant but were superseded by the flowering plants (Angiosperms) during the Cretaceous (135-65 my).

Following a discussion of the origin of the Angiosperms, I suggest that colonization of Earth by plants was not immediate but gradual. At the outset, relatively primitive plants could grow only in wet places but gradually more difficult habitats could be colonized. It is argued that even so it was only with the coming of the Angiosperms with their greater evolutionary plasticity and ability to adapt to adverse habitats, that the entire surface of the earth could be colonized for the first time and a complete plant cover established.

Introduction

Much has been written and much discussion has taken place about the evolution of the plant life of SW Australia, encouraged by the numerous special characteristics which the present-day flora possesses, but this interest has been devoted largely to the later stages subsequent to the appearance of flowering plants during which the present-day flora came into being. This paper attempts to fill in the picture by an account of the early times during which plant life on Earth first appeared, adapted, and gradually colonized the earth's surface.

The history of the vegetation of the Australian region as a whole has been addressed in two recent books by Smith (1982) and White (1986). The first comprises a collection of five papers prepared for the International Botanical Congress in Sydney. The second book gives the whole history of the evolution of Australian vegetation in a well illustrated book. The story told is not without its difficulties and inconsistencies, due to the uncertain evidence and conflicting theories.

The formation of Earth is generally accepted to have taken place between 4 500 and 5 000 million years ago. Just how or when life on earth originated is not known, but fossil evidence of very primitive forms of life has been detected in

rocks as old as 3 500 my. It is a strange fact that for the next 3 000 million years after that — an extremely long period — these forms of life underwent only a very slow development, and it was not until the geological period known as the Cambrian which began around 570 my ago that the evolution of life really got under way.

This horizon was originally chosen for the starting point of the Cambrian period and also for that of the whole Phanerozoic Eon (which means the period of visible life) because it is the point at which readily identifiable fossils appear. It was originally thought that earlier rocks were devoid of evidence of life on earth. With subsequent work it is known that humble forms were in fact there and slowly evolving. None the less it appears that at the opening of the Cambrian period a critical threshold was crossed, beyond which abundant life began to be possible.

Earth in Precambrian times was very different from today; the atmosphere was of very different composition, some say it consisted largely of methane and ammonia (Echlin 1966), others say water vapour, carbon dioxide, nitrogen and various sulphurous gases (Cloud 1968). They agree that it contained little or no free oxygen. Oxygen is vital to the functioning of life, and it is interesting that the supply of oxygen on which life depends had to be built up gradually by the action of life itself. The process of photosynthesis by which plants support their life processes, drawing energy from sunlight to combine carbon dioxide and water into sugars and higher compounds, involves liberating an excess of oxygen from these molecules.

* Presidential address 1987, delivered 22 July 1987.

For a very long time most of the oxygen produced in this way would have been absorbed again in the oxidation of iron and other surface minerals, a stage that may have lasted 2 000 my, but later the photosynthesis of primitive organisms gradually increased the free oxygen content of the atmosphere. Prominent among the early forms of life were the Cyanobacteria or Blue-green "Algae" whose colonies trapped sand and silt and form those curious structures known as stromatolites which we can still see today at Shark Bay (Fig. 1). Stromatolites have been detected in the early fossil record, and Western Australia can claim the oldest known deposit, at the locality "North Poie" in the Pilbara, 3 500 my old. By the beginning of the Cambrian it is supposed that the oxygen content of the atmosphere may have reached a critical level of perhaps 1% (whereas it is 20% today), permitting the evolution of life to progress more rapidly. In the words of Plumstead (1969): "When Phanerozoic time commenced 600 million years ago, the world stage was set for the great biological drama about to be enacted on its surface."

The Palaeozoic Era

At first, the developing forms of life which become abundant in the fossil record are found virtually only in marine deposits, and another 150 million years had to pass, until the oxygen content of the atmosphere had increased still further to perhaps 10%, before indisputably terrestrial vascular plants appear. One reason for this may have been that the early atmosphere, with its lack of oxygen, possessed little or no ozone layer to buffer harmful incoming radiation, so that early forms of life could only have survived under a protective cover of water at least 5m deep (Plumstead 1969).

It used to be tacitly assumed (eg Plumstead 1969) that as aquatic plants came first in the fossil record, land plants evolved from them by adaptation to sub-aerial conditions. Plumstead suggested that land plants evolved gradually at the margins of the sea or other large bodies of water, adapting the ability to survive short periods and even seasons of low water level, until complete adaptation occurred. Even then for a long time early land plants must have had to grow with their roots in water, as their tissues were not sufficiently evolved for efficient uptake and conductance of water, and they could not tolerate desiccation (Plumstead 1969).

More recently this has been questioned by Stebbins & Hill (1980) and others who suggest that large land plants evolved from unicellular soil algae independently of multicellular aquatic plants. If the new suggestion is true, the evolutionary process may have commenced in the Cambrian or earlier, and in fact some fossils found in the Middle Cambrian of Queensland have been claimed to represent land plants (Fleming & Rigby 1972). The occurrence of spores in the fossil record appears to document colonization of the land by non-vascular plants as early as the Ordovician (Gray 1985), but it is not until the Late Silurian about 410 my ago that we find megafossils definitely interpretable as land plants. Whether they evolved from aquatic plants or independently, terrestrial plants can be distinguished by the morphological characters needed to fit them for sub-aerial life, and generally if fossil plants possess cuticle, stomata or lignified vascular tissue they are assumed to be terrestrial.

During the Devonian period, 395 to 345 my, there was a rapid radiation of vascular plants, and it is possible to identify lycopods, ferns, pteridosperms (fern-like plants which were large woody trees and probably seed-plant ancestors), and



Figure 1 Living stromatolites on the shore of Shark Bay (White 1986).

possibly even the earliest seed-plants themselves. It has been suggested that this was an "experimental" phase of evolution, a time when evolution ran riot as innovators flourished in the largely unoccupied ecospace (Runnegar 1982). Except for the Angiosperms which did not appear in identifiable numbers until the Cretaceous, all the extant phyla of plants appeared together very early and were established if not during the Devonian, at least by the Carboniferous. All the same there is a definite progression in time of dominant plant forms, the simpler and more primitive being the more abundant in the early stages, and progressively more advanced forms becoming dominant later. The flora consists predominantly of relatively primitive forms such as lycopods in the Devonian, of ferns and seed-ferns in the Carboniferous and Permian, of gymnosperms by the Jurassic.

The earliest period in Western Australia for which adequate data show what the landscape and its vegetation really looked like is the Permian, 280 to 225 my ago, for two reasons: there is an exceptionally large amount of fossil material, and the geological events of that time have left some traces still recognizable in the landscape. At the outset of the Permian, Australia still formed part of a great continental landmass, Gondwana, from which the separate continents of today would later one by one split off, and it occupied a polar position.

To find the pole of those days one must resort to palaeomagnetic data which are confusing for Gondwana. However, a position for the Permo-Carboniferous South Pole was given by McElhinny & Embleton (1974) where readings from South America, Africa and Australia agree within a reasonable framework of confidence in placing it in the vicinity of Tasmania. Subsequent to the Permian the pole gradually moved away from Australia to its present position.

During the Sakmarian stage of the Early Permian, in keeping with the continent's polar position, the continental shield area of Western Australia was extensively glaciated. The sedimentary basins which surround it — the Perth, Carnarvon, Canning and Officer Basins — contain sediments dated to that time which are of glacial and fluvio-glacial origin. The widespread occurrence of these sediments indicates that the higher land was covered by a continental ice-sheet similar to that of Antarctica today, and the traces left indicate too that the country was extensively abraded by the ice. To form a picture of the landscape after the withdrawal of the ice-sheets one can refer to Québec and Labrador and Finland, where there is country of comparable geological structure based upon ancient crystalline rocks, which has been quite recently glaciated. Such country is of comparatively low relief, scoured into a structure of boss and hollow, and with the hollows now occupied by strings of long narrow lakes showing the direction of ice movement.

The nature of the plant cover in the early Permian of WA is shown to us by the fossiliferous coal beds which were laid down after the withdrawal of the ice, not only in the well known Collie Basin where the coal is mined commercially today, but in the Perth and Canning Basins also, in the eastern States and in other parts of Gondwana. The local plant macrofossils have been described by White (1961) and Rigby (1966) and demonstrate the presence of the "Glossopteris flora" which was widespread in the Southern Hemisphere at this period. An artist's reconstruction of it was published as a frontispiece to Plumstead (1969). While this illustration is from a South African source, Africa and Australia formed part of the same continental land mass in those days and shared the same flora.

The immense coal deposits laid down during the Permian are being exploited today both here at Collie and in the eastern States. The stereotype of coal swamps being steamy tropical swamp-jungles, as was the case in the northern hemisphere

during the Carboniferous, is not applicable to southern Permian coals. These coal deposits are the product of cold, swampy bogs in which Horsetails grew in immense profusion like rushes. Ferns and seed-ferns, and probably mosses as in modern peat, as well as herbaceous lycopods like *Selaginella* formed a low, dense, swamp vegetation. Trees and shrubs of the Glossopterids, with special aeration tissues in their roots suited to the boggy conditions, grew in the swamps and in adjacent areas with high water tables (White 1986).

It is impossible to reconstruct accurately the vegetation of any past period because relative abundance of species, dominance and structural features of vegetation cannot be known. One can only depict some typical plants whose form is known from macrofossil remains. The *Glossopteris* flora has been so named because that form-genus is the commonest element. Seven "species" have been identified in Western Australia and constitute 25% of all known macrofossil taxa of that period. *Glossopteris* is a name originally attached to fossilized leaves thought (at first) to represent a fern. Further study has shown that these plants are actually a diverse group ranking taxonomically more at the level of an Order according to White (1986). Glossopterids as they should preferably be called were trees (Fig. 2) with large tongue-shaped leaves up to 40 cm long which were deciduous in the cold winters, so that great mats of them have been preserved where they fell and were stratified in the swamp. The wood had annual rings and secondary thickening, and resembled modern *Araucaria*. Roots had a segmented internal structure which probably had an aerating function. Most interesting of all, the leaves bore various kinds of fruiting bodies which bore seeds, and may well have been the ancestors of later groups of plants such as the southern conifers, the cycads and even the angiosperms.

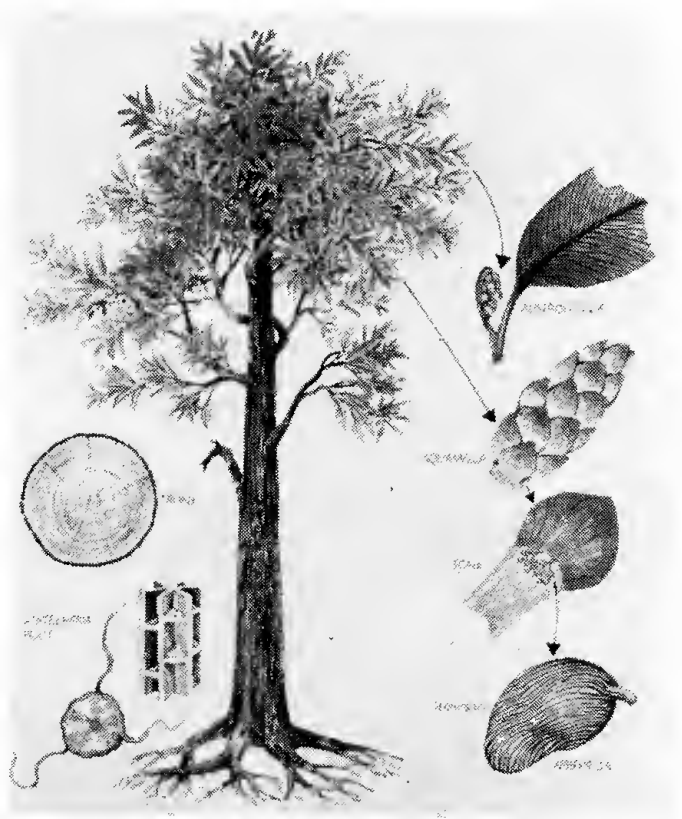


Figure 2 A *Glossopteris* tree with details of leaves, inflorescences, stem and roots (from White 1986).

The Lower Permian macrofossil record shows us vegetation of low-lying and swampy areas. What then was the vegetation of the much greater areas of upland? Did it exist at all? At that epoch most plants were still of a low grade of organization, eg mosses, hepatics, ferns, seedferns, whose modern descendants mostly inhabit wet places. Could they have colonized dry stony uplands in a cold post-glacial period? The answer is to be sought in high latitudes of the Antarctic today where we find communities of bryophytes, lichens and ferns.

A number of different cryptogam tundra communities have been described from the maritime Antarctic by Gimingham & Lewis Smith (1970) composed in order of abundance of the following classes of organisms: lichens, mosses, algae, hepatics, fungi, bacteria, and a few flowering plants. Considerable areas of low-lying ground may become free of snow in summer, a large number of habitats are available for cryptogam colonization, and water is locally plentiful during the short growing season. It is likely that these conditions prevailed also on our uplands in Western Australia during the immediately post-glacial Permian, and that the land was therefore occupied by similar cryptogam communities, while the *Glossopteris* forest occupied sheltered and low-lying places. A similar juxtaposition prevails today in Tierra del Fuego, with subantarctic tundra communities on higher ground, side by side with dense rain forests of *Nothofagus* on protected sites. The point here is that the cryptogam vegetation is able to tolerate cold but not drought. It must have sufficient moisture during the growing season.

The Mesozoic Era

Following the Permian the ensuing era of the Mesozoic spanned 160 my and is divided into the Triassic, Jurassic and Cretaceous periods. The fragmentation of Gondwana took place then (Owen 1983). The portion which is now Australia began to separate on the west from Greater India at the end of the Jurassic (Heitzler *et al* 1973) and from Antarctica during the Cretaceous (Owen 1983). Australia moved steadily towards the equator and experienced a warming of climate, much greater than could be expected merely from the equatorial movement. In the Jurassic and Cretaceous the global picture is of very widespread tropical conditions associated with a progressive warming of the entire earth. The Jurassic period is found to have been already warmer than the present, and by the end of the Cretaceous temperatures had risen to a maximum which according to Hughes (1976) was probably the hottest experienced at any time since land plants first appeared. Subsequently during Cainozoic time global temperatures have been progressively falling away from this maximum until glacial phenomena have once more appeared (Kemp 1978) and the earth has regressed to conditions approaching those of the Permian period.

Evidence for this is based primarily on the past temperature of the sea which is calculable for example by the well-known oxygen isotope determinations from belemnites which give apparently high values generally for Cretaceous seas and much higher temperatures than now in high latitudes (Lowenstam 1964). Hughes (1976) also cited the widespread carbonate sedimentation of the late Cretaceous which he attributed to high ocean temperatures, and pointed to the geographical distribution of certain types of pollen in the fossil record, eg *Classopollis*, as indicating that the equatorial belt was at least 80° of latitude wide (40° on each side of the equator). Under such conditions warmer temperatures would have prevailed in high latitudes as well with absence of glaciation and of polar ice caps. At a number of localities in both hemispheres which were situated at high latitudes in the Cretaceous, often between 70° and 80° from the equator, well within the polar regions, the fossil record shows luxuriant forests of warm-temperate

type, (eg West, Dawson & Hutchinson 1977 for the northern hemisphere, Douglas & Williams 1982 for the southern) and it is difficult to account for this unless the climate of the earth was radically different in late Cretaceous and early Tertiary time.

Various causes can be suggested to account for the situation, the most plausible being either variation in the amount of energy received in the earth's atmosphere, or variation in the tilt of the earth's axis relative to the plane of the ecliptic.

The principal difference between these two mechanisms would lie in the effect at high latitudes. With the obliquity as it is today and a higher solar output, it would be much warmer than now but there would still be seasonal variation in day length and continuous high illumination at high latitudes during the summer months only. With null obliquity there would be no seasonality, no summer or winter, no variation in day length but a low level of illumination, due to the low angle of the sun, during daylight hours throughout the year. Evidence from the late Cretaceous-early Tertiary vegetation of the Canadian high arctic (West, Dawson & Hutchinson 1977) supports the radiation hypothesis. The fauna, which included large land tortoises and alligators, indicates a frost-free climate, whereas the flora was deciduous and petrified wood shows well-marked annual rings indicative of seasonal growth. Furthermore there is an unusual leaf gigantism, inferred from modern studies to be a response to continuous photoperiod (Choi, Traverse & Hickey 1980). These facts appear to disprove any variation in obliquity. Australian evidence from an early Cretaceous flora of Victoria which lay at more than 70° south at that time (Douglas & Williams 1982) shows a similar warm-temperate fauna and flora, although in this case leaf gigantism has not been reported. Axelrod (1984) showed that it would be quite possible for mesothermal plants and animals to tolerate the light conditions and seasonality prevailing at high latitudes at the present day provided much more warmth were available.

Throughout the Mesozoic, therefore, climate was progressively changing, and at the same time the evolution of the Western Australian landscape continued, evolving from the glaciated landscape of the early Permian to a base-levelled landscape which we may call the Gondwana surface and which was perfected by the close of the Cretaceous. King (1972) recognized a series of erosional surfaces in Natal resulting from episodic continental uplift, the oldest of which is the Gondwana surface and is held to be a surviving portion of the surface of Gondwana as it was before rifting and separation. In South Africa the Gondwana surface has been uplifted to 3000m above sea level and most of it has been destroyed by erosion. In Western Australia it has been uplifted less than 300m and is visible as the Yilgarn Plateau, in the interior behind the Meckering Line, where it has remained substantially unmodified since at least the Eocene (Mulcahy 1967).

The fossil record shows us something of the evolution of plant life in response to all these changes. Whether Western Australia remained sufficiently humid in the Triassic for conjectural tundra vegetation of the early Permian to survive, is not known. The likelihood is that it became extinct with the warming and drying of the climate. We cannot be certain whether anything replaced it, because the macrofossil record is probably not showing us the upland flora, while with pollen material we cannot be certain what it represents nor where it came from. White (1986:97) wrote confidently that by late Permian times the drier hillsides and places away from permanent water were habitats for early conifers, Ginkgos and cycad-ancestors, but there is little evidence for this assertion. Microfossils are evidence for the existence of this flora but not for where it grew. An ecologist must examine the likely capabilities of the contemporary plants before making a guess

at their habitat and in this case it seems that they may well have been confined to river plains and other damp places upstream, and did not necessarily grow on hillsides.

Retallack (1977) dealt with the Triassic vegetation of eastern Australia. There is much more fossil material than in the West and Retallack adopted a new approach, treating the eleven different fossil plant assemblages which he found as plant associations in the modern sense, giving them names in Braun-Blanquet terminology, eg *Dicroidietum odontopteroideum*, and inferred habitats. Much of this may appear frankly far-fetched and fanciful. Seed-ferns such as *Dicroidium* (Fig. 3)



Figure 3 Reconstruction of *Dicroidium*, leaf and inflorescences (White 1986).

were dominant in most of the eleven associations, but one was a coniferous forest dominated by *Voltziopsis* a podocarpaceous conifer resembling modern *Dacrydium* (not to be confused with *Dicroidium*). Retallack took the view like so many other palaeobotanists that because terrestrial flora existed it necessarily occupied all habitats and formed a universal plant cover. I find this view hard to support. Retallack confidently drew several landscape diagrams showing the distribution of his hypothetical associations, making them extend to the tops of the hills, and asserting equally confidently that they grew up to 200 km inland from the coast of that time (Fig. 4). White (1986) says of this period that the conifers "grew on dry hillsides, remote from water", but how does she know? Careful reading of Retallack's paper shows no evidence that any association grew on a site where water was not plentiful, and I regard the existence of an upland flora as not proven.

During the ensuing Jurassic period in Western Australia the flora comprised as before lycopods, horsetails, ferns and seed-ferns, but dominance was assumed by gymnosperms. Many of these were cycad-like plants such as *Pentoxylon*, (Fig. 5) and others were coniferous trees belonging to those groups of southern conifers which still survive today, the Podocarps, Araucarias and Kauri Pines (*Agathis*), as well as *Ginkgo* of which a single species survives in China. Here for the first time we begin to find a vegetation which is recognizable in modern terms. A beautifully preserved Jurassic flora is found in the Talbragar Fish Beds of northern New South Wales which were laid down in an ancient lake and show us a forest of kauri pine interspersed with podocarps, and with *Pentoxylon* in the understorey. This is particularly interesting because relict *Agathis* forests on the Atherton Tableland have Podocarps growing among the Kauri Pines and a tree-like cycad, *Lepidozamia hopei*, is present in the understorey. Thus a modern assemblage of plants exists with the same basic composition (though at a more evolved stage). White (1986) claimed from this that "we know exactly what the Jurassic vegetation looked like". At least, we know what some Jurassic vegetation looked like. The Talbragar flora is likely to have grown under cool, constantly humid conditions as its modern counterpart does and cannot be assumed to have formed a universal cover extending over less favourable habitats.

This gymnosperm-dominated flora persisted through to the middle Cretaceous after which it was superseded gradually by a flora of angiosperms (that is, of flowering plants) of modern type and the earlier forms became extinct. This radical biological change was accompanied apparently by an increase in the number and variety of insects and birds, and their co-adaptation as pollinators with the developing angiospermous plants, by the radiation of mammals and the extinction of dinosaurs, not with precise contemporaneity but within the 70-million year timespan of the Cretaceous period. This period therefore witnessed a biological revolution as profound and important as that of the Cambrian when higher forms of life "suddenly" radiated in the sea, and transcending that of the Devonian when the first land plants evolved.

The appearance and early development of the angiosperms occurred from the Barremian to the Cenomanian stages of the Cretaceous and is usually described as "sudden", but actually spanned about 20 million years.

The flowering plants or angiosperms possess a whole range of well-marked characters readily recognizable even in fossil form which distinguish them from their precursors. In addition to their entirely new and distinctive reproductive system, they possess large reticulate-veined leaves, wood with vessels, and distinctive pollen. The earliest of this pollen, in an early and simple form, appears in the Barremian and radiates into more common and complex types by the Cenomanian (Wolfe, Doyle & Page 1975, Fig. 6). The earliest known fruits and seeds are Barremian, while leaves become generally recognizable in the Albian. The earliest known angiosperm remains are found in western Gondwana, and we have no records within Australia until the Albian.

The origin of these angiosperms is unknown. They appeared relatively suddenly and apparently already fully developed, leading to the postulate that angiosperms underwent a long previous period of development which failed to register in the fossil record.

The Russian botanist Takhtajan discussed the problem in the English version of his book (1969). Accepting that there is no factual basis for attempts to derive the angiosperms from ferns or other lower forms without a transitional gymnospermous stage, he proceeded to examine all the known

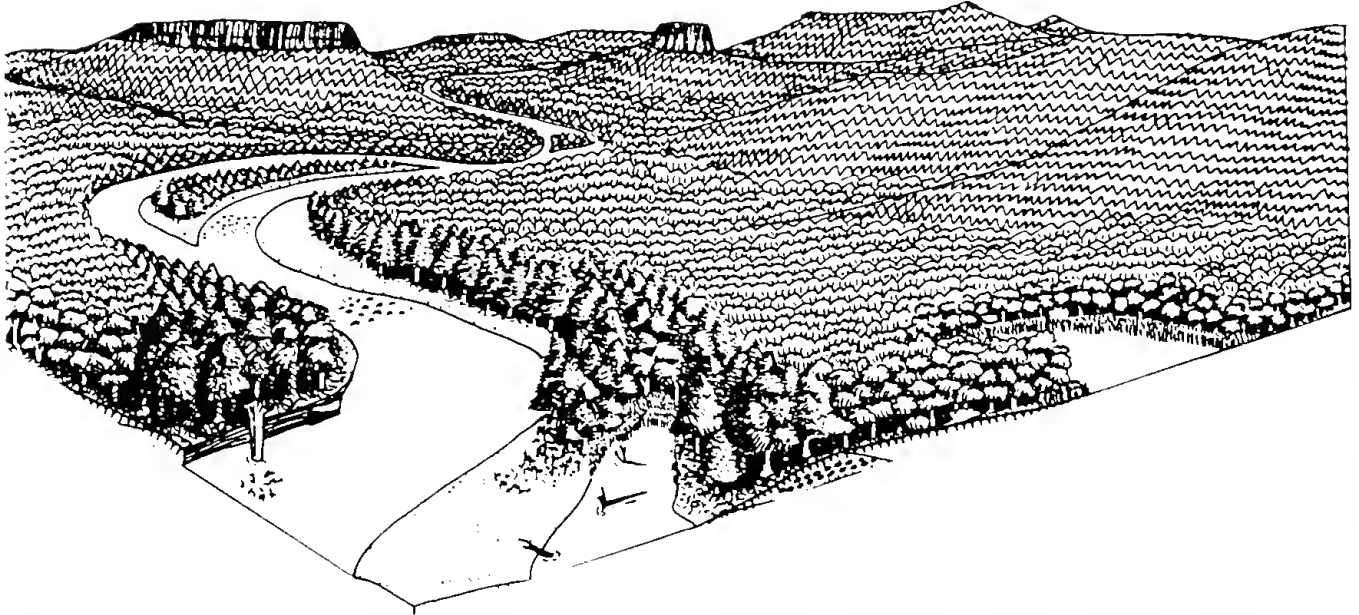
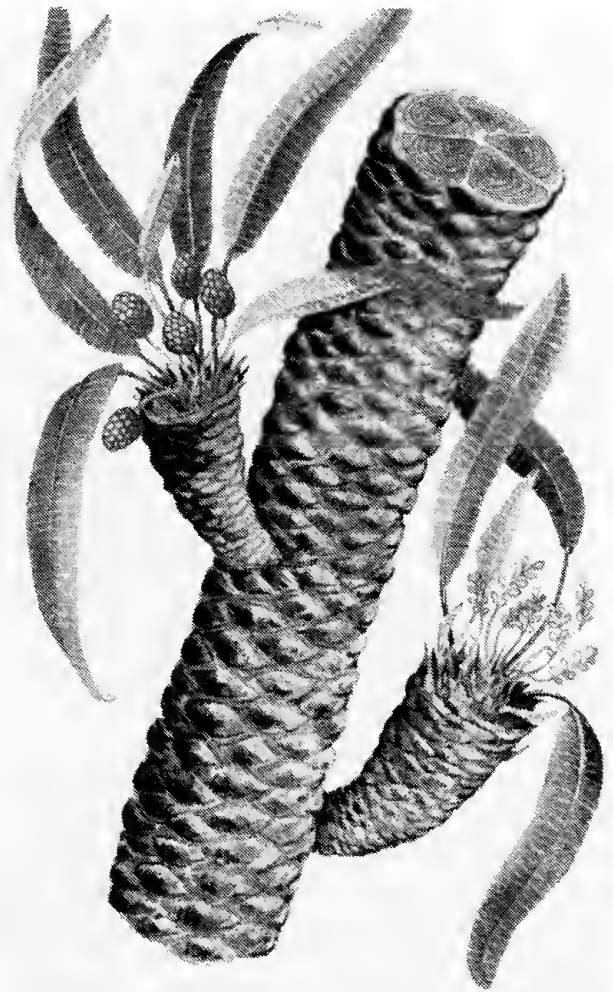


Figure 4 Reconstruction of Triassic vegetation cover at a site in present north-western New South Wales, after Retallack (1977). Communities shown are *Phoenicopsetum* levee scrub (dashed shading and conical pattern), *Dicroidietum* flood plain forest (rounded trees and undulating pattern) and *Johnstonietum* mallee-like woodland (serrated pattern on hillsides). This reconstruction implies total vegetation cover of the land area.

groups of Jurassic gymnosperms, looking for indications as to which might be candidates for angiosperm ancestry. In a sense this approach was unproductive, since it showed that all of them in one way or another, mainly in wood anatomy and the reproductive organs, possessed characters already too advanced along their own evolutionary line, so that they could not have evolved into angiosperm characters. Takhtajan eventually concluded that the angiosperms and their nearest Mesozoic gymnosperm relatives, the Bennettitales, probably had a common seed-fern ancestor as far back as the Carboniferous, although no trace of such an ancestor had been found. Stebbins (1976) wrote that "all we can say at present is that towards the end of the Palaeozoic era the evolutionary line leading to the angiosperms entered a dark tunnel of ignorance . . . and remained there until the angiosperms emerged, fully differentiated, in the early part of the Cretaceous period."

In the 1960s when Edna Plumstead in South Africa was engaged in her pioneer work on the Glossopterids, she suggested that these may have been among the missing angiosperm ancestors. Takhtajan's conclusion would support this but the idea found little favour among most botanists, who were wedded to the concept that the Ranales, with *Magnolia*-like flowers, were the sole ancestral type. Melville of Kew supported Plumstead from the beginning (Melville 1970) and recently (1983) came out strongly in favour, citing morphological evidence which he contended indicates that Glossopterids and Angiosperms "belong to one lineage which extends back in time for 300 million years". Recently White (1986) has given added support to Glossopterid ancestry. While of course the angiosperms must have had ancestors, we cannot satisfactorily identify them in the present state of our knowledge. It seems useful however to discuss further the why and the where of their origin, as it seems to me that certain points have been overlooked.



Reconstruction of Pentoxylon

Figure 5 *Pentoxylon*, a cycad-like plant of the Jurassic. The name is based on the division of the trunk into five stelae which have secondary thickening unlike modern cycads (White 1986).

