Journal of the Royal Society of Western Australia, 81:95-106, 1998

Passive clearing of native vegetation: Livestock damage to remnant jarrah (*Eucalyptus marginata*) woodlands in Western Australia

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Manuscript received March 1997; accepted October 1997

Abstract

In south-western Australia, areas of native forest and woodland on farmland left after agricultural clearing (remnants) have in recent times been subject to chronic disturbance by grazing livestock. We analysed adjacent grazed and ungrazed sites to assess the effects of grazing disturbance on the scleropyhll woodland community. Species richness and diversity were reduced in heavily-grazed sites and floristic dissimilarity between grazed and ungrazed sites was high. In the heavily-grazed sites, exotic species were 46% to 48% of the species recorded. Frequency and cover of native perennial species was significantly reduced in the heavily-grazed sites and in a lightly-grazed site. There was a significant increase in the frequency and cover of exotic annual grasses and herbs in the heavily grazed sites. Other life form groups such as geophytes, native perennial grasses and native annuals were not significantly affected by livestock grazing. Grazing also resulted in a significant increase in surface soil compaction and water repellency as well as concentration of soil N and P. Size-class distribution of the overstorey indicated that no recruitment had taken place for many years and, although germination of overstorey species occurred each year, no seedlings survived at the heavily grazed sites. In these sclerophyll woodlands, grazing has altered plant community structure, from a understorey dominated by perennial shrubs to one dominated by exotic annual grasses and forbs. Resilience of native perennial species is dependent on reproductive stategy, life form and morphology, life history and palatiblity. Annual exotic species are favoured by increases in soil nutrients and disturbance, reduction in competition and an ability to withstand a high level of disturbance.

Introduction

Management of native vegetation, as part of a landscape mosaic with cleared agricultural land, requires an understanding of its resilience to disturbance. Remnants of original vegetation tend to be small and isolated, and subject to many internal and external pressures including grazing (Saunders *et al.* 1991). In many parts of south-western Western Australia, clearing of remnant vegetation on farmland has been restricted by legislation for a number of years in an effort to combat land degradation such as salinization. However, although overt clearing now occurs only rarely, livestock (mainly sheep and cattle) are increasingly allowed to utilize remnant vegetation and cause varying degrees of change. While remnants may seem to be surviving well in the landscape at a superfical level, communities may be severely jeopardized in the long term, at a more detailed level.

Native eucalypt forest and woodlands with a sclerophyll shrub understorey in higher rainfall zones are not adapted to intensive herbivore grazing. Under natural conditions, these ecosystems would have been subject to sporadic grazing by sparse populations of macropods. With the introduction of domestic livestock, jarrah forest and woodlands were generally cleared and replaced with annual pasture rather than used for stock grazing. In consequence, the effects of greatly increased grazing disturbance in this environment is not well understood. For sub-alpine and semi-arid woodlands in south-eastern Australia, livestock grazing can change the vegetation structure from woodland to grassland (Chesterfield & Parsons 1985; Gibson & Kirkpatrick 1989). In other vegetation types such as Australian native grasslands, livestock grazing has resulted in an increase in unpalatable woody shrubs (Hodgkinson & Harrington 1985; Williams 1990). In plant communities that have had a long history of grazing disturbance, this disturbance is considered essential to maintaining species diversity (Carr & Turner 1959; McNaughton 1985; Noy-Meir *et al.* 1989).

Grazing affects the vegetation dynamics of remnants by influencing recruitment, mortality, dominance and age distribution of species (Wellington 1989). Direct effects of livestock grazing include the elimination of susceptible species (Wilson 1990) and the expansion of resilient species (Wimbush & Costin 1979). The need to identify susceptible (decreaser) and resilient (increaser) species is important for planning management of grazed sites (Hacker 1984). It may also be useful in ecological terms to classify species into functional groups (Hobbs 1992) based on life forms or reproductive strategies (Armstrong 1993). Maintenance of one or more species representative of each functional group may be an important strategy in restoration / management of degraded remnants (Hobbs 1992). The ability of an ecosystem to regenerate naturally may also depend on whether livestock disturbance has affected only the biotic components, such as the vegetation, or the resource base as well, such as the soil (Hobbs & Norton 1996).

Overstorey species, which in the remnants studied here are *Eucalyptus marginata* Donn ex Smith (jarrah) and *Corymbia calophylla* Lindley (marri), make up a critical functional group, through such processes as nutrient cycling, soil stabilisation and maintainence of hydrological balance, without which viability of vegetation of an area is seriously threatened. Recruitment of new trees is vital to the community's continued resilience to grazing disturbance.

A previous study (Pettit *et al.* 1995) examined the floristics of a large number of jarrah woodland remnants subjected to varying levels of livestock disturbance. This study reports on the results of a more detailed examination of 2 of these remnants, and clarifies the effects of livestock disturbance on; soil properties, survival of floristic life form groups and species with different reproductive strategies, and recruitment of overstorey species.

Methods

The study sites were located within remnants of native vegetation left after clearing for agriculture in the eastern portion of the Collie River catchment in the south west of Western Australia (33° 30' S, 116° 30' E). The landscape and soils of this area are typical of the Beraking valley landform with superfical deposits consisting mainly of sands, loams and sesquioxidic gravels up to several metres in depth on the valley slopes. These usually overlay pallid and weathered zones and granitic basement rock, with some ferruginous duricrust on the hilltops (Mulcahy & Bettenay 1972). Soil types at both locations were lateritic gravelly duplex soils with a sandy A horizon at location A and sandy loam at location B. The sites are at the eastern extent of the northern jarrah forest where jarrah and to a lesser extent marri and *Eucalyptus wandoo* Blakely (wandoo) form a woodland or open forest (Dell & Havel 1989). The understorey is dominated by perennial woody shrubs and herbs with the most abundant families being Proteaceae, Papilionaceae, Myrtaceae and Cyperaceae (Bell & Heddle 1989). The climate of the study region is Mediterranean-type with long term average annual rainfall of approxmately 650 ± 117 mm yr^{-1} of which approximately 80% falls between the months of May and October. Annual pan evaporation for the area is approximately 1600 mm and daily maximum temperature ranges from 31° C in January to 15° C in July. There are about 14 frosts per year.

