The effects of flooding and livestock on post-dispersal seed predation in river red gum habitats

N. MEESON, A.I. ROBERTSON and A. JANSEN

Johnstone Centre, School of Science and Technology, Locked Bag 588, Wagga Wagga, NSW 2678, Australia

Summary

1. Rates of seed predation are influenced by conditions that alter seed supply and the activity of seed predators. In southern Australia the potential seed supply for the dominant floodplain tree species, the river red gum *Eucalyptus camaldulensis*, has been reduced through forest clearing to support grazing by introduced livestock. River regulation and water extraction have reduced the frequency of flooding and thus the conditions that promote seed germination on floodplains. To determine if poor recruitment of river red gums could be caused by low seed supply, as a result of post-dispersal seed predation, we used field experiments and observations to investigate how post-dispersal predation on seeds of *E. camaldulensis* was affected by flooding, livestock management and their interaction.

2. Seed predation was measured before and after different flood treatments (0·5 m depth; short flood of 24 h, long flood of 30 days). Flooding of this kind (return frequency of once per year) did not have any significant effect on rates of seed removal by seed predators.

3. Rates of seed predation in floodplain habitats under widespread livestock management regimes changed seasonally. In all seasons seed predation was lowest at sites grazed by sheep. In winter seed predation was highest at ungrazed sites. In spring and summer seed predation was highest at sites grazed by cattle. Ant communities differed between forested and cleared habitats and seed-eating ant species were most abundant in cleared sites grazed by cattle.

4. Rates of seed predation in forested floodplain sites with different flood histories differed among sites with different livestock management histories. The impact of cattle exclusion on seed predation rates increased as the period since flooding increased.

5. Cattle grazing is widespread on the floodplains of rivers across the southern Murray-Darling Basin, and tree densities and hence seed supplies are low. In this situation small floods may not result in significant recruitment to river red gum populations because seed predation may reduce seed supply before and following flooding. Decreases in the frequency of flooding owing to river regulation and water extraction are likely to have exacerbated the influence of livestock on seed supply and thus reduced potential recruitment even further.

6. Efforts to rehabilitate large floodplain rivers based solely on the return of more natural flow regimes may fail if the effects of factors such as livestock grazing are not managed concurrently.

Key-words: ants, flooding regimes, floodplain, grazing, seed removal experiments.

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Introduction

Post-dispersal seed predation can be an important determinant of seed densities (Louda 1989). The importance

Correspondence: Professor Alistar Robertson, Johnstone Centre, School of Science and Technology, Locked Bag 588, Wagga Wagga, NSW 2678, Australia (fax + 61 269332737; e-mail arobertson@csu.edu.au).

of seed predation in recruitment to plant populations is a function of both seed density and environmental conditions necessary for successful germination (Grubb 1977). When conditions are favourable for germination and seed supply is low, post-dispersal seed predation can have a significant impact on recruitment (Crawley 1992).

Rates of seed predation vary with seed fall, seed predator densities and environmental conditions that

govern predator activity (Hulme & Borelli 1999). Changes to natural disturbance regimes can alter seed predator communities (Andersen 1990), and thus may influence patterns of recruitment to plant populations.

Natural disturbance regimes of riparian and floodplain habitats have been altered by river regulation and land management practices, including vegetation clearance, cropping and livestock grazing (Poff *et al.* 1997; Robertson *et al.* 1999). Such changes have influenced the spatial arrangement of plants and recruitment processes both directly and indirectly via alterations to hydrological links across land–water margins and processes occurring at the soil surface (Franz & Bazzaz 1977; Nilsson *et al.* 1991; Naiman, Decamps & Pollock 1993; Jansen & Robertson 2001a).

Floodplains of the Murray-Darling Basin of Australia are dominated by the river red gum *Eucalyptus camaldulensis* Dehnh. Optimal conditions for recruitment of river red gums are winter–spring flooding (when seed fall is at a peak) followed by spring–summer rainfall (Dexter 1970). Recruitment of river red gums is also dependent on seed supply, with trees producing between 100 and 150 million seeds before they are replaced by a single individual (Jacobs 1955). Trees produce large seed crops every 2–3 years but this cycle can be highly variable (Boland, Brooker & Turnbull 1980; Eldridge *et al.* 1993; Florence 1996).

In eucalypt forests ants are important post-dispersal seed predators and can exert a significant impact on recruitment (Andersen 1991). Ants can remove large numbers of river red gum seeds (Dexter 1970). However, in dense floodplain forests large numbers of germinants are always observed in years of high seed production, suggesting that seed loss to ants is insignificant. This may be a function of the large seed supply in these forests and the pattern of regular flooding that creates conditions unfavourable for ant colonies (Boomsma 1950; Jacobs 1955; Dexter 1970).

During the last 150 years the distribution of river red gum trees over most of the floodplain habitat in the southern Murray-Darling Basin has been altered directly or indirectly as a result of widespread changes in land and water management. Floodplain habitats once dominated by river red gums are now a mosaic of cleared land used for pasture and cropland, or sparse woodland used for livestock grazing (Crabb 1997).

Seed predation may be more significant in controlling recruitment to river red gum populations on floodplains used for agriculture than in less disturbed forests. The much lower tree densities on floodplains used for agriculture imply a greatly reduced seed supply relative to the few remaining dense forests that are managed for timber production. The ant faunas of grazing lands in Australia may also be dominated by seed-eating species (Andersen 1991).

