Assessing limitations on population growth in two critically endangered *Acacia* taxa

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Abstract

Flowering phenology, soil seedbank and the impact of fire, weeds and grazing were investigated in two rare *Acacia* taxa restricted to the agricultural district north of Perth Western Australia. *Acacia aprica* is known from six extant populations and one extinct population. Five of the extant populations are restricted to linear road reserves with the sixth population located in a small native vegetation remnant. *Acacia cochlocarpa* ssp. *cochlocarpa* is known from a single population also situated on a road verge. Size class structure, levels of canopy death and an absence of juveniles indicated that all populations are in decline. Flowering intensity and success varied between populations and years in *A. aprica* and between years in *A. cochlocarpa* ssp. *cochlocarpa*. Seed bank analysis indicated that seeds were patchily distributed while experimental fires demonstrated that such events could break seed dormancy and promote germination. Both taxa have similar germination physiologies and showed increased germination after seeds were exposed to heat. Following emergence, however, competition with annual weeds had a negative impact on seedling growth and survival in both taxa. While vertebrate grazing had some influence, weeds were the major inhibitory influence on recruitment. Reduced fire frequencies since fragmentation may be responsible for population decline in both taxa but other site specific factors such as weeds and grazing may affect the establishment of seedlings following fire. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Acacia; Rare; Weeds; Population constraints; Fire; Threatened species; Regeneration niche

1. Introduction

The southwest Botanical Province of Western Australia is species rich and recognised as one of 25 biodiversity hotspots in the world in terms of endemism and levels of threat (Myers et al., 2000). The flora is composed of relictual and more recently evolved species (Wardell-Johnson and Coates, 1996; Coates and Hamley, 1999; Byrne et al., 1999, 2001; Coates, 2000) with considerable radiation within genera of woody perennials (Beard et al., 2000; Paczkowska and Chapman, 2000). There is high local scale diversity within homogenous habitats (α diversity), high plant species turnover along habitat or environmental gradients (β diversity) and high plant species turnover among equivalent habitats across geographical gradients (γ diversity; George et al., 1979; Brown and Hopkins, 1983; Hopkins and Griffin, 1984; Lamont et al., 1984; Hopper, 1992; Cowling et al., 1994; Richardson et al.,

1995; Wardell-Johnson and Williams, 1996; Gibson et al., 2000). A large number of species have geographically restricted ranges (Hopper, 1992; Cowling et al., 1994; Wardell-Johnson and Williams, 1996; Gibson et al., 2000) and many species have naturally disjunct distributions associated with significant genetic differentiation between populations with any phylogenetic similarity now being due to common ancestry rather than any ongoing process of restricted gene flow (Coates, 2000; Gibson et al., 2000). A significant consequence of this is a large number of naturally rare species. Although these patterns are characteristic of the entire southwest, they are best expressed where average annual rainfall varies from 300 to 800 mm (the Transitional Rainfall Zone; Hopper, 1979).

The Transitional Rainfall Zone is now largely occupied by the Western Australian agricultural wheatbelt with approximately 75% of the native vegetation cleared (Beeston et al., 1994). The amount of native vegetation remaining varies across the wheatbelt being as low as 2% in some shires and up to 59% in others (Weaving, 1999). Consequently, a large part of Western

Australia's unique floral biodiversity exists in remnants of native vegetation of varying size, shape and connectivity in highly altered landscapes where disturbance and hydrological regimes have changed and exotic weeds and diseases have been introduced. It is therefore perhaps not surprising in such a diverse flora where natural rarity is common that 95 plant taxa are currently listed under IUCN guidelines as Critically Endangered, 128 Endangered, 104 Vulnerable, and 23 presumed extinct. In addition, a further 1708 taxa are considered as either rare or poorly known and in need of further survey to determine their conservation status (Priority Flora; Coates and Atkins, 2001). This is approximately 25% of the southwest Botanical Province's estimated 8000 plant taxa. These taxa occur across a variety of land tenures with some 70% of the threatened flora in Western Australia occurring outside the existing reserve system (Coates and Atkins, 1997).

Although the interaction of habitat destruction and natural rarity may be the reason for many plant taxa becoming threatened initially, there are continuing threats associated with the contemporary landscape that may be contributing to the continued decline of remaining populations. These include continued habitat destruction; the potential effects that being a small isolated population might have on attracting pollinators, producing sufficient quantities of seed and maintaining genetic diversity; altered fire regimes including reduced frequency of fire resulting in declines in taxa dependent on fire related cues for germination or alternatively increased frequency of fire resulting in declines of taxa which have long maturation times; and finally, declining rates of seedling establishment and increased rates of adult mortality through interactions with introduced exotic weeds, diseases, herbivores and rising saline water tables (Coates and Atkins, 1997).

Currently for many threatened plant taxa the relative importance of the contemporary ecological factors which constrain population growth are poorly understood and little is known about the management actions required to maintain stable populations of plants. Consequently, there is little scientific guidance for conservation managers to determine which threats/actions have the highest priority. Scientific investigations into the limitations on population growth in critically endangered and endangered plants can provide useful information in this regard. Pavlik and Manning (1993), Pavlik et al. (1993) and Pavlik (1994) have described the process of "factor resolution" which seeks to identify and rank constraints to the growth of endangered plant populations.

In regions such as southwest Western Australia where there are large numbers of rare and threatened plants, limited resources for research dictate that comprehensive population ecology studies may not be possible for all taxa. One solution to this problem may be to undertake factor resolution on carefully selected study species that will provide information that can be extrapolated to congeners or other species with similar functional attributes, life histories and landscape contexts. For example within the genus *Acacia*, of the 564 taxa known in southwest Western Australia, there are 12 Critically Endangered, seven Endangered and eight Vulnerable taxa and a further 162 taxa classed as Priority Flora. Moreover a considerable proportion (40%) of populations in threatened *Acacia* species occur on narrow linear remnants on road and rail reserves and as small populations on private lands and are therefore susceptible to many of the threats listed earlier. Knowledge of the relative importance of factors constraining growth in these populations is urgently needed. Similar statistics exist for many other genera in southwest Western Australia.

