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Death and Regeneration in Species Rich Kwongan Vegetation Affected by Drought.

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Abstract

This paper reports the response of native plant species in the Western Australian Kwongan to aseasonal water stress. Observations were made on a total of 124 vascular plant species in a 20 km^2 study area surveyed during the second consecutive year of below average rainfall. Individual plants with completely dead aerial parts were recorded, together with seedlings and individuals resprouting from below ground parts. Death and regeneration through both these mechanisms appeared successful for drought avoidance. The drought affected species in the families Epacridaceae, Legumiosae and Proteaceae more than species of other major shrubland families. The response of the vegetation to aseasonal drought is similar to the response to unpredictable fire, though this latter factor affects the vegetation more uniformly.

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Introduction

A detailed botanical survey of an area of the northern Kwongan of Western Australia (Beard 1976a) was carried out in 1977 during a period of aseasonal drought. Much of the vegetation of the study area was exhibiting symptoms of water (deficit) stress including brittleness, chlorosis, defoliation and death. Some species were also showing a response to the meagre winter rainfall. Systematic field observations were made at the time of the survey on death and mode regeneration of plant species in this Kwongan vegetation.

The aseasonal (unpredictable) drought was the result of two consecutive years of below average rainfall. The effects were superimposed on those normally prevailing in an area of general low water availability resulting from low rainfall and soils with poor water holding capacity, and seasonal drought associated with a pronounced mediterranean climate.

Despite the widespread nature of drought phenomena in

Australia, field studies on their effects on the native plant species are few. A physiological approach has been utilized to study the effects of general water stress in the arid zone (e.g. Connor and Tunstall 1968) and of seasonal drought in a Mediterranean climate area (e.g. Grieve and Hellmuth 1968). The effects of unpredictable water stress on native vegetation has been reported by Beard (1969), Heddle (1979) and Pook *et al.* 1966, but only the first two of these authors documented the recovery of species after first rains. This paper reports the observed effects of drought and subsequent regeneration on the vegetation of the Western Australian Kwongan.

The Study Area

The study area, covering 20km^2 of heath and shrublands, lies about 8 km south of Eneabba, Western Australia at 29°53'S, 115°16'E. It has been described in detail by Hnatiuk and Hopkins (1980). The area lies at the eastern margin of the coastal plain (Eneabba Plain) beside the Gingin escarpment, and straddles a Pleiostocene coastline at the edge of the lateritic plateau (Lowry 1974). The Eneabba Plain is largely composed of alluvial sand and low aeolian dunes. At the base of the escarpment there are complex colluvial deposits of sand, clay and lateritic gravel. The soils developed on these unconsolidated materials form a complex, fine-grained mosaic of units dominated by pale grey and yellow sand with variable interbedding of gravel and clay. The sand is mostly coarse (>0.5mm) whereas the clays are largely very fine (60μ). Nutrient levels are uniformly very low.

The area lies within the Tathra Vegetation System of Beard (1976b) which consists of fairly uniform "scrub-heath" with patches of *Melaleuca* thicket, with scattered trees and woodlands. The flora is extremely rich with over 400 species of vascular plants being recorded for the study area, of which 338 were found at the detailed study sites. There appears to be east-west gradients in species richness, with sites of greatest richness lying along the old strand line.

A number of endemic and undescribed species were recorded for the study area, which falls within a larger area of biogeographic importance delineated by George *et al.* (1979).

The area has a Mediterranean type climate (Thermomediterranean accentuated, UNESCO-FAO 1963) with an average annual rainfall of about 550 mm. Monthly rainfall exceeds evaporation only for June, July and August. Mean summer temperature is 21°C and that for winter is 13.5°C (Anon. 1968).

Field observations were made in late winter-early spring (September - October 1977) which was at the end of the usual annual "wet" season, and followed two years of much below average rainfall (Table 1).

METHODS

Observations on death and regeneration were made as part of a major study of the shrubland study area. It was sampled on a systematic grid at 400 m intervals. The drought observations were made in plotless samples of about 0.1 ha centred on each sample site. A total of 87 sites were available for study. At each site a list was compiled of all vascular plant species present, with special notations where individuals were found to be totally dead, resprouting, or occurring as seedlings. Seedlings were defined as plants with cotyledons attached or recently abscised. Doubtful determinations have not been included in this report. Resprouting from rootstock, rhizomes, etc. of individuals that were completely dead above ground occurred much less commonly than did complete death and seedling germination; thus records of resprouting events from between, as well as at the study sites have been included here. Individuals exhibiting resprouting but only partially defoliated were not recorded.