Over the last 70 years progressive river regulation and water extraction for irrigation in this region of the Murray-Darling Basin has caused a reduction in the frequency of small and medium floods (Dexter, Rose & Davies 1986; Maheshwari, Walker & McMahon 1995). Less frequent flooding since river regulation may also have provided more favourable conditions for ants (Dexter 1970).

Seedlings of river red gums are usually extremely rare in floodplain habitats used for agriculture (Jansen & Robertson 2001a). Grazing and trampling by livestock are important post-recruitment mortality agents for river red gums (Robertson & Rowling 2000) but the relative importance of factors that might control recruitment in these habitats is not known. Here, we investigated whether poor recruitment in floodplain habitats dominated by livestock grazing may be caused by low seed supply as a result of forest clearing and post-dispersal seed predation. We did this by using field experiments and observations to answer three specific questions. (i) Are the activities of seed-eating ants affected by flooding? (ii) How are rates of seed predation and seed predator communities influenced by variation in livestock management regimes in floodplain habitats once dominated by river red gums? (iii) What are the interactive effects of flooding history and livestock on post-dispersal seed predation?

Methods

STUDY SITES

All field sites were on the floodplains of the Murray and Murrumbidgee Rivers in the southern Murray-Darling Basin of Australia. We investigated the relationship between flooding and seed predation and the interactive effects of flooding and livestock on seed predation in the Gulpa Island State Forest, part of the Barmah-Millewa group of river red gum forests on the floodplain of the Murray River (35°49′S, 144°55′E). The climate is semi-arid, with a mean annual rainfall of 459 mm. Temperatures range from a mean winter minimum of 4·5 °C to a mean summer maximum of 30 °C (Leslie 1995).

In Gulpa Island State Forest, cattle are used to control fuel loads for fire prevention. Stocking densities average 0·8 dry sheep equivalents (DSE) ha⁻¹ year⁻¹. This forest is used primarily for timber production and was used for these investigations because of the infrastructure available for controlled experimental flooding (Bacon *et al.* 1993) and the known history of flooding (Robertson, Bacon & Heagney 2001).

Sites used for the investigation of the relationship between livestock management and seed predation were located in a 170-km long region of the Murrumbidgee River floodplain west of Wagga Wagga (between 34°34′S, 145°52′E and 35°05′S, 147°20′E). This region was used in our previous investigations of the impact of livestock on the ecological condition of floodplain habitats (Jansen & Robertson 2001a,b). The floodplain here varies in width from 3 to 20 km. The soils are characterized by deep alluvial loams, coarsely cracking clays, and calcareous earths. Average annual rainfall

for the region decreases east to west, from 500–600 mm at Wagga Wagga to 300–400 mm in the west. Mean annual evaporation ranges from 1600 to 2000 mm. Mean daily temperatures for the central section of the study area range from 19–37 °C in January to 4–14 °C in July (Buchan 1996).

Major land uses along the river are cattle and sheep grazing, and cropping. In these agricultural landscapes the river red gums often persist as a narrow band of trees along river banks (Crabb 1997; Jansen & Robertson 2001a). Relatively substantial stands of river red gum forest still exist in the west of this study region. These are in state forests managed for timber production, where low-density cattle grazing is used to control understorey fuel loads (Grant 1989; Crabb 1997).

The sites on the Murrumbidgee floodplain and Gulpa Island State Forest differed in geomorphology and understorey vegetation. In contrast to sites on the Murrumbidgee floodplain, which were on high banks (to avoid the complication of possible flooding), the Gulpa Island sites were located in flood runners (natural, shallow drainage channels in the forest; Robertson, Bacon & Heagney 2001). In addition, at the Murrumbidgee sites, the mean understorey vegetation cover was 94% and mean litter cover was 16%. In contrast, over all sites and seasons at the Gulpa Island sites mean understorey vegetation cover was 24% and mean litter cover was 80% (authors' unpublished data).

SEED PREDATION AND SEED PREDATORS

Petri dishes containing river red gum seeds were used as seed baits to assess relative rates of seed predation (Andersen & Ashton 1985). Plastic Petri dishes with a diameter of 6 cm were glued to 10×10-cm pieces of hardboard. Three holes (12–14 mm wide) were cut in the side of each dish through which ants could access the seeds once the lids were in place. Each seed bait contained 10 river red gum seeds. For experiments on the effects of flooding and grazing, seeds were collected in August 1999 from a site within the Murrumbidgee River study region. Seeds used in the experiment on the interactive effects of flooding and grazing were collected in September 2000.

All seed predation trials ran for 4 days, with seed removal recorded once per day. This provided sufficient time for ants to locate seed baits, as they often remove eucalypt seeds within 2 days following seed fall (Stoneman 1994).

In the comparison of livestock management regimes we quantified microhabitat in a 1-m² area around each seed bait because seed predation can be influenced by habitat features that affect the activities of seed predators (Andersen 1990). We made visual estimates of the maximum and average height of the understorey vegetation, the percentage cover of grasses, herbs, sedges and total live and dead plants, the percentage cover of bare ground, litter and coarse woody debris > 1 cm in diameter, and the depth of litter.