In this study, we aim to address the earlier problem by undertaking "factor resolution" within two Critically Endangered *Acacia* species that are restricted to linear remnants of native vegetation on road reserves and small remnants on private property. Specifically, we assess the relative importance of seed production and factors affecting seed germination and seedling establishment in constraining population growth.

2. Methods

2.1. Study taxa and study sites

The geographical range of both taxa is intensively farmed and has been extensively cleared. *Acacia aprica* is a winter flowering, leguminous open multi-stemmed shrub to 2 m tall. The species is known from six extant populations and one extinct population (Pop. 4) over a range of 10 km in the Carnamah area north of Perth (Fig. 1). Five of the extant populations (Pops. 1–3 and 5, 6) occur on highly disturbed linear road reserves that
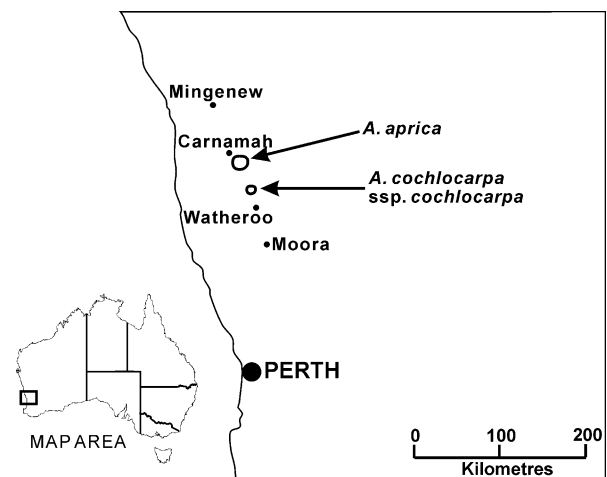

Fig. 1. Locations of the study taxa *Acacia aprica* and *Acacia cochlocarpa* ssp. *cochlocarpa*.

have been extensively invaded by exotic broadleaved annual herbs and grasses. Four of these populations consist of 15 or fewer plants. The sixth extant population (Pop. 7) of 103 plants occurs in relatively undisturbed scrub heath in a small remnant of native vegetation on private property.

Acacia cochlocarpa ssp. *cochlocarpa* is a winter flowering leguminous sprawling shrub to 0.7 m tall and up to 6 m wide. The taxon has been recorded over a 20 km range in the Watheroo area north of Perth but is currently known from a single extant population consisting of 117 plants (Fig. 1). This population occurs in a moderately disturbed scrub heath on linear road reserve and adjoining small remnant on private property.

The Watheroo-Carnamah area has a Dry Mediterranean climate with cool wet winters and hot dry summers. Mean annual rainfall at Carnamah is 389 mm most of which falls between May and September although unpredictable summer rainfall may occur. The mean maximum and minimum temperatures at Carnamah in the warmest month (January) are 35.9 and 18.3 °C and in the coolest month (July) 17.8 and 7.3 °C, respectively. Average monthly rainfall at Carnamah for the period of the study is presented in Table 1.

2.2. Size class structure and individual health

In four *A. aprica* populations (Pops. 1, 3, 5 and 7) and the single *A. cochlocarpa* ssp. *cochlocarpa* population the width of the living canopy at the widest point and the percentage of canopy which had died were measured in all plants. For each population the number of plants within canopy diameter classes (<25, 25–50, 50–100, 100–200, 200–300, 300–400, 400–600 and >600 cm) and the number of plants within each of the size classes that had 0, 1–25, 26–50, 51–75, 76–99 and 100% canopy death were calculated and plotted as stacked histograms.

2.3. Inflorescence, legume and seed production

Reproductive characteristics and potential in both taxa were investigated over three consecutive flowering seasons in 1999, 2000 and 2001. In *A. aprica* surveys were undertaken on five randomly chosen plants in populations 1, 3 and 7 and the single adult plant in population 5. In *A. cochlocarpa* ssp. *cochlocarpa* surveys

were undertaken on 20 randomly chosen plants. On each plant in both taxa, three branchlets spaced equidistantly around the canopy were selected and tagged 40 cm from the shoot apex. During peak flowering the number of inflorescences and inflorescence buds distal to each tag were counted. After legumes (fruit) had developed but not matured and dehisced, the branchlets were re-surveyed and the number of legumes distal to the tags were counted. For each plant in both taxa the mean number of inflorescences and legumes were calculated from the three branchlets.

In late spring in *A. aprica* a maximum of 10 unopened mature legumes were collected from each of the tagged plants in the four populations. In *A. cochlocarpa* ssp. *cochlocarpa* five unopened mature legumes were collected from 10 plants. Legumes were kept separate, returned to the laboratory and the number of seeds per legume counted. For each plant the mean number of seeds legume^{-1} was calculated.

In both taxa, for all plants in all populations an estimate of the number of seeds produced on each of the tagged branchlets was calculated using the formula:

$$\text{No. of seeds} = \text{no. of legumes}$$
$$\times \text{mean no. of seeds legume}^{-1}.$$

In *A. aprica* comparisons of the effects of population and year and the interaction between population and year on the number of inflorescences, the number of legumes, the number of seeds legume^{-1} and the number of seeds were analysed with repeated measures analysis of variance using the mean values for each plant as replicates. In *A. cochlocarpa* ssp. *cochlocarpa* the effect of year on the number of inflorescences, the number of legumes, the number of seeds legume^{-1} and the number of seeds were determined with repeated measures analysis of variance. Underlying assumptions of normality and equality of variance in the models were checked with residual plots and Levene's tests and no transformations were required. All analyses were undertaken using MINITAB Version 12.

