Selective feeding by macropods on vegetation regenerating following fire

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Abstract

The role of selective herbivory on plant mortality and density was investigated in naturally regenerating post-fire *Banksia* woodland at Whiteman Park Reserve, Western Australia. The western grey kangaroo (*Macropus fuliginosus*, Desmarest 1817) and black-gloved wallaby (*M. irma*, Jourdan 1837) are the largest native herbivores at the Reserve, and their impact upon the density of selected regenerating plant species in relation to time since fire was assessed. Both exotic and native plant species were well represented in the macropod diet. Density of plants within each species had no effect on selection. Defensive traits such as spinescence and tannin content also had no discernable effect on selection. The effect of herbivory and time since fire upon density was dependent upon plant species, with some species occurring at greater densities in exposed than protected areas. As expected, fire ephemerals declined in density with time, in particular *Austrostipa*, independent of level of herbivory. While herbivory appears to have a greater influence upon species density than fire, outcomes were highly species dependent. Results suggest kangaroos may assist in controlling introduced herbaceous species without detriment to native vegetation so long as populations did not exceed carrying capacities for the Park. The importance of continual monitoring of kangaroo populations is highlighted here, ensuring controlled build-up of combustible plant growth as well as maintaining kangaroo populations at a suitable carrying capacity for the environment.

Keywords: selective herbivory, macropod, post-fire regeneration, plant density.

Introduction

Seedlings and regenerating resprouters determine post-fire species composition in many Australian ecosystems (Leigh & Holgate 1979), with mortality during this vulnerable stage an important factor regulating the pattern of recovery (Harper 1977; Fenner *et al.* 1999). Herbivory may be a highly significant constraint on seedling recruitment (Crawley 1983; Hanley 1998). Selective predation of preferred seedling species has significant consequences for plant community development exerting a profound effect on community species composition (Hanley 1998), as well as on its structural components such as species density (Leigh & Holgate 1979). Substantial evidence indicates a decline in the populations of many plant species over time through selective elimination of their seedlings by herbivores (Lange & Graham 1983; Heinen & Currey 2000; Swihart & Bryant 2001).

For palatable plant species, browsing by native animals after fire may have a more profound effect on plant survival than the fire itself (Leigh & Holgate 1979). At Whiteman Park Reserve, Western Australia, preliminary fencing studies showed foliage cover of native species to be significantly greater after four years of kangaroo exclusion, implying possible adverse effects of kangaroos on native vegetation (Mattiske Consulting 2000). While declines in species abundance and cover are evident, however, it is important that species composition be also considered. Cover of the weed *Ehrharta calycina*, a major component of the kangaroo diet, was greater in kangaroo exclusion sites. The unpalatable weed *Ursinia anthemoides* was greatest in grazed sites, however, suggesting that feeding habits of kangaroos may favour some species to the detriment of others (Mattiske Consulting 2000).

Mattiske Consulting (1995) suggested that while large kangaroo populations may impact on native vegetation, their feeding activity may be beneficial in terms of fire control if they reduce the weed biomass. An understanding and management of factors affecting seedling survival and recruitment is therefore crucial for correct management of regenerating ecosystems. In 2001, Whiteman Park accommodated 900 western grey kangaroos with a breeding rate of 40 % per year. This breeding rate, facilitated by the presence of water and increased farmland area in the region, has led to a population size far exceeding pre-European estimates. These large numbers of kangaroos led to the implementation of a culling control program in 1991 under a Damage Control License, as it was thought that kangaroo herbivory was adversely affecting the native vegetation. While Mattiske Consulting (2000) reported that western grey herbivory had minimal impact on vegetation four years after plot exclusion, it was evident that kangaroos may reduce the cover of selected native plant species.

The range of plant species subject to damage from large native herbivores in south-western Australia is extensive. Palatable species show highly variable characteristics. At Whiteman Park, the two primary native herbivores are the western grey kangaroo (*Macropus fuliginosus*) and black-gloved wallaby (*M. irma*). To quantify the impact of these herbivores upon recovering vegetation, native species of high conservation value and introduced species, were monitored following fire in order to test the following hypotheses:

1. the densities of plants in areas protected from macropods should be greater than those of plants exposed in both the short (4 weeks) and long (2 years) term.
2. plant damage is positively correlated with the presence of macropods in the environment.
3. the response of plant species to macropod herbivory varies with differing morphological attributes.

Materials and Methods

Study site

Whiteman Park is situated 20 km north-east of Perth and consists of 3 600 ha of natural bushland and pasture. The vegetation is low woodland dominated by *Banksia attenuata, B. menziesii* and *Eucalyptus todtiana* on the upper slots, and *Melaleuca preissiana* and *B. littoralis* in the depressions. On 14 February 2001, a large fire affected much of the conservation area at Whiteman Park. Three sites within this burnt area were chosen to undertake the study. These were chosen to include varied plant communities, topography and soil types (two lowland sites and one elevated coastal dune site), in locations known to be frequented by macropods. These sites were not subjected to any adverse influence of fire fighting techniques (i.e. compaction, vehicle disturbance) to ensure a natural post-fire condition was maintained. Immediately following the fire, fencing was constructed around all study sites to omit all vertebrate access. Invertebrates could not be controlled via fencing, although daily monitoring of regenerating vegetation showed little herbivore activity from this group.

Species survey

A complete species list of naturally regenerating plant species observed growing at three sites of varying topography and soil type (two lowland sites and one elevated coastal dune site) at Whiteman Park was compiled from September to October 2001 (Appendix 2). This was the time of maximal species diversity of annuals. Most plants were identified to species level. Authorities for names follow Paczkowsaka & Chapman (2000). It was not possible to take specimens of the genera *Aira* or *Hypochaeris* to species level due to difficulties identifying individuals. Intermediates of both groups are common, hence it is possible individuals may belong to one of four or two species respectively, or hybrids of members of these species (Hussy *et al.* 1997). For all species encountered, signs of vertebrate herbivory were noted and numbers of eaten and uneaten plants recorded.