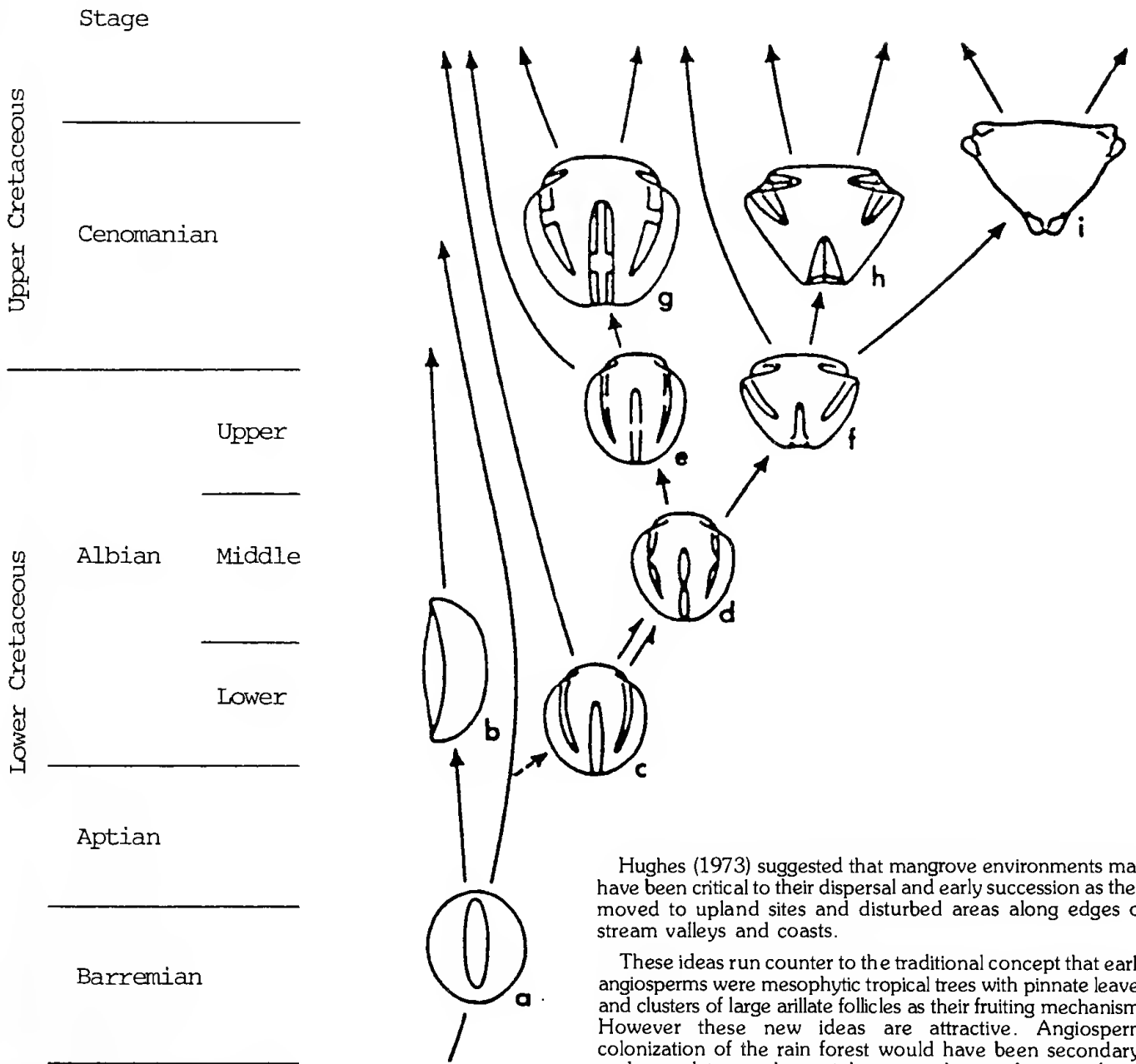


Figure 6 Evolution and radiation of Angiosperm pollen forms during the Cretaceous (after Wolfe, Doyle & Page 1975).

Authors dealing with pre-Cretaceous origins usually follow the "upland origin" hypothesis, whereby angiosperms evolved in rolling hilly terrain and the lower slopes of mountains in the ancient humid tropics. Because these sites were far from the depositional basins, the opportunity for material to become preserved in fossil form would be extremely low except as pollen. Various authors too have speculated as to what the earliest angiosperms were like and what habitats they occupied. On the basis of fossil evidence, the earliest angiosperms may have been small woody evergreen plants with simple, entire, pinnately veined leaves, their flowers pollinated by insects and their seeds distributed by animals (Takhtajan 1969). They may have originated in seasonally arid climates, migrating to more mesic regions later (Hickey & Doyle 1977) initially as riparian weeds or colonists of talus slopes, streambanks and other unstable habitats (Stebbins 1976).

Hughes (1973) suggested that mangrove environments may have been critical to their dispersal and early succession as they moved to upland sites and disturbed areas along edges of stream valleys and coasts.

These ideas run counter to the traditional concept that early angiosperms were mesophytic tropical trees with pinnate leaves and clusters of large arillate follicles as their fruiting mechanism. However these new ideas are attractive. Angiosperm colonization of the rain forest would have been secondary, and come later, perhaps at the stage when we begin to detect them in the fossil record. All of the new hypotheses have in common the concept of initial evolution to fill a vacant niche or niches which would comprise habitats too adverse in one way or another for the more simply organized earlier phyla of plants to tolerate. It seems to me that the logical conclusion of this approach is that it was only with the coming of the angiosperms that something approaching a universal plant cover of the continents was achieved. Even today it is not universal for plants do not grow where the ground is frozen for all or most of the year, or in deserts where too little moisture is available. Before the Cretaceous the range of unoccupiable habitats must have been much greater.

Hughes (1976) is the sole author I have come across who has not assumed that the earth essentially was completely colonized by early land plants in the Palaeozoic and Mesozoic. Hughes observed that if the time from the Devonian period to the present day has recorded progressive degrees of colonization of the land by plants, it follows that many possible habitats now filled would not have been filled in early Cretaceous time.

Support is given to this from a table given by Hughes showing the number of vascular plant taxa existing at various selected moments of geological time. The great diversity of form in the modern flora is expressed in the huge total of 300 000 living species, the great majority being angiosperms. The table shows however that the ferns and gymnosperms have also increased in number since the Cretaceous, having undergone a secondary adaptation to Cainozoic conditions mostly in forms different from those of the Mesozoic. The lower levels of the table give the number of taxa known from the fossil record and it is astonishing to find only 500 taxa of plants in the entire world at the end of the Carboniferous, and 2 500 in the Jurassic. Of course the record is distorted by the selectivity of fossilization, but if the numbers were multiplied by a factor of 10 they would still be astonishingly small.

I am convinced by this that the colonization of the land must have been a long and slow process, not completed before the coming of the angiosperms. I envisage the first small delicate land plants of the Silurian, confined to permanently wet places, perhaps the edges of lakes and ponds. Then in the Devonian and Carboniferous plants increase in size and occupy the deltaic habitats including coal swamps which the fossil record shows us. In the Permian in the southern hemisphere extensive coal swamps were formed and perhaps upland cryptogam communities in a sub-Antarctic climate. In the Triassic and Jurassic as the gymnosperms came to prominence they would first colonize river flood plains and lowlying ground. In the Triassic it is not uncommon to find petrified wood representing rafted tree trunks but these can only have come from the river-bank vegetation ripped away by floods. Trees growing on hills do not get washed down rivers, so that rafted logs are not evidence for upland forests. By the Jurassic, however, gymnosperm forests may have established themselves on favourable upland sites under humid climates, but there would still remain the unfavourable sites, the shallow rocky soils, the steep hillsides, and of course the less humid, hot and dry climates, all of which offered vacant ecospace for the later radiation of angiosperms.

It seems very unlikely that a mere 500 taxa of plants — or even 5 000 — known world-wide in the Carboniferous provided a complete cover for the uplands of the earth. 2 500 taxa or even 25 000 in the Jurassic can only represent a partial cover. The ecological amplitude required of those early taxa would have been far too great. Diverse habitats must have existed then as now, and required diverse adaptations to populate them.

A feature of the angiosperms, and the very basis of their success, is their immense evolutionary plasticity. They evidently radiated quickly in the Cretaceous into a multitude of new and specialized habitats. Ecological diversity is the basis for the great

number of angiosperm species in the world today. This plasticity far exceeds that of the ferns and gymnosperms as we can see from their relative numbers at the present time. Pre-angiosperm floras evolved slowly and lacked capacity to adapt to adverse habits.

This thesis is compatible with the conclusions of others that early angiosperms were small-leaved shrubs or small woody trees originating in dry climates. If "under adverse conditions" is substituted for "in dry climates", these are just the type of plants we should expect to be capable of first colonizing the previously empty spaces of the earth. Further supporting evidence for this comes from the global geological change to predominantly carbonate sedimentation which occurred in the second half of the Cretaceous. Whereas previously sediments had been mostly of erosional origin — sandstones, siltstones and claystones — now they become mostly depositional, *i.e.* limestones, which accumulated from the settling out of calcium carbonate in the skeletons of marine organisms. Hughes (1976) took account of this phenomenon but attributed it to the high temperature of the sea during his "Radmax" period. While this may certainly account for the high quality of the limestone in chalk deposits of that time, we must remember that during the subsequent Cainozoic era carbonate sedimentation has continued to predominate down to our own day even though global sea temperatures have been falling steadily. Other causes have been suggested such as the development of world oceans in the Cretaceous as Pangaea broke up, with their thermohaline circulations and concomitant evolution of calcareous plankton. Such no doubt were contributory but carbonate sedimentation may have been favoured by a reduction in sediment load, resulting in clearer water off shore, and this was the result of establishment for the first time of a general protective plant cover over the uplands. I suggest that by the close of the Mesozoic a general plant cover was more or less established for the first time, by an already ecologically diverse angiosperm flora which had radiated rapidly into a variety of habitats. This flora occupied not only the lowlands, mingling with the Jurassic gymnosperms, but a variety of upland habitats as well.

By the close of the Cretaceous, 65 my ago, there was a fairly general angiospermous vegetation diversified in form from scrub to rain forest, growing in a warm, non-seasonal, humid climate. Since the Western Shield of Australia lay above sea level during the Cretaceous, there is little fossil evidence of the vegetation and we have to rely heavily on data from eastern States sites, supported by local fossil evidence of slightly later date from the early Tertiary. These sources show us a flora whose modern counterparts occur in rain forests of the highlands of New Guinea and New Caledonia, with related types in New Zealand and Tasmania. We can recognize something similar to today's forests of southern beech (*Nothofagus*) and of southern conifers such as *Dacrydium* or mixtures of these, and with other living genera of sub-tropical trees including numerous Proteaceae.

Table 1
Estimated number of seed-plant and pteridophyte species
taxa existing at the selected instants of time (after Hughes 1976)

Selected instant	Time (my)	Gymno-sperm	Pterido-phyte	Angio-sperm	Approximate total
Recent	0	640	10 000	286 000	300 000
End Cretaceous	65	500	2 000	20 000	22 500
Beginning Cretaceous	135	1 500	1 500	0	3 000
Mid Jurassic (end-Bajocian)	170	1 500	1 000	0	2 500
Late Carboniferous (end-Westphalian)	300	200	300	0	500

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Spatial variation in fish communities in two South-western Australian river systems

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Abstract

The fish fauna of two river systems, the Canning and North Dandalup catchments, were sampled every 3 months over an 18 month period. Similar numbers of species and individuals were recorded from both systems. The majority of headwater streams were temporary, predominantly colonized by the native minnow, *Galaxias occidentalis*. Physical obstruction to the seasonal migration of this species by both natural and man-made barriers was evident.

At lowland sites an exotic, *Gambusia affinis*, was dominant in the Canning River, and was the second most abundant species in the North Dandalup River. The distribution of *G. affinis* is discussed in relation to streamflow regulation, disturbance and habitat requirements.

Introduction

The freshwater piscifauna of South-western Australia is considered a distinct element of the Australian fish fauna and has been described as depauperate, with a high degree of endemism (Whitley 1947, Allen 1982, Merrick & Schmida 1984). The fauna is represented by eight families (one monotypic and endemic) containing 12 genera and 17 species. Nine species and six genera, four of which are monotypic, are endemic to the State. Within the state, regional patterns of endemism are also apparent for some species (Christensen 1982). A number of exotic species are present, most notably the mosquito fish, *Gambusia affinis* (Bird & Girard).

Despite the low number of species, little is known of their biology, apart from the above gross patterns of distribution. In addition, little is known of the impact of introduced species. *G. affinis* is widespread throughout the South-west of Australia (Allen 1982) and much of the Australian continent (Merrick & Schmida 1984). This species has been implicated in the elimination of native species from many systems (Myers 1975, Mees 1977, Sarti & Allen 1978, Arthington *et al* 1983), yet little is known of the interactions between this and native species in South-western Australia.

This paper describes patterns in the distribution of the fish fauna of two river systems, the Canning and the North Dandalup and formed part of an extensive biological monitoring programme for environmental impact assessment and water quality using fish and macroinvertebrates.

Study areas

The location of sampling sites within each river system is illustrated in Figure 1. The headwaters of both rivers are situated in forested regions (*Eucalyptus marginata* and *E. calophylla*) of the Darling Scarp, the western edge of the Great Plateau of Western Australia (Jutson 1950). In the Canning catchment these streams are intermittent while in the North Dandalup they are more permanent. This is related to the higher annual rainfall and the presence of swamps on the headwaters of the latter system. The climate of the area is mediterranean (Seddon 1972) with predictable patterns of rainfall and stream discharge (Bunn *et al* 1986).

Both river systems are regulated, resulting in reduced summer flow at the majority of lowland sites. On the Canning River a large dam (built c 1932) is situated 2km upstream of site LC1. Below this dam a number of short tributaries, one of which is Stinton Creek, arise from adjoining sub-catchments. On the North Dandalup River a pipehead dam, which overflows each winter, is situated upstream of site ND5. In contrast this river receives little additional input from sub-catchments. Many of the streams of both catchments are impounded by V-notch weirs for gauging discharge. A riparian release valve, periodically opened to augment low summer flow, is situated immediately upstream of site LC6.

The headwater streams of both rivers are enclosed in a thick canopy of riparian vegetation, which is also a feature of some of the Lower Canning River sites (LC1-4). The lower reaches of the Canning system flow through urban areas, while downstream sites on the North Dandalup are situated in rural areas where riparian vegetation has been reduced by stock grazing.

¹ Correspondence

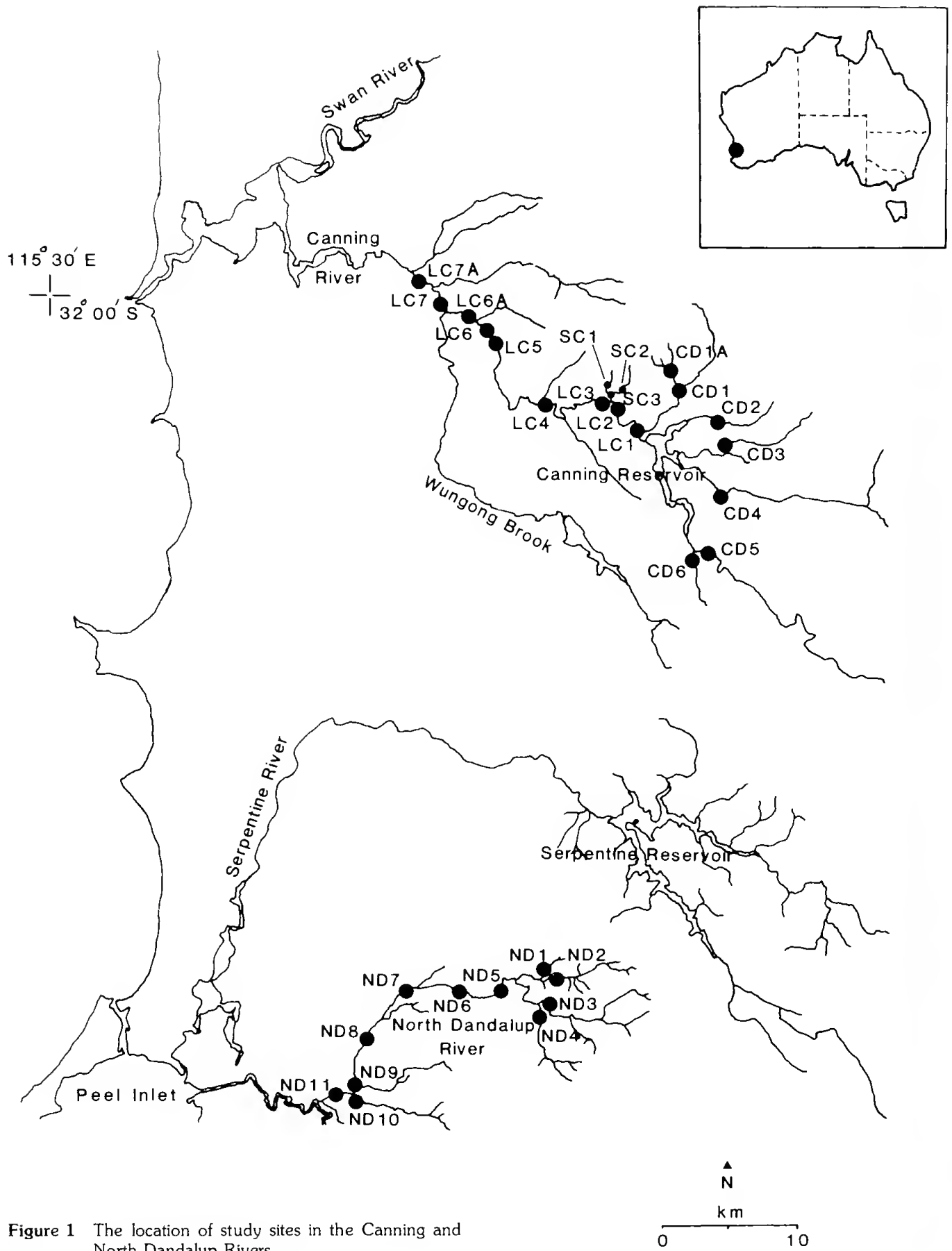


Figure 1 The location of study sites in the Canning and North Dandalup Rivers.

Methods

Sampling regime

Quarterly sampling was implemented from March 1985 to September 1986. A total of 30 sites was routinely sampled, with 11 sites in the North Dandalup and 19 in the Canning catchment. Sites were initially selected by the presence of riffle zones for macroinvertebrate sampling; however fish samples included both riffle and pool habitats.

At each site fish communities were sampled by seine and hand netting. The 5m wide purse type seine net, with a 9mm stretched mesh size, was placed across the stream and fish were driven downstream into the net over a 50-100m reach. Submerged vegetation, logs and large rocks were swept with standard FBA handnets (1.00mm mesh size). Sampling time was standardized to 2 person-hours at each site.

All fish taken were identified, enumerated and released. Species richness (S), taken as total number of species in each sample, was determined for each site on each sampling occasion.

Data analyses

One-way ANOVAs were used to test the significance of between-site changes in the above parameters. Prior to analyses, Cochran's C and Bartlett's Box tests were used to measure homogeneity of variances (Zar 1974). Square root or logarithmic transformations were used if variances were heteroscedastic.

Results

Composition of the fish fauna

Canning Catchment Eight species of fish were sampled (Figure 2). The most commonly taken fish was the exotic, *Gambusia affinis*, comprising 48.3% of the total. The pygmy perch, *Edelia vittata* Castelnau was the next most abundant species (23.5%), followed by the western minnow, *Galaxias occidentalis* Ogilby (16.9%). Two other species; silverside, *Atherinosoma wallacei* Prince, Ivantsoff & Potter and goby, *Pseudogobius olorum* (Sauvage) contributed 7.2 and 2.9% of the total respectively. The remainder (1.2%) was composed of the nightfish, *Bostockia porosa* Castelnau, the cobbler, *Tandanus bostocki* Whitley and the goby *Favonigobius suppositus* (Sauvage). A total of 2 593 fish was caught in the Canning River, 80.2% of which were collected from lower river sites, with the remainder spread evenly between the headwater streams. No fish were collected at the headwater sites SC1, SC2, CD1A & CD4.

North Dandalup Catchment Eight species of fish, totalling 2 182 individuals were sampled from the North Dandalup Catchment (Figure 3). This catchment contained one additional species, the exotic rainbow trout *Salmo gairdneri* Richardson. The goby, *F. suppositus*, present in the Canning Catchment, was not taken. The most common fish, comprising 71.5% of the total number caught, was *G. occidentalis*. *G. affinis* comprised 19.2% of the total and was the second most abundant species. *E. vittata* and *A. wallacei* made up 6.7% and 1.6% of the total respectively. The remaining four species; *B. porosa*, *T. bostocki*, *P. olorum* and *S. gairdneri*, comprised 1% of the total abundance.

Spatial variation in community structure

Canning Catchment Between-site differences in species richness (Figure 2) were significant (ANOVA $F=2.2062$, $P < 0.05$, $df 8,45$). Sites LC1, LC5 & LC6 had a lower species richness than all other lowland sites (Duncan's Multiple Range test (DMR), $P < 0.05$).

G. affinis, the dominant species in the lower Canning system, demonstrated a significant between-site difference in relative abundance (ANOVA $F=6.3905$, $P < 0.001$, $df 8,45$), with sites LC6 & LC7A significantly higher than all other lowland sites, with the exception of site LC2 (DMR, $P < 0.05$).

E. vittata, widely distributed throughout the lower Canning system (Figure 2), demonstrated significant between-site differences in relative abundance (ANOVA, $F=6.369$, $P < 0.001$, $df 8,45$). This species had a significantly higher relative abundance at sites LC1, LC3, LC4 and LC6A than all other lower sites (DMR, $P < 0.05$). *E. vittata* was not taken from site LC6.

G. occidentalis, the third most abundant species in the Canning system, was widely distributed throughout the catchment, with a higher relative abundance in the headwater sites.

The remaining five species were mainly restricted to lower sites, with low relative abundances. *A. wallacei* was an exception, comprising approximately 40% of the total catch taken from site LC4.

North Dandalup River Between-site differences in species richness were significant (Figure 3) (ANOVA, $F=6.5184$, $P < 0.05$, $df 10,66$). Sites ND4, ND6, ND8, ND9, ND10 & ND11 had a higher species richness than sites ND1, ND2, ND3, ND5 & ND7 (DMR, $P < 0.05$).

G. occidentalis, the most abundant species, was widespread throughout the North Dandalup catchment (Figure 3) and dominated the headwater sites.

G. affinis and *E. vittata*, the second and third most dominant species respectively, were common but restricted to the lowland sites, downstream of the dam. *P. olorum*, *A. wallacei* and *T. bostocki* were also restricted to the lowland sites but were neither widespread nor abundant (Figure 3).

The remaining two species, *B. porosa* and *S. gairdneri*, were uncommon and taken only from headwater sites.

Discussion

The majority of the native species of fish recorded in freshwater rivers within 160km of Perth (Allen 1982) were collected during this study. Those not collected are either migratory or estuarine species that occasionally penetrate freshwater. Of the native species collected, only one, *Favonigobius suppositus*, was not recorded from both rivers, being absent from the North Dandalup and rare in the Canning system.

The distribution of species in the Canning and North Dandalup rivers fits that predicted by Horwitz (1978) for temporally variable rivers. Both systems demonstrated a low overall species richness, increasing slowly downstream and within the common species there was no downstream replacement, only additions. The greatest within-system differences in species richness occurred between headwater streams and the lower reaches of both rivers. This may be a reflexion of the effects of physical barriers to fish movement.

Several sites exhibited a community composition different from that expected. Species richness at site LC6 was markedly reduced from site LC5, 100 m upstream. This site is downstream of a riparian release valve from which treated water (chlorinated to 1ppm) is periodically released to augment reduced summer flow. It is unlikely that the change in community structure was solely due to elevated chlorine levels. Increased siltation and a disrupted food chain (macroinvertebrate community structure) may also be important factors. The effects do not appear to be long-lived

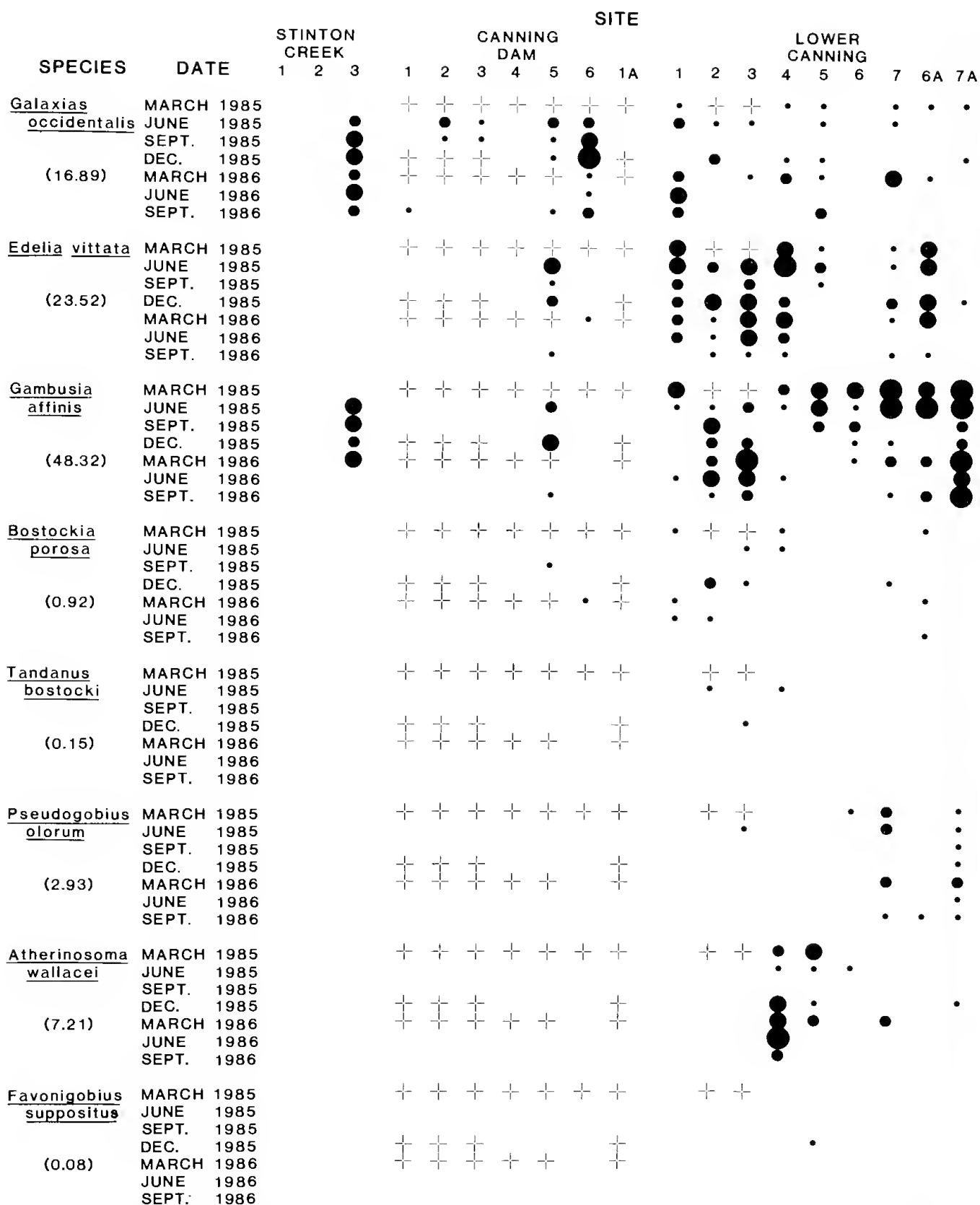


Figure 2 Spatial variation in the distribution of fish species in the Canning Catchment, March 1985 to September 1986 (Symbols indicate sample size: ●, 1-5; ●, 6-20; ●, 21-50; ●, > 50; +, site dry); Values in parentheses represent percentage of total abundance of each species over the sampling period.

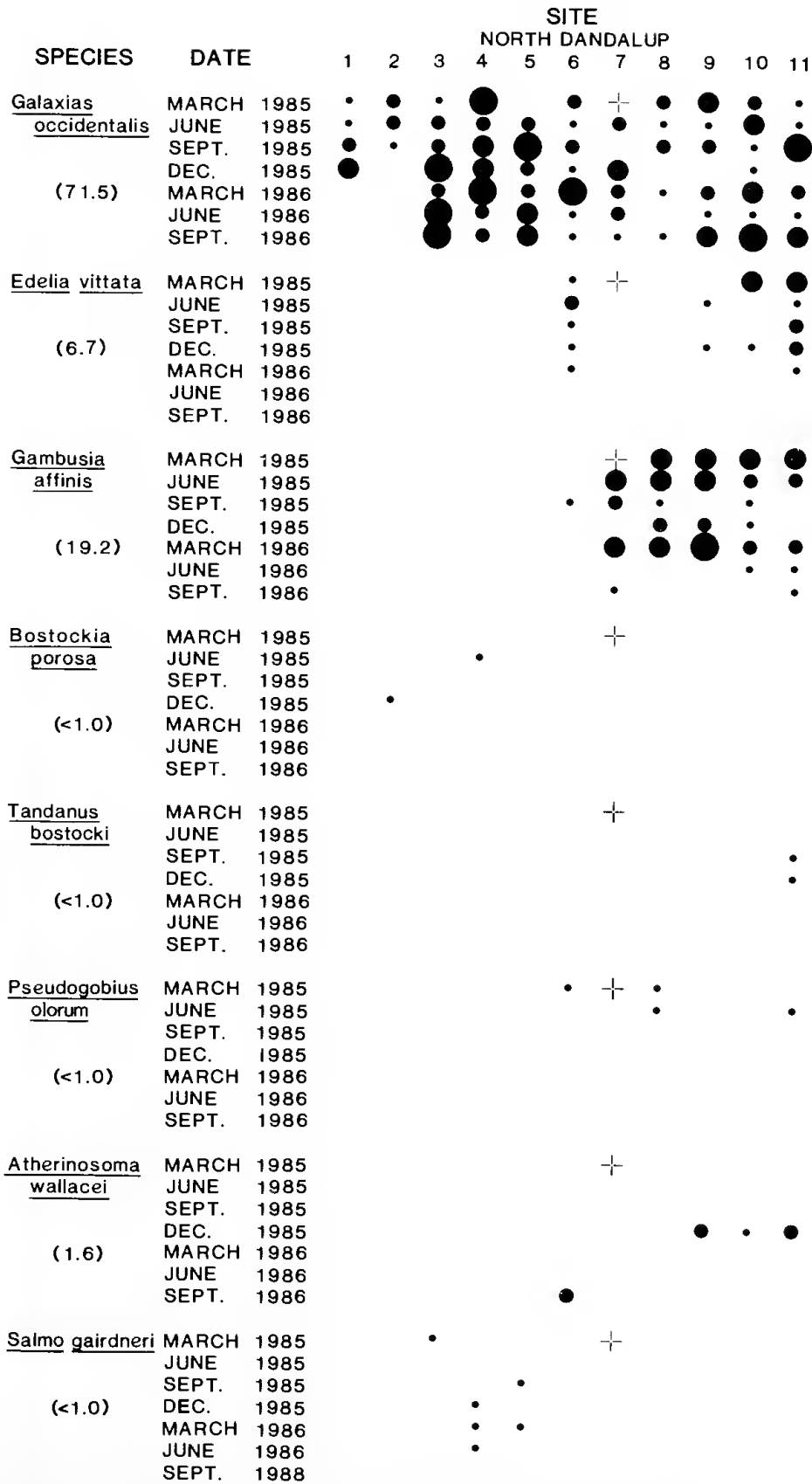


Figure 3 Spatial variation in the distribution of fish species in the North Dandalup Catchment, March 1985 to September 1986 (Symbols indicate sample size: •, 1-5; ●, 6-20; ●, 21-50; ●, > 50; +, site dry); Values in parentheses represent percentage of total abundance of each species over the sampling period.

with the river recovering by site LC6A, the next site downstream. Site LC7A, the most downstream Canning River site, also demonstrated a reduced species richness and diversity. This part of the river is both wide and deep reducing the effectiveness of the sampling method. More intensive sampling in the deeper sections of the river at this site may detect additional species.