To assess the potential post-dispersal seed predators in the Murrumbidgee River floodplain, we used pitfall trapping (Andersen 1990). Traps consisted of plastic cups (diameter 7 cm, height 7·5 cm) containing 30 ml of preservative and evaporation retardant (70% alcohol, 30% ethylene glycol). The traps were opened for 2 days during the 4-day seed bait trials in spring (November) and summer (January). Four traps were located randomly but at least 10 m apart, within the sampling grid at each site (see below). We restricted our investigation to ground-dwelling invertebrates because they are the most likely predators of the small (1-mm) seeds of *E. camaldulensis*. Ants made up more than 98% of the potential invertebrate seed predator catch in pitfall traps across all seasons and habitats (authors' unpublished data), so presentation and analyses of pitfall trap data are restricted to the ant community. Ants were identified to genera, and where possible to species or species group. Allocation to functional groups (seed eaters and non-seed eaters) followed Andersen (1991).

EFFECTS OF FLOODING

We used experimental floods to determine if rates of seed predation were affected by flood duration. Two shallow flood runner sites in the Gulpa Island State Forest were chosen, and one was flooded for 24 h (hereafter referred to as the short flood) and the other flooded for 1 month (the long flood). The two flood runners had been used as part of regular ongoing controlled flooding experiments by State Forests of New South Wales and Charles Sturt University (Bacon *et al.* 1993; Robertson, Bacon & Heagney 2001) and had similar flood histories for the previous decade. Tree densities were similar at the two sites.

In September 1999 (when natural seed fall was greatest) the short flood and long flood sites were blocked off from a nearby creek and water was pumped into them to create a flood (maximum depth 0·5 m, area flooded approximately 0·5 ha). After the predetermined lengths of flood time, water was drained from the flood runners with the aid of a pump. Draining took approximately 24 h. We assessed relative rates of seed predation under each flood treatment immediately prior to flooding and then within 24 h after flood recession. At each time seed predation was measured by placing two parallel rows of 15 seed baits along the length of the lowest sections of each flood runner.

EFFECTS OF LIVESTOCK MANAGEMENT

We chose four livestock management regimes representative of the major grazing practices on the floodplain of the Murrumbidgee River (Jansen & Robertson 2001a), namely no grazing by livestock in forests (hereafter referred to as no grazing); low-density cattle grazing in forests (low cattle); high-density sheep

grazing in mostly cleared paddocks (high sheep); and high-density cattle grazing in mostly cleared paddocks (high cattle). It was not possible to control for the length of time that particular livestock management regimes had been employed on the floodplain. Most regimes had been operating for more than 5 years at the time of sampling (August 1999 to January 2000). However, two of the three high sheep sites had had current management regimes in place for only 2 years. A measure of grazing pressure in each treatment was provided by normalizing stocking rates to DSE, where eight wethers (neutered male sheep) is equivalent to one cow (Jansen & Robertson 2001a). Ranges of DSEs for each of the livestock management regimes were: low cattle < 0·5–2·3 DSE ha⁻¹ year⁻¹; high sheep 7·7–11 DSE ha⁻¹ year⁻¹; high cattle 3·1–103 DSE ha⁻¹ year⁻¹. In the latter case cattle were hand-fed in the paddock, hence the very high stocking rate.

The sampling design could not be balanced as low-density grazing and no grazing rarely occur in paddocks, and high-density sheep and cattle grazing do not occur in forests. Three replicate sites were selected for each of the four livestock management regimes. Tree densities were similar across sites within the paddock and forest treatments. The treatments were not available across the entire study area, and all forest sites but one were in the west of the study region and all paddock sites were in the east.

Following Yates *et al.* (1995), at each site we established a 25 × 45-m grid located between 5 m and 20 m from the river bank. Within each grid 10 seed baits were randomly located so that all baits were at least 5 m apart. Over the three sampling seasons (see below) no specific location within the grid was sampled more than once.

To determine if rates of predation varied seasonally, sampling was conducted in late winter (August 1999), late spring (November 1999) and mid-summer (January 2000). It was expected that the rate of seed predation would increase as temperatures rose in spring and summer.

INTERACTION OF FLOODING AND LIVESTOCK

Flooding frequencies and livestock management regimes differ markedly across the floodplain landscape and through their impacts on soils and vegetation are likely to interact to influence seed availability, seed predators and patterns of post-dispersal seed predation. To investigate one possible interaction we took advantage of existing experimental sites in the Gulpa Island State Forest with known flood histories and cattle exclusion plots that had been established for 10 years (see below).

Detailed descriptions of the experimental sites are available in Bacon *et al.* (1993) and Robertson, Bacon & Heagney (2001). Briefly, in this region of the floodplain earthen walls were established at 15 sites in shallow

flood runners in 1990 so that water could be gravity fed and pumped to maintain replicate experimental flood regimes. At each site an area of approximately 0·5 ha was fenced off to exclude rabbits and livestock. Kangaroos were not excluded from plots by fences and kangaroo droppings are as abundant inside fenced plots as outside (A. Robertson, personal observation). The fenced area incorporated the lowest section of each flood runner and a section of the higher (1·5 m) floodplain. In 1990 the fences were rabbit-proof. However, gradual deterioration of wire mesh meant that by 1995 most fences had some holes. Thus for the 5 years prior to this work, fences excluded only livestock.

In the spring (November) of 2000 flood runner sites were available that had three different flood histories, namely no flood for 2 years (n = 3), no flood for 4 years (n = 3) and no flood for 6 years (n = 1). Tree (> 10 cm diameter at breast height) densities did not differ between flood runner sites with different flood histories, and averaged 208 trees ha⁻¹. In each of these sites there was a 10-year-old livestock exclusion plot (hereafter no cattle) and an area that had been grazed by livestock (hereafter cattle) for the same period. We placed nine seed baits inside and outside livestock exclusion fences in each of the seven flood runner sites.