Mortality and density: short and long term effects of herbivory

Study areas at the three recently-burnt sites were divided into 10 plots (5 x 5 m) and sectioned into four quarters, using compass bearings to orient the divisions. From the complete species list for each site, ten abundant species of differing morphologies were selected at each site for use in quantification of herbivore effects on plant survival. Study species differed between sites. Densities were calculated using the plotless density method, as described by Mueller-Dombois & Ellenberg (1974). Each individual of the selected species wasto be monitored and marked by a balsa wood pop stick with identification number. These were pushed into the soil, with 2 cm protruding to limit potential interference with herbivore feeding. In plots where plants were not found in designated quarters, densities for these plants were recorded as 200 cm, the maximum distance from the quadrat centre (see Mueller-Dombois & Ellenberg (1974) for density calculation details).

Exclosure fences were modified to expose five of the ten plots at each site to herbivores seven months following the fire, with the time of exposure selected in mid-spring to encompass the presence of annual and geophyte species in the study. Plots were inspected after 4 weeks, and alive/dead status of study individuals and plant densities were recorded again. This allowed assessment of macropod selection patterns, with feeding activity observed consistently over the period, while ensuring annual and ephemeral species had not died down due to natural causes. Weekly spoor assessment was completed, with scats identified and counted in each quadrat. Traces of other species participating in the trials (i.e. rabbits, bandicoot) were not evident throughout the monitoring period. Infrared video filming of site 1 over a four week period following fence amendment supported this assumption, with no other vertebrate herbivore species observed.

Plant species densities were again calculated in October 2003, two years following the first assessment and two and a half years following the fire. Values for exposed sites were compared with densities of those protected in plots of adjacent exclosures (separated by 50 m) that had been fenced from herbivores since the fire. A comparison of plant density for each species with time (2001 and 2003) and position (protected and exposed) was made.

Plant morphology

Two leaves were collected from each of ten plants of each species, and leaf mass:area, leaf thickness and dry density were determined as described by Witkowski & Lamont (1991). Amendment was made to the formula for leaf:mass area and density of needle leaved species, by dividing the standard formula by 0.7854. Leaf area was measured using the Dias system (Delta-T Devices, Cambridge, England). Other characteristics recorded included plant height and moisture content, and chemical attributes as described below. Attributes are provided in Table 1.

Chemical analysis

Whole plant samples (all above ground tissue) were collected during the first week of herbivore exposure

Table 1

Mean physical and chemical attributes of study species for each site. For all attributes, n = 20, except for n = 10 (species samples pooled) for chemical analysis. NSS denotes insufficient sample material. Units of measure expressed as follows: Plant height in cm, H_20 : % dry weight, leaf thickness in mm, LMA = leaf mass : area (mg mm^{-2}), tannin (total), Fibre (ADF), N, P, K, Na and Ca: % dry weight.

	Species	Height	H_2O	Thickness	LMA	Density	Tannin	Fibre	N	P	K	Na	Ca
	SITE 1												
1	*Aira sp.*	9.67	69.2	0.29	45	154	0.55	47.2	0.62	0.03	0.06	0.15	0.19
2	*Astrostipa compressa*	15.2	62.3	0.32	979	2990	0.50	NSS	2.10	0.25	1.52	0.21	0.38
3	*Dasypogon bromeliifolius*	14.2	68.8	3.14	249	90	2.36	44.1	1.39	0.04	0.87	0.16	0.20
4	*Gladiolus caryophyllaceus*	19.3	83.1	0.58	128	228	0.60	36.6	1.21	0.10	1.76	0.03	0.79
5	*Haemodorum spicatum*	47.5	85.0	0.66	158	249	0.60	28.9	2.52	0.15	3.46	0.12	0.72
6	*Hypochaeris sp.*	19.9	85.5	0.2	58	289	0.10	NSS	1.91	0.09	1.31	0.92	1.51
7	*Trachymene pilosa*	7.25	85.0	0.4	50	124	2.20	NSS	2.01	0.14	1.30	0.92	1.41
8	*Ursinia anthemoides*	20.5	75.2	0.25	81	314	0.77	33.9	2.10	0.09	1.11	0.97	0.58
9	*Waitzia suavolens*	9.0	82.9	0.43	36	81	1.20	48.8	0.78	0.04	1.37	0.46	0.69
10	*Xanthorrhoea preissii*	67.8	64.7	2.15	675	318	0.73	41.3	0.95	0.04	0.74	0.07	0.74
	SITE 2												
1	*Aira sp.*	8.9	69.2	0.29	45	154	0.55	47.2	0.62	0.03	0.06	0.15	0.19
2	*Chaemascilla corymbosa*	6.7	81.8	0.33	42	128	NSS	NSS	2.66	0.13	2.14	0.29	0.34
3	*Cyathochaeta avenaceae*	6.7	56.6	1.87	381	201	1.00	43.6	1.11	0.04	0.84	0.21	0.14
4	*Gladiolus caryophyllaceus*	15.7	83.1	0.58	128	228	0.60	36.6	1.21	0.10	1.76	0.03	0.79
5	*Hypochaeris sp.*	11.5	85.5	0.2	58	289	0.10	NSS	1.91	0.09	1.31	0.92	1.51
6	*Kennedia prostrata*	2.8	69.7	0.22	85	385	1.53	31.6	2.94	0.13	1.23	0.23	1.22
7	*Lyperanthus serratus*	9.9	86.8	0.44	168	391	5.50	22.2	2.49	0.12	2.22	0.57	0.28
8	*Angianthus humifusus*	1.8	91.3	1.14	49	43	NSS	NSS	NSS	NSS	NSS	NSS	NSS
9	*Waitzia suavolens*	9.1	82.9	0.43	36	81	1.20	48.8	0.78	0.04	1.37	0.46	0.69
10	*Xanthorrhoea preissii*	101.6	64.7	2.15	675	318	0.73	41.3	0.95	0.04	0.74	0.07	0.74
	SITE 3												
1	*Aira sp.*	7.8	69.2	0.29	45	154	0.55	47.2	0.62	0.03	0.06	0.15	0.19
2	*Astrostipa compressa*	16.3	62.3	0.32	979	2990	0.50	NSS	2.10	0.25	1.52	0.21	0.38
3	*Burchardia umbellata*	26.3	81.4	0.4	74	239	1.33	41.2	1.63	0.09	1.65	0.14	0.33
4	*Gladiolus caryophyllaceus*	11.85	83.1	0.58	128	228	0.60	36.6	1.21	0.10	1.76	0.03	0.79
5	*Desmocladus flexuosa*	7.2	47.6	1.16	549	475	1.05	32.2	0.97	0.02	0.68	0.21	0.30
6	*Haemodorum spicatum*	55.3	85.0	0.66	158	249	0.60	28.9	2.52	0.14	3.45	0.12	0.72
7	*Pattersonia occidentalis*	17.4	66.9	1.22	267	225	1.13	48.6	0.94	0.03	1.53	0.08	0.32
8	*Podotheca chrysantha*	19.5	88.9	0.41	70	173	1.03	27.3	2.55	1.12	0.92	1.63	2.92
9	*Trachymene pilosa*	6.2	85.0	0.4	50	124	2.20	NSS	2.01	0.14	1.30	0.92	1.41
10	*Ursinia anthemoides*	18.1	75.2	0.25	81	214	0.77	33.9	2.10	0.09	1.11	0.97	0.58