Conversely, species richness at site CD5 of the Canning Dam catchment was higher than expected, with this site comparable to lower river sites. This stream, unlike the other catchment streams, did not dry up totally, but remained as large isolated pools throughout the summer. These pools may act as refugia and hold residual populations of *E. vittata*, *B. porosa* and *G. affinis* which may then rapidly recolonize site CD5 and to a lesser extent site CD6. These three species were not collected from any other catchment streams. This may be a reflexion of their inability to colonize newly inundated streams demonstrating, like many small temperate streams, that these are not highly favourable environments for fish colonization (Moyle & Vondracek 1985).

E. vittata and *B. porosa* are known to colonize rapidly floodplains of the south-west of Western Australia (Pusey unpubl). Spawning of these and a number of other sympatric species on the floodplains occurs in spring with the young feeding predominantly on planktonic crustacea. Temporary catchment streams, because of the paucity of planktonic fauna, may represent areas unfavourable for the development of young and this may restrict the distribution of these species. Horwitz (1978) reported planktivores to be uncommon in the headwaters of mid-western American rivers, presumably due to the unavailability of a suitable food source.

The temporary headwater streams of both river systems were recolonized rapidly by *G. occidentalis* soon after flow resumed. Little is known of the life history of this species in the streams of Western Australia, but it is thought that *G. occidentalis* performs an upstream migration to spawn in tributaries and headwater streams (EPA 1987). During this study large aggregations of *G. occidentalis* were frequently sampled at the base of V-notch weirs and on one occasion fish were observed, fully emersed, mid-way up the concrete spill-way below a weir face. This supports the view of an intended upstream movement. Spawning in headwater streams is also supported by the collection of gravid females at these sites. The same process may be occurring in the lower river because larvae and fry have been regularly sampled from drainage channels and flooded areas of the Swan Coastal Plain in winter (Edward unpubl). Migration up drainage channels and lowland tributaries may be an adaptation of populations of *G. occidentalis* which are isolated downstream of physical barriers eg waterfalls, dams and V-notch weirs. The action of such structures as barriers to fish movement would explain the absence of fish from two of the headwater streams, sites CD1A & CD4, which were both upstream of V-notch weirs. Fish were also absent from sites SC1 & SC2 which were upstream of a steep waterfall. This natural feature may be acting as a physical barrier to fish movement since aggregations of *G. occidentalis* were present at the base of the waterfall, at site SC3.

The construction of dams and V-notches is likely to have had a significant impact on the seasonal movements of *G. occidentalis*, affecting its reproductive biology and the recruitment of juveniles. Temporary headwater streams may be recolonized by residual populations of *G. occidentalis* within the reservoirs. Adult fish may actively retreat to the reservoir as stream flow decreases and it is also likely that if larvae are pelagic they will be swept downstream into the reservoir.

Both river systems were shown to have the same species richness. In the North Dandalup catchment the native species *G. occidentalis* was dominant while in the Canning system the introduced species *G. affinis* was most frequently encountered.

G. affinis was first introduced to the fresh waters around Perth in 1936 (Mees 1977) to control mosquitoes. The species now dominates many streams and lakes in the Perth area and is widespread throughout South-western Australia. Sarti & Allen (1978), in a survey of the wetlands of the northern Swan Coastal Plain, found that *G. affinis* was the most abundant species present in lentic habitats. Where native species were present in such habitats they were in low densities and usually confined to inlet streams. Native species were abundant in lotic habitats only (Moore River; ten native and one exotic species, Ellen Brook; seven native and one exotic species).

It is not known when *G. affinis* was first introduced to the North Dandalup River but as it is capable of rapid increases in population size it is unlikely that the difference in abundance between rivers is due to differing periods of residency.

It is inferred from this study that between-system differences in the stream environment influence the population size of *G. affinis*. The Canning system is regulated by a substantial dam which rarely overflows. As a result, the lower reaches of this river are wide, deep and relatively slow flowing, especially so in summer. This habitat is comparable to the lentic environment to which *G. affinis* seems particularly suited. On the North Dandalup system the pipehead dam above site ND5 overflows each winter making this river more prone to spates. Also, the lower reaches of the North Dandalup system are shallower and faster flowing possibly reducing suitability for colonization by *G. affinis*.

The role of disturbance in structuring fish communities may be important. Meffe (1984) found that *G. affinis* populations introduced to a Sonoran Desert stream incurred great losses during flashfloods. The Sonoran topminnow, *Poeciliopsis occidentalis*, endemic to the region, did not suffer such losses as a result of behavioural responses. Meffe (*op cit*) argues that fish which evolve in habitats with frequent perturbations exhibit behavioural responses that minimize the impact of disturbance. It seems likely that this is also the case in the Canning and North Dandalup systems. The high level of endemism of the south-western fish fauna suggests that the evolution of the fauna has occurred *in situ* allowing sufficient time for the adaptation of behavioural responses to the seasonal regimes of stream discharge.

Meffe (1984) suggests that abiotic disturbance culminating in the almost complete removal of *G. affinis* allows the coexistence of this species and *P. occidentalis* in tributaries of the Santa Cruz River. A number of studies listed show replacement of *P. occidentalis* by *G. affinis* and all occurred in lentic environments.

Such a response, similar to the storage effect (Warner & Chesson 1985) in which coexistence is mediated by fluctuations in recruitment, may be involved in the coexistence of native species and *G. affinis* in streams and rivers of South-western Australia.

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A simple model to forecast wheat yield in Western Australia

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Abstract

Stress, defined as the lack of sufficient water to maintain maximum growth rates and yields, has long been recognized as a dominant factor in Australian wheat yield. Thus, by relating stress to crop yield and incorporating seasonal forecasts, a simple predictive crop model can be developed, the data requirements of which are commensurate with available meteorological seasonal forecasts. Such a model has been applied to the Merredin district of Western Australia and its potential is illustrated through the use of yield hindcasts for the 1984-1986 seasons.

Introduction

The growth and development of crops from sowing to harvest is influenced by a number of climatic and soil factors which interact in a very complex way. In recent years research has gone into the development of models to predict and simulate plant growth. Baier (1979) classified these crop-weather models into three broad categories: (i) crop growth simulation, (ii) crop-weather analysis, assessing crop response to weather and climate, and (iii) empirical-statistical models, where several weather variables are related to yields.

In Western Australian numerous studies have used the latter approach (Gentilli 1946, 1959; Fitzpatrick 1970; Hill & Goodchild 1981; Wigley & Tu Qipu 1983) to quantify the sensitivity of wheat yields to climate. They are particularly useful for zoning and mapping areas in terms of their suitability for growing crops and estimating yield potential. Nevertheless, statistical methods are limited for crop yield forecasting as they incorporate complex non-linear interactions between independent variables and there is no evidence to suggest normality of errors (Matis *et al* 1985). Baier (1977) and Hill & Goodchild (1981) noted interactions between weather and technology as well as weather variables themselves. Also, Hill & Goodchild (1981) found that long term historical data bases are likely to include unquantifiable historical events that have statistically intractable effects on yields.

A crop growth simulation model, adapted from CERES-Wheat (Ritchie & Otter 1985), has been developed for conditions at the Western Australian Department of Agriculture's Merredin Research Station (118.17°E, 31.29°S) in the eastern wheat belt of Western Australia (Perry 1986, pers comm). This model relies on a fallow-cereal crop water

balance and computes soil water flow, crop growth and phenological development (McMahon 1983). Yield predictions can normally only be made at the end of the season and are sensitive to daily changes in temperature, rainfall and radiation. Duchon (1986) used such a model, CERES-Maize, to predict yield, using a combination of current weather, and sequences of past weather for the time between prediction and harvest. Application of this approach to Merredin yielded a low correlation between predicted and observed yields for past trials. This is a reflexion of the present inability to simulate accurately the plant-environment system on a daily basis, when significant biological events happen in much shorter time intervals, beyond the resolution of available standard meteorological data.

However, it is neither essential nor practical to model at a level greater than that required for useful predictions and the model sophistication should be commensurate with routinely available input data, such as meteorological forecasts. Simple models can have a powerful predictive value when one or two major factors dominate the performance system (Ritchie 1983). Stress, defined as the lack of sufficient water to maintain maximum growth rates and yields (Mederski 1983) has long been recognized as dominating the performance of Australian wheat (Nix & Fitzpatrick 1969). Accordingly, a simple crop-weather analysis model that relates stress to crop yield (Frere & Popov 1979) was adapted to the Merredin Research Station using results from a ten year direct drilling wheat trial (1977-86) (Jarvis *et al* 1986). Incorporation of meteorological seasonal forecasts into the model, meant that yield predictions were possible and this procedure is illustrated with hindcasts based on the seasonal forecasts issued for 1984-86.

Model Description

The crop-weather analysis model we used was originally designed by Frere & Popov (1979). It was designed to provide developing countries in semi-arid conditions with a simple technique for monitoring crop conditions, thereby allowing the preparation of quantitative yield assessments. As such it requires a minimum amount of actual data and calculations. Central to the method is the determination of the crop water balance which shows directly whether the crop is experiencing stress or not. An accumulated stress factor (stress index) is determined from the water balance and as the season progresses better reflects the ability of the crop to produce yields. Crop assessments are based on the past relationship between final stress indices and actual yields.

The basis of the model is a cumulative water balance which is summed for 10 day intervals over the whole growing season. This is done by adding the difference between precipitation received and water lost by evapotranspiration, to the existing stored moisture which is first estimated at the sowing date. A potential evapotranspiration (PET) is defined as the maximum quantity of water which may be evaporated by a uniform cover of dense short grass when the water supply to the soil is not limited (Penman 1948). When the available water supply can satisfy the PET rate, maximum growth is assumed to occur; but when it does not, stress is implied so that growth rates and final yields suffer. The stress factor gives a direct measure of the expected reduction in yield.

The only input data needed throughout the growing season is the actual precipitation (Pa) received in 10 day periods (decades), ie from days 1-10, 11-20, and from day 21 until the end of the month for each month. The last decades of some months have 11 days to ensure continuity of the monthly notation and the use of standard meteorological information. Rainfall is rounded to the nearest millimetre to eliminate small showers (< 0.6 mm) which are considered to have little significance, being evaporated rapidly in most conditions. Runoff is not accounted for since no measurements of this are routinely available.

The average daily PET for a given month was calculated from the Penman formula (Penman 1948) using climatological records of mean monthly temperature, relative humidity, pressure, sunshine duration and wind speed (Frere & Popov 1979). Estimation of total radiation can be found from direct observations or measurements of sunshine duration (eg Frere & Popov 1979; Edwards & Lyons 1982), whereas the remaining input data are estimated from standard climatological observations.

Mean monthly wind speed was estimated from the Merredin wind rose. Monthly values were found by multiplying the average of the mean 0900 and 1500 wind speeds with a ratio, determined from the ratio maps of Hutchinson *et al* (1984). In the absence of significant errors in the 0900 and 1500 records the estimates obtained are expected to be within 10% of the actual values (Hutchinson *et al* 1984).

Frere & Popov (1979) found that the Penman formula under-estimated evapotranspiration in dry environments by not accounting for dry air advection. To rectify this, they modified the Penman coefficient affecting the wind speed whenever the average minimum temperature was above 5 C and the difference between monthly average maximum and minimum temperatures was more than 12 C. For larger temperature differences, a larger value of the coefficient was used. Consequently, for Merredin the coefficient was modified for the warmer months of September through to April, utilizing values given by Frere & Popov (1979).

Monthly values of PET were obtained by multiplying the mean daily PET by the number of days for each respective month. These values were then divided into decadal periods by a simple mathematical procedure based on the curve fitted to the monthly values X_c , for $c = 1$ to 12. By representing the three decades for each month by Y_1 , Y_2 and Y_3 , their individual values are determined by the equations:

$$Y_2 = (X_c/3) \quad (1)$$

$$Y_1 = (X_c/3) - (X_c - X_{c-1})/9 \quad (2)$$

$$Y_3 = (X_c/3) + (X_{c+1} - X_c)/9 \quad (3)$$

$$\text{such that } X_c = Y_1 + Y_2 + Y_3 \quad (4)$$

The values for the three decades (Y_1 , Y_2 , Y_3) were adjusted so that the monthly total X_c is preserved. If the total of the three decades is less than X_c , 1mm is added to the decade Y_3 or Y_1 , depending on whether the slope between X_c and X_{c+1} , increases or decreases from the previous monthly interval (X_{c-1} to X_c). Alternatively if the total is greater than X_c , 1mm is subtracted from Y_3 or Y_1 , depending on whether the slope decreases or increases from the previous interval. When a point of inflexion occurs at a particular month, Y_2 is given the largest (or smallest) decadal value depending on whether the curve is convex or concave.

The water requirements of the crop are found by multiplying the decadal PET (E7) with the respective crop coefficient (K_{cr}) for that period:

$$WR = E7K_{cr} \quad (5)$$

Such an equation allows for the fact that cultivated crops pass through several stages from emergence until maturity. Over this period the plant cover varies in comparison to the reference short grass used in defining PET and this variation is expressed as the crop coefficient, being the ratio of maximum actual evapotranspiration over PET.

The total water requirements of a potential highest yielding crop are based on conditions experienced at the trial site during 1974, when yields reached maximum expected values of 3 tonne/ha (Jarvis 1987, pers comm). For that year, the sum of stored soil moisture at sowing, estimated from the water balance subroutine of CERES-Wheat (McMahon 1983), and rainfall during the growing season came to 280mm. Therefore it was assumed, that if this amount of moisture was available and evenly distributed to a crop, no stress would be incurred and maximum yields close to 3 tonne/ha would result. The most regularly used crop coefficients of Doorenbos & Pruitt (1977) were slightly increased so that when they were multiplied with the decadal PET values the total water requirement for the season came to 280mm. At the same time the distribution of the decadal water requirements was related to the observations of French & Schultz (1984) which showed that 70% of the total water use occurred by anthesis. At Merredin, anthesis usually occurs in mid-September and hence the crop coefficients were adjusted to ensure that 70% of the total water requirement was between sowing and anthesis. The relative proportions of the total water requirement were approximated as 0.3 for the period (c 2 months) between sowing and tillering, 0.4 for the period (c 2 months) between tillering and anthesis, 0.2 for the following month up to soft dough, and 0.1 for the remaining time to maturity.

The current readily available moisture, RS_i , is found from:

$$RS_i = RS_{i-1} + (Pa - WR) \quad (6)$$

where the difference between actual precipitation and crop water requirements is added to the existing stored water, RS_{i-1} . RS indicates the amount of usefully stored or readily available water in the soil, and this is commonly referred to as the water reserve between the field capacity and the

permanent wilting point. The amount readily available depends on the depth of the soil exploited by the roots and the physio-chemical characteristics of the soil (Frere & Popov 1979). For the heavy, calcic red brown earth at Merredin, the maximum amount of stored moisture held in the 1.2 m depth rooting zone is 180 mm (Perry 1986 pers comm).

Originally designed for parts of Africa and Asia which experience a brief wet-season, this procedure assumes that there is no stored soil moisture before the first opening rain. Such an assumption cannot be applied to Western Australian conditions, where moisture is almost always carried through from either autumn or summer. Thus the validated water balance subroutine from CERES-Wheat (McMahon 1983), was used to estimate the stored moisture accumulated before the sowing date. The model was run with daily values of rainfall, radiation and temperature from the first of January through to the beginning of the 10 day period in which sowing occurred. Values of stored water determined varied from 0mm in 1985 to 64mm in 1984.

When the final stress factor was plotted against yield for the 10 years, two of the years, 1979 and 1984, heavily over-estimated the stress in comparison to the observed yield. However, the end of both 1978 and 1983 were very wet, suggesting that moisture could have been carried through from these years and this is not accounted for in initializing the soil moisture balance from January. By using the final soil moisture profile for the previous year to initialize the profile for the following year, very different soil moisture estimates were obtained for 1979 and 1984. For these two years the values increased from 53mm to 96mm and 64mm to 106mm respectively. Negligible increases of 1 to 4mm were found for the other years.

If RS is greater than the total possible stored water, in this case 180mm, a water surplus is registered and stress is assumed to occur. Likewise, if insufficient moisture is available to maintain maximum growth rates stress is also inferred. This is the case when RS becomes negative — a water deficit. As such, RS only relates what the available moisture content would be if a crop was to be growing at its potential rate not limited by stress. Because Merredin has a very high water holding capacity and a dry climate, only deficits were observed.

Stress is represented by a culminative stress index (I) and is calculated (for deficits, D) as:

$$I = I_{i-1} + (D/WRT) \quad (7)$$

where WRT represents the total water requirement for the growing season of the potential highest yielding crop, and I_{i-1} is the previous value of I. Expressed as a percentage, this factor indicates the extent to which the water requirements of a crop have been satisfied in a cumulative way up to that point in its development. At the beginning of the season, the index is given a value of 100. It will remain at that value for successive decades until a surplus or deficit appears. If a deficit of say 28mm appears, the quotient between 28 and 280 (the total water requirement) is 0.1. This corresponds to 10% of the water requirements not satisfied, so the index drops from 100 to 90. The calculation is continued through to maturity where the final stress index reflects the cumulative stress endured by the crop throughout the season. As such, it is usually closely linked with yield unless other harmful factors such as pests, diseases or frost have had an over-riding influence.

Results and Discussion

The accumulated stress-yield relationship for the 10 year direct drilling trial (Fig. 1) has a least squares regression of:

$$Y = 37.12 I - 1083.58 \quad (8)$$

where Y is the expected yield in tonne/ha and I the accumulated stress over the growing season. The

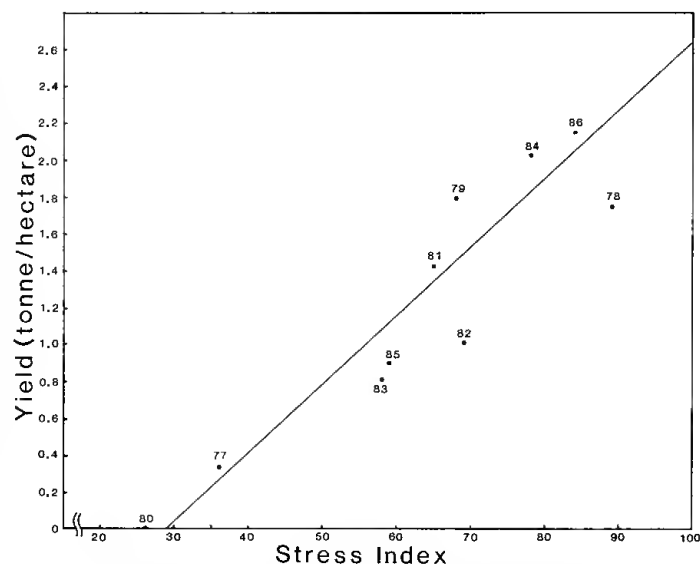


Figure 1 Comparison between yield and computed stress indices for the Merredin Research Station.

accompanying correlation coefficient is 0.94 ($r^2 = 0.88$) and is significant at $P = 0.001$. This illustrates that moisture stress is a significant yield determining variable for heavy soils in the Merredin district. The lower than expected yield in 1978 may have resulted from surface detention and evaporation of water due to poor soil structure at the start of the trial and the high rainfall (410 mm) in 1978 (Jarvis *et al* 1986). Equation (8) formed the basis of the predictive mode of the model.

Yield predictions made after the growing season but based on information available before the season are known as hindcasts. These were made by using decile rainfall corresponding to the seasonal forecasts issued by Austweather prior to the corresponding season. Such forecasts, based on large scale ocean-atmosphere indicators, endeavour to predict whether rainfall will be in one of three possible categories: (i) below normal (signifying the lower 30% of climate data), (ii) near normal (signifying the middle 40% of recorded values), or (iii) above normal (signifying the upper 30% of recordings).

Consistent with a similar decision-making model (Brown *et al* 1986), the three forecast categories were represented by the deciles 1.5, 5 (median), and 8.5 of the distribution of growing season precipitation. For certain situations, intermediate 2 event forecasts were made by Austweather and these were represented by decile 3 (for normal to below normal forecasts), and decile 7 (for normal to above normal forecasts), as these values are positioned at the boundaries between the two categories used in each respective 2 event forecast.

The hindcasts were first made for the beginning of the 10 day period in which sowing occurred and the initial soil moisture was estimated from CERES-Wheat. In place of actual rainfall, however, the decadal decile rainfall was used as an indicator of the distribution of the rainfall over the forecast period. Thus the level of sophistication of the climate data fits that of the seasonal forecasts. The monthly values were separated into 10 day intervals by the same mathematical procedure outlined in equations (1-4). Such a process was carried out for early winter (April-June), late winter (July-September) and early summer (October-December). Estimated stress was used to predict yield via equation (8).

An updated yield prediction followed at the end of June. Actual rainfall figures for June replaced the decile rainfall figures and another estimate was made. This updating continued until the end of the growing season when the final yield estimate was made. Initial and updated predictions for 1984-1986 are shown in Fig. 2.

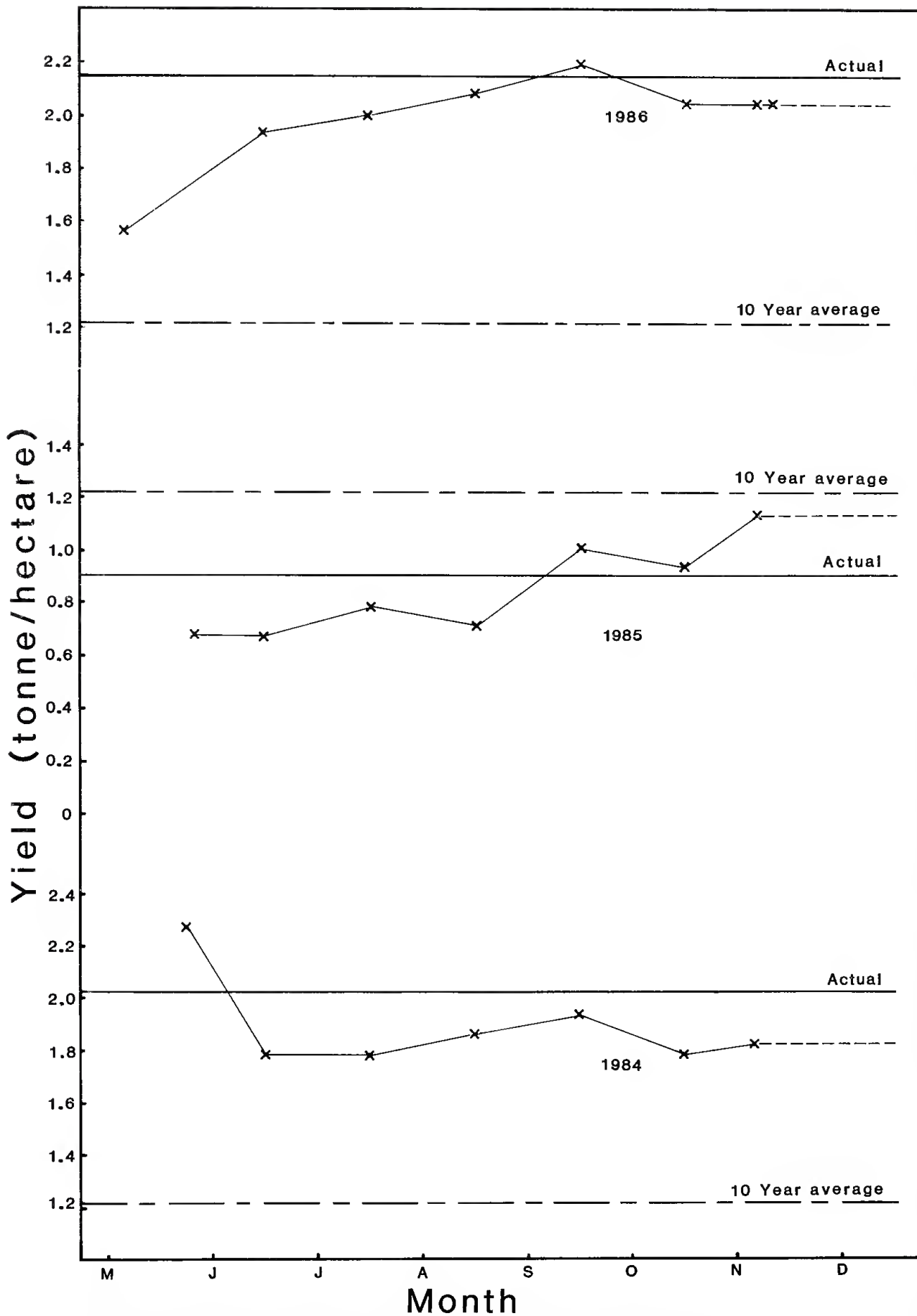


Figure 2 Yield predictions made at various stages during the growing seasons for 1984-1986 based on seasonal forecasts, compared with the 10 year average yield and the actual yield.

In 1986 the yield prediction gradually rose and levelled out near 2 tonne/ha. The rise in predicted yield was due to the actual rainfall being slightly wetter than the decile rainfall given by the seasonal forecasts. A similar result occurred for 1985 except that the predicted and actual yields were all about a tonne/ha lower.

In 1984 the reverse happened at the beginning of the season. An initial estimate of 2.26 tonne/ha declined to 1.78 tonne/ha at the end of June. This sudden change in yield estimate was essentially caused by the rigidity of the seasonal forecasts, individually restricted to a three month time-span. The outlook was for average to above average rainfall for the period April to June and below average rainfall from July through to September. What eventuated was an average to above average April and May, followed by below average rainfall for June, July and August. A rigid three month forecast could not account for such variation and thus the possibility of monthly forecasts is being considered.

Ultimately the value of the predicted yield is dependent on the stress/yield relationship and the accuracy of the seasonal forecasts. The relative success of the predictive model over the 1984-86 seasons is a direct function of the success of the input seasonal forecasts. Nevertheless, this simple model is commensurate with the available meteorological data and is able to express seasonal forecasts directly in terms of expected yield. The value of such predictions is not in the actual yield predicted, but rather as a comparative measure of how a particular year is expected to compare to previous years. At this stage, the model has only been applied to one soil type at one location. For other regions and soil types, different crop responses are expected but could easily be accounted for through modification of the maximum stored water and water required for maximum yield.

Conclusions

A crop-weather analysis model similar to Frere & Popov (1979) was developed and applied to the Merredin Research Station. By including soil moisture estimates at past sowing dates from CERES-Wheat, a correlation of 0.94 between yield and final stress was obtained. This strong relationship between stress and yield is in agreement with the observation of Nix & Fitzpatrick (1969) that lack of sufficient water to maintain maximum growth rates and yields is a dominant influence on Australian wheat. Such a relationship can be used to provide a direct link between expected seasonal weather conditions and yield as the data input required is of a similar sophistication to available seasonal forecasts. Hindcasts for the 1984-86 seasons illustrate the potential of the method as a basis for a dynamic decision making model.

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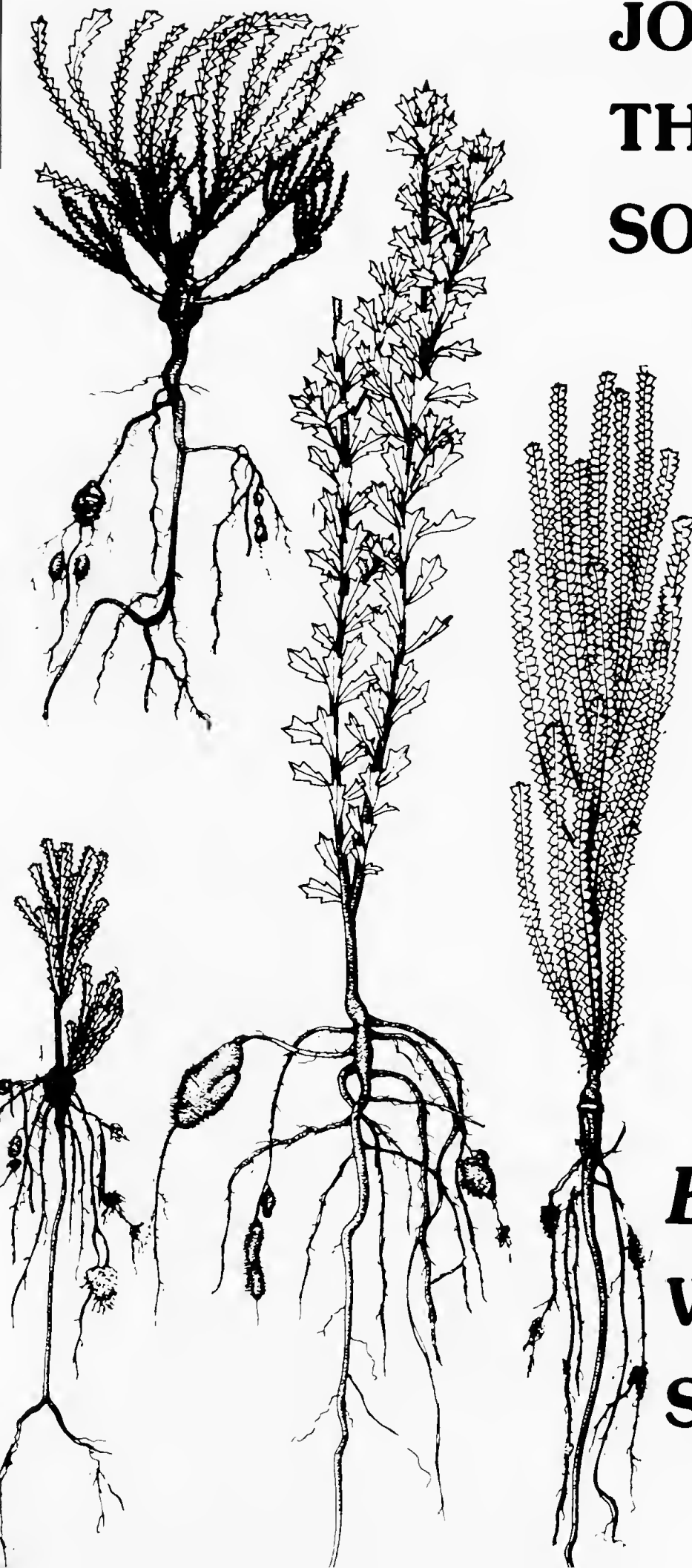
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**JOURNAL OF
THE ROYAL
SOCIETY OF
WESTERN
AUSTRALIA**

Volume 71, Part 4, 1989

***BANKSIA*
WOODLANDS
SYMPOSIUM**



The Royal Society of Western Australia

To promote and foster science in Western Australia
and counteract the effects of specialization

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Preface

J S Pate, FAA, FRS

President 1988/89
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The concept of holding a Symposium specifically on *Banksia* woodlands was the brainchild of the late Dr Jenny Arnold, to whom this volume is dedicated. In 1987 she approached the Royal Society of Western Australia as a possible host society for the Symposium, the Council of the Society agreed wholeheartedly, and, with Jenny as convener, the program which you now see recorded in this volume was generated.