Voucher specimens for species mentioned in this report are lodged at the Western Australian Herbarium (PERTH) and are annotated "Eneabba Survey 1977". Authorities for specific names are given in Hnatiuk and Hopkins (1980).

RESULTS

Eighty-six species of vascular plants representing 43 genera in 15 families, or 25% of the 338 species recorded at the detailed study sites, were found with dead individuals (Table 2). Seedlings of forty-nine of these species were found. Fifty-nine species with dead aerial portions (38 genera in 16 families, 17% of the flora) were recorded as resprouting from underground parts. Twenty-three of these species had no records of completely dead individuals. Fifteen species were recorded to have seedlings, but with no dead individuals found and only three of these species were recorded as resprouting. Thirty-one species were recorded as having dead individuals but with no seedlings or resprouting. No species was recorded only as dead individuals at all sites.

The species most frequently found with dead individuals was *Petrophile drummondii* (47% of plots). *Dryandra shuttleworthiana* and *Petrophile macrostachya* both had 36% of plots with dead individuals.

A systematic summary of the occurrence of deaths and regeneration in the major families is shown in Table 3. Also reported are the relative proportions of these families in the flora of the study sites, which can be compared with their proportional representation amongst affected taxa. The extent of mortality varied over the study area from an estimated high of >80% of above ground biomass, to a negligably small amount. The pattern of distribution of the mortality did not appear related to topography, soil type, vegetation type or species richness, although there was a tendency for sites on dune crests to have more species dead than sites in the swales.

DISCUSSION

The data presented here relate primarily to two mechanisms of drought avoidance (*sensu* Jessup and Moore 1957, Levitt 1972): defoliation to reduce transpiration with subsequent resprouting, and dormancy through death of the mature individual with subsequent regeneration from seed. The observations related to 25% of the species encountered during the survey. The remaining 75% of species could be avoiding stress through other mechanisms. The response of each species to the drought was not uniform throughout the study area. Clearly a species may avoid stress through the use of any one or combination of drought avoidance mechanisms, and the response at any site will depend on the type and magnitude of the stress and perhaps the genotype (cf. Ladiges 1976).

No regeneration was observed in about one-third of the drought affected species listed. It is possible that viable seed was still present in the soil. Alternatively those sites may not be suitable for long-term occupancy of the species which died.

The drought did not affect all plant families to the same extent. The relative proportions of the major families in the flora of the study sites relative to their proportional representation among the dead differ significantly (chi-square of expected and observed values (50-86) significant at $p < 0.001$). The Epacridaceae, Leguminosae and Proteaceae each had many more species killed by drought than would be expected by chance, whereas the other families were fairly close to their expected frequencies. It thus appears that species of these three families are least adapted to the conditions of drought experienced at Eneabba. The species concerned include both local endemics and widespread taxa.

The reasons for the different levels of drought sensitivity if these major families are not known. George *et al.* (1979) have speculated that the apparent predominence of Proteaceae species on lateritic soils and of Myrtaceous species on sandy soils reflects differences in root systems. Little however is presently known of the root systems of Western Australian heath species, though some studies analogous to those of Specht and Rayson (1957) have been carried out by Hellmuth (1963). Nutritional aspects have received some attention (e.g. Lamont 1972) and the importance of underground storage organs has recently been reviewed (Pate and Dixon 1979). Further detailed study of root architecture of these heath species is urgently needed.

The appearance of seedlings of forty-nine species was probably a response to the winter rains, however meagre. Seedlings of some species (*Beaufortia elegans*, *Conostylis* spp., *Hakea obliqua*, *Petrophile drummondii*) were particularly abundant, though not necessarily widespread. These observations of seedling recruitment conform to some extent with those reported by Specht (1979a) who found abundant seedlings in the first 1-2 years after fire, then relatively few until the vegetation began to degenerate at age 25-50 years after fire. Though the most recent fire in the Eneabba study area was *ca.* 10 years prior to this survey, the effect of drought on the vegetation is largely analogous to that of age senescence.