from protected sites to ensure no influence of herbivory on plant chemistry. These were dried at 60° C for 48 hours in an air-forced oven. Numbers of plants used varied according to species type; for some small annual species, sufficient samples could not be collected in the vicinity of the trials to provide the minimal mass required for some analysis. All samples were milled using a coffee grinder and run through a Culatti® beater mill with 1 mm gauze sieve. Attributes analysed were selected due to their relative importance in regards to palatability (Hanley 1998).

Nitrogen, potassium and phosphorus

Nitrogen content of whole plants was determined using 200 mg of plant sample digested with H_2SO_4 and H_2O_2 in the presence of salicylic acid (Bradstreet 1965), and analysed using a Technicon segmented analyser using Berthelot colorimetric determination (Searle 1984). Determination of total P and K were completed using similar methods, although molybdate/vanadate colorimetric reaction and flame emission spectrometry (Varley 1966) were used respectively.

Acid detergent fibre (ADF)

ADF gives a combined measure of cellulose, lignin and cutin. About 200 mg of plant material was simmered in an acidic detergent solution for 1 hour, filtered on a coarse sintered glass crucible and washed with acetone to prevent possible complex formation from the interaction of tannins and proteins, forming insoluble precipitates that elevate ADF values. Weight of dry residue gave ADF, allowing for ash content. AOAC (973.18) and RACI (03–01) methods were used.

Total tannins

200 mg of plant material was extracted in 70% acetone and tumbled overnight. 200 mL supernatant aliquots were complexed with 5 mL deionised water, 12.5 mL of 200 g. L^{-1} Na_2CO_3 and 2.5 mL of 50% Folin Ciocalteu reagent. Samples were stood for 30 minutes then centrifuged at 3000 rpm for 10 minutes. Absorbance was read at 725 nm on a UV-visible Spectrophotometer. Values were plotted against a standard curve produced from tannic acid analysis. Results were expressed as tannic acid equivalents.

Data analysis

Log-likelihood analyses were completed for surrounding survey data to test consistency of grazing between sites and effect of plant spinescence on herbivory. Alive/dead status of protected and exposed plants were compared using log-likelihood analysis. *P* values are given without Bonferroni correction (Rothman 1990). Correlations between plant damage and selected plant traits were determined using Microsoft Excel for Mac (2002) after arcsine transformation. Densities of study species at each site were analysed in relation to time (2001 and 2003) and position (exposed/protected) using univariate GLM ANOVA by SPSS 11 for Mac OS X (SPSS Inc 2002). Plant attributes most closely correlated to plant damage at each site were determined using canonical variance analysis (CVA). Plants were assigned to one of three damage classes: site 1: 0%, 1–9%, 10–100%; site 2: 0%, 1–10%, 11–100%; site 3: 0%, 1–20%, 21–100%. Damage classes differed between sites due to differences in the magnitude of herbivory experienced at each location. Distributions of non-normal attributes were transformed as follows: density (log), height (sqrt), leaf thickness (log), tannin (log) and K (sqrt). Due to insufficient sample material for tannin analysis of *Chaemascilla* (site 2) and lack of correlation of this compound with other measured plant attributes, an average tannin value for all species was calculated and used for CVA to allow the inclusion of the species.

Results

Surrounding herbivory

Over 100 species of plants are included in the diet of native vertebrate herbivores in southwestern Australia (Appendix 1). Legumes including *Acacia*, *Bossiaea*, *Daviesia* and *Gastrolobium* feature strongly, as do many of the Haemodoraceae, Cyperaceae and Restionaceae. Percentages of plants eaten varied markedly for species surveyed in the surrounds of the study sites, although trends for species and family groups often agreed with those from the literature and listed in Appendix 1. Grass-like genera of the families Cyperaceae, Haemodoraceae, Restionaceae and Xanthorrhoeaceae commonly showed herbivore damage. *Dasypogon bromelifolius* and *Patersonia occidentalis* were two exceptions of grass-like species that were not selected by herbivores (Appendix 2). All members of the Myrtaceae were avoided, as were

Table 2

Log likelihood ratio results for alive/dead in relation to protection/exposure to herbivores. For all comparisons, *df* = 1, n = 20, except for Site 2, *Aira* sp. n= 18, *Hypochaeris* sp. = 19 and *Xanthorrhoea* = 9. *P* values denoted as * < 0.05, ** < 0.01, *** < 0.001.

Species	Alive Protected	Alive Exposed	Dead Protected	Dead Exposed	χ^2
Site 1					
Aira sp.	0	0	20	20	0.0
Austrostipa compressa	9	0	11	20	15.1***
Dasypogon bromeliifolius	20	20	0	0	0.0
Gladiolus caryophyllaceus	2	17	18	3	25.4***
Haemodorum spicatum	20	20	0	0	0.0
Hypochaeris sp.	5	0	15	20	7.6**
Trachymene pilosa	0	0	20	20	0.0
Ursinia anthemoides	0	0	20	20	0.0
Waitzia suaveolens	0	0	20	20	0.0
Xanthorrhoea preissii	20	20	0	0	0.0
Site 2					
Aira sp.	0	0	19	18	0.0
Angianthus humifusus	0	0	20	20	0.0
Chaemascilla corymbosa	0	0	20	20	0.0
Cyathochaeata avenaceae	19	20	1	0	1.4
Gladiolus caryophyllaceus	15	18	5	2	88.1***
Hypochaeris sp.	0	2	20	17	3.0
Kennedia prostrata	20	20	0	0	0.0
Lyperanthus serratus	17	17	1	3	0.9
Waitzia suaveolens	0	0	20	20	0.0
Xanthorrhoea preissii	12	9	0	0	0.0
Site 3					
Aira sp.	3	0	17	20	4.3*
Austrostipa compressa	9	2	11	18	6.5*
Burchardia umbellata	10	17	10	3	5.8*
Gladiolus caryophyllaceus	9	6	11	14	0.9
Alexgeorgia nitens	19	18	1	2	0.4
Haemodorum spicatum	20	20	0	0	0.0
Pattersonia occidentalis	20	20	0	0	0.0
Podotheca chrysantha	13	1	7	19	17.9***
Trachymene pilosa	2	0	18	20	2.9
Ursinia anthemoides	4	0	16	20	6.0

many of the Proteaceae with the exception of *Banksia attenuata* and *Persoonia saccata*. The exotic *Carpobrotus edulis* was grazed relatively heavily at site 2, although for sites 1 and 3 none showed any sign of damage.