Two locations were chosen from an extensive survey of remnants occurring on agricultural land in the eastern Collie River catchment (Pettit *et al.* 1995). Location A consisted of a remnant that has been heavily grazed (5 sheep ha^{-1}) for at least the past 18 years, mainly by sheep (Table 1). This was separated by a fence and road from a remnant that has had no livestock grazing for at least 10 years and any grazing which took place before this was at low stocking rates (< 0.5 sheep ha^{-1}). The second location (B) consisted of a remnant which has been heavily grazed by sheep for approximately the past seven years. This site was separated by a fence from a lightly grazed site which has been leased for grazing at low stocking rates intermittently for the past 30 years. Although grazed at low stocking rates in 1991 and 1992, this site was not grazed by sheep during 1993. A third site at Location B was situated approximately 500 m from the other two sites on the next hilltop and has never been grazed by livestock. Farmland surrounding remnants consisted of clover (*Trifolium* spp) based pasture which is regularly fertilised with superphosphate. All sites would have been subject to grazing from rabbits and native herbivores (mainly kangaroos). However this was at low densities and there was no evidence that these animals had much impact on the vegetation, at least compared with domestic livestock, at these particular sites.

At each location, two 100 m transects were established, located approximately 50 m apart and at least 50 m from

Table 1

Site characteristics for the two areas of remnant vegetation studied here.

Location	Grazing [a]	Size Ha	Surrounding land use	Surface Soil texture	% clay[b]	% coarse sand[b]	% gravel[b]	Last Fire
A	heavy (' 10 dse ha^{-1})	40	pasture	sand	4.3 ± 0.9	60.6 ± 2.1	71 ± 2	1974
A	past light	150	pasture, reforestation	sand	4.5 ± 1.2	61.0 ± 4.4	73 ± 4	1974
B	heavy (' 10 dse ha^{-1})	230	pasture, native forest	sandy loam	6.2 ± 1.9	53.4 ± 1.8	68 ± 3	' 1984
B	light (' 0.5 dse ha^{-1})	230	pasture, native forest	sandy loam	7.3 ± 2.0	53.5 ± 2.6	72 ± 4	1989
B	ungrazed	230	native forest	sandy loam	7.5 ± 2.1	58.6 ± 2.3	64 ± 5	1989

[a] dse ha^{-1} = dry sheep equivilent per hectare
[b] Mean of 10 samples of the top 10 cm of soil at each site ± standard error. Percentage gravel is for the whole soil sample. Clay and coarse sand % are for the soil sieved to < 2 mm.

the remnant boundary, to minimise edge effects. At 20 m intervals along each transect, five adjacent 1 m^2 quadrats were placed parallel to the transect with the transect line forming one side of each quadrat. This gave a total of 50 x 1 m^2 quadrats in each site. Numbers of individuals and estimated percentage cover of all species within each quadrat were recorded. For overstorey species, seedlings and saplings up to 2 m in height that formed part of the understorey were also recorded . The survey was carried out initially in August 1992 and repeated in February 1993 and August 1993 to record any seasonal changes to the vegetation and phenology of selected species. Emergence of tree seedlings (*Eucalyptus marginata* and *C. calophylla*) along the transects was recorded and seedlings tagged and survival monitored monthly over two seasons. Numbers of surviving seedlings each month were averaged over the two years. Where possible, likely cause of death of seedlings was noted. Percentage of bare ground was measured in the 1 m^2 quadrats along each transect at each site in winter and summer.

Soil samples were taken in October 1992 at each site, adjacent to the vegetation quadrats, at a depth of 0-10 cm and at 20 m intervals along each transect. Samples were sieved to < 2 mm prior to analysis. Analyses performed on all samples were total N (Kjeldahl digestion method) and P (Olsen method), organic carbon (heat of dilution method), exchangeable K (ammonium chloride method) and particle size analysis (pipette method). Descriptions of the methods of soil analyses used are given by Page *et al.* (1986) for soil chemical properties and Klute (1986) for particle size analysis. Water repellency was also measured for soil samples using the ethanol method (King 1981) where a drop of aqueous ethanol of increasing concentration (0.2 molar intervals in the range 0 - 4 M) was placed on the soil surface and the time taken for the ethanol to enter the soil was recorded. The repellence of the soil was represented by the molarity of ethanol which penetrated the soil in 10 seconds. Surface soil compaction was measured using a hand held 'pocket' penetrometer which measures soil resistance to a probe pushed into the soil to a depth of 2 cm. Measurements were taken at 2 m intervals along each transect. Deeper soil testing for compaction was unreliable at these sites because of the high lateritic gravel and boulder content of the surface soils.

Diameters at 1.3 m (DBH) of all trees (*Eucalyptus marginata* and *C. calophylla*) within 10 metres of the transect were measured to determine size class structure of the overstorey species and infer age classes.

Floristic similarity between sites was calculated using the Czekanowski coefficient (Kent & Coker 1992). For most comparisons between grazed and ungrazed sites, species were grouped into life form groups. Perennial species were also grouped according to reproductive strategy using the categories defined by Bell *et al.* (1984) *i.e.* seeders, resprouters and facultative seeder / sprouters. Importance value was also calculated for all species occurring in quadrats along the transects. This was calculated for each site as; IV (Importance Value) = relative frequency + relative abundance + relative cover. Flowering, growth and seed production of selected species representative of life form and reproductive groups were monitored monthly from winter 1992 to winter 1993.