DATA ANALYSES

Exploratory data analysis of the number of seeds removed from each bait in the study on the Murrumbidgee River floodplain revealed that the data fitted a binomial distribution indicating that once a predator located a seed bait, all seeds from that bait were likely to be taken. Thus seeds from all 10 baits at each site did not have an equal chance of being removed. Consequently, individual seed baits were treated as replicates and these were recorded as 'visited' if any seeds were taken, and 'not visited' if none were taken. The independence assumption was satisfied by the random location of baits within sites, such that each bait had an equal chance of being visited. These data were analysed using binary logistic regression (Hosmer & Lemeshow 1989). We used Nagelkerke's R^2 (SPSS Inc. 1999) as an indication of the explanatory power of the models. A similar approach to analysing data derived from experiments using seed baits has been used in earlier studies (Yates *et al.* 1995). For each of the three field experiments, we observed seed baits each day for 4 days. Inspection of data revealed the day on which the proportion of seed baits visited in any one treatment reached 1·0. Logistic regression analysis for each experiment was performed on data from the day prior to the percentage of seed baits visited in any one treatment reaching 1·0. This varied among experiments (day 4 for the flood experiment, day 2 for the livestock regimes, and day 1 for the flood/livestock experiment), probably reflecting a variety of factors, including different microhabitat conditions, season and ant species

across sites and regions (see later). For each experiment, the mean proportion of baits visited over all treatments was 0·5 or less (see Results).

To compare seed removal in relation to flood duration we tested the effect of the sampling period (before flooding and one day after flood recession) on the proportion of baits visited. Due to differences in the timing of sampling for the short and long floods, and to seasonal changes in the proportion of baits visited (see below), the two different flood lengths could not be compared in the same analysis.

In the comparison of livestock management regimes we tested the effects of livestock management regime, season and their interaction on the proportion of seed baits visited. Baits (replicates) were treated as missing values if they had been disturbed or crushed by stock, birds or kangaroos. Disturbance was greatest in paddocks stocked with cattle. In the winter sampling season all seed baits were destroyed or disturbed by cattle at one high cattle site.

For the experiment where we investigated the effects of flooding and livestock on seed removal, we tested the effects of time since flooding, cattle grazing (presence/absence of cattle) and their interaction on the proportion of seed baits visited. In this analysis sites that had not been flooded for 4 years ($n = 3$) and 6 years ($n = 1$) were combined as > 4 years since flooding.

To investigate whether the microhabitat around seed baits influenced the likelihood of seed predators visiting baits, we used Mann–Whitney U-tests to compare the median value of each microhabitat measure around baits that were visited ($n = 217$) with that around baits not visited ($n = 124$) by seed predators. For the analysis data on baits visited and not visited were pooled over all sites and sampling seasons.

To compare ant community composition at sites with different livestock management regimes, we performed an ordination using non-metric multidimensional scaling (MDS) in PRIMER (Carr 1996). The analysis used data based on all ants captured in the four pitfalls at each site. Abundances of ant species were double square-root transformed before analysis, and similarities between sites were calculated using the Bray-Curtis metric. The significance of any differences between communities according to livestock management regimes and seasons were investigated using analysis of similarities (ANOSIM; Clarke & Warwick 1994).

A two-factor (livestock management regime, season) analysis of variance model was used to compare the mean abundances of seed-eating ants per pitfall trap. Owing to non-homogeneity of variances, the abundance data were log transformed (Ln + 1) before analysis. Differences between levels of significant factors were determined using post-hoc least significant difference tests in SPSS (SPSS Inc. 1999).

To determine if there was a relationship between the abundance of seed-eating ants and the proportion of baits visited across seasons and livestock management regimes, we ran the logistic regression model including the mean abundance of seed-eating ants per trap at each site as a covariate.

Results

EFFECTS OF FLOODS

For both the short and long floods there was no significant difference in the proportion of seed baits visited by seed predators before and immediately (24 h) after flood recession (short flood: mean before = $0·27 \pm 0·20$, mean after = $0·31 \pm 0·20$, $R^2 = 0·2\%$, model $\chi_1^2 = 0·06$, $P = 0·81$; long flood: mean before = $0·54 \pm 0·20$, mean after = $0·57 \pm 0·20$, $R^2 = 0·1\%$, model $\chi_1^2 = 0·06$, $P = 0·81$; $n = 3$ for all means).

EFFECT OF LIVESTOCK MANAGEMENT REGIMES

The proportion of baits visited by seed predators varied significantly according to livestock management regime, season, and their interaction (Fig. 1; $R^2 = 20·4\%$, $\chi_{11}^2 = 55·0$, $P < 0·001$). Owing to the significant interaction term, proportions of baits visited were analysed separately for each season to examine the effects of grazing regime (Table 1). In winter the proportion of baits visited was highest at the no grazing sites (mean $0·77 \pm 0·15$, $n = 3$), in spring it was highest at the high cattle sites (mean $0·92 \pm 0·11$, $n = 3$), while in summer it was highest at the low cattle sites (mean $0·93 \pm 0·09$, $n = 3$). In all seasons, it was lowest at the high sheep sites (winter mean $0·28 \pm 17$, spring mean $0·45 \pm 0·18$, summer mean $0·62 \pm 0·18$; $n = 3$ for all means).