Plant mortality

Hypochaeris sp. and *A. compressa* showed significantly higher rates of death in exposed plots than in those protected from herbivores (Table 2). At site 2, *G. caryophyllaceus* was the only species significantly affected by exposure. A number of species showed high mortality rates at site 3, including *U. anthemoides*, *P. chrysantha*, *B. umbellata, A. compressa* and *Aira* sp.

Plant density

Average densities of each of the ten study species per plot in the short- and long- term are given in Table 3. Plant density values after a short period (four weeks) of herbivore exposure were almost identical to pre-exposure values. Despite herbivore access, a high percentage of marked plants remained after herbivory, often as remnant stems, thus density was a poor indication of true herbivore activity after this time and was not included in further analyses. There was no relationship between the abundance of plant species in the environment and herbivory ($R = 0.333$).

Percentages of species showing herbivore damage differed greatly at each site after 4 weeks exposure (Table 3). *Austrostipa* was targeted at site 1 relative to other species (35% damaged). At site 2, *Waitzia* suffered the greatest of all the study species (35%), together with grassy *Aira* (30%). Grasses showed the greatest levels of damage at site 3, with *Aira* (50%), *Gladiolus* (30%) and *Desmocladus* (30%) commonly selected. *Podotheca* was also favoured (30%).

Damage values for plants surrounding each study site suggested herbivory differed greatly between plant species and sites. Of the individuals examined, the greatest proportions showing signs of herbivory were from families with typically grass-like morphologies: the Dasypogonaceae, Haemodoraceae and Restionaceae. The leguminous Fabaceae were one exception, with *Jacksonia*

Table 3

Densities of plants (No. per m^2, mean (SE)) at the beginning of the survey (2001), related to percentage of plants showing herbivore damage after four weeks of exposure and densities after 2 years (2003). Survey site for protected 2003 located approximately 20m from original site due to fencing amendment to facilitate ongoing herbivore monitoring.

Species	Plant density 2001		% Plants damaged	Plant density 2003	
SITE 1	**Exposed**	**Protected**	**Exposed**	**Exposed**	**Protected**
Aira sp.	201 (154)	1373 (878)	0	29595 (13005)	12620 (8142)
Austrostipa compressa	3793 (1346)	3372 (645.1)	35	1141 (357)	77 (28)
Dasypogon bromeliifolius	666 (329)	144 (66)	5	66 (12)	39 (10)
Gladiolus caryophyllaceus	726 (333)	936 (483)	0	41 (7)	162 (110)
Haemodorum spicatum	53 (18)	45 (5)	0	37 (7)	35 (3)
Hypochaeris sp.	69 (17)	638 (417)	0	488 (297)	14175 (10507)
Trachymene pilosa	1304 (944)	217 (63)	0	2693 (1141)	3605 (1738)
Ursinia anthemoides	174 (126)	1716 (1637)	5	675 (354)	1864 (694)
Waitzia suaveolens	280 (187)	1493 (725)	10	1519 (433)	6966 (5230)
Xanthorrhoea preissii	43 (5)	119 (37)	0	45 (11)	104 (44)
SITE 2					
Aira sp.	463 (438)	159 (108)	30	3856 (2712)	142929 (125009)
Angianthus humifusus	61 (34)	155 (53)	0	7746 (3302)	25 (0)
Chaemascilla corymbosa	1357 (1293)	159 (70)	5	60 (20)	25 (0)
Cyathochaeta avenacea	13098 (4422)	12592 (4670)	0	18891 (6960)	561 (442)
Gladiolus caryophyllaceus	59 (15)	54 (10)	5	25 (0)	25 (0)
Hypochaeris sp.	51 (16)	39 (4)	5	770 (364)	10362 (4358)
Kennedia prostrata	46 (17)	40 (5)	25	25 (0)	3569 (3276)
Lyperanthus serratus	37 (7)	29 (4)	0	43 (15)	25 (0)
Waitzia suaveolens	140 (114)	86 (46)	35	395 (242)	29 (3)
Xanthorrhoea preissii	35 (4)	32 (7)	15	34 (9)	132 (102)
SITE 3					
Aira sp.	70 (28)	3154 (3118)	50	5831 (3801)	6873 (4792)
Austrostipa compressa	762 (301)	270 (144)	25	178 (87)	304 (238)
Burchardia umbellata	72 (6)	146 (51)	15	64 (19)	194 (80)
Gladiolus caryophyllaceus	1566 (499)	1292 (641)	30	164 (109)	144 (78)
Alexgeorgia nitens	2276 (1392)	2946 (1687)	30	1428 (978)	92 (19)
Haemodorum spicatum	90 (32)	56 (5)	0	119 (44)	35 (4)
Patersonia occidentalis	25 (0)	30 (3)	5	33 (6)	37 (4)
Podotheca chrysantha	37 (8)	81 (21)	30	10816 (3518)	7956 (7088)
Trachymene pilosa	116 (36)	390 (264)	5	2247 (919)	586 (511)
Ursinia anthemoides	125 (43)	466 (348)	0	625 (286)	191 (76)

and *Kennedia* commonly selected. Species of Myrtaceae were never selected.