It was always Jenny's belief, now shared by many of us, that ecosystems close to the Metropolitan area are being so rapidly depleted and degraded that some form of widescale publicity was immediately required to evaluate their current state, and

suggest how future management might be implemented within the inevitable context of multi-purpose usage by a range of public bodies and interests. Having focussed previously on wetland habitats and to a certain extent on the virtually extinct tuart forest ecosystem, the *Banksia* woodlands of the Swan Coastal Plain seemed a highly appropriate topic for reasoned scientific evaluation and debate.

This is essentially what took place at our Symposium, and I commend this volume enthusiastically to you as a focus of current knowledge, and, hopefully, a basis on which future management strategies might be considered.

JENNIFER MARY ARNOLD B Sc, B A, M Sc, Ph D—An Appreciation

Jenny was born and spent her childhood on a farm which her parents pioneered near Waiki in the outer wheat belt of Western Australia, and although from primary school she had to board away from home she always retained an understanding of farming and a sympathy for farm life. It must have been there that her love of nature and concern for conservation was born.

She went to Northam High School and then came to the University of Western Australia where she studied Biology and completed a double major in Zoology and Botany in 1957. Shortly after graduating she went to work in the Climatology Section of the CSIRO Division of Land Research and Regional Survey in Canberra.

Then in 1961 she went to the University of Queensland as Senior Demonstrator in the Zoology Department before returning to a similar position at the University of Western Australia in 1964. There two of her many talents were displayed: her skill in writing and her deep concern for others.

Her doctoral thesis on the biology of the Native Cat was a masterful piece of writing which received the highest praise from the examiners, one of whom wrote:

"I have only high praise for this exceptionally fine thesis. Her perseverance and ingenuity has resulted in an impressive assembly of new information, which is well reported, and well related to the general subject...."

Jenny was a scientist, but her interests were much wider. She had a love of good literature and when she joined the Department of Conservation and Environment in 1977 she returned to the University to study English Literature and graduated again with a Bachelor of Arts Degree.

Her feeling for the language never allowed her to accept anything but the best in her writing. She was a perfectionist with her own work and drove herself hard to achieve a high standard, one that put a great strain on her at a time during her long illness when she might well have relaxed. But she was a kind and constructive critic of the work of others who sought her help.

Jenny's main job at UWA was in running first year laboratory classes and there she gave of herself in helping the many students. In the words of her Professor she was "almost obsessively conscientious." She was perceptive of student needs, she was interested in them personally and in what they were doing, and gave advice with sympathy and understanding, but without any pretence that she knew best.

The local branch of ANZAAS and the Royal Society of Western Australia especially owe her much for her tireless efforts in organizing their activities - which she was doing almost to the end - and in so doing endeared herself to her colleagues. One of her last responsibilities was to the Fitzgerald River National Parks Association and it was wonderful to see the high esteem in which she was held and the affection the members felt for her.



Another of Jenny's talents was as an artist, with a love of art, and only recently while she was fighting the cancer from which she died she took a course in drawing at the Fremantle Arts Centre. Her PhD Thesis is illustrated with her lifelike drawing of the animal she studied. She also had a love of good music and after she returned from Queensland she sang with the UWA Choral Society choir.

While she was with the Environmental Protection Authority Jenny worked for a year (1985-86) at the WA Water Authority where she was greatly respected and appreciated. There she compiled an inventory of the wetlands of the Swan Coastal

Plain, a mammoth job. This she did with her usual meticulous concern for accuracy and her distrust of the political demand for decisions before there was the relevant information on which to base judgements.

Those of us who visited Jenny in hospital in the last weeks of her life will remember with gratitude how through all her pain and distress she rallied to show her interest and involvement in our interests and activities, and to display her wonderful sense of humour and recall the fun she had shared with us. It was a joy to be with her.

Ernest P Hodgkin

Definition and location of the *Banksia* woodlands

J S Beard

6 Fraser Road Applecross WA 6153

A recent book (Pate & Beard 1984) entitled *Kwongan: the Plant Life of the Sandplain* dealt with the vegetation of sandplains in the Extra-Dry Mediterranean Bioclimatic Zone (Pate & Beard 1984) on which kwongan is the characteristic plant formation. *Banksia* woodland (technically *Banksia* low woodland) is the characteristic formation of sandplains in the more humid Dry Mediterranean Bioclimatic Zone where the length of the dry season averages 5-6 months as against the 7-8 months of the Extra-Dry Zone. *Banksia* woodland may be said to represent the plant life of the sandplain within this bioclimatic zone, which corresponds to the Darling Botanical District. Deep well-drained sandy soils form the characteristic habitat for *Banksia* woodland, and these occur principally within the Drummond subdistrict, which includes the Swan Coastal Plain and the Dandaragan Plateau.

Area calculations from the Vegetation Survey of WA (Beard & Sprenger 1984) estimate that *Banksia* low woodland originally covered 6 229 km² of which 61% is now alienated land where the vegetation is presumed cleared. *Banksia* woodland with scattered emergent eucalypts is estimated to have covered a further 680 km², all of which is now on alienated land. The amount of remnant vegetation on alienated land is not known.

The woodland is dominated by small trees of about 6-8m among which *Banksias* are the most numerous. On the Swan Coastal Plain these are *B. attenuata*, *B. menziesii*, less commonly *B. ilicifolia*, together with *Eucalyptus todtiana* and *Nuytsia floribunda*, and in the southern part *Casuarina fraseriana*. Further inland, in the northeastern occurrence on the Dandaragan Plateau, *B. menziesii* is replaced by *B. burdettii* and *B. prionotes*, while *Actinostrobus arenarius* and *Xylomelum angustifolium* also join the assemblage. Leaves of the *Banksias* are 10-15 cm long, rough, chartaceous, serrate; though large, they are relatively few so that the crown is thin, and branching of the trees is somewhat open. Bark is very thick, dark, scaly. The formation resembles the oak (*Quercus*) woodlands of other mediterranean regions, in particular the cork oak (*Q. suber*) woodlands of the mediterranean itself. Individually, *Banksias* resemble *Curatella americana* of savannas in tropical America, which significantly is named *chapparro*, Spanish for cork oak. Some convergence in evolution is perhaps impressed by the poor siliceous sands in these cases.

The *Banksia* woodlands have a well developed sclerophyll shrub understory for which Speck (1952) listed 28 spp of tall shrubs, 130 of low shrubs, and 182 spp of ground-layer plants including many Restionaceae, Cyperaceae and other herbaceous monocots, for the woodlands on the Swan Coastal Plain. Speck indicated for each of these components whether it occurred on limestone (i.e. on the Spearwood Dune System), on Bassendean sand or in a so-called "Moist Phase" which describes swampy areas which may be present throughout. These are the three most readily recognizable substrate types within the *Banksia* woodlands of the Plain.

Prior to Speck's detailed study, the *Banksia* woodlands had received scant attention in the literature. Diels (1906) did not recognize this formation precisely. The vegetation of the Bassendean sand was treated as "Mixed woodlands of the Coastal Plain" with emphasis on *Eucalyptus marginata* and *Casuarina fraseriana*. However Diels named the component *Banksia* spp (*B. attenuata*, *B. menziesii* and *B. ilicifolia*) as "several *Banksia* species which as smaller trees or tall-growing shrubs characterise many places in these woodlands of the plain" (p 228).

Gardner (1944) made no mention at all of these woodlands but as his treatment of the vegetation of the State was much briefer than Diels', it was necessary to omit describing many of the less extensive communities.

Subsequent to Speck's work, Havel (1968) published a study of the understory communities of the *Banksia* woodlands found in State Forest No. 65, employing mathematical analysis which distinguished 11 understory groupings associated with particular site conditions. 5 of these occurred on the Spearwood Dune System, 3 on the Bassendean System, 1 on the transition between the two, and 2 on swampy sites which might occur throughout the area, thus confirming Speck's earlier habitat divisions.

Subsequently again, Speck's work was summarized by Seddon (1972) together with a vegetation map scale 1:500 000 of the Swan Coastal Plain from the Moore to the Murray River, distinguishing 11 units. In 1979 as part of the System 6 study, Heddl published a vegetation map scale 1:400 000 covering the same part of the Swan Coastal Plain and extending further inland. F G Smith mapped vegetation in detail at 1:250 000 on the Busselton-Augusta sheet in 1973 and the Collie sheet in 1974. My own mapping at this scale of the Moora/Hill River, Perth and Pinjarra sheets was published in 1979. A composite map from these sources showing the extent of the *Banksia* woodlands is shown in Fig 1.

The mapping shows that *Banksia* woodland, while generally considered typical of the Swan Coastal Plain, is by no means confined to it. A substantial area, perhaps one third of the whole, occurs on the Dandaragan Plateau. There are even some minor occurrences east of the Darling Range. All these occurrences are within the Darling Botanical District. *Banksia* woodland occurs throughout the length of the Swan Coastal Plain, a distance of some 400 km north to south. Rainfall and temperature as well as soil and topography vary throughout this range, so that the distribution of the woodlands varies from point to point.

Banksia woodland reaches an optimum on the Plain between Muchea and Cataby, declining in both the northerly and southerly directions. In this central node it extends west onto the Spearwood Dune System and even reaches the sea in several places. It forms almost the total vegetation of the Plain here and extends widely over the Dandaragan Plateau immediately to the east. North of the central node the *Banksia* woodland is affected by declining rainfall so that it becomes restricted to the deeper sands. It is replaced by kwongan on the coastal limestone, and on the Dandaragan Plateau also except for a large extension from Moora to Watheroo. On the Coastal Plain the *Banksia* woodland finally pinches out near Jurien. The decline of the *Banksia* woodland is a gradual process and in many places there is a continuum from the woodland into *Banksia*-dominated kwongan which is much lower and more open than the woodland proper. In mapping in such cases one has to exercise a subjective decision and to decide somewhat arbitrarily where a boundary should be drawn. This applies particularly to the northern limit of inland *Banksia* woodland about the middle of the Watheroo National Park.

In a southerly direction the *Banksia* woodland is affected by increasing rainfall, the appearance of heavier soils, and of frequently more swampy conditions. South of Yanchep, tuart and tuart with jarrah form taller eucalypt woodlands on the coastal limestone. The *Banksias* persist as an understory. On the inland side of the Swan Coastal Plain south of Gingin there are heavier

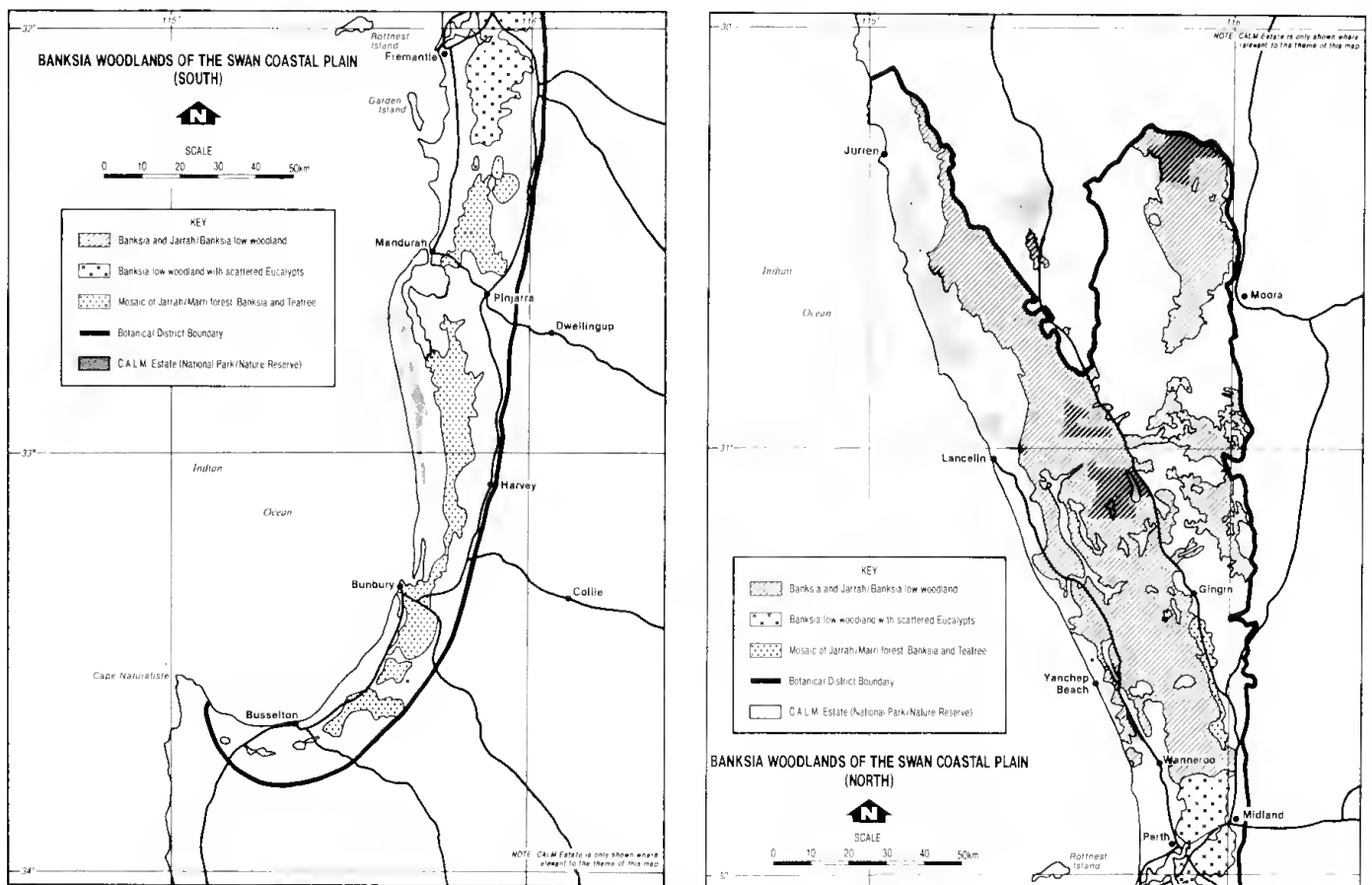


Figure 1 Distribution and extent of *Banksia* woodlands in southwestern Australia.

soils under jarrah-marri woodland and a swampy belt which has (or used to have before clearing) a mosaic of eucalypt woodland, *Banksia* woodland, paperbarks and *Casuarina obesa*.

South of Wanneroo the *Banksia* woodland, which has already acquired *Casuarina fraseriana* as a co-dominant since north of Yanchep, is further joined by scattered larger emergent jarrah trees, a structural type separately mapped. This occurs also at the southern extremity of the Dandaragan Plateau. At Wellard opposite Rockingham the last of the extensive stretches of *Banksia* woodland comes to an end, pinched out by the heavier soils at the foot of the escarpment and the increasing wetness of the Plain. From here southward the *Banksia* woodland forms a component of a tripartite mosaic with eucalypt and paperbark woodlands, or occurs as occasional patches within predominant eucalypt woodland. This situation is modified only in the extreme south where jarrah-marri forest (rather than woodland) is believed to have been the principal vegetation of the Coastal Plain. There are still some specific patches of *Banksia* on former coastal dunes, including one patch outside the Coastal Plain.

Along the south coast from Cape Leeuwin east to Albany a different bioclimatic zone is entered, the Mesomediterranean where the dry season is shortened to 3-4 months. *Banksias* continue of course to occur but mainly as components of other vegetation. *Banksia* woodland as such may occur on limited areas of well-drained sand forming an intermediate belt between jarrah forest and swamps, or on low sandy ridges rising from swamps (F G Smith 1972). Small patches of typical *Banksia* low woodland have been recorded in the Narrikup area (Beard 1979d). Apart from these instances sandy habitats are otherwise occupied. On south coast dunes *Agonis flexuosa* occurring in forms

from mallee to well-grown trees is the dominant species, rather than *Banksias*. Outwash plains of white sand carry *Casuarina fraseriana* low forest in pure stands or mixed with *Eucalyptus staeri* if there is poor drainage. A novel *Banksia* community in this region however consists of *B. verticillata* forming low forest under swampy conditions.

Further to the east there is a transition to kwongan as there is in the northern sandplains with *Banksias* continuing as a conspicuous element on deeper sandy soils as far east as Israelite Bay.

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Bassendean and Spearwood Dunes: their geomorphology, stratigraphy and soils as a basis for habitats of *Banksia* woodlands

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Introduction

Banksia woodlands and allied plant associations inhabit the extensive sandy soils of the Bassendean and Spearwood dune systems of the Swan Coastal Plain of SW Australia. These dune systems also have formed the basis for identifying vegetation associations in relationship to landscape (Heddle *et al* 1980, Cresswell & Bridgewater 1985). However, to date, there has not been a systematic description of the dunes in terms of their landforms, stratigraphy, soils, inter-relationships and age structure specifically for the purposes of landscape ecology, ie for delineation of vegetation habitats (cf Semeniuk *et al* 1989). This paper reviews the physical features of the Bassendean and Spearwood dunes as habitats for *Banksia* woodlands, describes some of the smaller scale variability of the dune systems as a basis for identifying potential habitats for vegetation, and suggests guidelines for identifying habitats.

Description of geomorphology, stratigraphy and soils

The Swan Coastal Plain is subdivided into 5 regional scale geomorphic units which are in narrow belts oriented north-south (McArthur & Bettenay 1960; Fig. 1). These units are: Ridge Hill Shelf - a landform underlain by Pleistocene laterite and sand; Pinjarra Plain - Pleistocene to Holocene fluvial landforms and sediments; Bassendean Dunes - undulating hills and degraded Pleistocene aeolian landforms underlain by yellow and white quartz sand; Spearwood Dunes - shallow to deep yellow quartz sand overlying shore-parallel ridges and depressions of Pleistocene aeolianite limestone (locally, there are ridges of yellow sand with little or no underlying limestone); and Quindalup Dunes - Holocene calcareous coastal dunes.

The Bassendean and Spearwood dunes dominate the longitudinally central part of the Swan Coastal Plain. Bassendean Dunes exhibit high relief (up to 80m above AHD) in the northern Swan Coastal Plain, and low relief in the south. Locally in both settings linear ridges and mounds of sand have a relief of 20-40m. In contrast, the Spearwood Dunes have a relief of c50-80m both in the northern and southern Swan Coastal Plain.

Geomorphologically, the Bassendean and Spearwood dunes can be subdivided into drylands and wetlands. Drylands can include dunes and interdunes. Dunes can be progressively subdivided into high dunes and low dunes, then into dune crests, dune flanks, and then into north flanks and south flanks. Similarly, interdunes can be systematically divided into thick sand sheets and thin sand sheets, then into sand sheets with a deep water table and sand sheets with a shallow water table. Alternatively, the dunes may be divided on geometry into simple linear dunes, composite linear dunes, sinuous linear dunes, star dunes, dome dunes, parabolic dunes, barchan dunes, and lunette dunes (Fig.1). Wetlands can be classified according to CASemeniuk (1987).

Stratigraphically, Bassendean Sand is equivalent to sands of the Bassendean Dunes, and Tamala Limestone is equivalent to the limestone portion of the Spearwood Dunes. The Tamala Limestone and Bassendean Sand interfinger along unconformity interfaces, the Bassendean Dunes may contain isolated lenses of limestone, and the yellow sands of the Bassendean and Spearwood dunes can be traced into each other (Fig.1). To date, the bulk of the yellow quartz sand

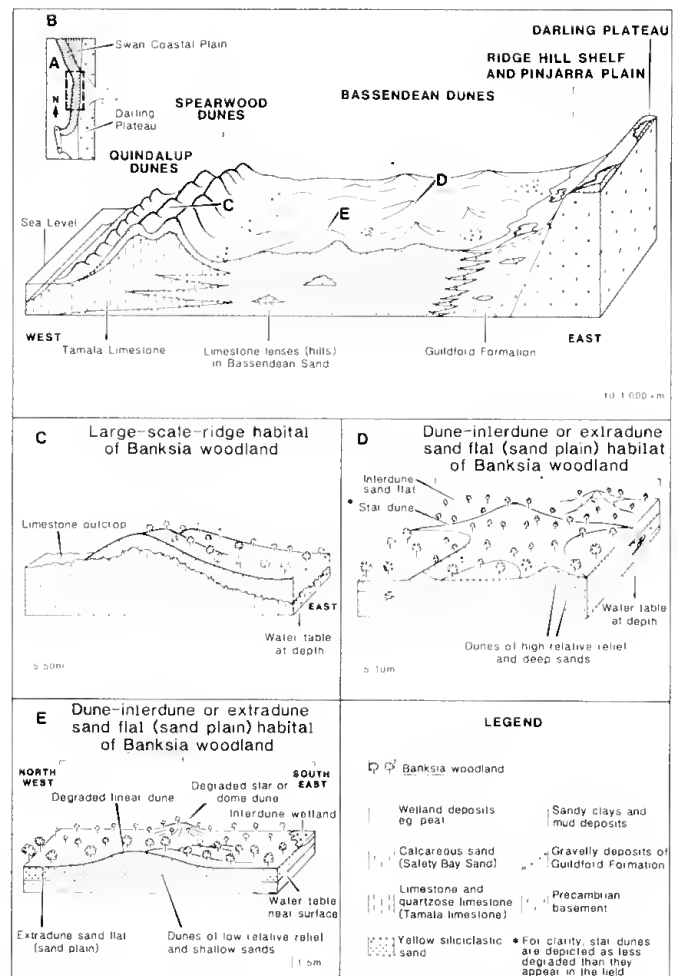


Figure 1 Schematic diagram showing distribution and relationships of the geomorphic units across the Swan Coastal Plain, the relationships between the underlying stratigraphic units, and details of the medium to small scale geomorphology of the Bassendean and Spearwood dunes as a basis for habitats of the *Banksia* woodlands. For details see Semeniuk & Glassford (1988) and Glassford & Semeniuk (1989).

overlying the Tamala Limestone has not been formally recognised as a separate formation, except in local areas (Glassford & Semeniuk 1989). Lithologically, yellow sands of the Bassendean and Spearwood dunes consist of quartz, feldspar, heavy minerals and kaolin. A goethite-stained coating of silt-clay sized kaolin and quartz on the grains imparts the yellow colouration (Glassford & Semeniuk 1989).

Information on the soils is difficult to review because the soil units have been inconsistently and imprecisely described, and inconsistently mapped; eg compare the definition of soil associations, series and phases (Bates & Jackson 1987; and discussion in Conacher & Dalrymple 1977), with the use of these terms in the local literature, and similarly, compare the various descriptions in map legends and texts of soil units which appear to largely overlap or be co-incident. Also, compare the different designations of landform-soil units near Mandurah (McArthur & Bettenay 1960, Churchward & McArthur 1980, McArthur & Bartle 1980), and the inconsistent location of the boundary of the Bassendean and Spearwood dunes in various maps. The definitions of the soil units do not differentiate between a stratigraphy resulting from complex and multiple pedogenic alteration, and the more simple, shallow products of pedogenesis superimposed on a complex primary stratigraphy, particularly where landforms are degraded, ie tending towards planation. Furthermore, primary sedimentary features and secondary alteration features frequently are not identified or separated. Further discussion of these aspects of landform-soil units of the Swan Coastal Plain are presented in Semeniuk (1989).

Soil and landform-soil units (Churchward & McArthur 1980) are the features most used by phyto-sociologists to correlate vegetation with physical setting, and so we summarise information on the soil units, without implication that we accept these subdivisions. Soils of the Bassendean Dunes are subdivided into Bassendean and Southern River soil associations. Bassendean soils occur on dunes and interdune sand sheets, and comprise deep grey sands with humic or ferruginous layers. Southern River soils are similar to Bassendean soils, but differ in the occurrence of sandy clay, clay and swamp deposits. Soils of the Spearwood Dunes are subdivided into Karrakatta and Cottesloe soil associations. Karrakatta soils comprise deep yellow sands over limestone, and are divided into yellow and grey soil phases. Cottesloe soils consist of exposed limestone, or shallow brown sands over limestone.

The deeper stratigraphy underlying the Bassendean and Spearwood dunes, rather than the actual surficial soils, has been the basis for subdividing soil units. Separation of soil types on the Spearwood Dunes has a genetic basis, ie yellow sand is assumed to be a residual soil derived by leaching from limestone, and depth of yellow sand is used as an index of soil development. If yellow sand overlying limestone has not formed by leaching in situ, the actual soils within the Spearwood dunes are humic and bioturbated surface alterations of a parent yellow sand of variable thickness (Glassford & Semeniuk 1989). However, even if it is assumed that yellow sands formed by in situ leaching, then these sands, which are mostly Pleistocene, are relict. Therefore, the parent material for present day soils is not limestone, but a relict, Pleistocene yellow sand. Accordingly, where limestone is covered by yellow sand, the soils of the Spearwood Dunes should be classed as humic and bioturbated quartz sand on a parent yellow sand. Where limestone is nearly exposed at the surface, the soils of the Spearwood Dunes should be classed as humic sands and rendzinas on limestone. Similarly, soils of the Bassendean Dunes have been separated on the basis of the stratigraphy underlying the dunes and interdunes, rather than on the actual surficial soils.

Vegetation habitats

The *Banksia* woodlands inhabit a dry, nutrient-poor, quartz sand terrain. In detail, other physico-chemical features may be habitat/vegetation determinants, particularly at the small scale (cf Semeniuk *et al* 1989). The following aspects can determine environmental conditions, and hence variations in habitats and understorey assemblages in the *Banksia* woodlands: location within dune type or interdune; depth to water table; aspect; organic soil development; kaolin content; Fe-mineral content; colour; thickness of bleached soil; moisture content in the vadose zone; and subsurface stratigraphic or pedogenic features, particularly for their influence on hydrology, and retention of water and nutrients. Some vegetation studies already have identified habitats, to various levels of detail, in terms of some of these edaphic features. Havel (1968) correlated vegetation types to some detailed edaphic information such as aspect, soil depth, soil moisture etc. Heddlie *et al* (1980) recognised landform and soil as determinants of vegetation floristics and structure, but did not proceed beyond correlating broad associations to the large scale geomorphic and soil systems of McArthur and Bettenay (1960) and Churchward & McArthur (1980). Cresswell and Bridgewater (1985) related vegetation associations within the Bassendean and Spearwood dunes to location on dune crests (tops), slopes, swales, an approach which effectively identifies location of habitat within dune terrain. However, we consider that to adequately address the variability of floristics in the *Banksia* woodlands of the Bassendean and Spearwood dunes, that phyto-sociologic studies should be undertaken in conjunction with a determination of the physical features listed above.

It should be apparent from the above, that the geomorphology, stratigraphy, and soils of the Bassendean and Spearwood dunes, in our opinion, have not been documented in sufficient detail, using modern systematic approaches, at the full range of large to fine scales. However, the development of an adequate descriptive framework of these physical features of the dune terrains should be an essential first stage requirement both for purposes of landscape ecological studies and for the identification of resource variability within *Banksia* woodland systems.

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Floristics of the *Banksia* woodlands

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Floristic studies are concerned with the botanical composition of vegetation. While the *Banksia* woodlands of the Swan Coastal Plain have been described in detail in recent vegetation surveys (eg Beard, this symposium, Hedde *et al* 1980), there is little published information on their floristic composition. The number of plant species in *Banksia* woodlands is relatively large and approaches that of kwongan (sclerophyllous shrublands), but is substantially lower than the Jarrah forest (Table 1). However, the *Banksia* woodland and kwongan values refer to individual vegetation types, whereas the Jarrah forest total covers a variety of vegetation types experiencing a range of topographic, edaphic and climatic factors. The limited data available suggest that species richness (species per unit area) of *Banksia* woodlands is less than in most heathlands (George *et al* 1979, Griffin *et al* 1983) but more than in some forest and woodland types such as Wandoo (Griffin & Hopkins, unpublished data from Mt Lesueur) and York gum/Wandoo (Lamont 1984). Milewski & Davidge (1981) recorded a cumulative total of 77 shrub species after sampling 52 consecutive 2 m² quadrats, while Dodd (unpublished) measured a mean richness of 28 shrub species and 3 tree species in 83 400 m² stands of *Banksia* woodland. The species richness is also very variable (16-53 species per stand; Dodd, unpublished), reflecting variation in edaphic, climatic and geographic factors (Havel 1968).

Broadly speaking, the *Banksia* woodlands are floristically representative of the State's south-western flora, since their dominant families and genera (measured by number of species) are also the dominant taxa throughout the south west. Although a large number of families is represented in *Banksia* woodlands, most species belong to only a few. The families of woody plants with the greatest number of species are the Proteaceae, Myrtaceae, Papilionaceae and, to a lesser extent, Epacridaceae (Table 1). Amongst non-woody plants, the most important families are the Orchidaceae, Cyperaceae, Haemodoraceae, Anthericaceae (part of Liliaceae *sensu lato*) and Asteraceae. These families, except the Orchidaceae, are also prevalent in kwongan. Indeed, the similarities are such in some areas that *Banksia* woodlands could be considered as kwongan with a *Banksia* canopy (but see Beard & Pate 1984). As in kwongan, some genera are often represented by several species within a single stand (eg *Banksia*, *Calytrix*, *Conostylis*, *Daviesia*, *Hakea*, *Hibbertia*, *Petrophile* and *Schoenus*). Other genera well represented throughout *Banksia* woodlands are *Acacia*, *Conospermum*, *Eremaea*, *Jacksonia*, *Leucopogon* and *Melaleuca*.