Student t-tests and analysis of variance were used to test for differences between sites for each variable tested, and where appropriate non-parametric tests were used (Zar 1984).

Results

Effects on soil properties

There was no significant difference in proportion of clay in the top soil between sites within location A (P = 0.825) or B (P = 0.687) although there was a significant difference in the average clay content of samples between location A & B (P = 0.03; Table 1). The similarity in clay content of the top soil, and therefore soil texture, within a location, as well as the close proximity of sites, and similar landscape position, aspect, slope and elements of the remaining native vegetation, would suggest that comparisons between sites within locations is valid.

Soil compaction was significantly higher in the heavily grazed sites at both locations (Table 2). There was a trend toward increasing surface compaction with increasing level of grazing at Location B. Water repellency was higher in the grazed sites compared to the ungrazed sites at both locations. However water repellency of the sandy soil at the ungrazed site at location A was greater than the sandy loam sites at location B. Concentration of soil phosphorus increased with increasing level of grazing at location B while soil nitrogen concentration was significantly higher in the heavily-grazed sites at both locations. Soil potassium and organic carbon concentrations were higher in the heavily-grazed sites while carbon to nitrogen ratios were significantly higher in the heavily-grazed site at location A. The lightly-grazed site at location B had significantly higher levels of N, P and organic C than the ungrazed site.

At location A, 3% of the ground surface was bare within the quadrats at the heavily grazed site in August (winter), increasing to 25% by February (mid-summer) when annual plants would have disappeared. At the ungrazed site (location A) bare ground was 1.1% in winter and 2% in summer. At location B, there was 4% bare ground in winter at the heavily grazed site, which increased to 35% in summer, whereas at the lightly grazed site the area of bare ground was 3% in winter which increased to 4% in summer. Percentage of bare ground in the ungrazed site remained around 1.5% in summer and winter.

Species diversity

In general, species richness and diversity were lower for the grazed sites than at the ungrazed sites at each location (Table 3). Although total species richness was similar at the heavily-grazed site and the lightly-grazed site at location B, exotics represented 46% of species in the heavily-grazed site compared with 22% in the lightly-grazed site and 5% at the ungrazed site. Therefore, species richness of native flora was much less with heavy grazing. The proportion of exotic species was also high (42%) at the heavily grazed site at location A. The presence of exotics at the ungrazed site at location A (12%) may reflect past disturbance.

The Czekanowski coefficient indicated there was a high degree of floristic dissimilarity between the heavily-

Table 2

Summary of soil physical and chemical properties and how these are affected by varying levels of grazing disturbance at both locations. Significance tests performed were unpaired t-test (location A) and ANOVA (location B). Student-Newman-Kuels multiple comparison was used to compare means at location B. Values with the same letter are not significantly different ($P < 0.05$).

	Location A			**Location B**			
Variable Means	Heavily grazed	Ungrazed	P	Heavily grazed	Lightly grazed	Ungrazed	P
Physical							
Surface compaction (kg/cm) n=100	1.93	1.52	0.005	3.80[a]	2.90[b]	1.84[c]	0.0001
Water Repellency n=10	2.44 (severe)	1.47 (moderate)		1.46 (moderate)	1.44 (moderate)	0.28 (very low)	
Chemical							
Total Nitrogen (%) n=10	0.27	0.19	0.009	0.22[a]	0.25[a]	0.12[b]	0.0001
Phosphorus (ppm) n=10	101.27	73.31	0.033	87.50[a]	66.80[b]	27.26[c]	0.0001
Potassium (ppm) n=10	148.19	116.82	0.075	238.32[a]	150.51[b]	91.33[b]	0.0002
Organic Carbon (%) n=10	6.00	4.98	0.187	5.79[a]	6.75[a]	3.57[b]	0.0007
C:N ratio n=10	22.27	26.73	0.0001	26.05	26.43	29.52	0.065

Table 3

Species richness, number of exotic species, species diversity (Shannon Weiner Index) and eveness (J) for the five sites at the time of the initial survey (August 1992).

	Location A		Location B		
	heavily grazed	ungrazed	heavily grazed	lightly grazed	ungrazed
Species Richness	52	67	48	46	57
Exotic species	22	8	22	10	3
Species Divesity (H)	2.91	3.07	2.48	2.82	3.17
Eveness (J)	0.72	0.73	0.63	0.70	0.77

Table 4

Czekanowski coefficient as an indicator of similarity/dissimilarity of the vegetation within and between the sites. Sites with totally similar vegetation would have a value of 1. Within site value is for the comparison between transects.

Sites	A heavily grazed	A ungrazed	B heavily grazed	B lightly grazed	B ungrazed
A heavily grazed	0.541	0.174	0.513	-	-
A ungrazed		0.569	-	0.233	0.321
B heavily grazed			0.676	0.228	0.105
B lightly grazed				0.756	0.475
B ungrazed					0.699

grazed and ungrazed sites within both locations (Table 4). By comparison, within-site floristic similarity was much higher, indicating the similarity between quadrats at each site. Due to the spatial separation of the different locations and the high level of floristic diversity in the jarrah forest (Bell & Heddle 1989), floristic similarity between the ungrazed sites at each location was low. However, similarity between heavily grazed sites at the two locations was much higher.

Changes to vegetation structure

There was a significant reduction in cover and abundance of both native shrubs and perennial herbs at the heavily-grazed sites at both locations (Table 5). In the ungrazed sites these life form groups make up 68% of the species and contribute 98% of the plant cover. At location B cover and abundance of native shrubs and perennial herbs decreased with increasing grazing pressure (Table 5). The opposite trend was seen for exotic annual grasses and forbs. Cover and abundance of native geophytes and annuals appeared not to be affected by grazing at either location. Cover and abundance of native perennial grasses was higher with heavy grazing at location A.