To examine seasonal effects, the proportion of baits visited was analysed separately for each livestock management regime (Table 2). At the no grazing sites there was no significant seasonal variation in the
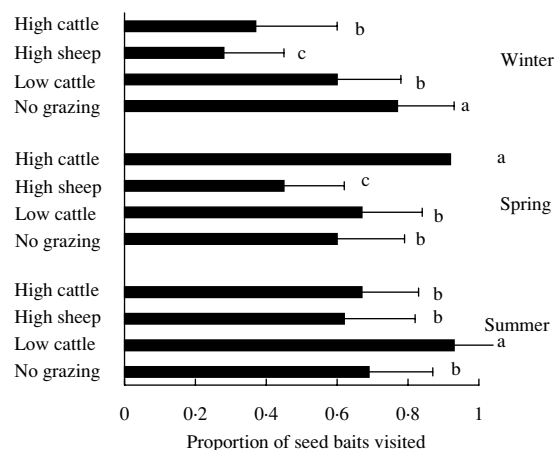
Fig. 1. Mean (+1 SE) proportion of seed baits visited by seed predators in winter, spring and summer in sites with different livestock management regimes. Letters indicate significant differences between grazing regimes within each season.

Table 1. Logistic regression analyses of the effects of livestock management regime on proportion of seed baits visited for each season. Significance of the test statistic (B) determined by comparing the mean of each livestock management regime to the overall mean for all livestock management regimes

Season (R^2, χ^2 value) and livestock regime	B	d.f.	P
Winter ($R^2 = 19\cdot9\%$, $\chi^2_3 = 17\cdot4$, $P = 0\cdot006$)			
No grazing	1·167	1	0·002
Low cattle	0·383	1	0·258
High sheep	−0·988	1	0·007
High cattle	−0·562	1	0·158
Spring ($R^2 = 17\cdot9\%$, $\chi^2_3 = 16\cdot0$, $P = 0\cdot011$)			
No cattle	−0·439	1	0·224
Low cattle	−0·151	1	0·682
High sheep	−1·052	1	0·004
High cattle	1·641	1	0·004
Summer ($R^2 = 12\cdot5\%$, $\chi^2_3 = 10\cdot6$, $P = 0\cdot014$)			
No grazing	−0·357	1	0·344
Low cattle	1·483	1	0·010
High sheep	−0·663	1	0·071
High cattle	−0·463	1	0·212

Table 2. Logistic regression analyses of the effects of season on proportion of seed baits visited for each livestock management regime. Significance of the test statistic (B) determined by comparing the mean of each season with the overall mean for all seasons

Livestock regime (R^2, χ^2 value) and season	B	d.f.	P
No grazing ($R^2 = 0\cdot03\%$, $\chi^2_2 = 1\cdot95$, $P = 0\cdot38$)			
Low cattle ($R^2 = 16\cdot9\%$, $\chi^2_2 = 11\cdot1$, $P = 0\cdot004$)			
Winter	−0·840	1	0·024
Spring	−0·553	1	0·142
Summer	1·393	1	0·007
High sheep ($R^2 = 10\cdot5\%$, $\chi^2_2 = 7\cdot1$, $P = 0\cdot028$)			
Winter	−0·738	1	0·025
Spring	0·019	1	0·951
Summer	0·719	1	0·023
High cattle ($R^2 = 28\%$, $\chi^2_2 = 16\cdot7$, $P = 0\cdot0002$)			
Winter	−1·419	1	0·001
Spring	1·605	1	0·003
Summer	−0·187	1	0·632

proportion of baits visited (range 0·60–0·77). A significant trend of increasing proportion of baits visited from winter through to summer occurred at the low cattle (range 0·60–0·93) and high sheep (range 0·28–0·62) sites. Proportion of baits visited at the high cattle sites was lowest in winter (mean 0·37) and highest in spring (0·92).

A comparison of microhabitat variables across livestock grazing regimes indicated that the average height of vegetation, leaf litter depth, the percentage cover of litter and the abundance of woody debris were greater in no grazing and low cattle sites than in high sheep and high cattle sites (ANOVA and least significant difference tests). Using data pooled over seasons and treatments it was clear that vegetation height and leaf litter depth were significantly higher at seed baits that were visited by seed predators (vegetation height, $Z = -2\cdot52$, $P = 0\cdot012$; litter, $Z = -3\cdot17$, $P = 0\cdot002$). The percentage cover of coarse woody debris and leaf litter was also significantly higher at seed baits that were visited (woody debris, $Z = -2\cdot24$, $P = 0\cdot025$; litter, $Z = -3\cdot28$, $P = 0\cdot001$). In contrast, the percentage cover of live vegetation was significantly lower at seed baits visited by seed predators ($Z = -2\cdot16$, $P = 0\cdot031$).

SEED PREDATORS

A total of 35 species of ants from six subfamilies was recorded in pitfall traps. The highest number of species was in subfamily Formicinae (15), followed by Myrmicinae (12) (see the Appendix). Six of the Myrmicinae species and one of the Ponerinae species were seed eaters. The total number of ants trapped was 17 211, and of these 18% were seed eaters. Of the seed-eating ants, 60% were *Monomorium* sp. B (*rothsteini* group), 25% were *Pheidole* spp., 15% were *Rhytidoponera metallica*, and less than 1% were *Meranoplus* sp. A.