A number of authors have correlated the bradysporous (thick fruited) habit of many Proteaceous genera with the prevalence of fire in the Australian environment (Carlquist 1974, Gardner 1957, Specht 1979b). The large woody fruits open after fire to liberate the hitherto protected seed onto a receptive ash bed. In this context the records of Proteaceous seedlings are of interest. Five of the ten *Banksia* species recorded in the survey, and six of the twelve *Hakea* species, were regenerating from seed. The seed shed appeared to follow soon after the death of the branch on which the fruits were borne. A similar pattern of twig death, seed release and germination was evident in many other taxa.

Clearly fire is not the only effective stimulant for seed release and germination in a large number of species including those with seeds held in large woody fruits. Seedlings of Fabaceous species with hard coated seed stored in the soil were also recorded.

The ability of woody perennial shrub species to resprout after defoliation has also been suggested as an adaptation to fire (Carlquist 1974, Gardner 1957) though a number of alternative views have been advanced (Gill 1975, Keeley and Zedler 1978, Mooney 1977). The fifty-eight species of perennial plants which were observed during this survey to have defoliated and to be resprouting represent some fifteen families, with most species in the Proteaceae, Myrtaceae and Leguminosae. About one third of the species in each of these major families were resprouting, and of these, many were also recruiting as seedlings.

The nature of the underground organ from which the resprouting took place remains for further study; for the present they are referred to as lignotubers except in the case of the rhizomatous *Mesomelaena stygia*. Specht and Rayson (1957) reported that the subterranean woody organs which they encountered at Dark Island were not lignotubers, yet in later papers (e.g. Specht 1979a, 1979b) the term appears to be more generally applied. It is not certain if these structures are morphologically equivalent to the better studied lignotubers of *Eucalyptus* (Bamber and Mullette 1978, Mullette 1978, Pryor 1976). The potential for lignotubers to store water, as observed on *Eucalyptus oleosa* by Black (1952 in Specht 1966) may further contribute to species' successful drought avoidance.

A pattern of partial defoliation during summer of species in Mediterranean climate areas has been reported by Hatch (1955) Mooney *et al.* (1970) and Specht *et al.* (1979). This is considered an effective drought avoidance mechanism by Kozlowski (1976). However, the premature and complete shedding of foliage in response to unpredictable water stress may involve other physiological mechanisms with implications for nutrient cycling, a factor which is important in nutrient poor environments.

Clearly there are similarities in the responses of these shrubland species to the two types of unpredictable environmental stress: aseasonal drought and fire. In both cases there is defoliation and/or death followed by resprouting and/or seedling regeneration. The effects of the two phenomena on the physical environment, however, differ markedly. Drought does not produce the massive mineralization of organic matter, but rather there is a slow decay of organic matter by wind, rain and decomposer organisms. After drought, regenerating individuals may be subjected to severe competition for nutrients, water and even light from the adjacent, living, mature plants not killed by the drought.

Regeneration after drought tends to be patchy. Where a minority of individuals in a small area are killed, there may be no recruitment of seedlings, merely an increase in the size of the remaining individuals. In other sites, abundant recruitment may occur thus the species composition and hence structure of the vegetation may be very different following drought than following fire.

The results of this study are biased by the relative ease of recording deaths in large perennial plants in contrast with the difficulty in observing the effects of stress on annuals or cryptophytes. No Asteraceae were noted as dead, for example, but this does not mean that individuals did not die for want of water before viable seed was set. Cryptophytes, such as species of *Drosera*, *Thysanotus* or *Stylidium*, that do not depend upon annual seed production but have shallow root systems which exploit water and nutrients in the surface layers of soil, may through water storage be able to withstand prolonged drought for longer periods than some evergreen shrub species.

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TABLE 1. Rainfall Records Eneabba Post Office.

Time Period	J	F	M	A	M	J	J	A	S	O	N	D	Annual Total
Mean (12 yrs*) (1964-1978)	4	10	9	34	67	135	104	77	42	28	12	7	529
1974	0	6	9	31	175	132	145	79	15	59	20	0	671
1975	0	9	49	56	42	106	126	44	47	38	9	1	527
1976	17	73	6	23	92	27	35	119	36	14	25	0	467
1977	2	1	1	25	52	65	41	97	23	40	3	22	372
1978	6	4	1	26	64	154	158	33	71	22	7	27	572

* Observations for years 1970, 1971 missing.