2.4. Soil seed bank

Investigations of the density of seeds in the soil were undertaken in April 1999, well after seeds from the

Table 1
Monthly rainfall for the study period 1999–2001 and average monthly rainfall recorded at Carnamah the nearest weather station to the study sites

	January	February	March	April	May	June	July	August	September	October	November	December
1999	0	0	77.9	13.4	182.1	83.9	71.1	38.6	36.7	33.6	18.6	38.8
2000	25.2	0	75.6	14.0	6.0	24.7	71.3	38.6	19.1	4.1	1.8	0
2001	13.9	8.4	11.2	0	61.7	20.1	81.4	38.5	46.1	19.3		
Mean	11.6	14.4	20.8	23.3	51.9	79.0	69.1	53.2	28.4	17.1	10.6	9

previous year's crop were dispersed. In *A. aprica* four soil cores (10×10×5 cm deep) were taken at randomly chosen points beneath the canopies of five reproductive plants in populations 1, 3 and 7 and from beneath the single adult plant in population 5. In *A. cochlocarpa* ssp. *cochlocarpa* four soil cores were collected from randomly chosen points beneath the canopies of 20 reproductive plants. The soil samples were air dried and successively passed through a series of differential sieves until two fractions remained above and below the normal size range of the seeds. The fraction below the size range of the seeds was discarded and the remaining fraction examined under a binocular microscope for seeds.

2.5. Fire and seedling emergence

The impact of fire on seedling emergence was investigated in *A. cochlocarpa* ssp. *cochlocarpa*. Six plants that were reaching the end of their lives with shoot growth restricted to a few branches and canopy cover reduced to a small percentage of the original cover were selected for burning. An additional six plants were chosen as controls for monitoring rates of seedling emergence in the absence of fire. Analyses of soil seed banks (Section 2.4) revealed that seed was very patchily distributed, consequently the magnitude of seed reserves beneath plants was unknown. To determine the effectiveness of the experimental fires in stimulating germination known quantities of untreated seed were sown in 50×50 cm plots beneath all plants including controls prior to burning using a technique modified from (Pavlik and Manning, 1993). One side of each plot was permanently marked with two 20 cm galvanised steel rods that protruded 5 cm above the soil. The rods were used to accurately position a perspex template for sowing seeds and monitoring subsequent emergence. The template contained a 6×6 grid of holes (36 holes) 2 cm in diameter and spaced 7.5 cm apart. In each hole a steel rod was pressed 1 cm into the soil and three seeds sown. Following sowing, holes were filled with soil and lightly firmed down.

The six plants chosen for burning occurred in two discrete clumps of three plants. Fuel loads in a 10×4 m area surrounding each clump of plants were manipulated with dead plant material collected on the site to create a continuous layer of loosely packed fuel approximately 30 cm deep across the quadrats. Plants were burnt in the two areas between 11:00 and 12:00 h in mid April 2000 prior to the beginning of the winter wet season. Conditions were clear and sunny and combustion of plants was complete. Following burning 1.3 m high fences were erected to exclude vertebrate herbivores. Seedling emergence from the manipulated and natural seed banks in burnt and unburnt areas were monitored in August and September in 2000 and March, June and September in 2001. The effect of fire on seedling emergence was assessed with an unpaired two tailed *t*-test using MINITAB Version 12.

2.6. The effects of seed coat scarification and grazing on seedling emergence

The effects of breaking seed dormancy and excluding vertebrate herbivore grazing on seedling emergence were investigated in *A. cochlocarpa* ssp. *cochlocarpa*. In April 2000 prior to the onset of the winter rains 30 quadrats (50×50 cm) were marked out and five replicates of each combination of seed treatment (treated and untreated seeds) and grazing (quadrats open or protected by an exclosure) were randomly allocated to the plots. Seed dormancy imposed by a hard seed coat was broken by nicking (scarifying) the seed coat with a scalpel. Grazing was excluded from plots with upended wire baskets 50×50×25 cm high fixed to the ground by steel pegs. In each plot 108 seeds were sown using the methods described in Section 2.5. Seedling emergence and survival were monitored in August and September in 2000 and March in 2001. All emergence data were adjusted to the proportion of viable seeds sown. The effect of seed treatments and excluding vertebrate herbivores on seedling emergence data were assessed with two way analysis of variance using MINITAB Version 12. Underlying assumptions of normality and equality of variance in the model were checked with residual plots and a Levene's test and an angular transformation (arcsine square root) performed to stabilise variances (Zar, 1999).

2.7. The impact of invasive weeds and grazing on seedling establishment

The impact of weeds and grazing on the establishment of *A. aprica* seedlings were assessed in populations 3 and 5. At each site in April 2000 eight 2×2 m plots were marked out and thatch from the previous winter's growth of annual weeds removed by hand. Following the onset of winter rains and the emergence of weeds four plots at each site were randomly chosen and weeded by hand, the other four plots were left untreated. All main plots were divided in two and a herbivore exclusion treatment randomly assigned to one half of each plot with upended wire cages measuring 1×0.5×0.5 m. The other half of each plot was left open to grazing. In each split plot eight seedlings were planted equidistantly apart on a 4×2 grid. Plots were monitored in August, September and November in 2000, and March, May and September in 2001. At each site for each monitoring period the effect of weeds and grazing and their interaction on the survival (arcsine) and growth (log) of seedlings were assessed with split-plot analyses of variance. Underlying assumptions of normality and equality of variance in the model were checked with residual plots and a Levene's test. Survival data was angular

transformed (arcsine square root) and seedling growth data log transformed to stabilise variances (Zar, 1999). In Population 5 by March 2001 all seedlings in unweeded plots had died and the effects of grazing on seedling survivorship and growth in weeded plots were assessed by unpaired two tailed t-tests. All analyses were undertaken in MINITAB Version 12.

2.8. The impact of grazing on seedling establishment

In *A. cochlocarpa* ssp. *cochlocarpa* weeds were not considered a threat and an experiment was designed to determine the importance of grazing on seedling establishment and growth. In June 2000, fourteen 1×0.5 m plots were marked out and eight seedlings planted equidistantly apart on a 4×2 grid. A herbivore exclusion treatment was randomly assigned to seven plots and upended wire cages measuring 1×0.5×0.5 m placed over the seedlings. Plots were monitored in August, September and November in 2000, and March, June and September in 2001. The effect of grazing on survival (arcsine) and growth (log) of seedlings were assessed with one way analysis of variance using MINITAB Version 12. Underlying assumptions of normality and equality of variance in the models were checked with residual plots and Levene's tests and survival data was angular (arcsine square root) transformed and growth data log transformed to stabilise variances (Zar, 1999).