The dominant canopy species are *Banksia attenuata* and *B. menziesii*, with *Eucalyptus todtiana* and *Nuytsia floribunda* occurring less frequently. In some wetter stands, *B. ilicifolia* is present. In southern areas of the Swan Coastal Plain, *E. calophylla*, *E. marginata* and *Allocasuarina fraseriana* become increasingly important and, eventually, dominate (Beard, this symposium)

while *B. menziesii* is absent. *Banksia prionotes* may be present in some areas and is the dominant tree in woodlands on the Spearwood dunes near Jurien. The understorey shows much greater variation than the canopy. Species found commonly on both Bassendean and Spearwood dunes are *Bossiaea eriocarpa*, *Eremaea pauciflora*, *Gompholobium tomentosum*, *Hibbertia hypericoides*, *Lyginia barbata*, *Petrophile linearis* and *Xanthorrhoea preissii* (Dodd, unpublished). Some species occur frequently only on one dune system eg *Calytrix flavescens*, *Conostephium pendulum*, *Hibbertia subvaginata*, *Leucopogon conostephioides*, *Patersonia occidentalis* and *Scholtzia involucreta* on Bassendean dunes and *Mesomelaena stygia*, *Petrophile macrostachya* and *Leptospermum spinescens* on Spearwood dunes. None of these understorey or canopy species is exclusive to *Banksia* woodlands, however, and all can be found in other vegetation types, especially kwongan on sand. Many of the characteristic species also occur in the understorey of those coastal plain woodlands south of Perth, in which *Banksia* form a secondary canopy beneath *E. calophylla*, *E. marginata* and *A. fraseriana* (Griffin, unpublished). *Banksia* woodlands lack floristic uniformity and, instead, consist of a number of different floristic types. Very few species are consistently found throughout the range of these woodlands. Only 13% of understorey species from 45 Bassendean dune sites and 11% from 31 Spearwood sites were found in more than 50% of stands surveyed by Dodd (unpublished). Havel's (1968) study of the vegetation of part of the northern Swan Coastal Plain defined seven types of *Banksia* woodland which reflected differences in topography and soil depth, moisture characteristics and degree of leaching. The two main factors that determined floristic composition, namely the degree of soil leaching and the moisture availability of the site (Havel 1968), have been found to apply to *Banksia* woodlands throughout the coastal plain (Dodd, unpublished).

Conclusions

Despite their simple structure and seemingly uniform appearance, *Banksia* woodlands are floristically rich and taxonomically diverse. Floristically, they appear to have close affinities to the kwongan of regions north of the Swan Coastal Plain. The woodland understorey exhibits a high degree of variability indicating responses by the component species to a range of environmental variables, of which edaphic factors are the most important. At the same time, the canopy shows little variation in composition. Hence, on the basis of their understorey composition, *Banksia* woodlands can be divided into a number of floristic types (mostly undefined as yet) in terms of topography, soil type and moisture status and geographic location. The degree of floristic variation found in *Banksia* woodlands has significant implications for conservation, since adequate conservation requires that the range of variation should be represented in reserves.

Table 1
Floristic composition of *Banksia* woodlands and adjacent vegetation types

	Families	Genera	Species	Dominant families of woody plants			Reference
Banksia woodlands							
Jandakot	31	-	122	Myrt. (13/11)*	Papil. (8/ 7)	Prot. (7/ 6)	Epac. (7/ 6) 1
Perth region	45	122	236	Prot. (29/12)	Myrt. (19/ 8)	Papil. (17/ 7)	Epac. (11/ 5) 2
Perth region	57	-	377 ⁺	Prot. (33/ 9)	Myrt. (33/ 9)	Papil. (32/ 9)	Epac. (26/ 7) 3
Swan Coastal Plain	59	78	187	Prot. (33/18)	Myrt. (33/18)	Papil. (27/14)	Epac. (22/12) 4
Brookton	24	63	98	Prot. (23/24)	Myrt. (18/18)	Epac. (5/ 5)	Papil. (5/ 5) 5
Kwongan							
Mt Lesueur	43	131	287	Prot. (46/16)	Myrt. (33/12)	Papil. (28/10)	Mimos.(12/ 4) 6
Badgingarra	41	112	238	Prot. (51/21)	Myrt. (30/13)	Papil. (25/11)	Epac. (13/ 6) 7
Eneabba	50	162	429	Prot. (71/17)	Myrt. (55/13)	Papil. (27/ 6)	Epac. (19/ 4) 8
Eneabba	38	125	317	Prot. (61/19)	Myrt. (37/12)	Papil. (28/ 9)	Epac. (15/ 5) 9
Tutanning	-	-	315	Prot. (45/14)	Myrt. (30/10)	Papil. (23/ 7)	Epac. (11/ 3) 10
Other							
York gum/ Wandoo woodland	36	-	85	Mimos. (4/ 5)	Papil. (4/ 5)	Prot. (3/4)	Myrt. (3/4) 11
Coastal heath	66	192	413	Myrt. (56/14)	Prot. (42/10)	Papil. (21/ 5)	Mimos.(18/ 4) 12
Jarrah forest	95	-	784	Prot. (70/ 9)	Papil.(68/ 9)	Myrt. (63/ 8)	Mimos.(37/ 5) 13
<i>References:</i>				1 Milewski & Davidge 1981	8 Hopkins & Hnatiuk 1981		
				2 Speck 1952	9 Griffin <i>et al</i> 1983		
				3 Marchant <i>et al</i> 1987	10 Brown & Hopkins 1983		
				4 Dodd, unpublished	11 Lamont 1984		
				5 Beard & Hnatiuk 1981	12 Wills <i>et al</i> 1989		
				6 Griffin & Hopkins 1985	13 Bell & Heddle 1988		
				7 van der Moezel <i>et al</i> 1987			

*First value = number of species; second value = percentage of total species

⁺Habitat descriptions suggest occurrence in *Banksia* woodlands

Endemic and rare species have not been assessed fully for *Banksia* woodlands. A number of rare and endangered species are discussed by Hopper & Burbidge (this symposium).

Until the regional variation of *Banksia* woodlands has been documented fully, the adequacy of existing reserves for encompassing the variation remains unknown.

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Water relations of *Banksia* woodlands

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Introduction

The interaction of the climate, soils and geology of the Swan Coastal Plain has an important bearing on the water relations of *Banksia* woodlands. The coastal plain experiences a dry Mediterranean climate (Beard 1981) with 5-6 dry months each year and receives 86% of annual rainfall between May and October. The deep, leached sands that support *Banksia* woodlands have an extremely low water holding capacity and, consequently, virtually no water is available from the top few metres of soil during the summer months. Paradoxically, the presence of groundwater, usually at several metres depth, provides a potentially unlimited water supply for those deep rooted plants capable of reaching it.

Water use by *Banksia* woodlands

Water use by *Banksia* woodlands and other native vegetation is estimated to return 70-90% of average annual rainfall to the atmosphere through evapotranspiration and therefore has a significant impact on the amount of water available to recharge the groundwater body. Net recharge of groundwater, estimated to vary from 9% to >30% of annual rainfall depending on location, is affected by plant water use since a) plants remove water from the soil profile, preventing that water - which arrived as rain - from reaching the groundwater body; and b) some plants with deep tap roots make direct use of groundwater. Net recharge is greatest at upland sites where the water table is many metres below ground surface, and virtually inaccessible to even the deepest root systems.

Rooting depth and root system morphology determine which source of water is utilized by plants. Excavation of the root systems of shrub and tree species from *Banksia* woodlands demonstrated a diversity of rooting types and a range of rooting depths (Grieve 1956, Dodd *et al* 1984). At Gnangara, shallow root systems that penetrated up to 1 m were the commonest, being found in 25 of the 43 shrub species examined, including *Acacia pulchella*, *Calytrix fraseri*, *Eriostemon spicatus*, *Bossiaea eriocarpa*, *Hibbertia aurea*, *H. helianthemoides* and several species of *Leucopogon*. Medium-depth root systems that penetrated 1-2 m were found in eight of the species, including *Gompholobium tomentosum*, *Scholtzia involucreta*, *Adenanthos cygnorum* and *Conostephium pendulum*. Woodland plants with shallow or medium depth root systems would depend on profile-stored water. Deep tap roots, potentially capable of reaching ground water, were found in 13 species, including *Banksia attenuata*, *B. menziesii* and *B. ilicifolia*. *Daviesia triflora*, *Jacksonia densiflora*, *Petrophile linearis*, *Calytrix flavescens*, *Melaleuca scabra*, *M. seriata* and *Stirlingia latifolia* (Dodd *et al* 1984). This diversity of rooting depths and

morphologies allows virtually complete occupation of the soil profile and leads to exhaustion of soil moisture reserves by late summer.

The moisture requirements of a large number of *Banksia* woodland species have been defined by Havel (1968). The trees *Melaleuca preissiana*, *Eucalyptus marginata*, *Banksia littoralis* and *B. ilicifolia* occur in moist sites near swamps, in depressions and on lower dune slopes. *Banksia attenuata* and *B. menziesii* characterize the drier upper slopes and dune crests, while *E. todtiana* and *Nuytsia floribunda* show no distinct preference. Havel (1968) also defined a number of understory species as indicators of particular combinations of site moisture characteristics, soil type and topography. The moisture requirements of the indicator species are reflected in the site conditions which they characterise.

Responses to annual fluctuations in water supply

The various seasonal patterns of transpiration and water stress which have been measured in a range of *Banksia* woodland trees and shrubs closely reflect plant rooting depths and, consequently, the nature and longevity of the water supply (Grieve 1956, Dodd *et al* 1984). At a site with a water table at 6-7 m depth, high transpiration rates and relatively low levels of water stress were measured throughout summer in the deep rooted *Banksia attenuata*, *B. menziesii*, *Stirlingia latifolia*, *Daviesia triflora* and *Petrophile linearis*, indicating continuous access to groundwater. *Eremaea pauciflora* and *Jacksonia densiflora* also showed these features until the abrupt onset of severe water stress in mid summer, which was due possibly to their roots losing contact with the falling water table. Deep rooted plants are not obligate users of groundwater, however, since some of the species exhibited reduced transpiration with relatively high levels of water stress during summer at other sites which lacked accessible groundwater (Grieve 1956, Grieve & Hellmuth 1970). Shallow rooted species generally showed severe water stress during summer, the early onset and severity reflecting the shallowness of the root system and the exhaustion of moisture reserves in the soils above the groundwater body (Dodd *et al* 1984). One consequence of these differences in water relations is that maximum transpiration occurs during spring and early summer in the understory, but during summer in the canopy.

Responses of vegetation to changes in water availability

Havel (1968) demonstrated that soil moisture conditions and the degree of soil leaching are the main determinants of the composition of the vegetation of the Swan Coastal Plain. This study involved detailed measurements of species composition and

plant cover at a large number of *Banksia* woodland sites on the northern Swan Coastal Plain in the mid-1960s, before the start of groundwater extraction and, therefore, constitutes a major base-line survey for subsequent ecological investigations. Havel's sites included nine transects which ran from swamp to dune crest, covering the range of topographical situations characteristic of the coastal plain. Four of these transects have been re-surveyed, first in 1976 (Hedde 1980) and at 1-3 year intervals subsequently, while several additional transects have been established to permit monitoring over a wider range of sites, including some close to groundwater pumping bores. Over the study period, since 1966, the Swan Coastal Plain has experienced a drought with 15 years receiving below average rainfall.

The results reveal certain trends in soil moisture conditions and in the vigour and composition of *Banksia* woodlands. There has been a reduction in soil moisture contents and a lowering of the water table on a regional scale throughout the coastal plain. At the same time, soils of the upper slopes and crests of dunes have remained relatively dry. This drying of coastal plain soils has been largely due to a reduction in annual rainfall. Land-use changes and groundwater pumping have also had an impact at some locations. Changes in vegetation include:

- a shift to drier types of vegetation with reductions in some tree and understorey species which tolerate wetter soils, eg *Eucalyptus marginata*, *Banksia littoralis*, *Hypocalymma angustifolium* and *Regelia ciliata*. This has been accompanied by replacement of older and larger trees with seedlings since 1966, as in *B. littoralis* and *B. ilicifolia*. Some trees, such as the paperbarks (*Melaleuca* spp), have responded to drought by producing additional stems. In contrast, at sites where soil moisture conditions have remained relatively stable, the composition and vigour of the canopy have been maintained.
- many species which tolerate drier soils or which are not site-specific in occurrence have maintained or increased their abundance. These include *Banksia attenuata*, *B. menziesii*, *Gompholobium tomentosum*, *Hibbertia subvaginata* and *Leucopogon conostephioides*.
- certain short-lived understorey species have declined, probably because of the lack of suitable conditions for germination and establishment.

Many of these changes had been predicted in earlier studies by Aplin (1976), Havel (1975) and Hedde (1980). The major cause of these changes in the *Banksia* woodlands has been the long-term drought which has caused a lowering of water table levels and has affected vegetation on a regional scale. The extraction of groundwater has added to these effects in sections of the Gnangara Mound.

Responses to ground water extraction

Many of the vegetational changes likely to be associated with groundwater pumping have already been observed as responses to long-term, regional drought. The major differences

would relate to the rapidity, extent and permanence of ground water draw-down, which would affect the banksias and a number of the understorey species. The majority of species are independent of groundwater, however, and should be little affected by pumping. Even where adult trees are killed, replacement from seed and from suppressed seedlings will occur, leading eventually to restoration of woodland. The resulting vegetation would probably have fewer and smaller trees and would resemble undisturbed woodland on dry, upland sites. In order to predict the effects of groundwater extraction and water table lowering in greater detail, further information is needed on the extent of groundwater use by the plants of the Swan Coastal Plain.

Conclusions

Plant species of the *Banksia* woodlands exhibit a variety of physiological responses to changes in water availability. Amongst many understorey species, the intensity of water stress is inversely related to rooting depth. This relationship does not hold for the canopy banksias and certain deep rooted shrubs which utilize groundwater at some sites and which are independent of soil-stored moisture. Knowledge of the water relations of plants from *Banksia* woodlands provides insights into the adaptations of plants in a Mediterranean-type environment and has helped explain the results of long-term monitoring, which in turn can be used for predicting the changes likely to occur in vegetation of the Swan Coastal Plain as a result of continuing droughts and/or increased groundwater extraction. Water use by existing vegetation is a major component of the water balance of the Swan Coastal Plain and is, therefore, of direct relevance to planning the development and management of the plain's groundwater resources.

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Fire in the *Banksia* woodlands of the Swan Coastal Plain

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Introduction

As is the case for most remnants of native vegetation in south western Australia, fire is an important management consideration for the *Banksia* woodlands of the Swan Coastal Plain. The proximity of these woodlands to the major urban and semi-rural developments within the State ensures that issues of fire protection have considerable prominence. Yet despite the ease of access for study purposes and the importance of effective fire management of these woodlands, relatively little is known of their fire ecology. In this paper we review briefly relevant information on this aspect and seek to provide guidelines for future management and research.

Historical burning

Judging by the records of observations compiled by Hallam (1979), there were concentrations of aboriginal people around the estuaries of the coastal plain from Moore River to Albany and perhaps further afield. These people did use fire: charcoal associated with artifacts in the Upper Swan archaeological deposit gave dates of almost 40 000 years (Pearce & Barbetti 1981).

The establishment of the Swan colony in 1829 would almost certainly have led to changes in frequency, intensity, seasonality, and spatial distribution of fires (regime, *sensu* Gill 1975, Hopkins 1985a). The nature of these changes can only be speculated although it is probable that useful information exists in various historical accounts. Some fire records have been kept by the Wanneroo District Office of the Department of Conservation and Land Management over the past 30 years; these show that there have been some fuel reduction burns, mainly in spring, and some wildfires, mainly in autumn and recurring at intervals of about 6-8 years.

Fire fuels

Burrows & McCaw (in press) have constructed fuel accumulation curves on the basis of extensive sampling of the *Banksia* woodlands in the Wanneroo area. After c 6 years the total available fuel stabilized at between 6 and 8 tonnes ha⁻¹ oven dry weight. These levels of fire fuels seem surprisingly low especially when compared with total above-ground biomass of *Banksia ornata* woodland at Keith, South Australia (460 mm annual rainfall) (Jones *et al* 1969). The curves, together with information on fire behaviour in these fuel types, suggest that repeated fuel reduction burning on a broad acre basis would be of limited practical value (Burrows & McCaw in press).

Effects of fire on plants

To provide this overview on the effects of fire regimes on the *Banksia* woodlands, we have focussed on selected aspects of the biology of the component species. This has enabled us to piece together the results of studies of fire on *Eucalyptus-Banksia-Allocasuarina* woodland at King's Park (Baird 1977), on *Banksia* woodlands at Mooliabeenee east of Gingin (R J Hobbs unpubl data) as well as studies on other aspects of *Banksia* woodlands (eg Dodd *et al* 1984).

The plant communities that now make up the *Banksia* woodlands of the Swan Coastal Plain contain very few long-lived perennial plant species that regenerate only from seed following 100% crown scorch (Table 1). Only 6 of the 13 species identified are in the most vulnerable category (Hopkins 1985b), being fire sensitive and having seed storage on the plant in brady spores. This feature, together with the general observation that significant areas of *Banksia* woodlands apparently in good condition still exist, indicates that the present-day plant communities comprising these woodlands must be tolerant of a wide range of fire regimes.

Generalizations about the impact of recurrent fire on the *Banksia* woodland communities could be developed by collecting data on the time it takes for species in Table 1 from germination of seed to production of sufficient, viable seed to permit population replacement in the event of a further fire. In the absence of detailed data, a rough guide of 2.5 to 3 times the time from germination to first flowering can be applied as a minimum between-fire interval if local extinctions are to be avoided (*cf* Gill & McMahon 1986).

There are no data from these *Banksia* woodlands that indicate best season of burn for conservation but the study of *Banksia burdetti* at Watheroo National Park by Lamont & Barker (1988) may be indicative. That study shows best seed release, germination and establishment after a hot fire in late summer/autumn.

Season of burn also has some bearing on fire intensity. Burrows (1985) showed that the extent of death of stems of *Banksia grandis* in the jarrah forest was a direct function of fire intensity: hotter fires kill more stems. A similar effect could be expected for *Banksia* spp on the coastal plain.

A conspicuous, complicating factor in the process of developing management guidelines is the likely invasion of burnt areas by weeds. As Keighery (this volume) points out, weeds are commonly associated with disturbed sites including many with a history of recurrent fire (see also Baird 1977, Bridgewater &

Backshall 1981). Not only does weed invasion lead to loss of nature conservation values, it also can lead to a vicious spiral of degeneration of the vegetation through recurrent burning because the presence of weeds alters the characteristics of the fire fuel bed, engendering an increase in flammability.

Fire and animals

The other important interaction associated with fire is between plants and animals. Whelan & Main (1979) showed how grasshoppers can modify regenerating vegetation by grazing selectively on seedlings and presumably on other types of shoots. The impact of herbivores is particularly acute after small and/or patchy burns.

Bamford (1986) also looked at effects of fire on invertebrates but more in terms of their role as a food resource for the vertebrates. Bamford's study area was east of Gingin but supported *Banksia* woodlands similar to those of the Swan Coastal Plain. He found that a spring fire reduced invertebrate numbers more than an autumn fire and suggested that the impact would be greatest on diurnal, terrestrial invertebrates and that this would have particular repercussions for the reptiles. This was not obvious in the trapping results; indeed the vertebrate fauna generally appeared to have coped quite well with the historical fires of the study area and the experimental fires. However, Bamford (1986) did observe that there had been some extinctions (three species of birds and perhaps some mammals) from the Swan Coastal Plain north of Perth which may be a consequence of the frequent, intense and extensive fires associated with European settlement (see also Bamford & Dunlop 1984).

The interaction between fires and weeds is also relevant when considering fauna. How & Dell (this volume) observe a decline in open area feeding reptiles with the invasion of the open areas by weeds. As noted above, weed invasion can be promoted by recurrent burning.

Concluding remarks

Because of the extensive clearing and disturbance of the *Banksia* woodlands of the Swan Coastal Plain these woodlands are now at a point where effective conservation and management is critical. Despite their proximity to Perth, these *Banksia* woodlands have been neglected scientifically; this applies as much to the issue of fire - its effects and its use in management - as to the many other important aspects of their biology. There is a real need to redress this situation.

In respect of fire alone, the present-day plant and animal communities of the *Banksia* woodlands appear to be relatively robust. They contain few plant species that we could describe as vulnerable. The fauna has also been shown to tolerate a certain regime of fire. We have, of course, no real insight into the extent of and reasons for disappearances of species from the Swan Coastal Plain in historical times. This apparent robustness is no justification for continuation of *laissez-faire* management; further species losses and degeneration are likely consequences of such an approach.

It would be a relatively simple matter to develop fire management guidelines for these *Banksia* woodlands starting with the gathering of data on rates of regeneration of vulnerable plant species provided that we are prepared to accept the rule of thumb suggested here as the basis for those guidelines. However, such an approach does not take into account the important interaction that we have identified here - that is the interac-

tion between fire (or any other form of disturbance) and weed invasion. Fire has the potential to promote weed invasion which in turn leads to increases in flammability of the vegetation and the loss of nature conservation values. This fire-weed interaction is probably the most important issue to be taken into account in the development of any fire management strategies in the future.

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Table 1

Long-lived perennial plant species which occur in *Banksia* woodland communities on the Swan Coastal Plain (from the list compiled by Griffin & Dodd for this symposium) and which are killed by fire causing 100% canopy scorch and which regenerate only from seed.

Species with seed storage on plant	Species with seed storage in soil
<i>Banksia prionotes</i>	<i>Adenanthos cygnorum</i>
<i>Dryandra sessilis</i>	<i>Astroloma xerophyllum</i>
<i>Hakea trifurcata</i>	<i>Leucopogon striatus</i>
<i>Hakea obliqua</i>	<i>Leucopogon cordatum</i>
<i>Beaufortia elegans</i>	<i>Lysinema ciliatum</i>
<i>Beaufortia squarrosa</i>	<i>Astroloma heterophyllum</i>
	<i>Acacia pulchella</i>

Terrestrial invertebrate fauna

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Introduction

The interactions between certain plant and invertebrate species in *Banksia* woodlands have been reviewed by Byron Lamont in this Symposium. This paper reviews what little information is known about the invertebrate communities of this plant formation. It is arranged in the following way. First, some thoughts on the species composition of invertebrate communities in *Banksia* woodlands are presented. This is then followed by a review of the effects of disturbance on certain components of the invertebrate fauna. Next, the few remaining invertebrate community studies which have been carried out in this vegetation formation are reviewed and, finally, a prognosis for the conservation of *Banksia* woodland invertebrates is presented.

Invertebrate communities in *Banksia* woodland

In simplistic terms, the *Banksia* woodlands consist of small trees of about 6-8 m under which there is a well developed sclerophyll shrub understorey. This formation tends to be bounded on the western edge by tuart (*Eucalyptus gomphocephala*) open-forest and to the east by jarrah (*E. marginata*)-marri (*E. calophylla*) open forest. Both of these formations have a well developed tree stratum of at least 25 m height and, like the woodlands, the latter of the two formations has a well developed shrub understorey. The *Banksia* woodland therefore differs from the adjoining formations in lacking a taller *Eucalyptus* tree stratum, and from the tuart open-forest in possessing a well developed shrub layer. The majority of the woodlands occur on the older Bassendean dune system which, in comparison with the adjoining soils, has soil of poorer nutrient status. Taking these factors into account, it is likely that the invertebrate community of the woodlands may differ from that of the adjoining plant formations.

There are few published accounts of the composition of individual invertebrate faunas in *Banksia* woodland and nearby plant formations. Abbott (1982) surveyed earthworm distribution in the Perth metropolitan area. He found seven native species, of which only two were confined to undisturbed habitat, principally woodland or swampland. The other species were also found in habitats which had been modified by humans. In reviewing the literature on earthworm distribution on the part of the Darling plateau close to Perth, Abbott (1982) found seven additional species which were absent from the metropolitan coastal plain area. It therefore appears that the coastal plain earthworm fauna differs substantially from that of the Darling plateau and this may be associated with differences in climate, soil type or other factors.

Rosbach & Majer (1983) surveyed the composition of the ant fauna in two coast-to-Darling Range transects which ran through the various plant formations. They found that while

many species occurred in a range of plant formations, some were confined to one type such as the *Banksia* woodland. An ordination of the various sites in terms of their ant species composition indicated that the jarrah-*Banksia* woodland sites had a characteristic ant fauna, which was allied to that of the tuart open-forest and the *Banksia*-sheoak (*Allocasuarina fraseriana*)-prickly bark (*E. todtiana*) woodland. The ant fauna of the woodland differed from that of the coastal scrub and the Darling plateau open-forest. On the basis of this rather limited information on invertebrate species composition in various plant formations, it seems likely that the overall invertebrate fauna of *Banksia* woodland is to some extent distinctive, although many species would probably be shared with adjacent plant formations.

Although not peculiar to the *Banksia* woodlands, the invertebrate fauna of this region also exhibits a strong seasonality. Koch & Majer (1980) and Majer & Koch (1982) compared the seasonality of surface-active invertebrates at Reabold Hill in tuart-jarrah woodland, where some *Banksia* spp. were present, with that of jarrah open-forest at Dwellingup and Manjimup.

Their data indicated that the various functional groups exhibited seasonal patterns which differed between the woodland and forests in their time or length of activity. This is well illustrated by the variation in duration of activity of slaters (Isopoda), a group which is involved in the decomposition of litter. The duration of activity increased progressively from Reabold Hill to Dwellingup to Manjimup, being restricted to the wetter months at Reabold Hill and Dwellingup, but active throughout the year at the southern-most site. This trend appears to be related to the duration of rainfall, which is least at the Perth site.

Effects of disturbance

John Beard has already pointed out that some 61% of *Banksia* woodland is now alienated land where the original vegetation has largely been cleared. A number of studies have looked at the effect of habitat modification on selected invertebrate groups in what was formerly *Banksia* woodland.

Springett (1976a) looked at the species richness and population density of soil microarthropods in three *Pinus pinaster* stands at Gnangara and compared this with densities in the native woodland of the area. Whilst the species richness of selected microarthropod taxa was generally halved by replacing the woodland with pines, the density of microarthropods in the pines was in the same range as that of the woodland. Accompanying decomposition studies indicated that the less species-rich soil fauna of the pine plots was unable to decompose pine or sclerophyll litter as fast as the fauna of the woodland.

Another fate of *Banksia* woodland is urbanization. Majer & Brown (1986) surveyed the ant fauna in 33 Perth gardens, most of which were situated in former woodlands. They found that

ant species richness was significantly reduced in gardens when compared to native vegetation. By quantifying the makeup and management practices of each garden and correlating these parameters with the ant fauna, they found that the variety of the ant fauna was enhanced by the length of time the garden had been established, by increasing the size of the garden and by providing a thick leaf litter and ground cover. Gardens where pesticides were used, where tall shrubs were dense or where management practices such as watering were intense, had a depauperate ant fauna. In view of the fact that the variety of ants tends to reflect that of other invertebrate groups, these conclusions might also apply to other components of the invertebrate fauna.

The remaining *Banksia* woodlands are subject to a number of pressures. One is the invasion of woodland by veldt grass (*Ehrharta calycina*). Barendse *et al.* (1981) surveyed the spider fauna of King's Park and found that areas colonized by veldt grass harboured a spider fauna of low abundance and species richness. Presumably this is either because the veldt grass occupies the feeding space which is normally used by spiders or because it harbours less invertebrate prey items than the native vegetation.

A widespread influence on *Banksia* woodlands is burning so, not surprisingly, a number of studies have been performed on this phenomenon.

Springett (1971, 1976b) looked at the effect of fire on soil fauna in woodland at Gngangara which had been replaced by pines. Discussion of this study is outside the scope of this paper. Around the same period Bornemissza (1969) described post-fire changes in the soil fauna within the woodlands of King's Park. Although this was an extensive long-term study, only an abstract of the results was ever published. It concludes that changes in numbers and species composition could be detected up to 5 years after a fire.

Whelan, Langedyk & Ashby (1980) and Bamford (1986) looked at the effects of burning on surface-active invertebrates. Pitfall trapping was employed in both of these studies. The former study, which was performed near Jandakot, found that invertebrate catch increased in the immediate post-fire period. Although this was in part an artifact of the sampling method, it does highlight the ability of a large component of the invertebrate fauna to survive a fire. Concurrent hand collections performed by Whelan *et al.* (*op cit*) revealed that many animals survived the fire by congregating in the crowns of *Macrozamia riedlei* and *Xanthorrhoea preissii* or under fallen logs.

Bamford's (1986) study was performed at Mooliabeenee and looked at both short-term (< 1 year) and long-term (1-22 years) impacts of fire. His monthly data collected within a year of burning indicated that spring burning had a greater impact on the 'ant' and 'other invertebrate' categories than did autumn burning. In the long-term, ant numbers declined to lower levels after reaching a peak one year after burning, while 'other invertebrates' progressively increased with time after fire as the litter layer built up. A more restricted program of sampling the understorey foliage invertebrates produced higher numbers 6 years after burning than those obtained after 23 years. This trend could be associated with the stimulation, and later the senescence, of vegetation after fire.

The relationship between invertebrates and post-fire plant succession was examined in more detail by Whelan & Main (1979). This work was carried out in small and large area burns near Jandakot. Whilst grasshopper invasion was rapid in the smaller burnt areas, grasshoppers were absent from the larger areas for 1-2 years after fire. This absence of grazing grasshoppers allowed escape of seedlings from predation, while in the smaller areas the susceptibility of seedlings to grazing was influenced by the relative palatability of species.

Other studies

Davidge's (1979) study of the herpetological community of a *Banksia* woodland near Jandakot included an analysis of the diets of the various frogs and lizards. Analysis of gut contents revealed that with the exception of the frog *Myobatrachus gouldii*, a termite specialist, all species were opportunistic feeders which fed on a wide range of prey items including vertebrates, plant material and sixteen categories of invertebrates.

The only other published community study from *Banksia* woodland which I am aware of is Bornemissza's (1957) analysis of arthropod succession in carrion. This study, which was carried out in King's Park, identified five different stages of carcass decomposition and these were correlated with the animal communities present in the decomposing tissue. Bornemissza also looked at the reinvasion of the carrion zone by soil arthropods and found that this was not complete after one year.

Conservation of *Banksia* woodland invertebrates

This review of the literature on terrestrial invertebrates has indicated how community composition can be altered by urbanization, veldt grass invasion, the frequency and season of burning, as well as by clearing of the original woodland for some new land use. Therefore, if the conservation of invertebrates in *Banksia* woodlands is to be catered for, we need to consider if, when, and how frequently to burn such areas and we also need more information on the impact of weed invasion on the terrestrial invertebrate fauna.

The fragmentation of the remaining woodlands by agriculture, roads, urbanization and other land uses is also reason for concern. However, unlike vertebrates, the conservation of relict areas of only a few hectares in size can be adequate to preserve almost all the invertebrate species of the community (Key 1978). This, of course, assumes that the relict areas are managed in an appropriate way to maintain environmental quality.

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Vertebrate fauna of *Banksia* woodlands

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Banksia woodlands with their floristic richness, extensive flowering regimes, juxtaposition to other vegetation formations and extensive distribution on deep near-coastal sands are important for vertebrates. However, no vertebrate species is unique to *Banksia* woodlands.