When perennial species were grouped according to reproductive strategy, all groups showed a significant reduction in cover and adundance in the heavily grazed sites ($P < 0.05$ in all cases). The exception was facultative seeder/sprouters at location A, with no significant difference in mean abundance between the heavily-grazed site (76) and the ungrazed site (95; $P = 0.23$). Cover of facultative seeder/sprouters at the lightly-grazed site location B (2.35%) was not significantly different from that at the ungrazed site (3.12%; $P < 0.05$). Cover of obligate seeders was also not signifcantly different in the lightly-grazed site (0.4%) from the ungrazed site (1.54%; $P < 0.05$) whereas for resprouter species cover in the lightly-grazed site (8.77%) was significantly less than at the ungrazed site (25%; $P < 0.05$).

Table 5

Comparison between different grazing intensities at location A & B of mean cover, abundance and number of species with species arranged into orgin and life form groups.

Location A

Life form*	Cover** Grazing			Abundance*** Grazing			Number of species Grazing	
	heavy	none	P†	heavy	none	P	heavy	none
Exotic annual grasses	2.22	0.06	0.012	127	12.9	0.014	10	4
Exotic annual forbs	3.2	0.13	0.024	190	8.1	0.005	12	4
Native annual forbs	0.08	0.03	0.196	38	28	0.534	3	3
Native perennial grasses	0.41	0.15	0.023	19.8	6.5	0.001	4	3
Native geophytes	0.52	0.78	0.68	89	35	0.12	13	13
Native perennial herbs	1.11	3.51	0.031	27	104	0.002	8	16
Native perennial shrubs	0.08	8.34	0.001	1	35	<0.0001	5	27
Total	7.62	13		491.8	229.5		55	67

Location B

Life form	Cover Grazing				Abundance Grazing				Number of species Grazing		
	heavy	light	none	P††	heavy	light	none	P	heavy	light	none
Exotic annual grasses	0.85a	0.05b	0.02b	< 0.0001	118a	7b	1b	< 0.0001	11	5	2
Exotic annual forbs	2.32a	0.18b	0.06c	< 0.0001	86a	23b	1c	< 0.0001	11	5	1
Native annual forbs	0.02	0.02	0.01	0.345	9	11	8	0.803	3	3	2
Native perennial grasses	0.08	0.13	0.03	0.096	8	8	3	0.113	3	3	4
Native geophytes	0.19	0.33	0.44	0.209	20	35	26	0.157	8	9	11
Native perennial herbs	0.04c	2.37b	10.80a	< 0.0001	6c	94b	154a	< 0.0001	6	12	20
Native perennial shrubs	0.42c	7.51b	21.87a	< 0.0001	6c	34b	59a	< 0.0001	9	12	19
Total	3.90	10.54	33.20		244	201	244		48	46	57

*Native perennial grasses are all hemicryptophytes which die back to ground level during the summer; native geophytes die back to subterranean organs during summer *e.g.* Orchidacae; native perennial herbs have non-woody above ground stems or leaves that persist through summer *e.g.* many Cyperacae. **Cover measurement is the mean cover value (%) of ten 5 m x 1 m quadrats. ***Abundance measurement is mean abundance from ten 5 m x 1 m quadrats. †Significance values given using Mann-Whitney non-parametric test between sites. ††Significance values given using Kruskall-Wallis non-parametric ANOVA between sites. Student-Newman-Kuels multiple comparison (non-parametric analog) was used to separate means at location B. Values with the same letter are not significantly different ($p < 0.05$).

Table 6

Frequency, cover and abundance of the five highest ranked species according to their importance value at each site. Importance value = relative frequency + relative cover + relative abundance. eag = exotic annual grass; eaf = exotic annual forb; naf = native annual forb; ng = native geophyte; nph = native perennial herb; ps = native perennial shrub; t = tree.

Species	Frequency total (%)	Cover (%) total 50 m^2	Abundance total	Importance value
Location A				
heavily-grazed				
Hypochaeris glabra (eaf)	98	0.84	1013	42.31
Aira caryophyllea (eag)	44	1.31	716	37.47
Trifolium subterraneum (eaf)	54	1.1	156	23.94
Hypoxis glabrella (naf)	74	0.08	432	17.31
Gahnia sp (nph)	20	0.95	45	16.21
ungrazed				
Loxocarya fasciculata (nph)	84	0.88	736	34.71
Scaevola striata (nps)	74	0.96	662	32.24
Gahnia sp (nph)	66	1.47	120	18.92
Acacia pulchella (nps)	52	1.2	44	13.68
Stylidium piliferum (ng)	44	0.2	148	9.33
Location B				
heavily-grazed				
Aira caryophyllea (eag)	60	0.54	880	53.78
Hypochaeris glabra (eaf)	84	0.85	396	44.55
Trifolium subterraneum (eaf)	80	1.24	124	42.1
Medicago sp (eaf)	50	0.23	115	15.62
Vulpia myuros (eag)	52	0.15	104	13.64
lightly-grazed				
Bossiaea ornata (nps)	96	4.45	195	51.81
Lepidosperma gracile (nps)	82	0.77	704	47.73
Eucalyptus calophylla (nt)	26	1.9	19	17.51
Gahnia sp (nph)	20	1.45	101	17.51
Lagenifera huegelii (ng)	62	0.13	134	13.73
ungrazed				
Bossiaea ornata (nps)	97	8.25	306	41.63
Gahnia sp (nph)	32	7.6	197	30.47
Lepidosperma gracile (nph)	78	2.28	359	26.67
Dampiera linearis (nps)	67	0.31	272	17.09
Hibbertia hypericoides (nps)	22	4.72	16	14.73