3. Results

3.1. Size class structure and individual health

The vigour and distribution of plants across size classes varied between *A. aprica* populations. The distribution of plants in populations 1 and 7 were skewed towards larger size classes with at least 20% of individuals in each class having greater than 50% of their canopy dead (Fig. 2a and d). Smaller plants with healthier canopies were more common in populations 3 and 5 but these consisted of very few plants (Fig. 2b and c). The common characteristic of all four populations was that no seedlings or juvenile plants were present.

The distribution of plants across size classes in *A. cochlocarpa* ssp. *cochlocarpa* was also skewed towards larger size classes although two younger non-reproductive plants were observed (Fig. 3). Like *A. aprica* there were considerable numbers of senescing plants with the proportion of plants with greater than 50% canopy death ranging from 2 to 77% across size classes.

3.2. Inflorescence, legume and seed production

For *A. aprica* the mean number of inflorescences, legumes and seeds produced varied significantly between populations and between years. For each of these factors there was also a significant interaction between populations and years (Table 2). The mean number of seeds per legume varied significantly between years and there was a significant interaction between populations and years (Table 2).

For all *A. aprica* populations inflorescence, legume and seed production were generally higher in 1999 than in other years. In 2000, all plants in all populations flowered and some plants produced legumes but no viable seeds were set. For each of the 3 years inflorescence, legume and seed production were consistently higher in populations 1 and 3 than in populations 5 and 7 (Fig. 4a–d, respectively).

For *A. cochlocarpa* ssp. *cochlocarpa* the mean number of inflorescences, legumes and seed production varied between years (Table 3, Fig. 5 and c, respectively). With the exception of the mean number of inflorescences which was higher in 2000 than either 1999 or 2001, the remaining parameters followed similar trends to that observed in *A. aprica*.

3.3. Soil seed bank

Acacia aprica seeds were recovered from soil samples in all populations. The mean density of seeds varied from 7.7 ± 4.3 seeds m^{-2} in population 1 to 47.4 ± 34.2 seeds m^{-2} in population 7 (Table 4). The distribution of seeds in the soil was extremely patchy with seeds being restricted to a small proportion of soil cores. Similarly in *A. cochlocarpa* ssp. *cochlocarpa* seeds were patchily distributed with a mean density of 72.5 ± 16.7 seeds m^{-2}.

3.4. Fire and seedling emergence

Fire killed the six adult plants and had a significant effect on seed gemination and seedling emergence in experimental plots where *A. cochlocarpa* ssp. *cochlocarpa* seeds were sown ($t_{(2), 5} = -5.75$, $P = 0.002$; Fig. 6a). Mean percentage seedling emergence in burnt plots was 8 ± 1.5 and in unburnt plots was 0.5 ± 0.3. Twenty-five seedlings emerged from the natural seedbank in the areas which were burnt while no seedlings were observed in the vicinity of the six unburnt plants. Seedling mortality was high in the first summer following emergence with 69% of seedlings from the artificial seedbank and 64% of naturally emerged seedlings dying (Fig. 6b).

3.5. The effects of seed coat scarification and grazing on seedling emergence

In *A. cochlocarpa* ssp. *cochlocarpa* seed coat scarification had a significant effect on seedling emergence ($F_{1, 16} = 44.38$, $P = 0.000$) but exclosures did not ($F_{1, 16} =$
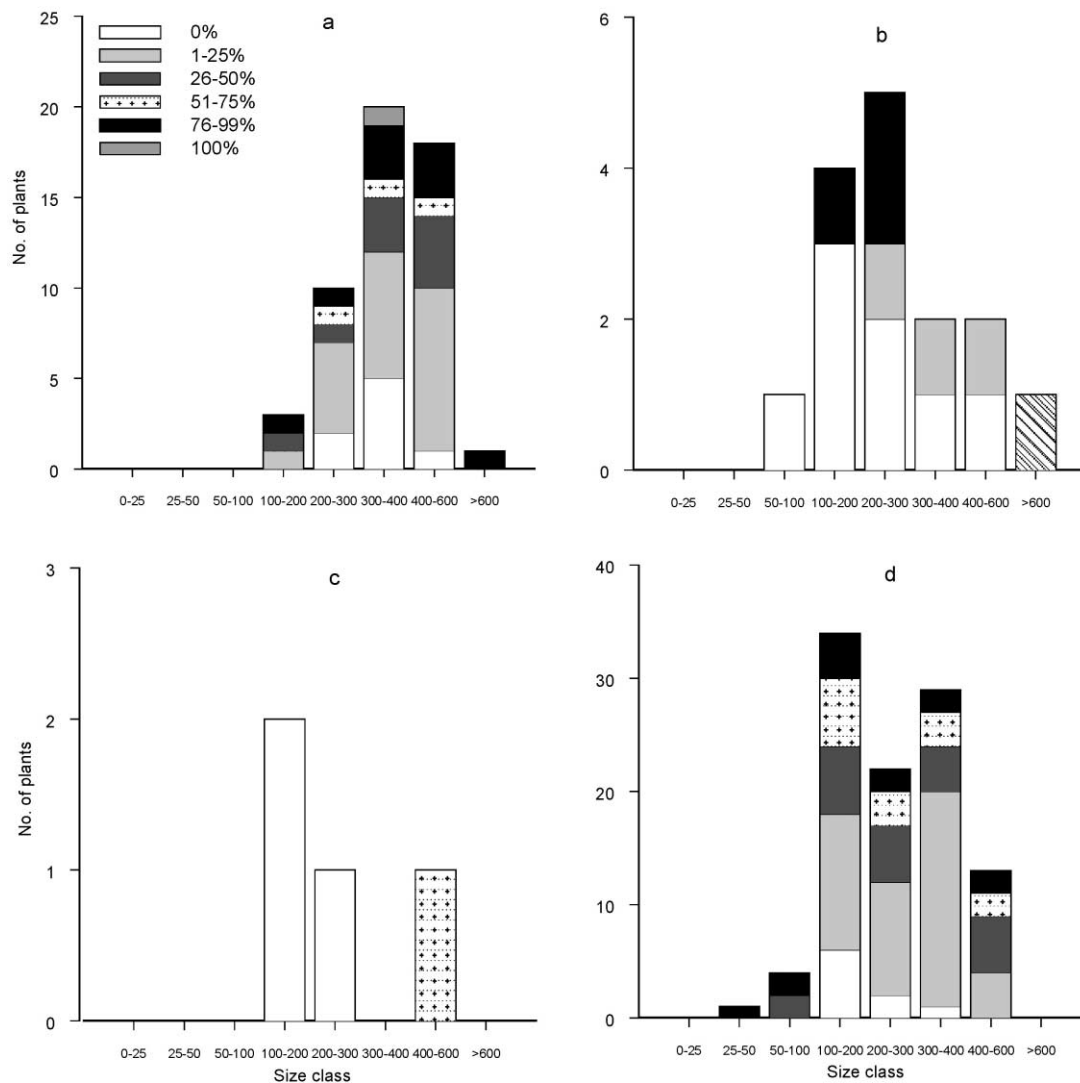
Fig. 2. The distribution of all *Acacia aprica* plants across size and vigour classes in population 1 (a), population 3 (b), population 5 (c), and population 7 (d). Vigour classes describe the proportion of the plant's canopy that was dead.