The ordination of ant communities (Fig. 2) revealed that forest sites (no grazing and low cattle, $n = 6$) had different ant communities to paddock sites (high sheep and high cattle, $n = 6$) in both spring and summer (ANOSIMS; spring global $R = 0\cdot863$, $P < 0\cdot01$; summer global $R = 0\cdot802$, $P < 0\cdot01$). There was also a seasonal
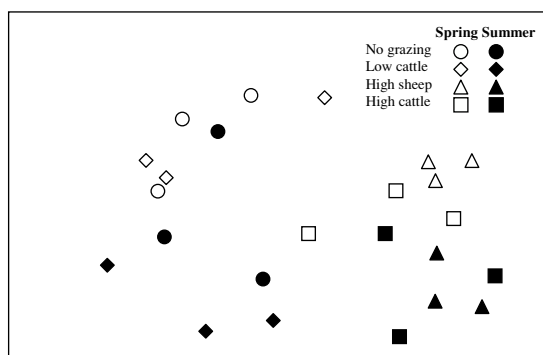
Fig. 2. Two-dimensional ordination of ant community composition at the site level for all livestock management regimes in spring and summer (MDS stress = 0·18).
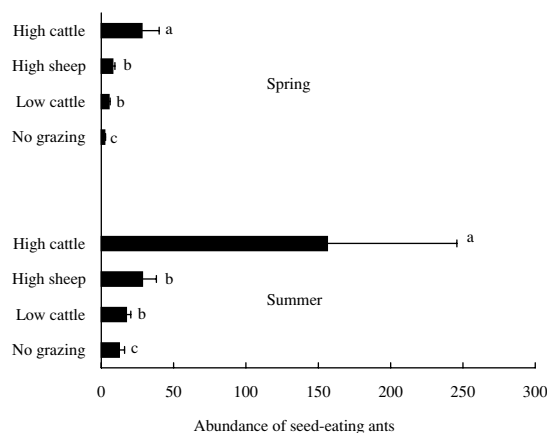

Fig. 3. Mean (+1 SE) abundance of seed-eating ants per pitfall trap for all livestock management regimes in spring and summer. Letters indicate significant differences between grazing regimes within each season.
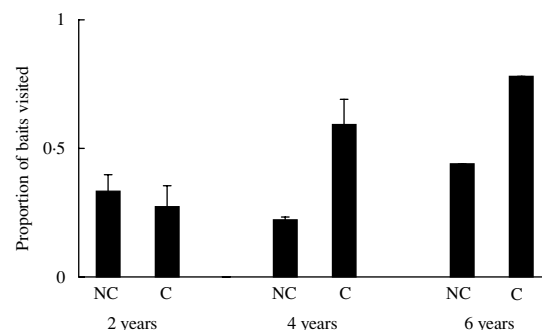

Fig. 4. Mean (+1 SE) proportion of seed baits visited by seed predators in cattle (C) and no cattle (NC) plots in shallow flood runners with different histories of flooding (2 years since flooding, $n = 3$; 4 years since flooding, $n = 3$; and, 6 years since flooding, $n = 1$).

as clear a relationship between seed-eating ants and seed removal at high cattle sites. In summer the number of seed-eating ants was not significantly related to the proportion of seed baits visited.

INTERACTION OF FLOODING AND LIVESTOCK

The impact of 10 years of cattle exclusion on the proportion of seed baits visited by seed predators increased as the period since flooding increased (Fig. 4; overall model $R^2 = 13·5\%$, $\chi_3^2 = 13·1$, $P = 0·004$; interaction $P = 0·020$). There was no difference in the proportion of seed baits visited in cattle and no cattle plots in sites that had been flooded most recently (2 years since flooding). In contrast, in sites that had not been flooded for more than 4 years the proportion of seed baits visited was significantly greater in cattle plots.

Discussion

SEED PREDATION RATES

Rates of post-dispersal seed predation were high in this study and seed predation is potentially an important factor affecting seed supply for recruitment to populations of *E. camaldulensis*. On sections of the floodplain of the Murrumbidgee River used for livestock management, the proportion of seed baits visited over 2 days ranged from zero at one high sheep site in winter to near 1·0 at several sites in spring and summer, with 0–96% of seeds removed (authors' unpublished data). In the flood experiments in the Gulpa Creek Island Forest, the proportion of seed baits visited ranged from 0·27 at the short flood site in September to 0·87 at the long flood site in November, with 6–67% of seeds removed.

A previous study of predation on river red gum seeds in a heavily forested section of the Murray River floodplain reported removal of 86–100% of seeds from trays containing ash bed material and bare soil left on the forest floor for between 32 and 85 days (Dexter 1970).

shift in ant communities from spring to summer in both forest sites and paddock sites (forest sites global $R = 0·341$, $P < 0·05$; paddock sites global $R = 0·365$, $P < 0·05$).

The mean abundance of seed-eating ant species (Fig. 3) varied significantly between grazing regimes ($F_{3,91} = 20·5$, $P < 0·001$) and seasons ($F_{1,91} = 46·4$, $P < 0·001$). Mean abundances were significantly lower at no grazing sites and significantly higher at high cattle sites than in all other livestock management regimes. Abundances were intermediate and similar at low cattle and high sheep sites (Fig. 3). Mean abundances of seed-eating ants increased significantly from spring to summer.

Inclusion of the abundance of seed-eating ants as a covariate in a re-analysis of the seed predation data showed that in spring the proportion of seed baits visited increased as the number of seed-eating ants increased, but there was an almost significant interaction with livestock management regime (overall model $R^2 = 28·3\%$, $\chi_7^2 = 26·4$, $P = 0·004$; number of seed-eating ants Wald statistic = 4·15, $P = 0·042$; interaction Wald statistic = 6·89, $P = 0·076$). The near significant interaction occurred because there was not

The higher rates of seed removal compared with our study reflect the difference in exposure time of seeds to predators.