Ranking species using the importance value showed the dominance of exotic species at the heavily-grazed sites (Table 6). *Gahnia* sp (Cyperaceae), the only native perennial species to rank in the top five at either of the heavily grazed sites, is relatively common at all five sites and ranked in the top five in importance value at four of the sites. At the lightly-grazed site at location B, no exotics ranked in the top five species indicating that although exotics are present their cover and/or abundance is low compared with native species. Although the cover of *Bossiaea ornata* (Lindley) Benth at the lightly-grazed site was only half that at the ungrazed site at location B, the importance value at the lightly-grazed site is much higher. Cover and abundance of *B. ornata* was significantly less with increased grazing disturbance at location B ($P < 0.0001$). The native perennial herb *Dampiera linearis* R Br (Goodeniaceae) ranked highly at the ungrazed site at location B but only two small individuals occurred at the lightly-grazed site and it was absent from the heavily-grazed site. A similar trend was seen for the native shrub and obligate seeder *Trymalium ledifolium* Fenzel and the native perennial herb *Scaevola striata* R Br (resprouter). Cover and abundance of the native geophyte *Chamaescilla corymbosa* (R Br) F Muell ex Benth, which has a flat rosette of leaves, was not significantly different at any of the sites indicating that this species is not adversely affected by grazing.

Results of six-monthly surveys of the vegetation data along the transects showed similar trends for both locations. At all sites there was a reduction in species, cover and abundance in summer (February) as annual species and geophytes were not present. This reduction is most pronounced in the heavily-grazed sites which had the greatest proportion of annual species. In August 1993, the mean cover or number of species did not change significantly in the heavily-grazed sites or the ungrazed sites from the August 1992 survey (Fig 1). At location B in August 1993, after grazing had ceased for

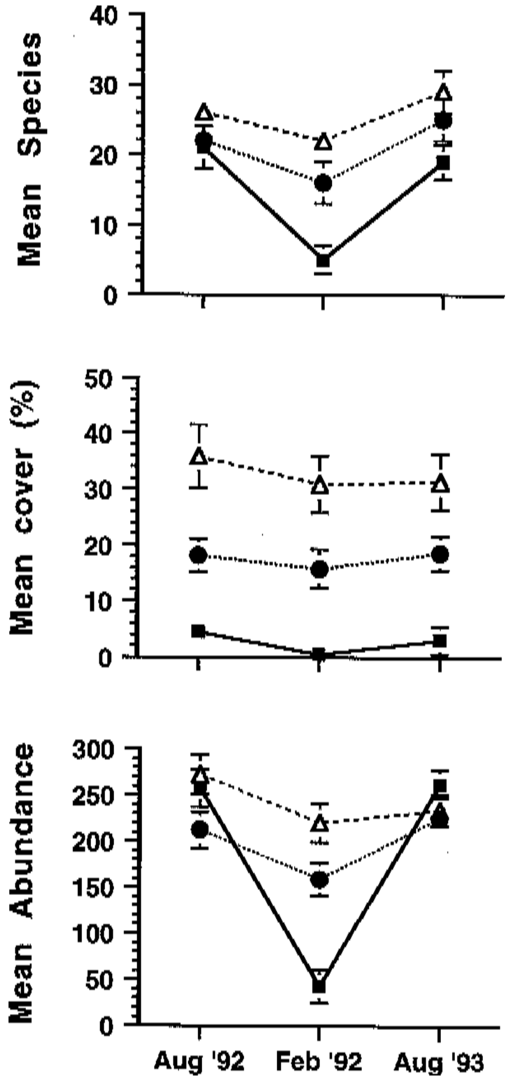

Figure 1. Mean number of species, cover and abundance (± se), along transects at each site at Location B over 12 month sampling period. Heavily grazed —▯—; lightly grazed ┈▯┈; ungrazed ---▯---.

six months, the mean number of species was significantly greater at the lightly-grazed site than at the heavily-grazed site (P = 0.004). This separation of sites was not apparent after the initial survey in August 1992.

Phenology of selected species

The phenology of species selected as representative of different life forms and reproductive groups and response to grazing was recorded over a 12 month period (Fig 2). The annual exotic herb *Hypochaeris glabra* L flowers and sets seed almost all year round. Other annual species such as *Lagenifera huegelii* Benth and *Vulpia myuros* (L) C Gmelin had a much more restricted period of flowering and seed set which is indicative of most therophytes in the area. The growth and flowering of perennial species occurs mainly in the period of warmer temperatures and when moisture is not limiting. Flowering and seed set of *Scaevola striata* and seed set of *Dampiera linearis* was entirely within the summer period which is the period of heaviest grazing within these remnants. Others such as *Trymalium ledifolium* , and to a lesser extent *Bossiaea ornata* and *Hakea lissocarpha* flower and set seed before the onset of summer.

Size class and recruitment of overstorey species

The size class analysis of the overstorey species (*Eucalyptus marginata* and *C. calophylla*) at the two locations showed a lack of individuals in the lower size classes at the heavily-grazed sites (Fig 3). This lack of trees in smaller size classes indicates that no recruitment has taken place at these sites for many years. Conversely, individuals in the the lower size classes at the ungrazed sites indicates that some recruitment has taken place at these sites. There was emergence of tree seedlings at the heavily grazed sites as well as ungrazed sites at both Locations (Fig 4). However, a high rate of mortality occurred at the heavily-grazed sites from early summer onwards with approximately half of the deaths due to grazing. Germination of tree seed at the lightly-grazed site (location B) was lower than at the ungrazed site but mortality rates were similar to the ungrazed site with only two deaths of seedlings at each site attributable to grazing. There was also a greater proportion of *E. calophylla* seedlings at the heavily-grazed sites and at location A despite a much lower ratio of *C. calophylla* to *E. marginata* trees at all sites.

Discussion

The lack of resilience of jarrah (*Eucalyptus marginata*) woodland to heavy grazing is well illustrated by the results presented here. Grazing disturbance has affected the three major determinants of vegetation dynamics, namely, soils, vegetation composition, and structure and population dynamics and recruitment. Similar effects have been reported for grazed eucalypt woodlands of western Victoria (Wellington 1989). The present study indicates that restoration of ecosystems such as these may not be a simple matter of excluding stock, as grazing has not only affected the biotic components but also the resource base in the form of the soil (Hobbs & Norton 1996).