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	Resprouting	Seedlings
Acacia auronitens	+	
A. barbinervis	+	
A. blakleyi		+
Actinostrobus acuminatus		
Adenanthos cygnorum		+
Andersonia heterophylla		
Astroloma pallidum		+
A. serratifolia	+	
Banksia attenuata		+
B. candolleana		+
B. grossa	+	
B. hookerana		+
B. lanata		+
B. leptophylla		+
Beaufortia bracteosa		+
B. elegans		+
Bossiaea biloba	+	
Calectasia cyanea	+	
Calothamnus sanguineous		+
Calytrix flaviscens		+
Casuarina humilis		
C. microstachya		
Caustis dioica		
Conospermum incurvum		+
C. triplinervum	+	+
Conostephium preissii		+ check RSH
Conostylis aurea (or C. sp. nov. aurea gp)		
C. crassinerva var. nov.		
C. cymosa		
C. sp. aff. crassinerva		+
Darwinia nieldiana	+	+
D. speciosa	+	
Dasypogon bromelifolius	+	
Daviesia divaricata	+	
D. juncea		+
D. rudiflora	+	+
D. pectinata	+	
D. pedunculata	+	
Diploloena ferruginea	+	
Dryandra bipinnatifida		+
D. carlinoides		? + check RSH
D. erythrocephala		
D. kippistiana		
D. nivea	+	
D. shuttleworthiana	+	+
D. sp. aff. falcata		
D. tortifolia		
D. tridentata	+	

	Resprouting	Seedlings
Eremaea acutifolia	+	
E. beaufortioides	+	+
E. violacea	+	+
E. sp. nov.		
Eucalyptus todtiana		+
Gastrolobium pauciflorum	+	
Gompholobium tomentosum		+
Grevillea didymobotrya		
G. polybotrya		
G. shuttleworthiana	+	
G. synaphea		
Hakea auriculata	+	
H. brachyptera		+
H. candolleana		+
H. cinerea		+
H. conchifolia	+	
H. costala	+	+
H. incrassata		
H. obliqua		+
H. prostrata		+
H. ruscifolia		
Hemiandra pungens	+	
Hibbertia crassifolia	+	
H. huegelii	+	
H. sp. aff. furfuracea	+	
Hypocalymma xanthopetalum var. linearfolium	+	
Isopogon adenanthoides	+	+
I. linearis	+	+
I. tridens	+	+
Jacksonia floribunda	+	+
J. spinescens		
Lambertia multiflora	+	
Lasiopetalum drummondii	+	
Laxmania sessiliflora		+
Lepidobolus chaetocephalus		
Leptomeria sp.		+
Leptospermum spiniscens	+	
Leucopogon ? conostephioides		
L. striatus		+
L. sp. indet. B.L. ? hispidus		
Loxocarya fasciculata		
Lysinema ciliatum		

	Resprouting	Seedlings
Macropidia fuliginosa		
Melaleuca tricophylla	+	+
Mesemelaena stygia	+	
M. uncinata		
Microcorys sp. nov.	+	
Monotaxis grandiflora	+	
Olax benthamiana	+	
Persoonia acicularis	+	
P. angustiflora		+
Petrophile drummondii		+
P. ericifolia		+
P. macrostachya	+	+
P. media	+	+
P. striata	+	
Phymatocarpus porphyrocephalus	+	
Pimelea angustifolium	+	
P. sulphurea	+	
Petyrodia bartlingia	+	
P. hemigenioides	+	
P. verbascina		
Restio sphacelatus		
Scaevola canescens	+	
Sedge indet. (golden based)		
Stirlingia latifolia	+	
Synaphea polymorphea	+	
Tetrariopsis octandra		
Thysanotus spiniger		
T. rectanthus		
Verticordia chrysantha	+	
V. grandis		
V. grandiflora	+	
V. ovalifolia		
V. sp. aff. nitens		

	Resprouting	Seedlings
Xanthorrhoea reflexa		
Xylomelum angustifolium		+
Indet Goodeniaceae RJH 771375.	+	

Table 3. Summary statistics of the effects of drought on native species-rich ~~shrubland~~ Kwongan. Families are arranged from those with most to fewest no. of species with individuals affected by drought.