Effects of herbivory and time

Time significantly affected the density of all genera with the exception of *Haemodorum*, *Trachymene* and *Xanthorrhoea*. Effects appeared highly variable between species, however, with some densities greater in exposed plots than protected, suggesting herbivory did not directly determine abundance (Table 4). The effect of exposure to herbivory upon species density was less than for time, having a significant influence upon *Austrostipa*, *Dasypogon* and *Hypochaeris*. An interaction effect was only noted for *Austrostipa* and *Xanthorrhoea*. Time was less influential upon density at site 2 than position, only effecting *Aira*, *Gladiolus* and *Hypochaeris* (increased density) and also *Cyathochaeta* (decreased density). Densities of *Aira*, *Cyathochaeta* and *Hypochaeris*, but not *Gladiolus*, were affected by exposure to herbivory. An interaction effect was evident for *Angianthus*, *Cyathochaeta* and *Hypochaeris*, with the densities of *Angianthus* and *Cyathochaeta* increasing significantly in the exposed area over time, while decreasing in the protected area. For *Hypochaeris*, density increased significantly in the exposed and protected sites with time. Fewer effects were evident at site 3. Time affected densities of *Aira* and *Alexgeorgia* (decreased density) and *Gladiolus* and *Podotheca* (increased density), although position had little effect, with the exception of *Haemodorum*. An interaction between position and time was noted for *Trachymene*. *Austrostipa* was not influenced by either variable.

Table 4

Results of tests upon densities of plants in relation to position (protected/exposed) and time (year – 2001/2003). For all species df=3, univariate GLM ANOVA.

Species	*P* Position	Time	Interaction
Site 1			
Aira sp.	0.000	0.579	0.191
Austrostipa compressa	0.000	0.025	0.007
Dasypogon bromeliifolius	0.002	0.024	0.331
Gladiolus caryophyllaceus	0.001	0.325	0.585
Haemodorum spicatum	0.225	0.952	0.952
Hypochaeris sp.	0.012	0.028	0.479
Trachymene pilosa	0.072	0.884	0.210
Ursinia anthemoides	0.045	0.115	0.608
Waitzia suaveolens	0.015	0.114	0.433
Xanthorrhoea preissii	0.599	0.599	0.011
Site 2			
Aira sp.	0.005	0.703	0.840
Angianthus humifusus	0.152	0.045	0.002
Chaemascilla corymbosa	0.068	0.413	0.794
Cyathochaeata avenacea	0.009	0.003	0.001
Gladiolus caryophyllaceus	0.000	0.899	0.876
Hypochaeris sp.	0.000	0.008	0.005
Kennedia prostrata	0.275	0.089	0.100
Lyperanthus serratus	0.799	0.119	0.603
Waitzia suaveolens	0.550	0.101	0.065
Xanthorrhoea preissii	0.470	0.530	0.335
Site 3			
Aira sp.	0.009	0.725	0.633
Austrostipa compressa	0.150	0.399	0.342
Burchardia umbellata	0.887	0.056	0.553
Gladiolus caryophyllaceus	0.000	0.826	0.549
Alexgeorgia nitens	0.022	0.585	0.078
Haemodorum spicatum	0.533	0.032	0.224
Pattersonia occidentalis	0.069	0.206	0.951
Podotheca chrysantha	0.000	0.477	0.066
Trachymene pilosa	0.052	0.203	0.035
Ursinia anthemoides	0.372	0.925	0.229

Table 5

Ranking of correlation coefficients from strongest to weakest for plant attributes with percentage of plants eaten for each site after 4 weeks exposure. Symbol in brackets denotes positive or negative relationship. No correlations were significant ($P > 0.05$, $df = 8$ for sites 1 and 3, $df = 7$ for site 2).

Rank	Site 1	Site 2	Site 3
1	Na (-)	H_2O (+)	Leaf density (-)
2	H_2O (+)	Leaf thickness (-)	Na (-)
3	LMA (-)	Na (+)	Plant density (+)
4	Leaf thickness (-)	Plant height (-)	LMA (+)
5	N (-)	Plant density (-)	P (-)
6	Ca (-)	Phenolics (+)	N (-)
7	Phenolics (-)	LMA (-)	Phenolics (-)
8	Plant density (-)	Ca (+)	Ca (-)
9	Leaf density (-)	P (+)	H_2O (+)
10	P (-)	N (-)	Leaf thickness (-)
11	Plant height (-)	Density (-)	Plant height (+)

Plant attributes

A rank of correlations of plant attributes with plant damage was constructed by completing Principal Components Analysis for species at each site (Podani 1994). Plant damage was not significantly correlated with any facet of plant morphology at any site, and ranks varied between sites (Table 5). Sodium had a negative influence on selection at sites and 1 and 3, although for site 2 this trend was absent. This trend was similar for calcium, although the influence of this salt was less profound than with sodium. Moisture content had the most influence upon selection at site 2, although for site 3, leaf density had the greatest effect. Plant height had the least influence on selection at sites 1 and 3, while leaf density was of least influence at site 2. Plant density had little effect on selection at any site.

Discussion

Feeding preferences of macropods at Whiteman Park were similar to those of many native herbivores in southwestern Australia (Bell 1994; Shepherd *et al.* 1997; Bell *et al.* 1987). Tables 1 and 2 highlighted a preference for grass-like species, while Myrtaceous species were considered less palatable. Tolerance for aromatic species such as *Corymbia calophylla* and *Eucalyptus marginata* is prevalent for some possum species (Appendix 1) and has also been reported for *M. eugenii* and *M. irma*, but not *M. fuliginosus* (Shepherd *et al.* 1997; Wann & Bell 1997). Similarly, feeding upon *C. calophylla* and *E. marginata* was never observed at Whiteman Park throughout the duration of the study.

Density comparisons two years after fire were very useful in demonstrating the long-term impact of selective feeding. Of particular interest were changes in populations of weed species, with densities of many species significantly affected by time. The direction of the effect (i.e. increase or decrease in density) and ecology of individual species was an important consideration when assessing these results. For some species (e.g. *Aira*, site 1, 2003), exposed plots had greatest densities, suggesting microsite differences, such as light availability or differential seed set in previous years, may be more influential than herbivore activity, although sites were selected where possible to minimise such extrinsic factors. Alternatively, *Aira* may benefit from macropod feeding upon other species, reducing competitive impacts of surrounding vegetation. Differences in density between exposed and protected plots at the beginning of the study (Table 3) further emphasize this potential for species density to vary greatly at the microsite level.