The high floristic dissimilarity between adjacent sites indicates the changes to the floristic structure brought about by grazing disturbance. High floristic similarity between heavily-grazed sites at the 2 locations despite the ungrazed sites having low similarity suggests that effects of grazing are overriding the usual determinants of floristic composition such as location, soil type, topography and moisture availability. The effects of light grazing are not as pronounced but are nonetheless significant. Species diversity and richness has also decreased under livestock grazing disturbance. This contrasts with environments that have had a long history of grazing disturbance and are dominated by herbaceous grasses and forbs(Milchunas & Lauenroth 1993). In other plant communities which are dominated by perennial shrubs such as heath, species diversity is also reduced (Williams & Ashton 1987).

Changes in soil characteristics under the present grazing regime benefit exotic “grazer-increaser“ species while disadvantaging native species. This is characterized by increased soil compaction, water repellancy and nutrient

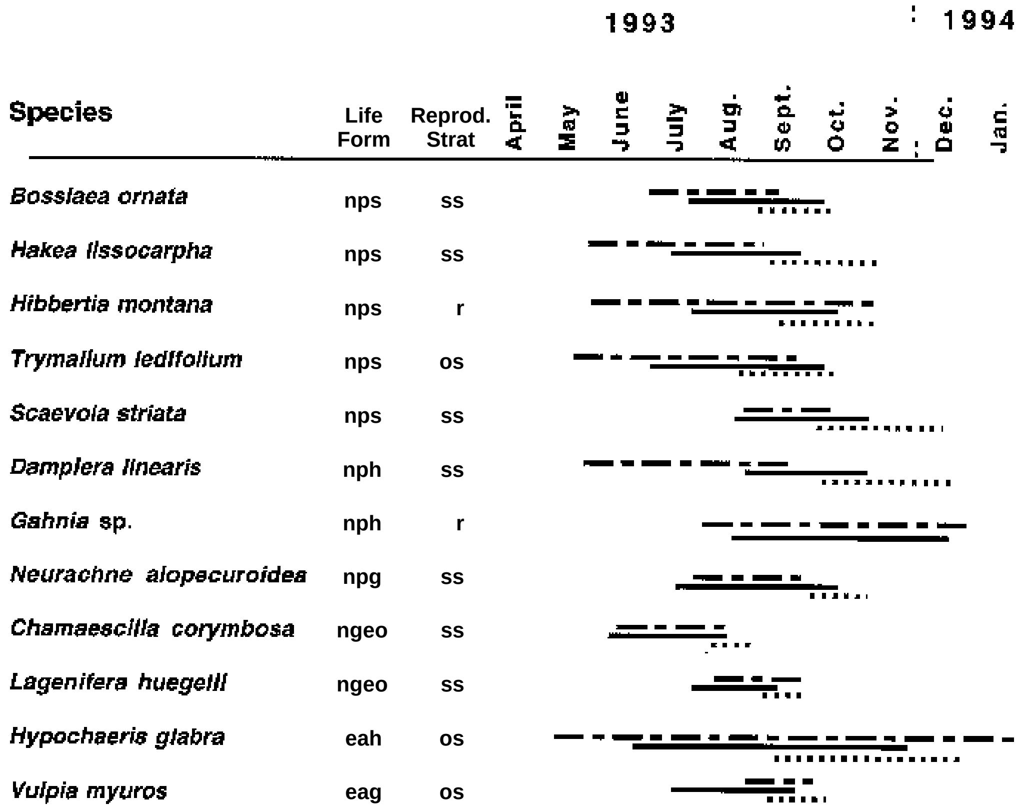

Figure 2. Phenology over 1993/1994 of selected species. Species are representative of the different life form groups and reproductive strategies of the vegetation at the 2 locations. Life form groups: nps, native perennial shrub; nph, native perennial herb; npg, native perennial grass; ngeo, native geophyte; nah, native annual herb; eah, exotic annual herb; eag, exotic annual grass. Reproductive strategy; ss, facultative seeder/sprouter; r, resprouter; os, obligate seeder. Phenology; flowering period — - — - ; growth — ; seed development ……….

concentrations. Surface soil compaction, caused by trampling of the soil by livestock, may have adverse effects on moisture status and may provide a physical barrier to seedling emergence and root growth. While water infiltration in the wetter part of the year may not be affected, during summer and autumn (*i.e.* throughout the dry season) compaction may decrease infiltration of any rain which does fall and increase the risk of erosion (particularly high intensity thunderstorms) over that likely in the wet season. Annual exotic weed species which utilise only a shallow section of the topsoil through winter and spring will not be affected by decreased water infiltration in the dry season, while native perennial species establishing at the end of spring and having to survive a long dry summer/autumn may be severely affected.

The high nutrient status of grazed sites is most likely caused by drift from fertilisers applied to adjacent pasture (P) and livestock excreta and invasion of legume pasture species (N). Under fertilised regimes many native sclerophyll species develop increased shoot growth out of proportion to root growth (Specht 1963). In the dry season, the relatively under-developed root system cannot relieve the severe water stress that develops in the shoots, leading to plant death (Specht 1963).

The increase in major soil nutrients (N, P and K) and proportion of organic carbon, and the subsequent decrease in C:N ratios seen in the heavily-grazed and the lightly-grazed remnants indicate that there are dramatic changes in the nutrient cycling within remnants caused primarily by livestock disturbance. Disruption to nutrient cycling is a major cause of the deterioration of remnants (Main 1981; Hobbs 1993), especially in an environment such as jarrah woodland where the vegetation is well-adapted to nutrient poor soils (Lamont 1983). High concentrations of N and P can affect the survival of some native species (Groves & Keraitis 1976; Specht *et al.* 1977), especially the Proteaceae. Elevated concentrations of nitrogen in the leaves have also been implicated in the decline of eucalypt species as they become more attractive to insect herbivores (Landsberg 1990).