0.42, $P = 0.526$). In open plots the mean percentage seedling emergence was 44.3 ± 12.7 while in exclosure plots the mean was 33.7 ± 8.6. In plots where untreated seeds were sown the mean percentage seedling emergence in open and exclosure plots were 0.7 ± 0.4 and 0.6 ± 0.2, respectively. No seedlings survived the first summer following emergence.

3.6. The impact of invasive weeds and grazing on seedling establishment

In both populations 3 and 5 the presence of weeds had a significant effect on the survival of *A. aprica* seedlings but exclusion of grazing had no effect (Figs. 7a and b). In population 3 seedling survival was significantly higher in weeded plots than in unweeded plots in March 2001 ($F_{1, 5} = 8.03$, $P = 0.030$), May 2001 ($F_{1, 6} = 21.62$, $P = 0.004$) and September 2001 ($F_{1, 6} = 26.44$, $P = 0.002$). In September 2001, in population 3 mean

percentage seedling survival in weeded plots was 83.5 ± 4.86 and in unweeded plots was 14.1 ± 6.0. In population 5, all seedlings in unweeded plots had died by March 2001. Mean percentage seedling survival in September 2001 in weeded plots was 62.5 ± 5.3.

In population 3, the presence of weeds had a significant effect on the growth of *A. aprica* seedlings but the exclusion of grazing had no effect (Fig. 7c). The magnitude of the effect of weeds on seedling growth changed through time. The mean height of seedlings in weeded plots was significantly greater than in unweeded plots in November 2000 ($F_{1, 6} = 38.22$, $P = 0.001$) and March 2001 ($F_{1, 4} = 33.10$, $P = 0.005$). In May 2001 seedlings in weeded plots were taller than in unweeded plots but this effect was not significant at the accepted α level of 0.05 ($F_{1, 4} = 6.23$, $P = 0.067$). However, by September 2001 seedlings in weeded plots were again significantly taller than in unweeded plots ($F_{1, 4} = 32.76$, $P = 0.005$).

In population 5, both the presence of weeds and the exclusion of grazing had a significant effect on the growth of *A. aprica* seedlings (Fig. 7d). The mean height of seedlings in weeded plots was significantly greater than in unweeded plots ($F_{1, 6} = 26.27$, $P = 0.002$). However, all seedlings in unweeded plots had died by March 2001. In weeded plots the mean height of seedlings was significantly greater in plots where grazing was excluded than in plots open to grazing in March 2001 ($t_{(2), 4} = -3.38$, $P = 0.028$), May 2001 ($t_{(2), 3} = -4.40$, $P = 0.022$) and September 2001 ($t_{(2), 5} = -2.88$, $P = 0.035$).

3.7. The impact of grazing on seedling establishment

The exclusion of grazing had no significant effect on the survival of *A. cochlocarpa* ssp. *cochlocarpa* seedlings (Fig. 8a). In both open and exclosure treatments, the patterns of mortality were similar. Rates of seedling deaths were highest in the first winter and summer following planting but stabilised with no mortality being observed in the second winter. The mean percentage survival of seedlings at the end of the second winter in

exclosure treatments was 26.8 ± 8.38 and in treatments open to grazing was 21.43 ± 9.34.

In contrast the exclusion of grazing did effect the growth of *A. cochlocarpa* ssp *cochlocarpa* seedlings with the effect increasing in magnitude with time since planting (Fig. 8b). Seedlings in exclosure treatments were significantly higher than seedlings open to grazing in March ($F_{1, 11} = 12.89$, $P = 0.004$), June ($F_{1, 10} = 8.25$, $P = 0.018$) and September 2001 ($F_{1, 10} = 25.17$, $P = 0.001$). There was a considerable decrease in plant height in both exclosure and open plots in June 2001. By September, however, plants in exclosures had regrown to a height similar to that of the previous March. In contrast, plants in open plots only attained approximately half of the height measured in March.

4. Discussion

The maintenance of stable populations is contingent on birth rates equalling death rates. In both *A. aprica* and *A. cochlocarpa* ssp. *cochlocarpa* the predominance of plants in larger size classes, absence of seedlings, large proportion of plants with greater than 50% of their canopy dead and presence of dead plants suggests ageing demographic structures and declining populations. Most deaths in populations were recorded in 2001 after two exceptionally dry years when rainfall was well below average. The recruitment of seedlings into a population is contingent on numerous factors. Plants must flower, the flowers must be pollinated and produce viable seeds which must escape predation and persist in a seedbank until suitable conditions for germination. The seedlings must then survive and grow to reach reproductive maturity (Harper, 1977).