Previous studies on other eucalypt species have employed a variety of techniques to measure rates of seed predation. They have shown that between 33% and 100% of seeds are removed by invertebrate predators within a matter of days (Withers 1978; Ashton 1979; Drake 1981; Andersen 1982; Andersen & Ashton 1985; Wellington & Noble 1985; Clayton-Greene & Ashton 1990; Yates *et al*. 1995).

Ants dominated pitfall trap catches in our study and were likely to be the main seed predators. On several occasions seed-eating ants were observed carrying seeds away from seed baits (N. Meeson, personal observation). Twenty-five per cent of the seed-eating ants captured were *Pheidole* spp. Large numbers of *Pheidole* spp. worker ants forage specific areas and can remove many seeds very rapidly (Briese & Macauley 1981; Clayton-Greene & Ashton 1990; Shattuck 1999). The pattern of seed disappearance observed in our study corresponded to the foraging behaviour of some seed-eating ants. Once a seed bait was located by ants, all the seeds were often removed within 24 h (N. Meeson, personal observation).

EFFECTS OF FLOODING

Floods that are retained within flood runners in Gulpa Island State Forest occur naturally with an average frequency of one per year (Robertson, Bacon & Heagney 2001). Our results indicate (i) that flooding of this kind does not affect rates of seed removal by seed predators, and (i) that earlier opinions regarding regular flooding being unfavourable for ant colonies (Boomsma 1950; Jacobs 1955) are not justified.

It is feasible that ants and any other invertebrate seed predators retreat from the flood runners as floodwaters rise, and return to forage in the area from trees or the adjacent dry ground following flood recession. In our study, many ants were seen on and around seed baits immediately after the short and long floods (N. Meeson, personal observations). Dexter (1970) also observed ant activity when the ground was still moist immediately following spring flooding in river red gum forests.

Certain species of Australian ants are found in habitats that are periodically inundated (Shattuck 1999). Two ant species have even been reported nesting in the intertidal zone of a Northern Territory mangrove community (Clay & Andersen 1996). Hoyt (1996) suggests that some ant species living close to periodically flooded areas have adapted to submersion for long periods through the ability to reduce their oxygen intake, or even extract oxygen from the water.

While we found no effect of small flood events on the activities of seed predators, river regulation has not reduced the frequency of large flood events in floodplain habitats in the southern Murray-Darling Basin

(Bren 1987, 1988; Page 1988). Whether ants have the ability to survive large flood flows of a long duration requires further work.

EFFECTS OF LIVESTOCK MANAGEMENT

Disturbance, such as grazing, frequently leads to a change in ant communities (Andersen & McKaige 1987; Keals & Majer 1990; Bromham *et al*. 1999), with seed-eating species, *Rhytidoponera, Monomorium* and *Pheidole* spp. (all abundant in this study), becoming more abundant in disturbed sites (Andersen 1990). High numbers of seed-eating ants have been linked to high rates of seed predation on agricultural land (Andersen 1991).

Livestock has been grazing the floodplains of the southern Murray-Darling Basin for 150 years. Grazing has resulted in changes to soil structure and understorey vegetation community structure and composition at the landscape scale (Margules *et al*. 1990; Bacon *et al*. 1994; Buchan 1995; Jansen & Robertson 2001a). Disturbances to soils and vegetation influence ant community composition (Andersen 1986; Keals & Majer 1990) and hence the potential for seed predation (Andersen 1991).

Our data indicate a difference in the effect of cattle and sheep on rates of seed predation. The abundance of species of seed-eating ants across livestock management regimes increased in the order no livestock < high sheep stocking = low cattle stocking < high cattle stocking, and rates of seed predation were lowest in sites stocked with sheep in all seasons. Owing to differences in their foraging behaviour and size, sheep and cattle can have different impacts on soil structure, vegetation composition and litter layers (Arnold & Dudzinski 1978; Noble & Tongway 1986; Wilson 1990; Robertson & Rowling 2000). We found little evidence of differences in ground cover layers in high sheep and high cattle sites in this study, indicating that differences in soil compaction may have been important in influencing the community composition of ants. It is also apparent that these changes in the ant communities on the floodplain of the Murrumbidgee River have developed quite quickly, since the sites grazed by sheep had only been converted from cattle grazing 2–5 years before this study.

In spring the proportion of seed baits visited was related to the abundance of seed-eating ants at each site. However, this pattern broke down in summer. For various reasons it is not surprising that we did not find a consistent relationship between seed predation and the abundance of seed-eating ants. Seasonal differences in the relative availabilities of river red gum seeds and alternative food sources across sites and their interaction with the depth of leaf litter will affect any relationship between seed predators and river red gum seeds. It is also possible that at small scales (metres) the main determinant of seed predation rates is the spatial arrangement of predators in relation to baits, and not

the overall abundance of predators (Hulme & Borelli 1999). Finally, the probability of capture for ants in pitfall traps may vary across season, species and sites (New 1998; Melbourne 1999) and thus mask the true relationship between ant abundance and seed removal.

INTERACTION OF FLOODING AND LIVESTOCK

Our field experiment indicated that the impact of cattle on seed predation by ants is greater in areas that receive less frequent floods. Stocking rates of cattle at the Gulpa Island State Forest field site are relatively low and comparable to those in the low cattle sites we investigated on the floodplain of the Murrumbidgee River (Table 1). Tree densities were similar across treatments, so it appears unlikely that differences in seed supply accounted for differences in rates of seed removal. The no cattle plots used in our experiment had been established for 10 years (Bacon *et al.* 1993). It appears that such a period of exclusion of cattle activity has been sufficient to alter the ant community and reduce the numbers of seed-eating ants.