The exotic annual weeds benefit from the increased nutrient levels of the grazed sites (Panetta & Hopkins 1991) but do not have to survive the dry season. Invading exotic annual species have a competitive advantage over perennial species in highly disturbed environments. Their rapid development from germination to reproductive maturity in winter-spring enables them to grow and reproduce within the short time of relatively low grazing intensity (Miles 1979). Seed dormancy is also important in allowing these species to withstand high frequency disturbance (Grime *et al.* 1986). Invasion by exotics at the lightly grazed site was widespread although they have not yet become dominant. This may be due to there being sufficient cover of native perennial

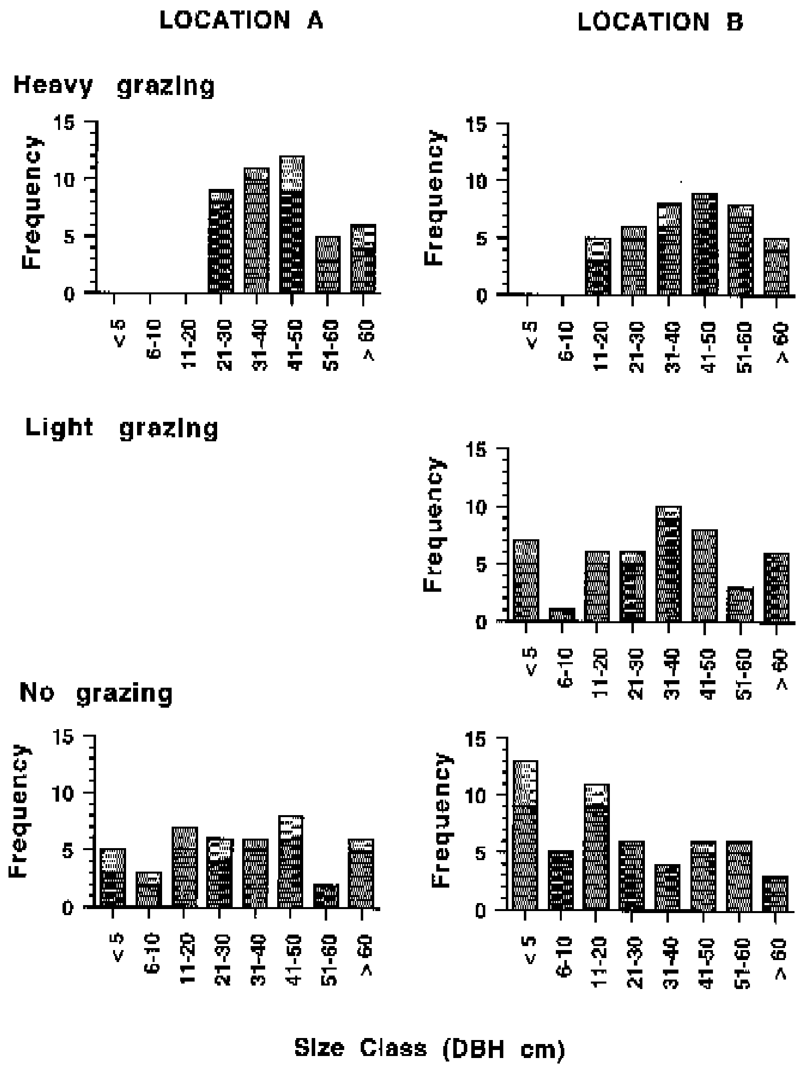

Figure 3. Size class distribution of the overstorey species measured along transects at each site at both locations. Size class measured as tree diameter overbark at breast height (1.3 m). ■ *Eucalyptus marginata*, □ *C. calophylla*

species to prevent exotics from moving into the phase of rapid spread (Hobbs & Mooney 1993). In contrast to the situation in some arid inland areas (Hodgkinson & Harrington 1985) and in the alpine region of eastern Australia (Wimbush & Costin 1979), "woody weeds" do not appear to be a problem in jarrah forest remnants. In late winter and spring, exotic annuals are prominent while in summer and autumn cover of all understorey vegetation is much reduced in comparison with ungrazed sites.

Life form groups show clear relationships with grazing pressure. Therophytes benefit from grazing due to the increase in area of bare ground that permits establishment and reduces competition from perennial plants which have been removed. The growth phase of therophytes is at a time (winter/spring) when there is maximum herbage available, especially in the adjoining pasture, so grazing pressure in remnants is reduced. Other life form groups such as geophytes and native perennial grasses (hemicryptophytes) also benefit in this regard because they are unobtainable by exotic grazers during the time of greatest grazing stress (post spring). Although some native herbivores dig up the perennating organs of geophytes (Taylor 1992), livestock such as sheep or cattle do not seem to do this.

Among the native perennial herbs and shrubs, facultative seeder/sprouters seem less affected than obligate seeders or taxa which are strongly resprouting and have sparse seed regeneration. Facultative seeder/sprouters are thought to be the most resilient (Keeley 1986) as they are able to resprout from storage organs and regenerate freely from seed whereas populations of obligate seeders can persist only as long as seed is available in the seedbank. Resprouters need time to recover starch reserves so that they can resprout (Bowen & Pate 1993); frequent or persistant grazing therefore can exhaust reserves and eventually lead to their loss.