In this study the intensity and success of flowering varied between populations and years in *A. aprica* and between years in *A. cochlocarpa* ssp. *cochlocarpa*. The reasons for this variation are unknown but clearly the relationship between flowering intensity and seed production is not simple. The amount of seed produced following flowering is dependent upon resource availability (Huber et al., 1996; Zimmerman and Pyke, 1988), pollinator abundance (Jennersten, 1988; Agren, 1996; Mustajrvi et al., 2001) and pollen quality (Ramsey and Vaughton, 2000; Wolf and Harrison, 2001) and
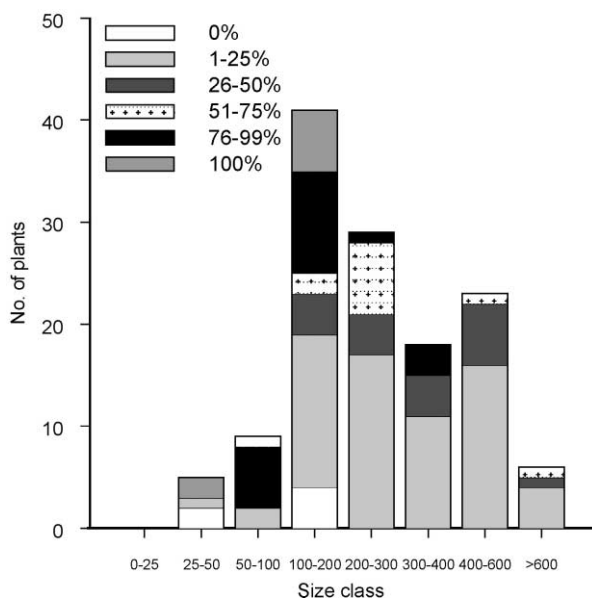

Fig. 3. The distribution of all *Acacia cochlocarpa* ssp. *cochlocarpa* plants across size and vigour classes. Vigour classes describe the proportion of the plant's canopy that was dead.

Table 2
Results of analyses of variance examining effects of population, year and their interaction on inflorescence production, legume production, number of seeds legume^{-1} and seed production in *Acacia aprica*

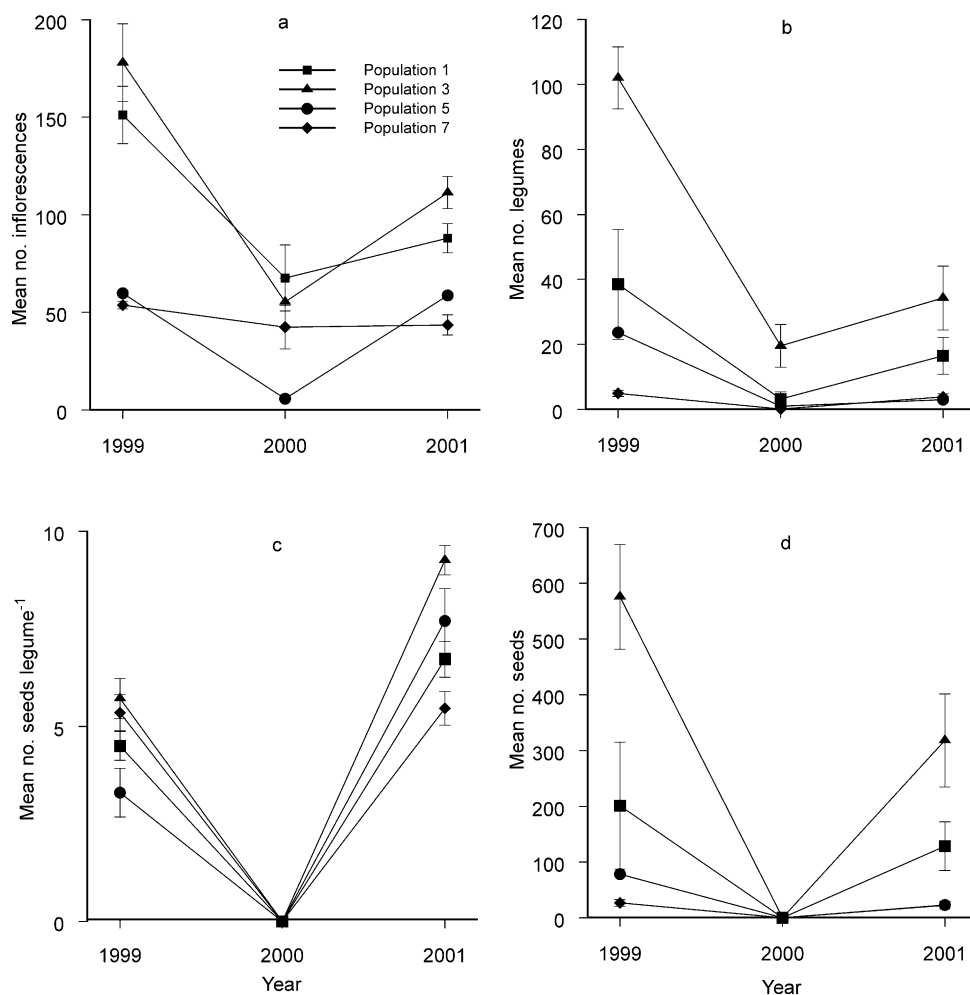| Measurement	Population	Year	Population×year
No. inflorescences	$F_{3, 12} = 18.22$, $P = 0.000$	$F_{2, 24} = 16.76$, $P = 0.000$	$F_{6, 24} = 4.24$, $P = 0.005$
No. of legumes	$F_{3, 12} = 17.64$, $P = 0.000$	$F_{2, 24} = 14.71$, $P = 0.000$	$F_{6, 24} = 4.24$, $P = 0.005$
No. of seeds legume^{-1}	$F_{3, 12} = 2.49$, $P = 0.110$	$F_{2, 24} = 47.71$, $P = 0.000$	$F_{6, 24} = 2.67$, $P = 0.005$
No. of seeds	$F_{3, 12} = 9.65$, $P = 0.002$	$F_{2, 24} = 10.18$, $P = 0.001$	$F_{6, 24} = 6.51$, $P = 0.005$

Fig. 4. Mean ($\pm$SE) (a) number of inflorescences; (b) number of legumes; (c) number of seeds legume^{-1} and (d) number of seeds produced on a 40 cm length of branch beneath shoot apex in 1999, 2000 and 2001 in four populations of *Acacia aprica*.