Amphibians

Nine species may occur in *Banksia* woodlands (Davidge 1979, Murray 1980, Bamford 1986, A H Burbidge pers comm, How & Dell unpubl). Most require water for larval development, consequently their entire life cycle cannot occur in *Banksia* woodlands; they are captured throughout the year after rain, but activity peaks in spring (How & Dell unpubl).

The two arboreal hylid species (*Litoria moorei* and *L. adelaidensis*) are seldom found far from water and thus occur as transients and then only peripherally in *Banksia* woodlands. Species of the leptodactylid genera *Heleioporus*, *Limnodynastes*, *Pseudophryne* and *Ranidella* also depend on water, but have the ability to burrow while *H. eyrei* and *L. dorsalis* have been caught in *Banksia* woodlands several kilometres from the nearest water.

The Turtle Frog *Myobatrachus gouldii* has direct development, ie no tadpole stage is involved (Watson & Saunders 1959, Roberts 1981), and is independent of water for its development making it the only species capable of surviving entirely in *Banksia* woodlands.

Reptiles

Studies of major geographic regions (Kitchener *et al* 1980, McKenzie *et al* 1987) have found that few, if any, reptile species have disappeared since European settlement. The goannas *Varanus gouldii*, *V. rosenbergi* and *V. tristis* have become less numerous in *Banksia* woodlands due to habitat fragmentation and changing resource availability and there are no recent records of the Carpet Python *Morelia spilota*.

Two arboreal geckos, *Diplodactylus spinigerus* and *Phyllodactylus marmoratus* are widespread and abundant, while the terrestrial, *D. polyophthalmus* and *D. ornatus* are infrequently recorded (Davidge 1979, Murray 1980, Bamford 1986). Agamids whose distributions encompass the extent of *Banksia* woodlands (*Pogona minor* and *Tympanocryptis adelaidensis*) are recorded on most sites, however, *Banksia* woodlands occur outside the main geographical distribution of most geckos and agamids.

Skinks are the richest family with 10 genera. The arboreal *Cryptoblepharus plagioccephalus* is widespread and common as are the terrestrial *Ctenotus fallens*, *C. lesueurii*, *Lerista elegans*, *Menetia greyi*, *Morethia obscura*, *M. lineocellata*, *Tiliqua rugosa* and the fossorial *Lerista praepectata*. Several species in *Banksia* woodlands are near the limits of their range; these include *Ctenotus impar*, *C. schomburgkii*, *Egernia multiscutata*, *Lerista christinae*, and the rare *L. lineata*. It is probable that *Leiopisma trilineatum*, *Egernia napoleonis* and *Omolepida branchialis* only occupy those woodlands adjacent to denser and moister vegetation types. *Hemiernis quadrilineata* and *Lerista lineopunctulata*, appear to be more common in woodlands occupying the coastal Spearwood Dune systems.

The blind snake *Ramphotyphlops australis* occurs in many *Banksia* woodlands and elapid snakes are recorded in most *Banksia* woodlands that have been sampled for more than a year. Bamford (1986) recorded *Demansia reticulata*, *Notechis*

curtus, *Rhinoplocephalus gouldii*, *Vermicella calonotus* and *V. bertholdi* at Mooliabeenie while at Bold Park (How & Dell unpubl) *V. bertholdi*, *V. calonotus*, *V. bimaculata*, *V. fasciolata* occur sympatrically with *Pseudonaja affinis*. The diversity of *Vermicella* can be explained by the abundance of fossorial and epigaic lizards which constitute their principal food source.

The composition of the reptile assemblage reflects the sandy substrates of *Banksia* woodlands. Genera that are fossorial (eg *Lerista* and *Vermicella*) are well represented, while those that use burrows (eg *Diplodactylus* and *Egernia*) are poorly represented. Litter inhabiting genera (*Hemiernis*, *Morethia*, *Menetia*) occur in most habitats, although this is correlated with time since fire (Bamford 1986).

In some isolated patches of *Banksia* woodlands extensive weed invasion (Keighery this publ) covers the ground between shrubs. This has severely impinged on reptiles which forage in the open between bushes eg *Tympanocryptis adelaidensis* and *Ctenotus lesueurii*. Dense rooting patterns may also inhibit the movement of near-surface fossorial species.

Birds

Bird studies have focussed on the importance of *Banksia* species to the maintenance and structuring of both nectar and insect feeding groups and entire assemblages.

Bamford's (1986) detailed study on *Banksia* woodlands of different ages after fire provides the most detailed account of the annual composition of the avifauna. Bamford recorded 86 bird species within his study area at Mooliabeenie; 17 were principally birds of *Banksia* woodlands, 48 occurred in both woodland and adjacent farmland and 21 occurred principally in cleared farmland. Of the 86 species, 19 were migratory or present for only part of the year, 24 were rare or uncommon vagrants, 35 showed marked seasonal variation and 8 slight variation in numbers. The strong seasonality in bird numbers of these *B. menziesii*/*B. attenuata* woodlands resulted principally from migratory species, particularly insectivores, moving in towards the end of spring to make use of increased invertebrate availability.

Honeyeaters showed a bimodal peak in numbers of individuals (Bamford 1986) that corresponded to the peak flowering of *B. attenuata* (Dec.-Jan.) and *B. menziesii* (June-July). Insects are taken by all honeyeater species (Tullis *et al* 1982, Collins 1985) and form an important protein source, while nectar is the principal energy source. Tullis *et al* (1982) indicated the importance of *Banksia* woodlands to honeyeaters in winter, but their study only covered the period April-July. Newland & Wooller (1985) compared nectar feeding and insectivorous honeyeaters and other insectivores in *Banksia littoralis* woodland and adjacent *B. menziesii*/*B. attenuata* woodland. They present important data on the flowering phenologies of *Banksia* and understory species in explaining contrasting richness and abundance in honeyeaters over the year. *B. littoralis* had more species and individuals during the winter, when peak nectar occurred; adjacent woodlands had more constant numbers throughout the year resulting from overlapping flowering times of the dominant species. Large and moderate sized honeyeaters predominated in *B. littoralis* woodland while smaller species dominated in other *Banksia* woodlands.

Migratory insectivores, eg Bronze Cuckoos, Bee-eaters, move into *Banksia* woodlands to take advantage of seasonal peaks in arthropods, while resident insectivores, eg thornbills,

silvereyes, retain relatively constant numbers throughout the year with fluctuations in numbers attributed to recruitment of the young (Newland & Wooller 1985).

Most resident species breed during winter-early spring so that food resources are maximized for nesting and breeding when energetic costs are greatest.

Banksias themselves infrequently develop hollows consequently, parrots and cockatoos that are dependent on tree hollows for nesting rely on adjacent eucalypt woodlands, or use hollows in the few emergent eucalypts in *Banksia* woodlands.

Fire in *Banksia* woodlands advantages those species which prefer to forage in open vegetation (Bamford 1986). These are generally colonizing species that can take advantage of modified environments. Small resident species, especially insectivores, are disadvantaged by a loss of the structurally diverse and dense understory species after fire. These birds are generally those that need special conservation measures since they are susceptible to local extinctions after major environmental modifications.

Storr & Johnstone (1988) presented a list of birds of the Swan Coastal Plain and commented on status changes since European settlement. Unlike birds of other associations, such as Tuart forests and woodlands fringing lakes, *Banksia* woodland birds have not declined to the same extent.

Mammals

Range reductions of mammals since European settlement have been attributed to several causes, principally habitat alteration, changed fire frequency and predation. (Kitchener *et al* 1978, How *et al* 1987). Consequently, the fauna of *Banksia* woodlands has probably changed substantially since European settlement.

The most abundant and widespread mammal in *Banksia* woodlands is the introduced Mouse *Mus domesticus*. Other species that have established feral populations since European settlement and which also occur in *Banksia* woodlands are the Black Rat *Rattus rattus*, Red Fox *Vulpes vulpes*, Ferret *Mustela putorius*, Cat *Felis catus*, and European Rabbit *Oryctolagus cuniculus* (Kitchener *et al* 1978). The Dingo *Canis familiaris*, Tamar *Macropus eugenii*, Quokka *Setonix brachyurus* and Woylie *Bettongia penicillata* may all have used *Banksia* woodlands but are unlikely to maintain viable populations in these habitats.

Of the small native semi-arboreal mammals, the Honey Possum *Tarsipes rostratus* occupies many *Banksia* woodlands, while the Western Pigmy Possum *Cercartetus concinnus* may also occur in woodlands that have remained unburnt for a long period. Small native terrestrial mammals are never abundant in this habitat, although 3 species of dunnart, *Sminthopsis dolichura*, *S. griseoventer*, *S. granulipes* and the Ashy-grey Mouse, *Pseudomys olbocinereus*, have been recorded in the more northern woodlands (Murray 1980, Bamford 1986).

Little is known of the bats occupying *Banksia* woodlands as no systematic surveys have been done. However, the Lesser Long-eared Bat *Nyctophilus geoffroyi* frequently roosts under the bark of dead *Banksia* trees (Kitchener *et al* 1978). The Echidna *Tachygllossus aculeatus* probably feeds on termites within and adjacent to these woodlands. Similarly, the marsupial carnivore Chuditch *Dosyurus geoffroyi* may have foraged in *Banksia* woodlands and adjacent areas. The Brushtail Possum *Trichosurus vulpeculo* occurs in *Banksias* only where there are emergent eucalypt trees that provide the necessary hollows for dens; there are no records of this possum feeding on *Banksia* flowers, fruit or leaves. The Quenda *Isodon obesulus*, occurs in *Banksia attenuata*/*B. menziesii* and swamp *Banksia* (*B. littoralis*) woodlands where these surround ephemeral swamps and lakes.

The effect of fire on small mammals in *Banksia* woodlands has been documented by Bamford (1986). Fire coupled with habitat fragmentation, has greatly reduced the range and abundance of most species. Recent work in three isolated *Banksia* woodlands within the metropolitan area show that *Mus domesticus* occurs in all three and *Isodon* in only one (How & Dell unpubl) despite the apparent suitability of these woodlands for other species.

Conclusions

The vertebrate fauna occupying *Banksia* woodland consists of species that generally have distributions focussed on the south-west of the state with its Mediterranean type climate. The great majority of vertebrates breed in late autumn to early summer and the young become independent when food is most abundant. Several species of reptile are more characteristic of semi-arid and arid parts of the state, and frequent more northern *Banksia* woodlands where the higher temperature and sandy soils are determining factors. Similarly some arid-zone bird species are moving into areas where *Banksia* woodlands occur adjacent to cleared land.

Strong patterns of seasonal abundance are apparent in many species and these result from different causal mechanisms. For highly mobile bird species, numbers fluctuate in response to changing food resources such as nectar or insects. Reptile abundance reflects changes in temperature, while seasonality in amphibians is associated with changing temperature and moisture regimes. Mammals show only slight seasonal patterns that generally reflect recruitment into the population after breeding.

Unlike many eucalypts, *Banksia* trees do not readily form hollows in limbs or trunks, consequently, species such as parrots and Brushtail Possums, which are obligate hollow users, seldom occur exclusively in *Banksia* woodlands. Land clearing and fire have both affected the composition of vertebrate species occupying *Banksia* woodlands. The frequency and time since burning can be shown to have a pronounced effect on species composition; species dependent on vegetation that has been unburnt for long periods have been greatly reduced since European settlement.

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Biotic and abiotic interactions in *Banksia* woodland

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Introduction

The aim of this synopsis is to explore interrelationships between representative plant species in banksia woodland and their environment. The two species selected are *Banksia menziesii* and *Adenanthos cygnorum*. Both are characteristic species of the Swan Coastal Plain, but extend further north on the coastal sands and, to a lesser extent, south-east in sandy pockets on the plateau (Nelson 1978, Taylor & Hopper 1988).

Banksia menziesii

This banksia flowers in winter, when few other species are available for nectar-dependent animals, especially honeyeaters (Newland & Wooller 1985). Florets open in response to foraging by honeyeaters (Ramsay 1988). These birds probably play a major role in pollen transfer as this species is self-incompatible (Scott 1980). There is minor consumption of pollen by staphylinid beetles (Ramsay 1988), while specialist moth and weevil larvae may feed on the flower heads (Scott 1982). Insect damage affects fruit set markedly. Cockatoos may feed on these larvae, giving some biological control (Cowling, Lamont & Pierce 1987, Lamont & van Leeuwen 1988).

Less than 1% of florets produce follicles, for various reasons (Fig. 1). A beetle larva feeds only on the seed of *B. menziesii* (Scott 1982). This banksia stores little seed in its canopy, although the proportion increases northwards, corresponding to an increase in likelihood of fires reaching the canopy to release the seed (Cowling & Lamont 1985). Otherwise, mature seed is released in late autumn. The seed and young seedlings are highly nutritious (S Holman & B Lamont unpubl) and are eaten by granivores and herbivores (Fig. 1; Whelan & Main 1979, Cowling & Lamont 1987). Seedling establishment is negligible in the absence of a post-fire seed bed, and rare even in its presence (Cowling & Lamont 1987). This is an evolutionary tradeoff with the ability of the parent plants to resprout after fire. The first summer drought plays a major role in seedling death, but there are other causes as well (Fig. 1).

Adult trees harbour many small animals, providing food and shelter, although there are no details in the literature (Fig. 1). Whole branches sometimes die and the loosened bark and dead wood are sources of food and shelter for additional small primary consumers, carnivores and parasitoids. *B. menziesii* is one of the few species susceptible to a minor disease which causes a coralloid distortion of the branches. The symptoms are consistent with invasion by a mycoplasma carried by cicadelloid leafhoppers, but the phenomenon has received no study.

The leaves drop after 4-5 years. The litter serves as food and shelter for decomposers but the rate of decomposition is extremely slow. Proteoid roots from the surface laterals grow up into the fresh litter. These hairy rootlets probably short-circuit the nutrient absorption path by adhering directly to the litter particles and promoting nutrient release (Lamont 1986). The proteoid roots mat the surface soil and increase its stability for geophytes and other small plants, but make inter-fire seedling establishment less likely. The sticknest ant, *Iridomyrmex conifer*, uses the litter for nest-building and is a major 'robber' of banksia nectar - it is believed to site its nest near nectar-rich trees (R P MacMillan, pers comm).

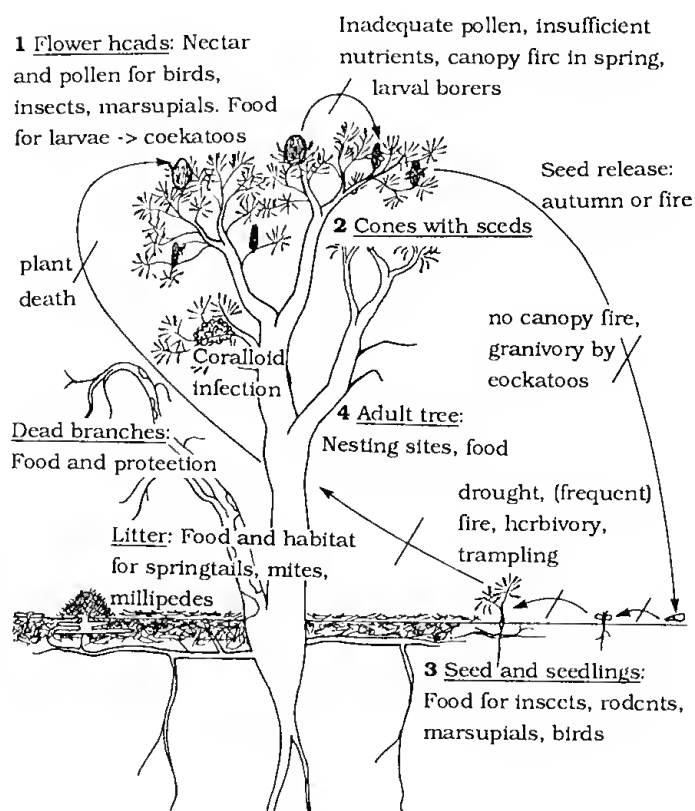


Figure 1 Interactions between *Banksia menziesii* and other components of banksia woodland on the Swan Coastal Plain. Line through arrow refers to inhibition of the process.

Adenanthos cygnorum

The woolly bush has many unusual features which give it a special place in the ecology of the region. It is a colonizer of soil- and fire-disturbed sites, growing as a thicket. This species is the tallest shrub and yet one of the few to be killed by fire. Unlike *B. menziesii*, the woolly bush flowers from spring to autumn, and has a major role in maintaining resident nectar-feeding birds throughout the year (Newland & Wooller 1985). The single flower is immersed in a terminal whorl of leaflets whose overlapping hairs, together with the constricted neck of the perianth, prevent access to nectar-robbing ants (Fig. 2). About 1.3% of the flowers are converted to fruits whose fate may follow three paths: (a) The green fruit is eaten by parrots on the plant. (b) The bracts surrounding the fruit open out pushing the leaflets into a cup from which the fruit drops to the ground (Fig. 2). Here it is eaten by granivorous birds and probably rodents. (c) The fruit usually remains in the cup where it is visited by ants. Most ants remove the fruits to their nests where they consume the basal elaiosome (Lamont & Grey 1984).

The fruits remain dormant until the soil is disturbed or a fire occurs. Presumably in response to a change in the temperature regime (Brits 1987), most then germinate during the next winter from an average depth of 35 mm. As with banksias, drought probably greatly influences eventual recruitment into the new stand, but this has not been studied directly. Apart from the cotyledons, the foliage is fibrous and probably not very attractive to herbivores. However, there is a specialist phytophagous moth, *Xylorycta* sp., which webs together the terminal leaves. It is preyed upon by a parasitoid wasp, *Campoletis* sp. Seven of 10 xyloryctid pupae we hatched yielded these ichneumonid wasps (Grey & Lamont unpubl).

The first leaves of the new season's branchlets in mature shrubs bear extrafloral nectaries on their tips (Fig. 2). Seventeen species of ant, as well as the *Campoletis* sp. and other nectar-seeking insects, visit these glands. The nectaries are a reliable, albeit small, source of sugar for the predatory ants and wasps throughout the year. The location of the elaiosome-bearing fruits and xyloryctid larvae respectively are secondary and irregular events for these insects, but vital in maintaining the fitness of this species. *A. cygnorum* tends to collapse as it senesces and is readily invaded by termites which eventually consume the woody stems after death, before or after fire.

Discussion

There are major obstacles to the completion of one phase and commencement of the next in the life cycle of these two indicator species of banksia woodland. None of the threats to this fine balance as imposed by nature in the past are of the same order as currently caused by wholesale clearing for urban and rural expansion. For the remnants that escape the bulldozer, new obstacles remain, such as fertilizer and herbicide application or drift, weed invasion, *Phytophthora* dieback disease, trampling by hooves and shoes, frequent fire and unprecedented changes in soil water levels. As outlined here, the demise of these two species alone will take with them many dependent animals, to varying degrees. Although the honeyeaters readily switch to new nectar sources, some of the plant-insect relationships outlined here appear to be obligate. From a biological point of view, there is much to commend the conservation of this threatened ecosystem.

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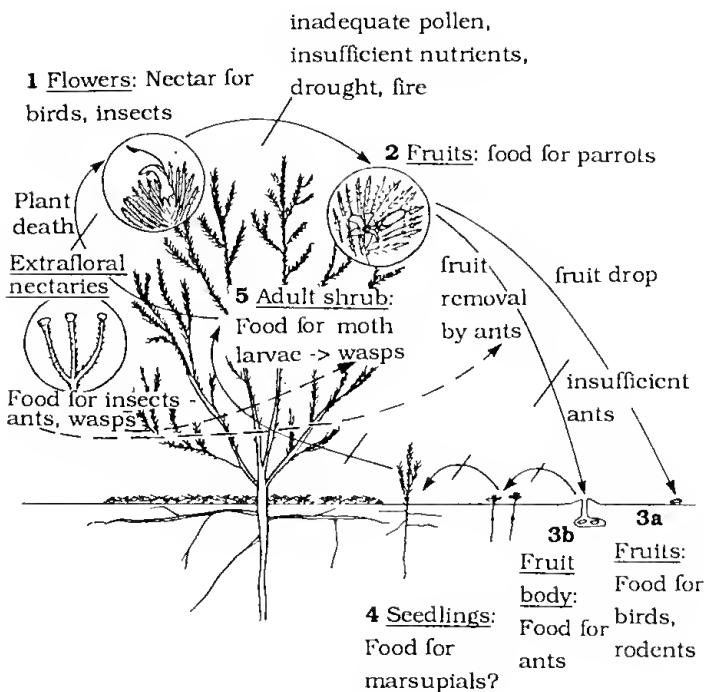


Figure 2 Interactions between *Adenanthos cygnorum* and other components of banksia woodland.

Management of groundwater resources for protection of native vegetation

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Introduction

The Perth region, which has a population well over one million people, is underlain by significant fresh and brackish groundwater resources. These resources play a very significant role in the lifestyle of the people who live in the area. The increasing demand for these groundwater resources among competing users is requiring more effective planning and management strategies.

Water Authority activities have considerable potential to impact on wetlands and *Banksia* woodlands, as direct impacts from the provision of water services such as the construction of water and sewer mains and the less obvious impacts from the management and development of the groundwater resources.

The Resource

Underlying the Swan Coastal Plain to depths of 14 km are large groundwater resources. These occur as the unconfined water-table aquifers which constitute the major Gnangara and Jandakot groundwater mound systems and as confined groundwater. Recharge to these systems is directly from rainfall. Some of the confined groundwater is artesian to the extent that pressure heads are above the land surface.

Whilst these groundwater sources are relatively large, at least in the local context, the increasing demands are such that careful management is required to ensure equitable use and to protect water quality. Unlike many other commodities, management of Perth's groundwater resources is undertaken in accordance with the concept of sustainable yield as defined under the State Conservation Strategy (Department of Conservation and Environment 1987).

The concept of sustainable yield applies particularly to fresh resources and requires that abstraction is maintained within limits that can be sustained in perpetuity without adverse effects on the beneficial uses of the resource.

Current Water Use

Total water consumption within the Perth region (between Gingin and Rockingham) is close to 400 million m³ annually of which approximately half is supplied by the Water Authority and the remainder is extracted by private users (Webster 1989). In 1985, 262 million m³ were obtained from groundwater sources of which 206 million m³ were extracted privately and the remainder was pumped by the Water Authority from public water supply areas.

The importance of the shallow unconfined aquifer can be seen by the fact that of the 262 million m³ of groundwater used some 223 million m³/annum were from the shallow aquifer.

This water is used for a range of purposes, namely private domestic irrigation, local authority and institutional parks and gardens, Water Authority public supplies, horticulture and industrial and commercial purposes.

Other important users of the shallow unconfined groundwater in the Perth metropolitan region are the wetlands and the areas of lowland vegetation including *Banksia* woodlands.

Future Water Use

The Source Development Plan for future development of water supply sources for Perth's public water supplies identifies sources for the next 25 years of Perth's development (Water Authority of WA 1987). Within this plan, groundwater sources continue to play a prominent role, with groundwater being expected to contribute in similar proportion to the current one-third of the total public supply.

By the year 2000, based on current trends, it is estimated that the total water consumption in the Perth metropolitan region could be close to 550 million m³/annum of which 350 million m³/annum could come from groundwater resources.

The value of these resources is considerable. If the fresh shallow groundwater resources in the Perth region were valued entirely in terms of their potential for public water supply, their net present worth would be in excess of \$1000 million. Their value in terms of other potential uses would be less in some instances, and more in others. The value in environmental terms is difficult to estimate but relates at very least to the high value of the quality of life that we enjoy in Perth.

The importance of groundwater to existing future public water supplies lies in its proximity to centres of demand. For example, the Gnangara Mound is adjacent to the North West Corridor, and its attribute of large storages compared to replenishment rates allows water to be borrowed from these storages in drier periods.

There are, however, some quite contrary aspects to these positive attributes. The proximity of groundwater to the urban demand centres is seeing pressure for the urban development to move onto the primary groundwater source areas with the consequential threats of degradation of these sources. The need to maintain groundwater levels within limits necessary to support environmental requirements is requiring the Water Authority to review its use of unconfined groundwater as a drought protection strategy and to review its policy of firm licensed allocations to private users. These conflicting requirements of the groundwater resource increase the need for management of not only the water resources but of the land uses in the surrounding area.

The main pressure regarding groundwater quantity relates to the increasing competition from the users of these resources.

Groundwater Allocation Strategy

Deciding how to manage groundwater resources to meet increasing competition is not easy. In broad terms, the competing uses are public water supplies, private use, and the environment. It is thus a matter of determining how a finite resource can be shared equitably between the users.

In the past, the management of water resources of the State has been undertaken largely through the proclamation of water resource management areas ie Catchment Areas, Water Reserves, Groundwater Areas and Public Water Supply Areas. This provides the Water Authority with statutory mechanisms to ensure that activities do not degrade the quantity and quality of water and to allocate the resource.

To a large extent, the proclamation of water resource management areas has also allowed for protection of the environment. A good example of this is the Gngangara Water Reserve. This area of 835 km² on the Gngangara Mound between Gngangara Road and Gingin Brook was proclaimed in 1973. Although a considerable proportion of this area is pine plantation, the largest part is either State Forest or vacant crown land which is mainly vegetated with *Banksia* woodland. Large areas of the Gngangara Mound *Banksia* woodland are now proposed for more secure vesting in the Department of Conservation and Land Management's latest regional management plan-eg Carabin, Wabling and Yeal Nature Reserves (CALM 1987). Without the proclamation which was originally aimed at protecting the water resource, some of these areas would probably have been subdivided for agricultural purposes.

Because of increasing competition for a limited resource, management of water resources is now significantly more complicated. Satisfying this emerging competition and resolving the conflicts are the fundamental objectives of the water allocation process. This process will become increasingly complex as community water demands grow.

For water allocation strategies to be successful, they will need to become part of a wider strategic plan. The traditional approach of allocating water to specific individual users for specific purposes needs to become part of a process of developing regional land and water resource strategy plans.

These strategy plans should include a hierarchical process that will ensure adequate protection of the water resource for the intended uses. The highest level within this hierarchical process should be allocation of priority beneficial uses to the water resources of a region or basin. Such an allocation defines the primary desirable use or uses for a specific water resource in the long term.

These priority beneficial uses fall into two broad categories of:

- environmental and recreational uses; and
- consumer uses (public and private water supply).

The next level of allocation should specify the bulk allocations for particular uses within the identified priority beneficial use. An example of bulk allocation within the consumer uses category is between public and private water supplies where the usage by each is broadly constrained within specified annual abstraction volumes.

The lowest level of allocation that has been actively used in resource management is the individual user allocation or licenced allocation.

It is proposed that these water allocation principles will be embodied into a Environmental Protection Policy under the Environmental Protection Act, for the Gngangara Mound. This will offer greater protection to both the water resource and the environment.

Protection of Lowland Vegetation

The Water Authority is very aware of its responsibility to manage groundwater levels to protect the environment. The Minister for Environment has set a number of conditions on the next phase in the development and management of the Gngangara Mound groundwater resources. These conditions are founded on ensuring adequate conservation and management of wetlands. In protecting wetlands, they also protect lowland vegetation surrounding wetlands.

Future extensions of wellfields on the Gngangara Mound are aimed at keeping wells in upland areas where the vegetation is not dependent on the water table for its water supply.

The Water Authority now monitors a significant number of vegetation transects on both the Gngangara and Jandakot Mounds. Monitoring commenced on some of the 14 sites in the Gngangara Mound as early as 1966 when the Forests Department established four transects. The monitoring has so far shown that climatic factors have the major effects on the *Banksia* woodlands with many areas being drought affected in recent years and succession occurring from water loving species to more drought resistant species. (Mattiske & Associates 1988).

Certainly there have been some dramatic effects on local areas in the vicinity of wells which must be attributed to pumping. These are now being carefully monitored. It appears the main reason for *Banksia* deaths was the sudden drop in water table level occurring soon after the commissioning of wells. The Water Authority is looking at means of avoiding this such as developing the full yield for new wells over more than one year to give the trees time to adapt to lower water tables. An additional new transect has also been established radiating out from one of the new Pinjar bores to monitor the effect of the pumping strategy.

Five vegetation transects have recently been established on the Jandakot Mound to provide baseline monitoring as part of the Environmental Impact Assessment for the Jandakot Groundwater Scheme Stage 2. Developing environmental criteria for valued areas of the environment including *Banksia* woodlands in Jandakot area is a key component of the early stages of this environmental assessment.

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Urban development

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There is little doubt that urban growth and consolidation will result in deterioration of many of the natural plant communities along the Swan Coastal plain, even though the people responsible for directing that urban growth may do their utmost to protect these plant communities (or at least representative samples) through the various legislative powers that are available.

To illustrate the methods of controlling urban expansion, some history of regional planning needs to be outlined.

In 1955, the State Government commissioned consultant town planner Gordon Stephenson to prepare, in conjunction with the Town Planning Commissioner, Alistair Hepburn, a regional plan for Perth and Fremantle. This was the state's first attempt at regional planning. It did little for the *Banksia* woodland areas, other than identify them as suitable for "development as woodlands and forests".

The Stephenson Hepburn Plan, formed the basis of the Metropolitan Region Scheme, which was gazetted in 1963. As a statutory Scheme, it was the first in Australia, and is still the basis for urban development and expansion within the Perth area. It zones land for industrial, rural and urban uses and reserves land for a variety of purposes, including parks and recreation.

As a policy guide to identify future expansion needs for Perth, the Corridor Plan was adopted in 1970. This, although somewhat controversial, set down the basis for a series of urban corridors. The rural wedges between the corridors will experience significant pressures from growth that will affect the remaining areas of *Banksia* woodlands.

During the late 1970s a Conservation-through-Reserves Committee was established by the Department of Conservation and Environment in an attempt to identify those areas of Western Australia that needed to be protected from development. The Darling System, System 6, covered the Perth area. Recommendations made in the System 6 study have been endorsed by the State government, and will eventually be recognised in the Metropolitan Region Scheme. Several areas contain *Banksia* woodlands, but generally the wetlands received greater attention by this committee.

The future expansion of the region is now being re-examined as a result of a formal review of the Corridor Plan. This review is examining the various choices available for the region's future growth. These are:

1. Continued corridor growth as outlined in the Corridor Plan.
2. Peripheral Expansion.
3. Easterly Expansion.
4. Coastal Expansion.

In order to make these decisions, there must be some awareness of the nature of the expansion and the constraints. The following gives a broad basis for understanding the growth rates applicable to the Perth region.

- The region's population will continue to grow at a rate of between 1.5 and 2% or some 30 000 people per year. This means an increase in excess of 800 000 people by the year 2021.