Perennial species which flower and/or set seed in the period of heavy grazing in summer are the most vulnerable to livestock grazing. Two such species seen here were the perennial shrubs *Scaevola striata* and *Dampiera linearis.* In a grazing simulation experiment on

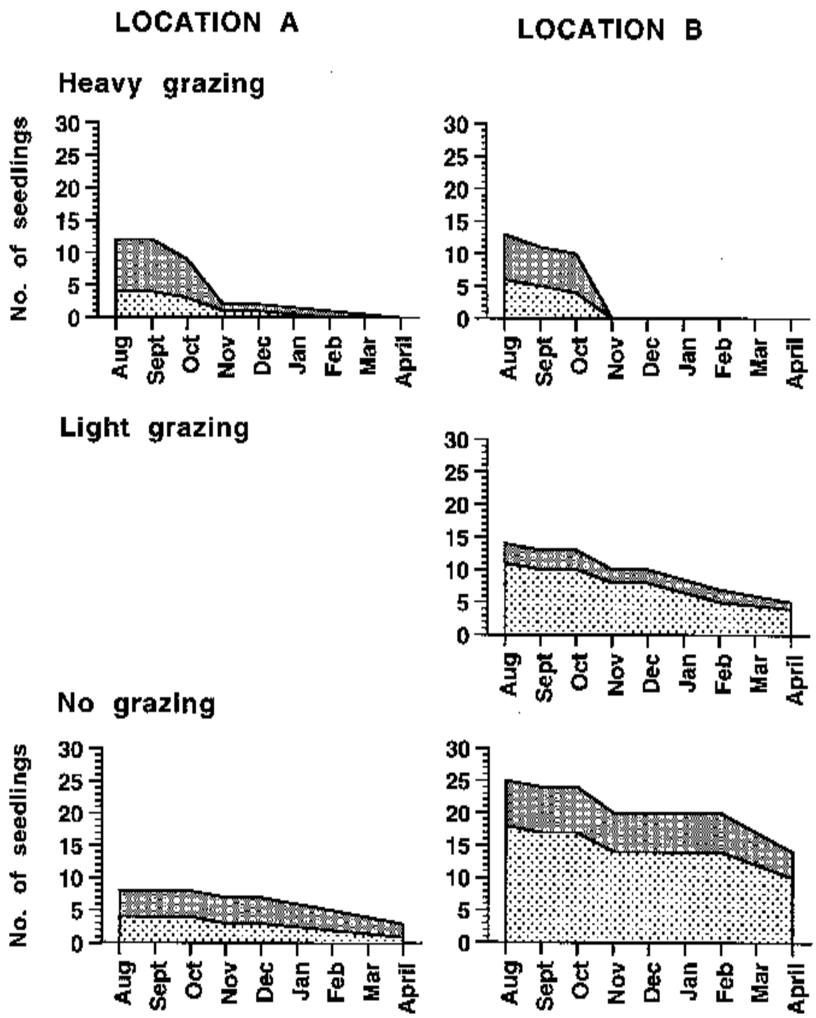

Figure 4. Occurrence and survival over a season for seedlings of overstorey species along the transects in each site at both locations. *Eucalyptus marginata*; *C. calophylla*

sub-alpine herbs, grazing in spring and summer reduced flowering and increased plant mortality (Leigh *et al.* 1991). Large reductions in seed production even for adapted species has been reported in grazed sub-alpine grasslands in eastern Australia (Wimbush & Costin 1979). This potential loss of seed production further reduces the vegetation's resilience to grazing pressure, especially of obligate seeders.

In the ungrazed jarrah forest there is normally a high proportion of trees in the lower size classes *i.e.* younger trees (Abbott & Loneragan 1986). In the heavily-grazed sites these younger size classes are absent, indicating that there has been little recruitment for a number of years. The disturbance of the ground under grazing provides sites for seed germination, leading to large numbers of seedlings emerging in the winter. However, the combination of grazing pressure when other herbage is sparse in summer/autumn, together with the low soil water content exacerbated by soil compaction and poor wetability, lead to virtually complete mortality of seedlings after the summer/autumn period. Seedlings of *C. calophylla* are larger and more drought tolerant than *E. marginata* seedlings, which may explain their greater abundance at the heavily-grazed sites where disturbance has created less hospitable conditions for seedling survival. The greater clay content of the surface soil at location B may also have contributed to the greater recruitment of eucalypt seedlings (particularly *E. marginata*) at the ungrazed and lightly-grazed sites. Jarrah flowers only intermittently (Abbott & Loneragan 1986) therefore seed is not always available in large numbers for regeneration. Some regenerative capacity is maintained through canopy seed store and coppice growth from lignotubers, although seed harvesting ants and livestock grazing further reduces the possibility of recruitment and regeneration.

The lack of resilience of jarrah forest remnants to heavy grazing appears to be partly the result of intensity rather than the type of grazer. Native plant species are adapted to some grazing pressure from native herbivores but they are not adapted to high intensity grazing by exotic herbivores such as sheep or cattle. Also, livestock unlike the native herbivores are hard-hoofed causing the problems of soil disturbance outlined above, especially when they are numerous. Resilience of native plant species to grazing will depend on a number of attributes. These include reproductive strategy, life form and morphology, life history and palatability.

Heavy grazing affects the 'skeleton' of the jarrah forest community (the trees and shrubs), most severely with a change in the lifeform complement of a remnant occurring progressively. Phanerophytes are replaced by mostly introduced species of therophytes, either weeds or pasture plants, and some geophytes. The long life span of the overstorey species means that visual disintegration of the woodland will take some time. However, without recruitment of these species the nature of the *Eucalyptus* spp woodland will eventually change totally. At a relatively early stage of the decline in a remnant, the structure and composition of the native community can be re-established by excluding stock (Pettit *et al.* 1995). However, under severe and prolonged grazing the lignotuber bank of resprouters and the seedbank of seed regenerators will be lost and regeneration will become very difficult.

Acknowledgements: The authors wish to thank M Angeloni for assitance with fieldwork and D Ashton for providing useful comments on the manuscript. This research was funded by the Water Authority of Western Australia.

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