Family	no. of genera		no. of species			spp. with seedlings		spouting		% of Total flora	% of dead
	alive	dead	alive	dead	dead as % of live	no.	%	no.	%		
Proteaceae	13	12	60	40	67	28	47	19	32	17	47
Myrtaceae	15	7	40	11	28	8	20	11	28	12	13
Epacridaceae	5	5	10	7	70	1	10	1	10	3	8
Leguminosae	8	3	27	8	30	4	20	7	35	8	31
Haemodoraceae	5	2	16	5	31	2	13	0	0	5	6
Cyperaceae	8	3	14	4	29	1	7	1	7	-	-
Liliaceae	9	1	14	2	14	1	7	0	0	4	2
Restionaceae	8	2	9	2	22	0	0	0	0	-	-
Asteraceae	8	0	9	0	-	-	-	-	-	-	0

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Table 1. Species of plants that were found with individuals dead, with seedlings, or with resprouting from underground parts after the above ground parts had died (* = resprouting).

		No. plots with sp. found dead individuals	% of total	No. plots where seedlings found	% of total
Casuarinaceae					
Casuarina humilis		2	2.3	1	1.1
Casuarina microstachya		1	1.1	.	
Cypressaceae					
Actinostrobus acuminatus		9	10.3	.	
Cyperaceae					
Caustis dioica		9	10.3	.	
indet.		1	1.1	.	
Mesomelaena stygia	*	5	5.7	.	
Mesomelaena uncinata		2	2.3	.	
Tetrariopsis octandra		.		1	1.1
Dicrastylidiaceae					
Pityrodia bartlingii	*				
Pityrodia hemigenioides	*				
Pityrodia verbascina		2	2.3	.	
Dilleniaceae					
Hibbertia crassifolia	*	.		4	4.6
H. huegelii	*				
H. furfuracea	*				
Epacridaceae					
Andersonia heterophylla		4	4.6	.	
Astroloma pallida		1	1.1	1	1.1
Astroloma serratifolium	*	1	1.1	.	
Conostephium preissii		3	3.4	.	
Leucopogon ? hispidulus		2	2.3	.	
Leucopogon ? striata		1	1.1	.	

		No. plots with sp. found dead	% of total	No. plots where seedlings found	% of total
Epacridaceae (cont.)					
Lysinema ciliata		4	4.6	.	
Euphorbiaceae					
Monotaxis grandiflora	*		4.6	.	
Fabaceae					
Bosseaea biloba	*				
Daviesia divaricata	*	7	8.0	.	
Daviesia juncea		4	4.6	1	1.1
Daviesia nudiflora	*	5	5.7	1	1.1
Daviesia pectinata	*				
Daviesia pedunculata	*	.		1	1.1
Gastrolobium pauciflorum	*				
Gompholobium tomentosum		.		1	1.1
Jacksonia floribunda	*	5	5.7	.	
Jacksonia spinescens		2	2.3	.	
Goodeniaceae					
Scaevola canescens	*	2	2.3	.	
indet.	*				
Haemodoraceae					
Conostylis aurea		2	2.3	.	
Conostylis crassinema ~~var. nov.~~		1	1.1	.	
Conostylis cymosa		1	1.1	.	
Conostylis sp. (aff. crassinerva)		14	16.1	11	12.6
Conostylis sp. indet.		.		6	6.9
Macropidia fuliginosa		2	2.3	.	
Lamiaceae					
Hemiandra pungens	*	1	1.1	.	
Microcorys sp. ~~nov.~~ undescribed	*				
Liliaceae					
Laxmania sessiliflora		.		1	1.1