- Residential development is the largest consumer of land, requiring some 12 000 lots per annum or 1 500 ha.
- There will be a need for up to 50 000 extra ha of land by the year 2021.
- 97% of the metropolitan population lives in the urban zone.
- There is expected to be a decline in the average number of persons per household from 2.84 in 1986 to 2.51 in 2001 and 2.38 in 2021.
- The North west corridor is experiencing the highest rate of lot consumption comprising nearly 25% of the metropolitan total.
- Increased population and urban expansion will place further pressure on the finely balanced and limited capacity of the metropolitan environment.

The team undertaking the corridor review is using a constraints mapping system to identify that land most suitable for urban development. The various constraints to development were identified and mapped. These include environmental constraints such as:

- The geomorphology of the coastal plain (V Semeniuk & D K Glassford - This publication).
- The water resources. The groundwater resources in particular are a constraint to further urban development, and a bonus to the further protection of the *Banksia* woodlands (J Kite & K Webster - This publication & J S Beard - This publication).
- The natural vegetation (J S Beard - This publication). There is some natural vegetation remaining on the coastal plain, but even this is often contaminated with weed species, and dieback disease (G J Keighery - This publication, S D Hopper & A H Burbidge - This publication).
- Significant landscape. These landscapes have been identified and plotted, and are considered of sufficient importance to be protected where possible. It is expected that the Metropolitan Region Scheme will be the primary vehicle for this protection.

The above constraints and others were used in the preparation of a comprehensive constraints map and, as a result of this, areas for urban expansion were identified.

The planning process does not stop there, as it involves public participation through submissions from individuals and groups that have studied the published concepts. These submissions will influence the final decisions on the future patterns of urban development.

There are two choices available for future urban expansion in Perth. Either, the environmental and planning recommendations are adhered to and development is restricted to the already established urban corridors, and therefore protect the wetlands and the *Banksia* woodlands from urban development, OR peripheral urban expansion is allowed, which will result in eventual destruction of the wetlands and woodlands.

Obviously every effort will be made to follow the first option, and to use the Metropolitan Region Scheme to reserve the valuable environmental areas between the urban corridors. The Proposed Metropolitan Parks system, outlined in Figure 1, is the preferred means of protecting these areas. One wonders, however, just how much protection will be forthcoming, given the

Impact of horticulture on *Banksia* woodlands

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Introduction

Horticultural production in Western Australia was valued at \$200M for the year ending 30/6/87 of which 44% (\$90M) was vegetables, 35% (\$70M) fruit and 20% (\$40M) nurseries and cut flowers. The sands (Spearwood, Karrakatta and Bassendean) are important soils for the production of vegetables, flowers and to a lesser extent fruits such as citrus, avocados and strawberries. The alluvial soils of the Pinjarra plain such as the neutral red earths (Belhus) in the Guildford/Swan area are preferred for the production of grapes.

About 40% of Western Australia's vegetables (2 726 ha) are grown on these sands in the Perth region (Moore to Serpentine River) of the coastal plain. The area planted to fruit on the sands (including some grapes) is much less significant being currently c 4.0% of total State plantings (301 ha). It has increased substantially in recent years with a big increase in plantings of avocados (45% of WA) and citrus (especially oranges) near Gingin (20% of WA). There are about 360 ha of nurseries and flower crops (both sheltered and field plantings) representing about 36% of the State total.

Most of the vegetables grown in the region are exported. They set the quality standard in Asia and distinguish the Swan Coastal Plain as one of the most important of vegetable production regions in the southern hemisphere.

In this paper we summarize the impact of horticulture on the coastal plain, make some projections for the future, and discuss what is currently being done to reduce problems and minimize any in the future.

Current Management and Impact

Total area

The total area of land in the Perth region of the coastal plain (Moore to Serpentine Rivers) is 380 000 ha or about 34% of the total area of the coastal plain (1.125 Mha)(Allen 1981). Nearly 80% of the total area (c 300 000 ha) of the plain in the Perth region is sands (Bassendean, Karrakatta, Spearwood). The area of sands under horticultural crops in the Perth region is around 3 400 ha or just over 1.0% of the total area. This is small compared with the area of other activities such as urbanization and pine forests which currently cover c 55 000 and 22 000 ha respectively. The impact of horticulture on other components of the system (soils, water) is now considered.

Soil

Physical properties

The soils of the *Banksia* woodlands have little natural structure. The negative impact of horticulture on the structure of the Bassendean, Karrakatta and Spearwood sands has therefore been negligible. In fact the structure of these sands has almost certainly been improved by extensive additions of organic amendments such as poultry manure (10-100 m³ ha⁻¹).

Clearing land usually exposes the soil to erosion of some type (wind, water). The Bassendean (Jandakot, Joel, Gavin) sands have developed on wind blown material thus they are particularly vulnerable to wind erosion following the removal of vegetative cover. Sprinklers are used to stabilize sandy soils during windy periods to prevent sand blasting of tender seedlings or rendering leafy vegetables unmarketable through direct wind damage or sand. There is some use of artificial windbreaks such as Paraweb® for protecting vegetable crops on the coastal plain but little use of trees.

Chemical properties

The sands of the coastal plain are highly leached and therefore very infertile in their natural state with the Bassendean and Karrakatta sands being more infertile than the Spearwood sands. Almost all the macronutrients (N, P, K, S, Mg, Ca) and micronutrients (Cu, Zn, Mn, B, Mo, Fe) regarded as essential for plant growth must be added as inorganic or organic fertilizers for the production of vegetables, fruits and exotic flowers on the coastal sands.

In addition these sands have low capacity to adsorb cations and anions. As these nutrients readily leach, it is not possible to build up a nutrient bank in these sands to any extent and regular applications of fertilizers for crop production are required. The sands differ in their capacity to adsorb P with the Bassendean sands having the lowest adsorption capacity (< 2 ppm P) and the Spearwood sands the highest (10-15 ppm P) (Ozanne & Shaw 1967). Nutrients not used by the crop are prone to leaching from the soil into ground and surface waters. This problem is exacerbated by over-irrigation. Bassendean and Karrakatta sands have been extensively leached of CaCO₃ and have low pH (≤ 5.0-6.5) in their natural states. These soils require liming prior to fruit and vegetable production as only a limited number of crops are productive at low pH (potato, sweet potato, watermelon, rhubarb). The Spearwood sands are not as leached and are normally neutral to alkaline in reaction in their virgin state. Regular liming of Bassendean and Karrakatta sands is necessary to maintain pH when used for vegetable production.

As the coastal sands have low capacity to hold either water or nutrients, salt build up is not a problem since it is readily leached.

Water

Quantity

The annual consumption of groundwater from the superficial aquifer was 223x10⁶ m³pa in 1985/86 of which 38x10⁶ m³ (17%) was for irrigated agriculture. The quantity used for horticulture is c 32x10⁶ m³ or c 15% of total ground water consumption. Thus the impact of horticulture on total water supplies is much greater than on total land area (c 1%) in the Perth region. The future of horticulture on the Swan coastal plain depends on an adequate supply of good quality (≤ 500-750 mg salts L⁻¹)

ground water. Currently about 66% of the total annual renewable recharge of groundwater in the superficial aquifers in the Perth region is consumed ($337 \times 10^6 \text{ m}^3 \text{ pa}$). Much of the remaining 33% in the superficial aquifers would also be suitable for irrigation of most crops.

Quality

Groundwater sources in the Jandakot and Wanneroo licence areas are used for blending with dam water for drinking. Fertilizers leached from horticultural properties on sands may lead to increased levels of nutrients in ground water especially when irrigation is in excess of soil water holding capacity. Nutrients of most concern are nitrate, sulphate and salt.

Nitrate and sulphate

High levels of nitrate in drinking water have led to health problems such as methaemoglobinaemia in infants. Thus upper limits (10 mg L^{-1} , $\text{NO}_3 \text{ N}$) are put of the level of nitrate considered safe in water destined for human consumption. Nitrate is very mobile in soils and is leached even in heavily textured soils. There is a positive correlation between urbanization, horticultural activities and nitrate levels in groundwater in the superficial aquifers on the Swan Coastal Plain (Cargeeg *et al* 1987). Nitrate in groundwater is higher ($> 10 \text{ mg L}^{-1} \text{ NO}_3 \text{ N}$) under suburbs with a high incidence of septic tanks (eg Applecross). Vegetable production has been implicated in high levels of nitrate found in some bores ($1.29 \text{ mg L}^{-1} \text{ NO}_3 \text{ N}$) in the Gwelup groundwater area. Nitrate levels in water outside the urban areas is well below potable limits. Sulphate (SO_4) concentrations in excess of 400 mg L^{-1} are considered unsafe for drinking. High concentrations of sulphate ($> 200 \text{ mg L}^{-1}$) have been recorded in groundwater near the coast between Woodman Point and Kwinana. This is probably associated with industrialization rather than any other activities. Fertilizers applied to vegetables may have resulted in elevated sulphate levels in the groundwater in some bores in the Gwelup area. Nevertheless these were well below potable limits of 400 mg L^{-1} .

Salt

High salt in water ($\geq 500\text{--}750 \text{ mg L}^{-1}$) severely limits the range of crops than can be grown. Very few vegetable crops (Asparagus, Silver beet) can tolerate high salinity. The best quality water ($< 150 \text{ mg salt L}^{-1}$) occurs at the crest of the Jandakot and Gnarara groundwater mounds. Salinity increases ($> 500 \text{ mg L}^{-1}$) from the crest of the mound to the coast. By far the biggest risk to the quality of groundwater in the Perth region of the coastal plain is the intrusion of the salt water wedge in coastal areas due to overpumping from the large number domestic (88 000) and agricultural bores.

Surface Waters

Oligotrophic surface water systems such as estuaries, rivers and lakes are characterized by low levels of P (ie usually $< 0.1 \text{ mg L}^{-1}$). These systems are vulnerable to eutrophication if P inputs increase substantially. P L^{-1} leached from soils where fertilizers have been applied to agricultural (pastures) and horticultural (vegetables) crops in the catchments of the Harvey, Murray and Serpentine Rivers have been implicated in the eutrophication of the Peel Inlet and Harvey Estuary. Whilst most (85%) of the P originates from fertilizers applied to agricultural land about 5% originates from vegetable land and 10% from intensive animal (piggeries, sheep holding yards) industries. Given the high rates of P applied to horticultural crops such as vegetables ($30\text{--}120 \text{ kg P ha}^{-1} \text{ crop}^{-1}$) cf pastures ($8.5 \text{ kg P ha}^{-1} \text{ yr}^{-1}$; Kinhill Engineers 1988) any large scale expansion of horticultural activities on sands with very low P absorption capacity (eg Bassendean sands) could see this quantity increase substantially. At present horticultural crops are grown on 536 ha representing 0.26% of the coastal plain portion of the catchment area. Only a small percentage of wetlands of the *Banksia* woodlands are close to their pristine condition (Halse

1988). Almost all the remaining wetlands are nutrient enriched ie P concentration of water in excess of 0.04 mg L^{-1} (Chalmers & Davis 1988). Horticulture along with intensive animal enterprises, industry and urbanization has contributed to this nutrient enrichment and associated algae pollution.

Future Impact and Management

Horticultural production in Western Australia is predicted to at least double by the year 2011. The greatest impact will be on the water resources (both quantity and quality) of *Banksia* woodland.

Water quantity

Demand for groundwater will intensify considerably above the current $32 \times 10^6 \text{ m}^3 \text{ pa}$ with the predicted expansion in horticulture. Horticulture will most likely be forced to access more unconfined groundwater either further north (Lancelin) or south (Scott River). Confined water from the Leederville and Yarragadee formations may increasingly be used for horticulture although supplies from this source are much smaller than the unconfined sources. Growers will be pressured to improve their efficiency of water use through crop selection and irrigation management. Improved irrigation management will also aid in the reduction of nutrient leaching. Movement of horticulture especially vegetables greater distances from the metropolitan area will increase costs (freight) and reduce quality (especially leafy vegetables).

Fertilizer Management and Water Quality

Increased horticultural production will increase the pressure on groundwater and surface water quality.

Improved fertilizer management to reduce nutrient pollution of ground and surface waters of the coastal plain is a major challenge facing horticulture currently. Fertilizers have not traditionally been a major production cost (c 5-15% of direct costs of production) in horticultural crops and growers have tended to oversupply fertilizers since the financial penalties of under fertilization, especially with vegetables, are severe. Growers will be pressured to increase their efficiency of fertilizer management as water pollution presents a major cost to the community. Management strategies likely to be employed include preservation of better quality soils (Spearwood rather than Bassendean sands) for vegetable production, more regular fertilizer applications in smaller quantities (compared with less frequent and larger applications) to more closely match nutrient supply to crop demand and the use of soil and plant testing to monitor fertilizer programmes. The use of amendments high in Fe and Al oxides and hydroxides such as 'red mud' (Barrow 1982) and lateritic loams to increase the P absorption capacity of the Bassendean and Karrakatta sands may also be included in a strategy to minimize the impact of horticulture of the ground and surface waters of the coastal plain. Improved irrigation management (as mentioned above) will be an integral part of this programme.

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Forestry and *Banksia* woodlands on the Swan Coastal Plain

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Introduction

From earliest settlement days the forests and woodlands of the Swan Coastal Plain were heavily exploited for their wood resources. The target species was jarrah used for fuel and pit sawn and later milled for heavy structural timber. Tuart was revered for its structural qualities and since early days has been managed for special timbers for flooring and waggon construction. Tuart management and preservation was a major concern of early forest management and State forests 1 and 2 were established for this purpose. *Banksia* was used as firewood but was of secondary interest.

Early Management

Apart from tuart management the first organized forestry attention saw the Coastal Plain as an opportunity to grow pines and reduce the heavy costs to the Colony of importing softwoods. For this purpose the Spearwood and Bassendean Dune systems offered the following advantages:

- 1 The apparently otherwise "worthless nature" of much of the woodlands for alternative economic purposes (ie for agriculture, urbanization).
- 2 The close proximity to the main centres of development (wood markets).
- 3 Relatively gentle topography and cheap clearing costs for plantation establishment.
- 4 The example of afforestation with *Pinus pinaster* in a climate and on sands considered to be similar in the Gascony region of France during the period 1781 to 1864.

The first initiative to convert areas of the Swan Coastal Plain woodlands to pine is recorded in an annual report submitted in 1987 by Ednie-Brown, Conservator of Forests. He noted that an endeavour should be made to favour plantations of some of the softwoods of commerce and thus make the Colony independent of outside supplies. Trial plantings were made that year on coastal sand dunes near Bunbury. They failed. Other sites were tried and early reports on the growth of pines at Hamel and Ludlow were enthusiastic. *Pinus radiata* was favoured because of its great success in South Australia. The early promise with coastal pine planting was not maintained and in 1916 most of the failed *P. radiata* was felled and replaced by *P. pinaster*.

In 1916, Sir David Hutchins, a prominent British forester employed to report on the forestry situation in Western Australia observed that "one problem was to fill up the sparse stocking of

the jarrah forest with the stocking of timber that the climate fits it to carry and so improve the yield and straighten up the too often crooked jarrah" (Hutchins 1916). He noted that pines naturally suggest themselves and favoured *P. pinaster* of the Portuguese provenance for the coastal sands.

Plantation Development

Three centres of interest were concentrated on for pine planting on the coastal sands—Ludlow, Myalup and Gnangara. Ludlow operations were largely in conjunction with managing the tuart reserve. The few stands that remain are the best and were concentrated on the Tuart sands of the Spearwood Dunes types. Most of the Ludlow plantings were, however, on the poorer non-tuart sites on the Coolilup sands. These had a high banksia component in the original flora and have now been largely removed in a mineral sands operation.

The Gnangara area was first considered as a pine planting proposition by C E Lane Poole in 1917. He was greatly influenced by the similarity of the sandy areas available to those of the Landes in Gascony. Some 3 100 ha were subdivided into compartments and a railway was surveyed from Bayswater to market the logs and firewood removed in clearing the sites. A number of trial plots were cleared and planted with *P. pinaster* raised in nurseries or direct sown.

Plantings at Myalup and Gnangara concentrated on sands of the Spearwood (Myalup) and Bassendean Dunes types. Problems with nutrition, establishment, genetics and spacing (Kessell 1927; Kessell & Stoate 1938, Perry 1939, Stoate 1939, 1946, Hopkins 1960a, b Perry & Hopkins 1967, Havel 1968, Butcher & Havel 1976; Butcher 1977a, b) needed to be overcome.

Up to 1988 c 28 000 ha of pine plantation had been established on sands of the Swan Coastal Plain. Of this area c 10 500 ha and 5 730 ha are on grey and transitional sands of the Bassendean System and 11 000 ha are on yellow sands of the Spearwood System.

Extension has now ceased due largely to the changing values placed on the land types by a developing urban population.

Current Plantation Values

Ludlow is now managed completely for conservation values of the native forests. Ludlow plantations will only remain until they can be converted to best suit the new national park role of the area.

Myalup-McLarty plantations have provided a small but strategic source of pines which can be logged in winter when logging is difficult in the major *P.radiata* plantations of the Blackwood Valley. It is probable much of the *P.pinaster* will be converted to *P.radiata* to provide a valuable economic resource.

For Gngangara, Pinjar and Yanchep the prime value of the area is now recognized as water production from the Gngangara mound (Butcher 1979a, b). A fibre board plant is projected for 1989 to provide for commercial thinning of the plantations and from approximately 1990, the saw log yield will increase to support a significant milling industry. Whether these northern pines will be replanted for a second rotation to favour water management and wood production is yet to be determined.

Recreation in these coastal plantations is an increasing benefit to population development.

Impact on *Banksia* Woodland

Havel (1968) has described the site types considered for pine planting in State forest 65 on the northern Swan Coastal Plain. On the Bassendean Sands and Transition Areas the *Banksia* dominated woodlands have proved unsuitable for commercial pine planting due to both low fertility and poor water relations. Generally only the sites carrying jarrah and marri have been suitable.

On Spearwood Dunes, favourable sites containing tuart and or jarrah cease north of Yanchep and most areas planted are on *banksia* woodland types with deep yellow sands. In the absence of moisture associated species such as jarrah, tuart, *B.grandis* and *B.ilicifolia*, pine planting is of questionable value without supporting heavy thinning costs.

Unplanted areas of the original forestry reserves are now managed as portion of the major conservation reserves to remain on the Swan Coastal Plain. Apart from the plantation areas, conservation is now the highest value to be managed for. This is a challenging requirement as the increasing population, adjacent urbanization and high value for recreation renders management of fire and public access a major problem.

Of 60 573 ha of State forest north of Perth, 23 050 ha have been converted to pine, 10 000 ha have been singled out for conservation reserves and some 27 500 ha of *Banksia* woodland remain for general conservation and recreation purposes. For the 9 000 ha of State forest on the Swan Coastal Plain south of Perth, 4 000 ha have been cleared for pine plantation, 1 400 ha have been selected for conservation reserves and 3 600 ha are managed for general conservation and protection purposes.

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Mineral resources and mining of the Spearwood and Bassendean Dune Systems

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Introduction

The development of Perth is very much dependent upon an assured access to reliable supplies of industrial minerals (sand, limestone, clay, gravel and hardrock) which are essential for road and building construction.

The *Banksia*-dominated woodlands of the Spearwood and Bassendean Dune Systems contain all the limestone resources and some of the more significant sand resources of the metropolitan region (Fig. 1).

Deposits of sand and limestone have always been thought to be abundant and freely available in the metropolitan area. These materials do occur extensively throughout the region, but the occurrence of economic deposits is limited, and proven resources are generally restricted to isolated pockets in specific geological units (Metropolitan Region Planning Authority 1984).

Sand resources

Geology

Although several geological units in the Perth area contain sandy strata, most sand supplies come from the Bassendean Sand and Tamala Limestone which form the Bassendean and Spearwood Dune Systems respectively (Fig. 1). The main areas of extraction are Wanneroo, Gnangara, Beechboro, Henley Brook, Jandakot, Spearwood and Baldivis (Biggs 1979).

The Bassendean Sand is typically yellow at depth beneath a surface cover of pale to dark grey humic sand. The sand comprises fine - to medium - grained, general subrounded quartz with occasional feldspar and heavy minerals. It is moderately well sorted with a low silt and clay content.

In the Spearwood Dune System a residual sand formed as a product of weathering of the underlying Tamala Limestone. It is humic-grey at the surface and yellow at depth, becoming orange close to the parent limestone bedrock. The sand comprises fine-to medium-grained, subangular to subrounded quartz with rare feldspar and heavy minerals, and is moderately well sorted with a small, but significant, clay and silt content. In general, it is coarser than the Bassendean Sand but the difference is slight and cannot be detected in all samples.

Uses

The major use of sand in Perth is for land fill - freeway construction, bridges, housing pads and rubbish disposal by sanitary land fill all require sand filling. Sand is also used as bedding for pipes to prevent damage, especially in the hills area where soil movement may cause problems. Standard specifications require that the sand be free of vegetable matter.

Construction sands - those used in concrete, brick work and plaster - need to meet a set of standards relevant to their end use. These standards set permissible percentages of various grain sizes, the rate of water absorption, particle shape, and the amount of contained impurities.

In Perth the most valuable sands are those with a high silica content, such as those found in the Gnangara and Jandakot areas. These are exported to Japan for glass manufacture and for some types of moulding, and to the Philippines for cement manufacture.

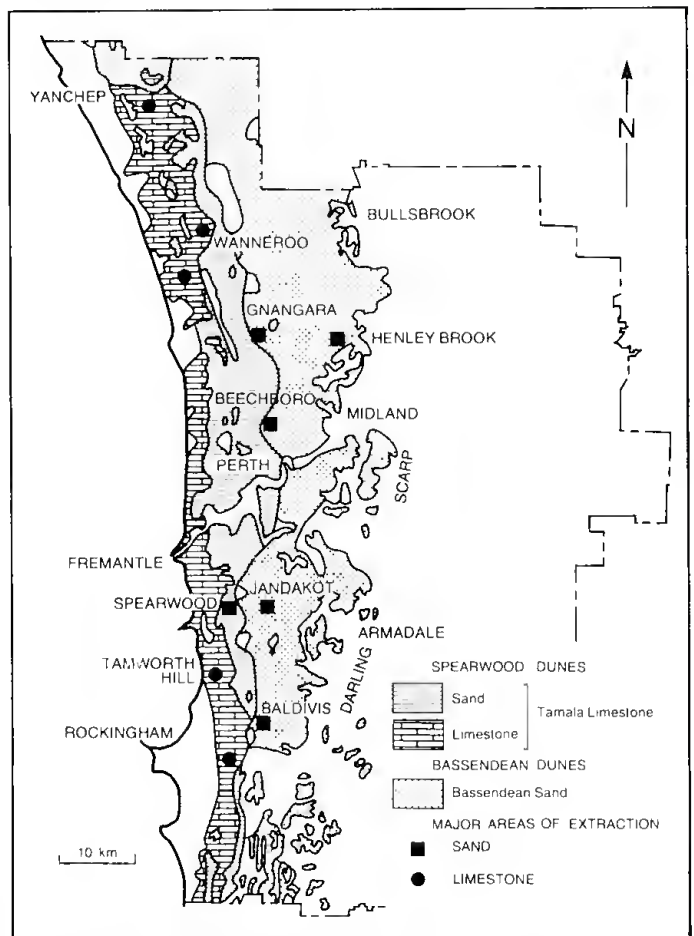


Figure 1 Sand and Limestone resources of the Spearwood and Bassendean Dune Systems

Mining and treatment

Because large areas of Perth are built on sand, there is a generally held belief that supplies of sand are cheap and unlimited. However, as urbanization advances, potential resources are sterilized, existing pits are forced to close and relocate, and transport costs increase.

In 1986 there were 49 actively worked sand pits in the metropolitan area. These were worked by a total of 32 operators, many of whom operated pits on a full time basis. The remaining pits were worked on an ad hoc basis according to the operators' needs. It is partly due to the simplicity of pit operation that the number of operations is high and ex-pit prices are very low.

Sand is the least expensive of all raw materials to extract, and the simplest to exploit. A typical operation involves a dozer, a front-end loader and a screening plant.

Once the vegetation is cleared, the overburden is stripped and stockpiled for future rehabilitation. In the case of sands not requiring treatment, the sand can be loaded directly from the pit face to the truck. Construction and other specialized sands usually require either dry screening or washing to remove organic matter and oversize material.

Limestone resources

Geology

The Tamala Limestone contains all of the limestone resources of the Perth region (Gozzard 1987). It occurs as a series of ridges parallel to the coast, and most is dunal in origin although marine beds are also present. The limestone typically ranges between 50% and 90% calcium carbonate (CaCO_3). The magnesium content is normally low, ranging from 0.5% to 1.5% MgCO_3 , but in exceptional cases it may be as high as 3% MgCO_3 . Silica (SiO_2), in the form of quartz grains, is the only significant contaminant and usually exceeds 12% of the rock. Average concentrations of minor constituents are: 1.1% Al_2O_3 , 1.1% Fe_2O_3 , 0.5% K_2O , 1.14% Na_2O , and 0.013% Cl. The *in situ* moisture content is normally about 5%.

The higher grade material is only found in isolated pockets within two areas. One is between Spearwood and Tamworth Hill, and the other is to the north west of Wanneroo (Fig. 1).
Uses

There are three industries that require high-grade limestone and cannot function with any substantial proportion of lower grade calcium feed. These are cement manufacture, lime production, and iron and steel smelting. The main use for high-grade material is in cement manufacture, which requires limestone with a CaCO_3 content of at least 80%.

Currently the two cement companies (Swan Portland Cement and Cockburn Cement) operating in the metropolitan area use this rock to produce at least 600 000 tonnes of cement annually.

The main uses of low- and medium-grade limestone include soft material for building, hard caprock for groynes and breakwaters, and rubble for road construction.

Mining and treatment

In 1986 a total of 24 operators had licences issued by local authorities to extract limestone within the metropolitan area. These operators include three local authorities and the Main

Roads Department. Six of the operators had interests in three or more sites. In addition there are approximately 100 mining tenements for limestone extraction within the metropolitan area.

The quarrying of limestone generally proceeds in stages, the first of which is the removal of overburden. This material, consisting principally of uncemented silica sand and variable quantities of caprock derived from limestone pinnacles, is normally used for the restoration of worked out areas. Initially the overburden is stockpiled, but, as the quarry is developed, all overburden is transferred directly into the worked-out areas to effect progressive restoration, thus avoiding double handling. Following this, weathered limestone is removed to expose the usable material.

Whenever possible, higher and lower grade materials are blended in order to extend the life of a quarry but this practice is too expensive when the quarry is yielding only low- and medium-grade material. Low-grade limestone can be mixed with binders such as bitumen, lime, clay, fly ash, and Portland cement, and used in road construction.

Environmental Aspects

Approval to operate sand or limestone pits depends on the proposed use of the material and the tenure of the land. These factors will determine whether the operations are approved under the Mining Act or under the Extractive Industries By-laws of Local Government. If the location is in an area that is environmentally sensitive approval may also be required from the Environmental Protection Authority.

In all cases the proponent is required to prepare a mine plan, operational guidelines, final landform and a rehabilitation program. The final landform and method of rehabilitation depends very much on the final use envisioned for the site.

In some cases pits have been used for landfill waste disposal sites and in other cases suburban development has occurred over worked-out pits. In recent months an old limestone pit north of Wanneroo, which was in operation before the creation of the Neerabup National Park, has been re-contoured and rehabilitated to encourage forest regeneration to a standard acceptable for return of the area to National Park status.

The environmental aspects of these types of extractive industries are presently under review by a Government Committee into Conservation and Rehabilitation in the Mining Industry. This committee will formulate recommendations aimed at ensuring that basic raw materials supplies are always available while ensuring that final landform objectives are met.

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Banksia woodland weeds

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Introduction

Floristic studies of *Banksia* woodlands usually mention introduced species (Milewski & Davidge 1981, Bell *et al* 1979, Foulds 1988), but no comprehensive survey has been undertaken of these taxa. This paper reports a survey of the naturalized flora of 100 sites distributed between Mandurah and Moore River.

Results

120 species were recorded as naturalized in *Banksia* woodlands within this region (Table 1). Most are Eurasian (chiefly Mediterranean) or South African in origin (Fig. 1a); However, a small but growing group originates in Eastern Australia and the Americas. This may have considerable implications for future composition of this area's weed flora. In life form the majority of weeds are annual or bulbous (chiefly the South African species) herbs, and the trees and shrubs are Australian species (Fig. 1b).

Half of the naturalized taxa were recorded at one (41 taxa) or two sites (19 taxa). Another 37 were located at fewer than 10 sites. Only 5 species (*Ehrharta calycina*, *Ehrharta longiflora*, *Lagurus ovatus*, *Romulea rosea*, *Hypochaeris glabra* and *Ursinia anthemoides*) were recorded at more than 30 sites.

Naturalized taxa occurred in a variety of disturbed areas or micro habitats within each site. Some were restricted to natural openings (*Pelargonium capitatum*) or moss swards (mainly Caryophyllaceae), edges of the remnants, tracks (43 taxa confined to track edges) or in litter under trees. Only 7 taxa were found to be abundant throughout remnants (*Avena barbata*, *Ehrharta calycina*, *Ehrharta longiflora*, *Romulea rosea*, *Gladiolus caryophyllaceus*, *Pelargonium capitatum* and *Homeria flaccida*).

The major avenue of introduction of weeds was rubbish dumping and soil transportation. Spread within a site was primarily via too many tracks being created in each remnant. Other disturbance factors were present and past grazing, clearance, frequent fires and tree felling.

From this survey the major weeds of *Banksia* woodlands are *Ehrharta calycina*, *Avena barbata* (chiefly in *Banksia prionotes* woodlands), *Gladiolus caryophyllaceus*, *Pelargonium capitatum* and *Homeria flaccida* (the last two mainly in Spearwood dune woodlands). Two special microhabitats are under threat; moss swards (Spearwood dunes invaded by small annuals) and deep litter under trees (invaded by *Myrsiphyllum* species, *Freesia leichtlinii* and *Fumaria* species).

Management of *Banksia* woodlands should aim to lower disturbance and prevent further introductions occurring.