Table 3
Results of analyses of variance examining effects of year on inflorescence production, legume production, number of seeds legume^{-1} and seed production in *Acacia cochlocarpa* ssp. *cochlocarpa*

Measurement	Year
No. inflorescences	$F_{2, 38} = 3.76, P = 0.032$
No. of legumes	$F_{2, 38} = 18.53, P = 0.000$
No. of seeds legume^{-1}	$F_{2, 38} = 15.29, P = 0.000$
No. of seeds	$F_{2, 38} = 5.77, P = 0.000$

seed predation (Andersen, 1989). These in turn may be affected by factors such as population size, remnant area, landscape context and level of degradation. Rainfall was well above average in 1999 but in 2000 and 2001 was below average with later than usual beginnings to the winter wet season. It is possible that the higher rainfall in 1999 resulted in heavier flowering and fruiting and the shorter duration of the wet season and lower rainfall in 2000–2001 were responsible for reduced flowering, fruiting and seed production. Gaol and Fox (in press) reported similar trends for eight common *Acacia*

species from southwest Western Australia over the same time period. This commonality of response between rare and common species suggests that rainfall and resource availability are important factors limiting seed production in both rare and common *Acacia* species. However, possible effects of variability in pollinator abundance or pollen quality between years cannot be discounted.

The pattern of vegetation clearing and the probable geographic restriction of the two *Acacia* taxa makes replication of remnants and populations with the same characteristics impossible, and it is, therefore, difficult to draw firm conclusions from the data about the impact of population size and site characteristics on seed production. However, studies on the impacts of population size on seed production have found in some cases that seed production declines with decreasing population size (Lamont et al., 1993; Morgan, 1999; Cunningham, 2000; Hendrix and Kyhl, 2000; Hackney and McGraw, 2001; Wolf and Harrison, 2001) while others have found that population size has no impact on reproductive success (Cunningham, 2000; Costin et al., 2001; Mustajrvi et al., 2001). On the available evidence
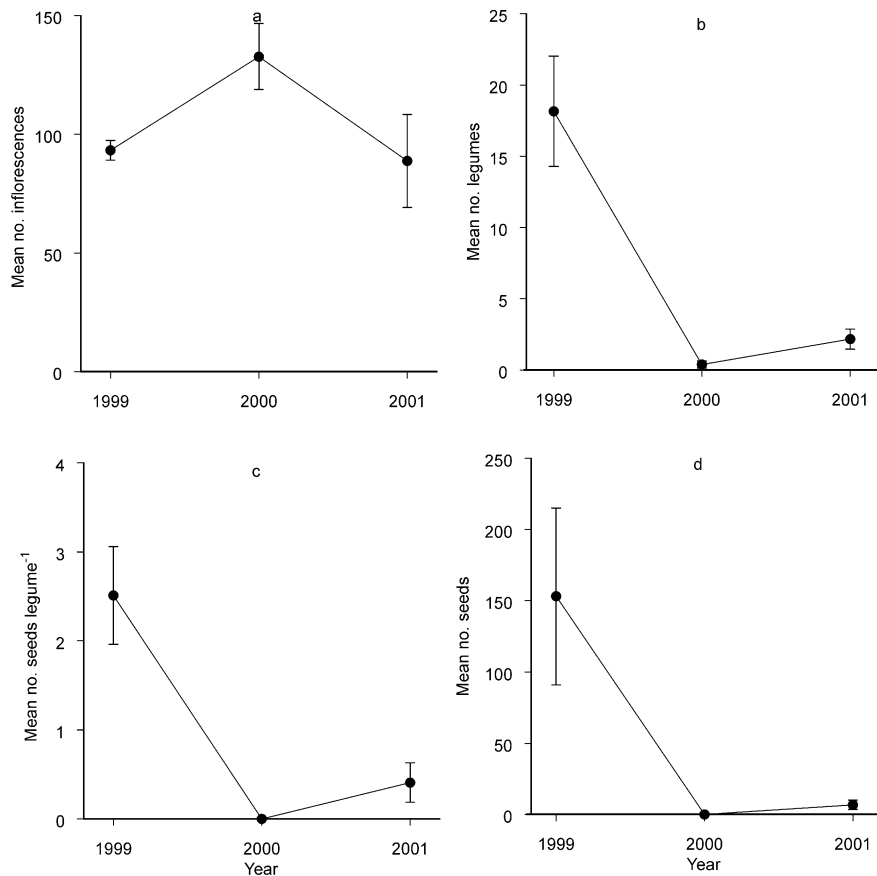
Fig. 5. Mean ($\pm$SE) (a) number of inflorescences; (b) number of legumes; (c) number of seeds legume^{-1} and (d) number of seeds produced on a 40 cm length of branch beneath shoot apex in 1999, 2000 and 2001 in *Acacia cochlocarpa* ssp. *cochlocarpa*.

Table 4
The density of seeds in the soil for *Acacia aprica* and *Acacia cochlocarpa* ssp. *cochlocarpa*

Taxon	Pop	No. soil cores	No. cores with seeds	Mean seeds m^{-2} ($\pm$SE)
Acacia aprica	1	40	3	7.7$\pm$4.3
	3	20	1	14.3$\pm$14.3
	5	4	1	25.0$\pm$25.0
	7	40	7	47.4$\pm$34.2
Acacia cochlocarpa		80	24	72.5$\pm$16.7

it is difficult to make generalisations about the impact of population size on reproductive success. Without reference to larger populations it is difficult to determine whether seed production is lower in the remaining populations of *A. aprica* and *A. cochlocarpa* ssp. *cochlocarpa* than it was prior to fragmentation. Study populations were all small ranging from 4 to 117 plants. Interestingly in *A. aprica*, population 3 consisting of 15 plants on a disturbed road verge had higher numbers of inflorescences and produced more legumes and seeds per plant than the largest population 7 consisting of 117 plants in a relatively undisturbed larger remnant of native vegetation. These limited observations suggest

that the reproductive biology of *A. aprica* may be relatively robust to the impacts of population size and that factors such as landscape context may be as important as population size when considering the impacts of fragmentation.