Effects of herbivory and time were of particular interest in regards to fire ephemeral species, such as *Austrostipa compressa*. *A. compressa* density decreased significantly with time since fire at site 1, as has been observed in other systems (Baird 1984). Germination and flowering of this species are typically stimulated by fire, and it appeared to make up an important component of the kangaroo diet following fire relative to other species (35% plants damaged after four weeks' exposure). With time, however, herbivory did not appear to have a detrimental effect on density of the species, with values in exposed plots significantly greater than in protected plots in 2003. Effects were absent at site 3, although overall densities for the species at this site were less overall throughout the study. Dry conditions observed within the study area on the dune slope at site 3 may have outweighed any herbivore or time effects on more sensitive plant species. For sites 2 and 3, mortality of species was rarely increased by macropod feeding, and with the exception of *Austrostipa*, those significantly affected were primarily introduced species. Harsh environmental conditions at site 3, where plants were exposed on the dune crest, may have contributed simultaneously with herbivory to increase mortality relative to other sites.

Examination of death rates of species in protected and exposed sites revealed that non-geophytic resprouters tended not to be eaten, while annuals were preferentially selected. Among the sites, the mortality of *Cyathochaeta*, *Dasypogon*, *Patersonia* and *Xanthorrhoea* were low, with species usually exempt from browsing. This contrasted with many of the smaller annuals and geophytes, including *Aira*, *Austrostipa*, *Hypochaeris* and *Podotheca*, where lower survival rates were attributed to macropod feeding. Perennials and shrubs, including *Desmocladus*, *Haemodorum* and *Kennedia*, were commonly grazed. Mortality of such species appeared unaffected by Macropod feeding, however, suggesting plant growth form is a major influence in determining the herbivory outcomes in many instances.

Densities of short-lived annuals, particularly after the fire, typically exceeded longer-lived species. Shorter-lived annuals are typically fast growing, reproducing rapidly, and thus are available to herbivores for a short time in great abundance (personal observations). Investment in herbivore defence may be minimal, with the individuals escaping in space and time (Briner & Frank 1998). While repeated grazing of many resprouters is observed to lead to their eventual death (Leigh & Holgate 1979; Wahungu *et al.* 1999), there appeared to be few long-lived species among the study selection with enhanced defence mechanisms such as secondary metabolites (e.g. tannins). *Dasypogon*, *Trachymene* and *Lyperanthus* had the greatest tannin levels, although all three have markedly different life strategies and suffered variable herbivore damage. With the exception of *Dasypogon* with serrated leaf margins, none of the species had physical defence mechanisms, suggesting other cues were driving macropod selection habits.

Correlation coefficients confirmed that the plant attributes analysed had little influence on feeding selection. The lack of correlation between plant density and percentage eaten emphasizes the highly selective feeding behaviour of macropods at the reserve. Certain plants, especially grasses, *Austrostipa, Desmocladus* and *Aira*, were favoured over more abundant, larger species (Appendices 1 and 2). At site 1, however, *Aira* escaped attention, possibly due to the high density of palatable alternatives such as *Austrostipa*. Introduced species featured strongly, indicating weeds are equally subject as native plant species to macropod feeding. Macropod grazing may act to reduce weed cover to a significant extent in some areas, although as shown by differences in grazing damage of *Aira* between the three sites, feeding activity was independent of weed density, contrasting with the findings of Mattiske Consulting (1995).

It is likely that pre-European fire regimes encouraged the regrowth of undefended seedling species, with fire often affecting large tracts of land (Flannery 1994). Such vast areas were unlikely to be reinhabited by vertebrates for some time, allowing substantial development of small herbaceous species, as well as larger resprouters, providing cover for smaller recruits. Although fire regimes were variable throughout the continent, a general reduction in the size and number of fires since European settlement typically facilitates rapid movement of large herbivores into post-fire areas. An increase in the effects of herbivory are therefore inevitable, with plants unable to evolve functional defensive strategies in such a short time. Effects are typically more significant to some plant species relative than others, which has been a key finding of my study. Understanding the factors influencing mammalian browsing can facilitate the development of management strategies. Current fire management regimes typically result in the burning of smaller areas, which are often reinhabited by herbivores within days. The ability of kangaroos to feed on lush post-fire growth, coupled with their increase in numbers in these remaining habitats with the availability of free water, undoubtedly impacts upon post-fire recruitment of species with little or no defence strategy. While herbivory appears to have a greater influence upon species density than fire, outcomes are highly species dependent. The selection of a number of weed species in the post-fire diet of macropods must also assist in native regeneration to some extent, reducing competition and decreasing fuel loads over time.

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Appendix 1

List of known food plants of Western Australian native marsupials. Leaf types denoted as spinescent = S, non-spinescent = NS; spinescence determined from Perth Flora (1987) and B. Lamont (pers. obs.). Methods of detection as food source denoted as F = faecal analysis, S = stomach content analysis, O = observed eating, P = plant damage. Native herbivores denoted as E = *Macropus eugenii* (tammar wallaby), F = *M. fuliginosus* (western grey kangaroo), I = *M. irma* (black-gloved or brush wallaby), P = *Pseudocheirus occidentalis* (western ring-tail possum), T = *Trichosurus vulpecula* (common brush-tail possum). Reference sources denoted as 1 = Halford, Bell & Loneragan (1984), 2 = Bell (1994), 3 = Shepherd, Wardell-Johnson, Loneragan and Bell (1997), 4 = Bell, Moredoundt & Loneragan (1987), 5 = Wann & Bell (1997). Exotic species denoted by *.