The clear interaction between flood frequency and the presence or absence of cattle has important implications for future floodplain river management in the Murray-Darling Basin. River regulation and water extraction have decreased the frequency of small and medium flood events in large sections of the rivers of the southern Murray-Darling Basin (Bren 1987, 1988; Page 1988). Our results indicate that, where this occurred, cattle grazing may have exacerbated the impact of reduced flooding on river red gum regeneration by promoting greater rates of post-dispersal seed predation by ants.

Despite the impact that ants have on reducing the supply of river red gum seeds on floodplains cleared for agriculture, germination of river red gum seedlings is a common but patchy event in most years (A. Robertson, personal observation). However, comparisons of floodplain sites with and without access to grazing by cattle and sheep indicate that those seedlings that survive dry summer conditions are trampled or eaten by livestock (Robertson & Rowling 2000). The impacts of livestock on seed predation and post-recruitment mortality ensure that regeneration of river red gum populations is poor at a landscape scale in most years (Jansen & Robertson 2001a).

We used experimental floods of a magnitude that would have a return period of 1 year, and hence our manipulations did not inform us about what happens in larger floods. River regulation has had little effect on the frequency and duration of large floods in the rivers of the south-eastern Murray-Darling Basin (Page 1988; Maheshwari, Walker & McMahon 1995). It is possible that recruitment to river red gum populations in areas of floodplains used for agriculture occurs only following large flood events.

Conclusion

Most floodplains of the Murray-Darling Basin are used for agriculture, and river red gums have been cleared to promote livestock grazing and cropping. In these areas tree densities, and hence seed production, are very low relative to intact river red gum forests. The results of our investigation of the effects of different livestock management regimes on the Murrumbidgee River floodplain indicate that seed predation is highest at sites grazed by cattle, probably as a consequence of the greater abundances of seed-eating ants in these areas. The results of our flooding experiment suggest that rates of seed predation are not affected by small-scale flooding. Based on the experiment in which we investigated the possible interactive effects of livestock and flooding, it was clear that decreases in the frequency of flooding owing to river regulation and water extraction are likely to have exacerbated the influence of livestock on seed supply, and thus reduced potential recruitment to river red gum populations.

The restoration of floodplain rivers depends on return of at least parts of the natural flood regime (Sparks 1995; Poff *et al.* 1997; Molles *et al.* 1998). In Australia significant efforts have been made by governments and agencies to use environmental flow releases from headwater dams to restore ecological function to lowland rivers (EPA 1997). Our previous research has shown the importance of the appropriate seasonal timing of flows to achieve positive conservation outcomes for plant communities in floodplain habitats (Robertson, Bacon & Heagney 2001). However, the research reported in the present paper, taken together with other work on the role of disturbance by livestock in riparian habitats (Fleischner 1994; Robertson 1997; Robertson & Rowling 2000; Jansen & Robertson 2001a), indicates that efforts to rehabilitate large floodplain rivers based solely on the return of more natural flow regimes may fail if the effects of factors such as livestock grazing are not managed concurrently.

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Appendix

Ant subfamilies and species captured in pitfall traps on the floodplain of the Murrumbidgee River in spring and summer of 1999–2000. Allocation to functional groups (seed eaters and non-seed eaters) followed Andersen (1991)

Subfamily	Species	Seed eater
Cerapachyinae	*Cerapachys* sp. A (*singularis* group)	No
Dolichoderinae	*Doleromyrma* sp. A (*darwinianum* group)	No
	Iridomyrmex sp. B (*mattiroloi* group)	No
	Iridomyrmex sp. C (*mattiroloi* group)	No
	Iridomyrmex sp. A (*rufoniger* group)	No
Formicinae	*Camponotus aeneopilosus*	No
	Camponotus obniger	No
	Camponotus sp. A (*claripes* group)	No
	Melophorus sp. B (*fieldi* group)	No
	Melophorus sp. D (*fieldi* group)	No
	Melophorus sp. D (*froggatti* group)	No
	Melophorus sp. A (*mjobergi* group)	No
	Melophorus sp. C (*mjobergi* group)	No
	Melophorus sp. E	No
	Notoncus sp. A (*enormis* group)	No
	Notoncus?ectatommoides	No
	Paratrechina sp. B (*minutula* group)	No
	Paratrechina sp. A (*obscura* group)	No
	Stigmacros aciculata	No
	Stigmacros sp. A	No
Myrmeciinae	*Myrmecia* sp. nr *pilosula*	No
Myrmicinae	*Cardiocondyla nuda*	No
	Meranoplus sp. A	Yes
	Meranoplus sp. B	No
	Monomorium sp. D (*laeve* group)	No
	Monomorium sp. C (*nigrius* group)	No
	Monomorium sp. B (*rothsteini* group)	Yes
	Monomorium sp. A (*sordidum* group)	No
	Pheidole sp. B (group A)	Yes
	Pheidole sp. A (group D)	Yes
	Pheidole sp. C (group D)	Yes
	Pheidole sp. D (group D)	Yes
	Podomyrma sp. A (*elongata* group)	No
Ponerinae	*Rhytidoponera metallica*	Yes
	Rhytidoponera sp. A (*mayri* group)	No