		No. plots with sp. found dead	% of total	No. plots where seed-lings found	% of total
Liliaceae (cont.)					
Thysanotus rectantherus		2	2.3	.	
Thysanotus spiniger		3	3.4	.	
Mimosaceae					
Acacia blakleyi		.		1	1.1
Acacia auronitens	*				
Acacia barbinervis	*				
Myrtaceae					
Beaufortia bracteosa		1	1.1	.	
Beaufortia elegans		23	26.4	27	31.0
Calothamnus sanguineus		9	10.3	4	4.6
Calytrix flavescens		.		1	1.1
Darwinia nieldiana	*	.		1	1.1
Darwinia speciosa	*				
Eremaea acutifolia	*				
Eremaea beaufortioides	*	1	1.1	2	2.3
Eremaea violaceae	*	13	14.9	3	3.4
Eremaea sp. ~~nov.~~ [undescribed]		4	4.6	.	
Eucalyptus todtiana		1	1.1	1	1.1
Hypocalymma xanthopetalum var. linearifolium	*				
Leptospermum spinescens	*	4	4.6	.	
Melaleuca trichophylla	*	3	3.4	9	10.3
Phymatocarpus porphyrocephalus	*				
Verticordia chrysantha	*				
←Verticordia grandiflora	*				
Verticordia grandis	*	1		.	
Verticordia sp. (aff. nitens)		3	3.4	.	
Olacaceae					
Olax benthamiana	*				
Proteaceae					
Adenanthos cygnorum		8	9.2	7	8.0

		No. plots with sp. found dead	% of total	No. plots where seedlings found	% of total
Proteaceae (cont.)					
Banksia attenuata		7	8.0	1	1.1
Banksia candolleana		.		2	2.3
Banksia grossa	*	3	3.4	.	
Banksia hookerana		7	8.0	1	1.1
Banksia lanata		18	20.7	1	1.1
Banksia leptophylla		3	3.4	1	1.1
Conospermum incurvum		5	5.7	6	6.9
Conospermum triplinervium	*	8	9.2	10	11.5
Dryandra bipinnatifida		.	.	1	1.1
Dryandra carlinoides		7	8.0	1	1.1
Dryandra nivea	*	10	11.5	.	
Dryandra sessilis		2	2.3	.	
Dryandra shuttleworthiana	*	31	35.6		
Dryandra tortifolia		10	11.5	.	
Dryandra tridentata	*	18	20.7	.	
Dryandra vestita		1	1.1	.	
Grevillea didymobotrya		1	1.1	.	
Grevillea polybotrya		1	1.1	.	
Grevillea shuttleworthiana	*				
Grevillea synaphaea/rudis		2	2.3	1	1.1
Hakea auriculata	*	3	3.4	.	
Hakea brachyptera		5	5.7	5	5.7
Hakea candolleana		1	1.1	1	1.1
Hakea cinerea		15	17.2	5	5.7
Hakea conchifolia/smilacinifolia	*	6	6.9	.	
Hakea costata	*	27	31.0	9	10.3
Hakea incrassata		4	4.6	.	
Hakea obliqua		11	12.6	9	10.3
Hakea prostrata		4	4.6	2	2.3

		No. plots with sp. found dead	% of total	No. plots where seed-lings found	% of total
Proteaceae (cont.)					
Hakea ruscifolia		2	2.3	.	
Isopogon adenanthoides	*	5	5.7	1	1.1
Isopogon linearis	*	1	1.1		
Isopogon tridens	*	18	20.7	3	3.4
Lambertia multiflora	*	6	6.9	1	1.1
Persoonia acicularis	*	1	1.1	.	
Persoonia angustiflora		.		1	1.1
Petrophile drummondii		36	41.3	31	35.6
Petrophile ericifolia		9	10.3	3	3.4
Petrophile linearis		.		2	2.3
Petrophile macrostachya	*	31	35.6	2	2.3
Petrophile media	*	22	25.3	5	5.7
Petrophile striata	*	2	2.3	.	
Stirlingia latifolia	*	7	8.0	1	1.1
Synaphaea polymorphea	*	3	3.4	.	
Xylomelum angustifolium		.		1	1.1
Restionaceae					
Loxocarya fasciculata		2	2.3	.	
Restio sphacelatus		9	10.3		
Rutaceae					
Diplolaena ferruginea	*				
Santalaceae					
Leptomeria sp.		.		2	2.3
Sterculiaceae					
Lasiopetalum drummondii	*	1	1.1	.	
Thymelaeaceae					
Pimelia angustifolium	*				
Pimelia sulphurea	*				
Xanthorrhoeaceae					
Calectesia cyanea	*	2	2.3	.	
Dasypogon brome[illegible]folius	*	1	1.1	.	

	with sp. found dead	% of total	where seedlings found	% of total
Xanthorrhoeaeceae (cont.)				
Xanthorrhoea sp.	2	2.3		