Plant species	Family	Woody shrub (w), Non-woody shrub (n), Grass-like (g)	Spinescent (S), Non-spinescent (N)	Native herbivore	Method of detection	Reference
Acacia celastrifolia	Mimosaceae	w	N	F	F	1, 2
Acacia extensa	Mimosaceae	w	N	F		2
Acacia pulchella	Mimosaceae	w	S	F, E	F	2, 3
Acacia rostellifera	Mimosaceae	w	N	E	F, S, O	2, 4
Acacia stenoptera	Mimosaceae	n	S	I	F	5
Adenanthos cygnorum	Proteaceae	w	N	F	F, P	1, 2, 5
Alexgeorgea nitens	Restionaceae	g	S	I	F	5
Allocasuarina sp.	Casuarianaceae	w	N	F		2
Allocasuarina sp.	Casuarinaceae	w	N	F	F	1
Anthocercis littorea	Solanaceae	w	N	F	P	1, 2
Arnocrinum preissii	Anthericaceae	g	N	I	F	5
*Ashodelus fistulosus**	Asphodelaceae	g	N	E	F, S, O	2, 3
*Asparagus asparagoides**	Asparagaceae	n	N	E	F, S, O	2, 4
Astroloma ciliatum	Epacridaceae	w	S	F	F	2, 3
Austrotipa flavescens	Poaceae	g	N	E		2
Austrotipa sp.	Poaceae	g	N	F	F	5
Baeckaea camphorosmae	Myrtaceae	w	N	F		2
Beaufortia elegans	Myrtaceae	w	N	I	F	5
Billardiera variifolia	Pittosporaceae	n	N	F	F	3
Boronia spathulata	Rutaceae	n	N	F, I	F	3, 5
Bossiaea eriocarpa	Fabaceae	n	N	F	F, P	1, 2, 5
Bossiaea linophylla	Fabaceae	n	N	E, F		2
Bossiaea ornata	Fabaceae	n	N	F, I	F	2, 3, 5
Burchardia multiflora	Colchicaceae	g	N	F	P	1, 2
Callitris preissii	Cupressaceae	w	N	E	F, S	4, 2
Calothamnus sanguineus	Myrtaceae	w	N	F	F, P	1, 2
Carprobrotus edulis	Aiozaceae	n	N	F, I	F	5
Cassytha sp.	Lauraceae	n	N	E, I	F	3
Centaurium erythraea	Gentianaceae	n	N	E	F	3
Clematis pubescens	Ranunculaceae	n	N	E, F		2
Conostylis setigera	Haemodoraceae	g	N	F	F, P	1, 2
Corymbia calophylla	Myrtaceae	w	N	E, F, P, T	F	3
Corynotheca micrantha	Anthericaceae	g	N	F, I	F	5
Cyathochaeta avenacea	Cyperaceae	g	N	E		2
*Cynodon dactylon**	Poaceae	g	N	F, I	F	5
Dampiera lavandulacea	Goodeniaceae	n	N	F	F, P	1, 2
Dampiera linearis	Goodeniaceae	n	N	F, I	F	5
Daviesia decurrens	Fabaceae	n	S	F	F	1, 2
Daviesia gracilis	Fabaceae	n	S	F	F,P	1
Daviesia preissii	Fabaceae	n	S	F	F	2, 3
Desmocladus fasciculata	Restionaceae	g	N	F		2
Desmocladus flexuosa	Restionaceae	g	N	F	F	1, 5
Dianella revoluta	Phormiaceae	g	N	F	P	1, 2
Dichopogon sp.	Anthericaceae	g	N	F	P	1
Dicotyledon sp.			N	F, I	F	5
Drosera spp.	Droseraceae	n	N	F	P	1
Dryandra carduacea	Proteaceae	w	S	F	F, P	1, 2
Ehrharta calycina	Poaceae	g	N	F, I	F	5
Eremophila glabra	Myoporaceae	w	N	E	F, S	4, 2
Eucalyptus marginata	Myrtaceae	w	N	E, I, P, T	F	5, 3
Gastrolobium bilobum	Fabaceae	w	N	E, F, I, T	F	3
Gastrolobium calycinum	Fabaceae	w	S	F	F, P	1, 2
Gastrolobium trilobum	Fabaceae	w	S	F	F, P	1, 2
Glischrocaryon aureum	Haloragaceae	n	N	F	F, P	1, 2
Gompholobium preissii	Fabaceae	w	N	F	F	1, 2
Gyrostemon subnudus	Gyrostemanaceae	n	N	F	P	1, 2
Hakea ambigua	Proteaceae	w	N	F	F	1, 2
Hakea lissocarpha	Proteaceae	w	S	E, F, I, T	F	3

Appendix 1 (cont.)

Plant species	Family	Woody shrub (w), Non-woody shrub (n), Grass-like (g)	Spinescent (S), Non-spinescent (N)	Native herbivore	Method of detection	Reference
Hakea trifurcata	Proteaceae	w	S	F	F, P	1, 2
Hakea undulata	Proteaceae	w	S	F	F	1, 2
Hibbertia cunninghamii	Dilleniaceae	w	N	E		2
Hibbertia racemosa	Dilleniaceae	w	N	F		2
Hypocalymma angustifolium	Myrtaceae	w	N	E		2
Jacksonia furcellata	Fabaceae	w	S	F	F	5
Jacksonia restioides	Fabaceae	n	N	F	F, P	1, 2
Juncus pallidus	Juncaceae	g	N	E, F, I	F	3, 2
Kennedia carinata	Fabaceae	n	N	F	F	3
Lasiopetalum molle	Sterculiaceae	n	N	F	P	1, 2
Lasiopetalum oppositifolium	Sterculiaceae	n	N	E	F	4, 2
Lepidosperma angustatum	Cyperaceae	g	S	F	F	3
Lepidosperma scabrum	Cyperaceae	g	S	F	F, P	1, 2
Lepidosperma tenue	Cyperaceae	g	S	E, F	F	3
Leptomeria cunninghamii	Santalaceae	n	N	E	F	3
Leucopogon capitellatus	Epacridaceae	w	S	E, F, I	F	2
Leucopogon conosteophioides	Epacridaceae	w	S	F, I	F	5
Leucopogon pulchellus	Epacridaceae	w	N	F		2
Leucopogon sp.	Epacridaceae	w	N	F, I	F	5
Leucopogon verticillatus	Epacridaceae	w	N	E, F, I	F	2, 3
Lomandra effusa	Haemodoraceae	g	N	F	F, P	1, 2
Lomandra hermaphrodita	Haemodoraceae	g	N	F	F, P	1, 2
Lomandra preissii	Haemodoraceae	g	N	F		2
Lomandra sericea	Haemodoraceae	g	N	E, F, I	F	3
Lomandra sonderii	Haemodoraceae	g	N	E	F	3
Lomandra sp.	Haemodoraceae	g	N	F	F	2, 3
Loxocarya sp.	Restionaceae	g	N	E, F, I	F	3
Lysinema ciliatum	Epacridaceae	w	N	I	F	5
Macrozamia riedlei	Zamiaceae	w	S	F, I	F	2, 5
Melaleuca viminea	Myrtaceae	w	N	F, I	F	3
Mesomalaena stygia	Cyperaceae	g	S	I	F	5
Mesomalaena tetragona	Cyperaceae	g	S	F		2
Mirbelia ramulosa	Fabaceae	n	N	F	F, P	1, 2
Monocotyledon sp.		g		F, I		5
Native grasses (non-flowering)		g	N	F	P	1
Neurachne alopecuroidea	Poaceae	g	N	F	F, P	1, 2, 3
Notodanthonia setacea	Poaceae	g	N	E, F, I	F	5, 3
Nuytsia floribunda	Loranthaceae	n	N	F, I	F	5
Opercularia hispidula	Rubiaceae	n	N	E, F, I	F	3
Opercularia vaginata	Rubiaceae	n	N	F	F, P	1, 2
Oxylobium capitatum	Fabaceae	w	S	F, I	F	5
Patersonia occidentalis	Iridaceae	g	N	F, I	F	5
Persoonia longifolia	Proteaceae	w	N	F		2
Petrophile serruriae	Proteaceae	w	S	F	P	1, 2
Phyllanthus calycinus	Rosaceae	n	N	E	F, S, O	2, 4
Schoenus cyperacea	Cyperaceae	g	N	E		2
Solanum symonii	Solanaceae	n	N	E	F, S, O	2, 4
Stylidium affine	Stylidiaceae	n	N	F	F, O	2, 4
Stypandra imbricata	Phormiaceae	g	N	F	F, P	1, 2
Tetraria octandra	Cyperaceae	g	N	F	F	1, 2
Tetrarrhena laevis	Poaceae	g	N	F	F	3
Tetratheca confertifolia	Tremandraceae	n	N	E, F	P, F	1, 2
Thomasia cognata	Sterculiaceae	n	N	F	F, O	2, 4
*Trachyandra divaricata**	Asphodelaceae	g	N	E	F, S	2, 4
Tribonanthes uniflora	Haemodoraceae	g	N	F	P	1, 2
Tricoryne elatior	Anthericaceae	g	N	F, I	F	5
Xanthorrhoea preissii	Xanthorrhoeaceae	g	S	F, I	F	1, 5