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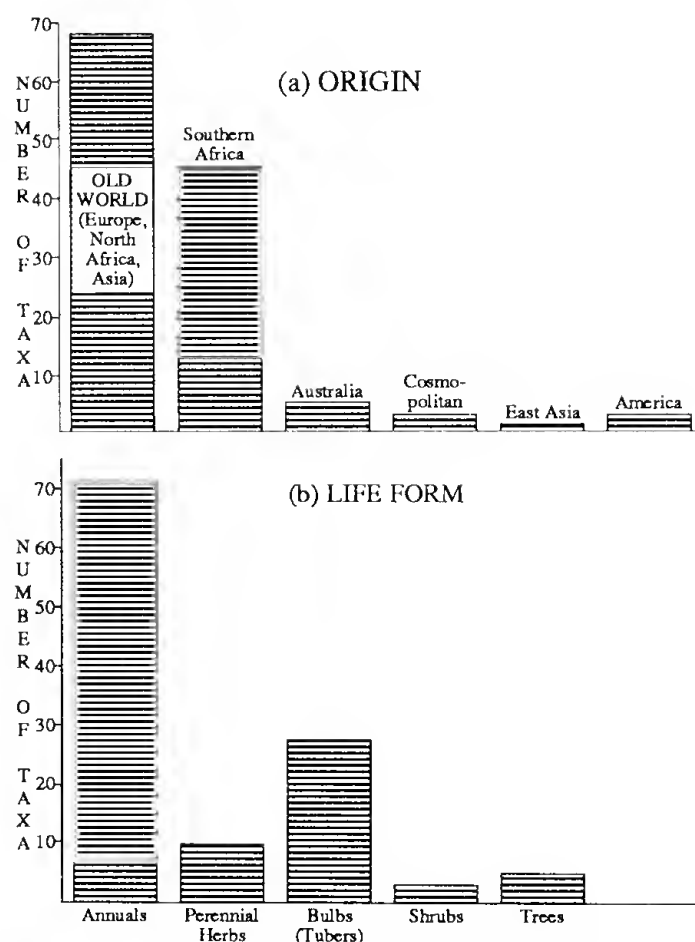


Figure 1 Area of origin and life form of *Banksia* woodland weeds.

Table 1

Species recorded as naturalized in Swan Coastal Plain *Banksia* woodlands. Figures in parentheses indicate number of times each species was recorded.

List is arranged in systematic order, after Green (1985).

Gymnosperms	
Pinaceae	
<i>Pinus pinaster</i> Ait. (1)	<i>Avena barbata</i> Link. (21)
Angiosperms	
Monocotyledons	
Poaceae	
<i>Aira cupiana</i> Guss. (22)	<i>Avena fatua</i> L. (6)
<i>Aira caryophyllea</i> L. (3)	<i>Briza maxima</i> L. (11)
	<i>Briza minor</i> L. (9)
	<i>Bromus diandrus</i> Roth. (17)
	<i>Bromus hordeaceus</i> L. (2)
	<i>Bromus madritensis</i> L. (1)
	<i>Cynodon dactylon</i> (L.) Pers. (2)

- Ehrharta calycina* Sm. (72)
Ehrharta longiflora Sm. (74)
Eragrostis curvula (Schrud.) Nees (2)
Hordeum leporinum Link. (14)
Hyparrhenia hirta (L.) Stapf. (1)
Lagurus ovatus L. (37)
Lolium rigidum Gaud. (17)
Pentaschistis thunbergii Stapf. (4)
Stenotaphrum secundatum (Walter) Kunze. (1)
Trachynia distachya (L.) Link (1)
Vulpia bromoides (L.) Gray (7)
Vulpia myorus (L.) C. Gmelin. (4)
- Asparagaceae
Myrsiphyllum asparagoides (L.) Willd. (2)
Myrsiphyllum declinatum (L.) Oberm. (1)
- Agavaceae
Agave americana L. (1)
- Asphodelaceae
Trachyandra divaricata (Jacq.) Kunth. (2)
- Hyacinthaceae
Albuca canadensis (L.) F.M. Leighton (1)
Lachenalia reflexa Thunb. (1)
Lachenalia orchioides L. (1)
Cyanella hyacinthoides L. (1)
- Iridaceae
Babiana disticha Ker. Gawler (1)
Babiana stricta (Ait.) Ker. Gawler (1)
Chasmanthe floribunda (Salisb.) N.E. Br. (2)
Ferraria crispa Burman (1)
Freesia aff. leichtlinii Klatt (4)
Gladiolus angustus L. (4)
Gladiolus caryophyllaceus (N. Burm.) Poir. (17)
Gladiolus undulatus L. (1)
Hesperantha falcata (L.f.) Ker. Gawler (1)
Homeria flaccida Sw. (4)
Ixia polystachya L. (2)
Romulea rosea (L.) Ecklon (41)
Romulea flava (Lam.) De Vos (7)
Sparaxis bulbifera (L.) Ker. Gawler (4)
Watsonia aletroides (Burm. f.) Ker. Gawler (1)
- Orchidaceae
Monadenia bracteata (Sw.) T. Durand et Schinz. (2)
- Dicotyledons
- Polygonaceae
Rumex acetosella L. (1)
Emex australis Steinh. (4)
- Phytolaccaceae
Phytolacca octandra L. (1)
- Aizoaceae
Carpobrotus edulis (L.) L. Bolus (5)
- Caryophyllaceae
Arenaria serpyllifolia L. (1)
Cerastium glomeratum Thuill. (3)
Minuartia hybrida (Vill.) Schischkin (2)
Petrohagia velutina (Guss) P. Ball et Heyw. (16)
Polycarpon tetraphyllum (L.) L. (1)
Sagina apetala Ard. (4)
Silene gallica L. var. *gallica* (9)
Silene gallica var. *quinquevulnera* (L.) Koch (1)
Silene nocturna L. (1)
Spergula arvensis L. (1)
Stellaria media (L.) Villars (2)
- Fumariaceae
Fumaria capreolata L. (3)
Fumaria muralis Sond. ex Koch. (2)
- Brassicaceae
Brassica juncea (L.) Czernj. (1)
Brassica tournefortii Gouan. (7)
Diplotaxis muralis (L.) DC. (1)
Heliophila pusilla L.f. (11)
- Crassulaceae
Crassula thunbergiana Schultes (1)
- Resedaceae
Reseda alba L. (1)
- Fabaceae
Lupinus angustissimus L. (4)
Lupinus cosentinii Guss. (3)
Medicago polymorpha L. (17)
Ornithopus pinnatus (Mill.) Druce (1)
Trifolium angustifolium L. (1)
Trifolium arvense L. (3)
Trifolium campestre Schreber (4)
Trifolium dubium Sibth. (7)
Trifolium glomeratum L. (9)
Vicia hirsuta (L.) Gray (1)
Vicia sativa L. (7)
- Geraniaceae
Erodium botrys (Cav.) Bertol (2)
Erodium cicutarium (L.) L'Her. (2)
Erodium moschatum (L.) L'Her. (4)
Geranium molle L. (3)
Pelargonium capitatum (L.) L'Her. (12)
- Oxalidaceae
Oxalis pres-caprae L. (4)
Oxalis purpurea L. (2)
- Zygophyllaceae
Tribulus terrestris L. (1)
- Euphorbiaceae
Euphorbia peplus L. (2)
- Malvaceae
Malva parviflora L. (1)
- Sterculiaceae
Brachychiton populneus (Schott) R.Br. (2)
- Myrtaceae
Agonis flexuosa (Spreng.) Schau. (1)
Eucalyptus citriodora Hook. (1)
Eucalyptus maculata Hook. (1)
Leptospermum laevigatum (Gaertn.) F. Muell. (1)
- Primulaceae
Anagallis arvensis L. var. *caerulea* Gonan. (5)
Anagallis arvensis L. var. *arvensis* (1)
- Gentianaceae
Centaurium erythraea Rafn. (4)
- Lamiaceae
Stachys arvensis (L.) L. (3)
- Solanaceae
Solanum nigrum L. (2)
- Scrophulariaceae
Dischisma arenarium E. Mey. (3)
Dischisma capitatum (Thunb.) Choisy (2)
Parentucellia latifolia (L.) Caruel (7)
Kickxia spuria (L.) Dumort. (1)
- Orobanchaceae
Orobanche minor Sm. (1)
- Rubiaceae
Galium murale (L.) All. (1)
- Campanulaceae
Wahlenbergia capensis (L.) A.DC. (29)
- Asteraceae
Arctotheca calendula (L.) Levyns (7)
Conyza bonariensis (L.) Cronq. (5)
Cotula bipinnata Thunb. (1)
Hypochaeris glabra L. (89)
Hedynopsis rhagioides (1)
Lactuca serriola L. (2)
Osteospermum clandestinum (Less) Norlindh (14)
Pseudognaphalium luteoalbum (L.) Burt et Hillard (16)
Sonchus oleraceus L. (5)
Urospermum picroides (L.) Scop. ex F.W. Schmidt (6)
Ursinia anthemoides (L.) Poir (94)
Velleroeophyton dealbatum (Thunb.) Hilliard et Burt (4)

Diseases of *Banksia* woodlands on the Bassendean and Spearwood Dune Systems

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Current knowledge

Diseases of *Banksia* woodlands have been a neglected area of plant pathology. Of the c 250 000 publications on plant diseases abstracted in the Review of Plant Pathology since 1922, only about 30 refer to diseases of *Banksia*. Only 6% of these 30 publications refer to diseases of *Banksia* in woodlands compared with 55% for forest and 39% for *Banksia* species used in floriculture. Observations on the impact and spread of *Phytophthora cinnamomi* by Podger (1972) and Havel (1979) are the only published account of disease on *Banksia* woodlands of the Bassendean Dune system. Nevertheless, despite the lack of published information, disease is an important factor affecting the ecology of *Banksia* communities.

Phytophthora species have been the most frequent cause of disease of *Banksia* (73% of the 30 publications) followed by wood rots (12%), leaf spots (9%) and *Cylindrocladium scoparium* (6%). The leaf spot *Asterina systema-solare* (Shivas in press), wood rots caused by *Armillaria luteobubalina* (Shearer & Tippett 1988), *Ganoderma*, *Polyporus*, *Poria* and *Stereum* (Hilton collection, WA Herbarium) and the canker pathogen *Botryosphaeria ribis* (Shivas in press) have been recorded on *Banksia* species occurring on the Bassendean Dunes. However the most destructive impact on the *Banksia* community of the Bassendean Dune system is disease caused by *Phytophthora* species, especially *P. cinnamomi* (Podger 1968, 1972).

Phytophthora cinnamomi is distributed widely in *Banksia* woodlands of the coastal plain killing most of the overstorey and shrub layers in affected areas (Podger 1972). Incidence of disease is greatest south of Perth, decreasing north of Wanneroo (Havel 1979). The Moore River National Park is the most northerly known occurrence of *P. cinnamomi* on the coastal plain. Geographically restricted and susceptible *B. laricina* is being killed in affected areas in this park. The incidence of *P. cinnamomi* on the Spearwood Dunes is much less than on the Bassendean Dunes (Podger 1968), even though plant species are susceptible and disturbance from human activity is high (Havel 1979).

Phytophthora cinnamomi is an introduced soil-borne fungus belonging to the Oomycetes or "water moulds". As the name "water mould" suggests, the life cycle of *P. cinnamomi* depends on moist conditions that favour survival, sporulation and dispersal of the fungus, and host infection. Warm, moist conditions and interactions with soil microflora favour vegetative production of sporangia and thick walled chlamydospores from mycelial strands in the soil or host tissue. Interaction of mycelium of different mating types may produce thick-walled sexual oospores. However reproduction in soil is mainly by the asexual

sporangium-zoospore cycle which produces large numbers of infectious spores when conditions are favourable.

Sporangia release motile zoospores in free water. Zoospores can swim over short distances in water, but are mainly dispersed over large distances in flowing water or in infected moist soil moved by human activity. Zoospores in moist soil are chemotactically attracted to root surfaces where they germinate to produce germ tubes that penetrate roots. Infection by *P. cinnamomi* is probably favoured by the thin bark and proliferation of rootlets associated with the specialized proteoid roots of the *Banksia* species occurring on the Bassendean Dunes. The fungus actively grows through root systems or is passively dispersed in infected roots transported in soil. Root to root contact facilitates mycelial growth between root systems and initiation of new infections.

The pathogen infects at least 1000 species of known hosts from taxonomically diverse families (Zentmyer 1980). The families Epacridaceae, Myrtaceae and Proteaceae, important components of *Banksia* woodlands, contain many susceptible species.

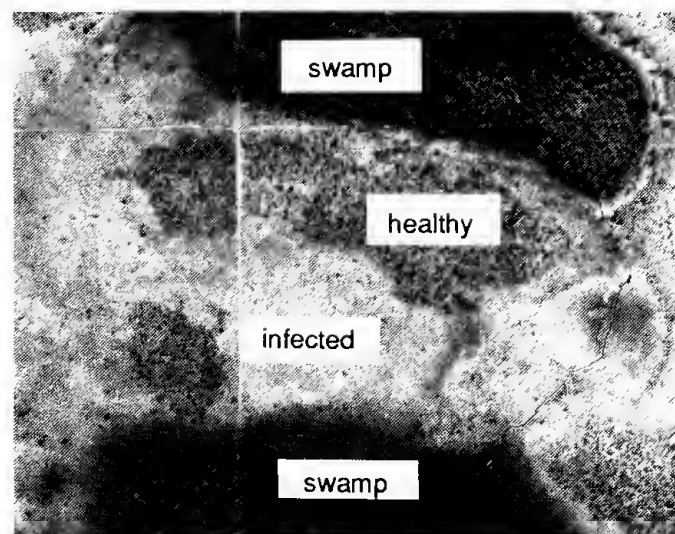


Figure 1 Destruction of *Banksia* woodland following infection by *Phytophthora cinnamomi* (light grey) compared with remnants of healthy woodland (dark grey) on a gently sloping Bassendean Dune between two swamp systems at Gngara on October 1964. The infected area was healthy woodland prior to 1953. Scale 1:12 500.

Current research

Following Podger's (1968) initial monitoring of sites from Ravenswood to Moore River, little research has been done on the occurrence of *P. cinnamomi* in *Banksia* woodlands on the coastal plain. Investigations are now in progress to determine the factors influencing disease development, impact and methods of control of *P. cinnamomi* and other *Phytophthora* species in *Banksia* woodlands.

Disease Development

The spread of *P. cinnamomi* in 132 ha of Bassendean Dunes at Gnangara has been mapped from aerial photographs. The area includes 97 ha of *Banksia* woodland and 35 ha of ephemeral swamp. Four small patches of dead vegetation totalling 0.15 ha occurred in 1942 alongside tracks that radiated from nearby strawberry farms. The area of infected woodland and swamp had increased to 55 ha by 1959, because of expansion of original infections, new infections from a nearby farm and contamination of the swamp system with associated destruction of low lying *Banksia* woodland (Fig. 1). These disease fronts expanded at 1.0 m yr⁻¹ and 67 ha was infected by 1974, increasing to 82 ha (63%) in 1988. Slope or depth to water table did not appear to influence the rate of spread. However the rate of spread at Gnangara was slower than a mean downslope spread of 8 m yr⁻¹ observed by Podger (1968) on a gently sloping dune of Gavin sand in the Bassendean system near North Dandalup.

The pattern of disease development at Gnangara reflects the ability of *P. cinnamomi* to exploit various mechanisms of spread. Disturbance associated with market gardening, roads, tracks and off-road driving have resulted in the dispersal of *P. cinnamomi* in infected soil, and is responsible for the widespread distribution of the pathogen throughout the coastal plain. Active and passive dispersal of zoospores in free water contributes to spread within an area and results in the contamination of swampy areas. Zoospore dispersal in coarse-textured sands may also be assisted by movement of the water table or by lateral drainage from perched layers of saturated soil over clay or iron hardpan. We have recovered the fungus from groundwater at 3 and 5 m below the soil surface in affected *Banksia* woodland on Gavin sand near Hamel and south of Busselton. Growth of *P. cinnamomi* in roots of susceptible hosts ensures continued spread through summer, even though activity of the fungus in dry soil ceases. For example, *P. cinnamomi* can grow up to 1 cm day⁻¹ in roots of susceptible *B. grandis* in summer when temperatures are optimal for fungal growth (Shearer *et al* 1987).

The destructiveness and persistence of *P. cinnamomi* in *Banksia* woodlands is partly determined by the ability of the pathogen to survive the dry soil environment over summer and resume activity when moist conditions return. The fungus survived throughout the year in soil sampled from a depth of a metre in an affected *Banksia* woodland on Gavin sand south of Busselton. Recovery rates at depth from this site were often higher than those obtained from a high impact site in the jarrah forest.

Infected host tissue provides a buffered environment for *P. cinnamomi* survival during dry conditions. For example, the fungus survived summer in 65% of colonized pine plugs buried at 30 cm in an affected area at Gnangara, even though soil moisture at this depth decreased to 0.6% in February.

Impact

Phytophthora cinnamomi infection destroys the structure and diversity of *Banksia* woodland. The dominant overstorey of *B. attenuata*, *B. ilicifolia* and *B. menziesii* is killed and only scattered *Eucalyptus todtiana* and *Nuytsia floribunda* remain in affected areas. Many understorey shrub species are similarly affected. Species richness in 64 m² quadrats decreased from 56 species

in healthy woodland to 41 species in an affected area. Biomass can be reduced by up to 90% following infection (Fig. 1). Despite the impact of *P. cinnamomi* on *Banksia* woodland, information is lacking on the long term structural and floristic changes in affected areas.

Other *Phytophthora* species

Phytophthora citricola, *P. cryptogea* (A₁), *P. megasperma* var. *megasperma* and *P. megasperma* var. *sojiae* have been isolated from dying vegetation on Bassendean Dunes north of the Moore River. Many of the affected areas were low-lying and seasonally inundated or received off-road drainage. The susceptibility of native vegetation to these *Phytophthora* species needs to be determined before their relative significance to the health of native plant communities can be accurately evaluated (Shearer *et al* 1988).

Control

Eradication of *P. cinnamomi* from spot infections by Ridomil and fumigation with formaldehyde is being assessed in Jandakot sands of the Bassendean Dunes at Gnangara with promising results. In addition, the systemic fungicide phosphorous acid has arrested lesion extension in *B. grandis*. Evaluation of these control methods is continuing.

Conclusions

Systematic surveys of *Banksia* woodlands in southwestern Australia are needed to address the lack of information on diseases of *Banksia*.

Phytophthora cinnamomi and other *Phytophthora* species are major factors affecting the ecology and management of the diverse, but susceptible, *Banksia* communities on leached sands. Information is lacking on the specific requirements for pathogen survival, sporulation and spread as well as host infection and susceptibility in sandy soils. Such information is essential for the development of hazard and risk systems to minimize introduction and spread of *Phytophthora* species.

Knowledge of the diversity of *Banksia* woodlands, similar to the site-vegetation classification of Havel (1979), is needed in the development and application of hazard and risk systems. Long term effects of *Phytophthora* spp on diversity clearly needs to be quantified.

An understanding of the low incidence of *P. cinnamomi* on Spearwood Dunes may provide clues for the control of the disease. Control strategies must be developed and applied to prevent spread and intensification of disease favoured by disturbance caused by increasing urbanization and sand mining.

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Conservation status of *Banksia* woodlands on the Swan Coastal Plain

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Introduction

Banksia woodlands are such a familiar sight to urban Perth dwellers that few would consider these communities to be of serious conservation concern. However, many areas of woodland have been cleared of native vegetation recently, and an assessment of the conservation status of *Banksia* woodlands is, therefore, both appropriate and long overdue.

The *Banksia* woodlands chosen for study were those confined to the Bassendean and Spearwood dune systems of the Swan Coastal Plain from Lancelin southwards, and in mapped vegetation complexes in which banksias were described as being dominant by Heddle *et al* (1980). Using satellite imagery at a scale of 1:250 000, the area of *Banksia* woodland communities on the Swan Coastal Plain extant in 1986 was determined and compared with original areas (see Burbidge & Rolfe, in prep., for a detailed account).

Clearing of *Banksia* woodlands

By 1986 an estimated 55% of the 281 000 ha of *Banksia* woodland complexes between Lancelin and Capel on the Bassendean and Spearwood dune systems had been cleared entirely of native vegetation (Table 1). The destruction of the seven complexes varied from 90% for the small area of Bootine Complex (north of Gingin) to only 2% of the equally small Karrakatta Complex-North-Transition Vegetation Complex (NE of Lake Pinjar).

The two largest complexes, Bassendean—North and Bassendean—Central and South, differed substantially (37% vs 85% respectively cleared). Essentially, little remains of the once extensive *Banksia* woodlands from Perth southwards to Busselton. Only in the Moore River National Park—Yeal Swamp—Melaleuca Park areas north of Perth are large tracts of *Banksia* woodlands still to be found.

Conservation on reserves

Only 7% of the original 281 000 ha of *Banksia* woodlands investigated was on conservation reserves (Table 1, and Fig. 1 of J.S. Beard, this volume), and those reserves were uneven in geographical distribution and among vegetation complexes. Some of these deficiencies will be addressed by proposed additions to the conservation estate in CALM's Northern Forest and Central Forest Region Management Plans 1987-1997. However, in these and other areas the conservation of remnant *Banksia* woodlands currently lies very much in the hands of owners of private property or Crown lands set aside for purposes other than flora and fauna conservation.

Rare and threatened species

Although poorly studied, *Banksia* woodlands appear to contain few rare localized endemic species. However, the extensive clearing of these woodlands has resulted in some plants and vertebrate animals declining in numbers to the point where they are now considered highly vulnerable or endangered.

Two declared endangered reptiles occur in the *Banksia* woodlands of the Swan Coastal Plain. The Carpet Python (*Morelia spilota*) is widespread in Australia but scarce throughout its range. The Black-striped Snake (*Vermicella calonotus*) is almost confined to the Swan Coastal Plain, from Lancelin to Mandurah and most commonly in the deep white sands of the Bassendean and Spearwood dunes. A third reptile, the Lined Skink (*Lerista lineata*), is not declared endangered but is of limited occurrence, being found only on the Swan Coastal Plain from Perth to Yalgorup. Varanid lizards have also declined markedly in *Banksia* woodlands (How & Dell, this publ.).

Many species of birds have declined in numbers on the Swan Coastal Plain (Storr & Johnstone 1988) although no bird species is restricted to the area and the *Banksia* woodlands do not constitute a major part of the breeding habitat of any declared endangered bird species. However, the *Banksia* woodlands do provide an important feeding resource for non-breeding flocks of Carnaby's Black-Cockatoo (*Calyptorhynchus funereus latirostris*) which has declined markedly due to clearing of native vegetation in the wheatbelt (Saunders *et al* 1987).

Amongst the mammals, it is possible that only a few species of small mammal maintain viable populations in *Banksia* woodlands (How & Dell, this publ.). For example, the Western Quoll (*Dasyurus geoffroii*) is possibly locally extinct and in *Banksia* woodlands the Numbat (*Myrmecobius fasciatus*) is now restricted to a small, highly vulnerable population in the Canning Vale area.

Little is known about the conservation status of *Banksia* woodland invertebrates (Majer, this volume).

The King Spider Orchid (*Caladenia huegelii sens str*) and two hammer orchids (*Drakaea jeanensis* and *D. micrantha* Hopper *ined*) are the only plants currently declared as rare flora that occur mainly in *Banksia* woodlands on the Swan Coastal Plain. However, ephemeral wetlands dotted through the *Banksia* woodlands have three additional declared rare plants—Purdie's Donkey Orchid (*Diuris purdiei*), Stalked Water Ribbon (*Aponogeton hexatepalus*) and Minute Pygmy Sundew (*Drosera occidentalis*).

Table 1

The area of *Banksia* woodland vegetation complexes still extant on the Swan Coastal Plain in 1986, and their representation in the total CALM estate and in conservation reserves.

Woodland Complex*	Original area (ha)	% extant† in 1986	% in CALM estate	% on reserves
37 Bootine	3 911	9.8	1.0	1.0
43 Bassendean-North	78 261	63.0	32.8	11.1
44 Bassendean-Central & South	86 123	14.5	8.8	1.6
45 Bassendean-North-Transition	20 845	86.5	44.9	39.3
47 Karrakatta-North	43 868	41.0	42.6	0
48 Karrakatta-North-Transition	5 282	97.7	10.7	0
51 Cottesloe-North	43 062	55.6	34.5	4.5
Totals	281 353	45.2	27.3	7.2

* as defined and mapped by Heddle *et al* (1980)

† these figures represent very conservative estimates of the amount of habitat destruction in the *Banksia* woodlands. Much of the remaining woodlands exists only in small patches and in many of these the understorey is highly modified by disturbance agents such as grazing.

While still locally common, several other plant species endemic or nearly so to *Banksia* woodlands need to be monitored in the future, eg *Banksia laricina*, *Eremaea pupurea*, and *Caladenia speciosa* Hopper *ined.* The woodlands also contain a number of outlying populations well removed from their main areas of occurrence, eg southern populations of Winter Bells (*Blancoa canescens*) and *Conostylis latens* in Canning Vale.

Management for conservation

Other papers in this publication allude to major management concerns facing *Banksia* woodlands—fire, dieback disease, herbivory by rabbits, fertilizer drift, groundwater extraction and weed invasion to name but a few of the most important. To this list might also be added various recreational activities (trail bike riding, off road vehicle use) and commercial pursuits (wildflower picking, bee keeping, grazing by stock) that require management.

While these issues deserve our concerted efforts, perhaps of greatest and immediate concern is the ongoing pace of clearing of *Banksia* woodlands for agricultural, urban and industrial development projects. While some land uses such as mining are obliged to go through an environmental impact assessment process before they can clear native vegetation, this does not apply under current legislation to others such as residential developments. Any program to rectify this situation must include a concerted effort at public education concerning environmental issues.

The management of remnants of *Banksia* woodlands set aside for conservation poses a number of problems, as does the management of remnants of native vegetation generally (Saunders *et al* 1987). It seems likely that inappropriate fire regimes can promote invasion of perennial weeds such as veldt grass, and

lead to gradual degradation of conservation values (Hopkins, this publ). We know little of the population ecology of *Banksia* woodland species, and require this sort of understanding to plan future management strategies (eg Lamont, this publ).

Future Directions

New initiatives are needed to improve on the conservation estate in both Crown and private ownership. Those proposed and already reviewed in the public arena (System 6, CALM Regional Management Plans) need to be implemented as soon as possible if the land involved is not to suffer degradation through other inappropriate land uses. Indeed, biologists will have to work harder at communicating the value of conserving *Banksia* woodlands if we are not to witness the rapid attrition of these communities over the next few decades.

Few rare and threatened species are known to be endemic to these *Banksia* woodlands, but there are some among plants. These require research and the development of appropriate management strategies. The possible local extinction of predatory medium sized mammals like Quolls is, however, an early warning that many common *Banksia* woodland species will become threatened unless we research, plan for and actively manage the remnants extant today.

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Banksia woodlands: Summary and conclusions

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Introduction

The *Banksia* woodlands that have been the subject of these series of papers are surprisingly poorly studied and documented. Perhaps this is due, at least partly, to their location close to Perth—they are too familiar to many scientists who have preferred to work in less familiar and perhaps more “exotic” surroundings. However, it is their closeness to Perth that makes the *Banksia* woodlands an ideal place for scientific research since they are ideally located for low cost studies and have been and are subjected to various land-use pressures that are causing many changes.

Environment and Conservation

The *Banksia* woodlands of the Swan Coastal Plain grow on deep Quaternary sands with a very low nutrient level. They are subjected to a typically Mediterranean climate of cool, mild winters and hot, dry summers. They have a rich flora and fauna, with much variation over 4° of latitude and between the different soil types. However, there are relatively few endangered species.

Because of their proximity to Perth, *Banksia* woodlands are being destroyed at a rapid rate. While some conservation reserves protect samples of *Banksia* woodland, not all the types of woodland are protected at present, nor are all the reserves large enough to be viable. Additionally, the reserves are threatened by a variety of disturbers.

Resources

The resources of the *Banksia* woodlands can be divided into three categories:

Land Resources

The land is used for urban and industrial purposes, food growing, horticulture and pine plantations, and recreation. Urban development and its associated land uses are leading to the destruction of increasing areas of *Banksia* woodland.

Natural Non-renewable Resources

The chief demands for non-renewable resources are for basic raw materials used in construction, brick making, road building, etc. and for minerals. The demand for minerals is low and restricted mainly to silica and limestone. The amount of *Banksia* woodland destroyed by demand for basic raw materials is related largely to the growth of Perth.

Natural Renewable Resources

The most important of these are groundwater and the biological resources—the indigenous plants and animals that make up a genetic storehouse for the future. Demand for groundwater is related to the growth of Perth.

Disturbers of Natural *Banksia* Woodlands

Those *Banksia* woodlands that are not cleared for urban or other use are subject to many disturbers. Among the most important are:

Fire

Mediterranean climatic areas are typically affected by high intensity summer wildfires and the *Banksia* woodlands are no exception. Aboriginal firing would have occurred for many thousands of years but there are few data on their extent, frequency or timing. With recent urbanization and increases in human population fires are likely to have increased in frequency at least.

Disease

Phytophthora cinnamomi, an introduced fungus that destroys roots, is now a major disease of native and exotic plant communities of the *Banksia* woodlands. Other *Phytophthora* spp. occur also.

Weeds

Numerous environmental weeds are now established in *Banksia* woodland communities. They are competing with and probably eliminating some native species.

Feral Animals

A variety of introduced animals has become feral in *Banksia* woodlands. This includes the rabbit, house mouse, black and brown rats, cats, foxes, dogs and, near Perth, even polecats (or ferrets). Their effects on plant and animal communities are only beginning to be understood. Overgrazing and selective grazing are destroying components of the flora, and predation has eliminated or is eliminating some native animals.

Pollution

Urban and industrial pollution has so far had the greatest effect on wetlands, via increased nutrients in the water table, rivers, estuaries and lakes.

Groundwater Extraction

Groundwater extraction can lower the water table and lead to the death of some plants and a reduction in the size of wetlands or the length of time that they contain water.

Recreation

Human use can lead to degradation of the land and its plant and animal communities. Damage can come from off-road vehicles, rubbish-dumping and walking paths.

Synergism

A major problem of understanding the effects and relative importance of the various disturbers is that most of them are inter-related and, indeed, their effects may be synergistic. For example, frequent fires combined with exotic grazing and

browsing animals will lead to the degradation of the vegetation much faster than would be expected from the simple addition of the effects of the two disturbers measured in isolation, and the invasion of weeds is much faster in the presence of soil disturbance or frequent fire.

Future Management Strategies

If *Banksia* woodlands are to be used for the long-term benefit of the people of Western Australia it is clear that strategies will have to be developed and applied to prevent their total destruction or near destruction plus degradation of the remnants. Of particular importance are:

- 1** Further documentation of biological resources and environmental dynamics.
- 2** Increased research into and management of
 - plant disease, especially *Phytophthora cinnamomi*
 - fire regimes
 - groundwater extraction
 - recreation
 - the "greenhouse effect"
- 3** Continued land-use planning, including a refinement of the system of nature conservation reserves.
- 4** A continuing debate in the community about the acceptable limits to the growth of Perth.
- 5** Education. Without improved education about *Banksia* woodlands, most of the above points are unattainable.

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Book Jacobs M R 1955 Growth Habits of the Eucalypts. For Timb Bur, Canberra.

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