Appendix 2

Naturally regenerating plant species observed in 2 km radius of each study site. A maximum of 15 plants were examined where possible and macropod damage noted. N : non-spinescent foliage, S : spinescent foliage.

Family	Species	Spinescence	Site	No. plants examined	Plants eaten (%)
Aiozaceae	*Carpobrotus edulis*	N	1	15	0
Aiozaceae	*Carpobrotus edulis*	N	2	15	47
Aiozaceae	*Carpobrotus edulis*	N	3	15	0
Cyperaceae	*Cyathochaeta avenacea*	N	2	15	67
Dasypogonaceae	*Dasypogon bromeliifolius*	S	1	15	0
Dasypogonaceae	*Dasypogon bromeliifolius*	S	2	15	0
Dasypogonaceae	*Dasypogon bromeliifolius*	S	3	15	0
Dasypogonaceae	*Lomandra caespitosa*	N	1	10	80
Dasypogonaceae	*Lomandra caespitosa*	N	2	15	53
Dasypogonaceae	*Lomandra caespitosa*	N	3	10	80
Dilleniaceae	*Hibbertia huegelii*	N	2	5	60
Dilleniaceae	*Hibbertia vaginata*	N	1	15	0
Dilleniaceae	*Hibbertia vaginata*	N	2	15	0
Dilleniaceae	*Hibbertia vaginata*	N	3	15	0
Epacridaceae	*Conostephium pendulum*	S	1	10	0
Epacridaceae	*Conostephium pendulum*	S	3	10	0
Fabaceae	*Jacksonia floribunda*	S	1	15	93
Fabaceae	*Jacksonia floribunda*	S	3	15	93
Fabaceae	*Jacksonia sternbergiana*	S	2	15	60
Fabaceae	*Kennedia prostrata*	N	2	13	69
Haemodoraceae	*Conostylis setigera*	N	2	15	80
Haemodoraceae	*Haemodorum spicatum*	N	1	15	46
Haemodoraceae	*Haemodorum spicatum*	N	2	15	13
Haemodoraceae	*Haemodorum spicatum*	N	3	15	46
Iridaceae	*Patersonia occidentalis*	N	1	15	0
Iridaceae	*Patersonia occidentalis*	N	2	15	0
Iridaceae	*Patersonia occidentalis*	N	3	15	0
Mimosaceae	*Acacia pulchella*	S	2	4	25
Myrtaceae	*Calytrix flavescens*	N	1	15	0
Myrtaceae	*Calytrix flavescens*	N	3	15	0
Myrtaceae	*Corymbia calophylla*	N	1	15	0
Myrtaceae	*Corymbia calophylla*	N	2	15	0
Myrtaceae	*Corymbia calophylla*	N	3	15	0
Myrtaceae	*Hypocalymma angustifolium*	N	1	15	0
Myrtaceae	*Hypocalymma angustifolium*	N	2	15	0
Myrtaceae	*Hypocalymma angustifolium*	N	3	15	0
Myrtaceae	*Melaleuca preissiana*	N	2	5	0
Myrtaceae	*Pericalymma ellipticum*	N	2	15	0
Myrtaceae	*Regelia ciliata*	N	1	15	0
Myrtaceae	*Regelia ciliata*	N	3	15	0
Myrtaceae	*Scholtzia involucrata*	N	1	9	0
Myrtaceae	*Scholtzia involucrata*	N	2	11	0
Myrtaceae	*Scholtzia involucrata*	N	3	9	0
Proteaceae	*Banksia attenuata*	S	1	15	27
Proteaceae	*Banksia attenuata*	S	3	15	27
Proteaceae	*Dryandra lindleyana*	S	1	15	0
Proteaceae	*Dryandra lindleyana*	S	3	15	0
Proteaceae	*Persoonia saccata*	S	2	4	25
Proteaceae	*Stirlingia latifolia*	N	1	15	0
Proteaceae	*Stirlingia latifolia*	N	3	15	0
Restionaceae	*Alexgeorgea nitens*	S	1	15	100
Restionaceae	*Alexgeorgea nitens*	S	3	15	100
Restionaceae	*Alexgeorgea sp.*	S	2	15	87
Restionaceae	*Lygenia barbata*	S	2	15	100
Restionaceae	*Lyginia barbata*	S	1	15	100
Restionaceae	*Lyginia barbata*	S	3	15	100
Rutaceae	*Philotheca spicatum*	N	2	15	0
Xanthorrhoeaceae	*Xanthorrhoea preissii*	S	1	15	13
Xanthorrhoeaceae	*Xanthorrhoea preissii*	S	2	15	20
Xanthorrhoeaceae	*Xanthorrhoea preissii*	S	3	15	13