Other studies have observed that landscape context can influence reproductive output. For example, Lamont et al. (1994a, b) found that fruit and seed production were higher in road verge plants of *Banksia menziesii* compared with non-verge plants and attributed this to greater access to water and nutrients from road runoff, and reduced root competition. However, Cunningham (2000) in a study of the effect of landscape context on the reproductive ecology of four taxa observed that net seed production in linear strips of vegetation compared with large remnants was higher in one species, lower in one species and not significantly different in two species.

The limitations imposed by the number of populations and plants in this study do not allow absolute conclusions to be made as to whether *A. aprica* and *A. cochlocarpa* ssp. *cochlocarpa* are producing enough seed to maintain viable populations. However, similar trends in fruit production in common *Acacia* species for the period of the study (Gaol and Fox, in press) and higher
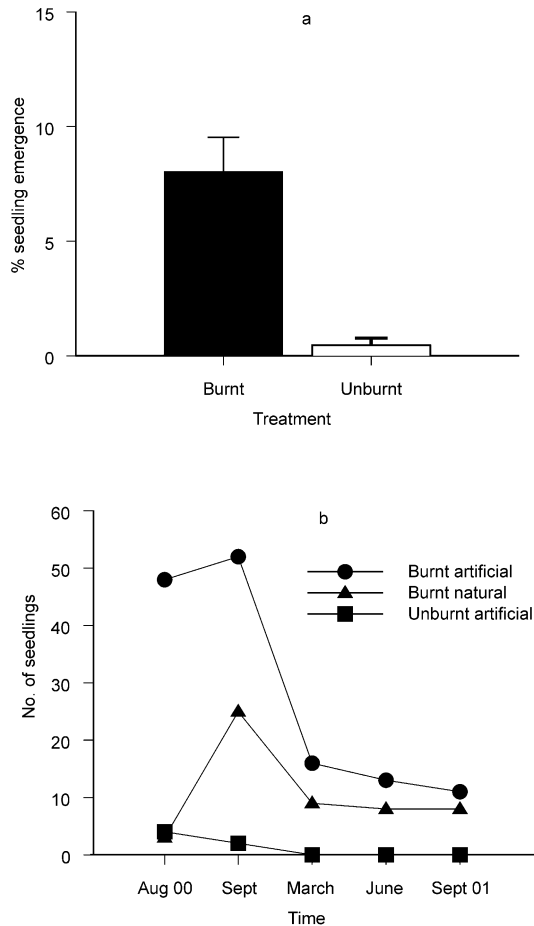
Fig. 6. (a) Mean (±SE) cumulative emergence of *Acacia cochlocarpa* ssp. *cochlocarpa* seedlings from experimentally sown plots following experimental fires and in the absence of fire, and (b) the total number of seedlings emerging and their survival from experimentally sown plots and the natural seed bank following the experimental fires.

rates of reproductive output in a small population compared to a relatively larger population suggest that seed production may not be constraining population growth. Moreover, the relationship between seed production and population viability may not be linear. Obviously in populations where seed production is zero, extinction will occur unless the plants can reproduce vegetatively. However, in populations where plants are producing viable seeds, the absolute number of seeds required to maintain viable populations may be hard to determine. This may be particularly evident in species that rely on the occurrence of infrequent unrelated events for recruitment. For example, plant species in fire prone Mediterranean shrublands where the two study species are found may rely on fire and above average rainfall in the first winter following the fire for successful recruitment (Lamont et al., 1991; Bond and van Wilgen, 1996; Enright et al., 1998). In these species, populations numbers are limited by both seed reserves and factors which control germination and establishment of seedlings. Lamont et al. (1991) observed in an

obligate seeding shrub dependent on fire for recruitment, that despite there being a large canopy stored seed reserve (17,100 viable seeds), emergence was poor (<5% of the seed reserve) and seedling survival even poorer (0.1%). Lamont et al. (1991) attributed the poor recruitment to below average rainfall in the first winter following the fire and concluded that population size was not limited by the size of the canopy seed bank but by the weather pattern following fire induced seed release. Similarly Bradstock (1991) reported that for fire dependent recruiting shrubs population size was influenced more by recruitment related events than a 50% reduction in seed production. Clearly, in such species, population viability may be more sensitive to factors that effect seed germination and seedling survival than reductions in seed production caused by declines in population size.

In both *A. aprica* and *A. cochlocarpa* ssp. *cochlocarpa* soil seed reserves were found. The density of seeds observed were within or greater than the range reported by Auld (1986) in the common *A. suaveolens* but may be biased by restriction of sampling to beneath plant canopies. The germination physiology of *A. aprica* and *A. cochlocarpa* ssp. *cochlocarpa* suggests that these reserves are persistent with germination being initiated by events which rupture the hard seed coat. The dynamics and longevity of these seed reserves is unknown but in the similarly hard seeded *A. suaveolens* seeds may have half lives of 10 years and may remain viable for greater than 50 years (Auld, 1986). The formation of persistent soil seed reserves may buffer populations of both taxa against the impacts of reduced seed production. Importantly, the inferred ability of *A. aprica* and *A. cochlocarpa* ssp. *cochlocarpa* seeds to survive for long periods in the soil may enable both taxa to persist independently of living plants.

The absence of seedlings and juveniles in all populations of both study taxa may be due to factors associated with seed germination and seedling establishment (the regeneration niche) (Grubb, 1977). Studies of plant population viability in fragmented landscapes have primarily focused on factors associated with seed production but have ignored the availability of the regeneration niche. In Mediterranean climate southwest Western Australia vegetation is prone to burning in the dry summer months and it is generally accepted that fire has been a force of evolutionary significance in many plant groups (Gill, 1981). Indeed studies in the region have revealed taxonomically diverse groups of plant species that exhibit morphological, phenological and functional characteristics which suggest a commonality in evolutionary response to recurrent fire (Gill, 1981; Bell et al., 1984; Whelan, 1995; Bond and van Wilgen, 1996). These include fire survival characteristics (Gill, 1981; Bell et al., 1984) and fire related germination cues (Bell et al., 1984; Dixon et al., 1995) with recruitment in
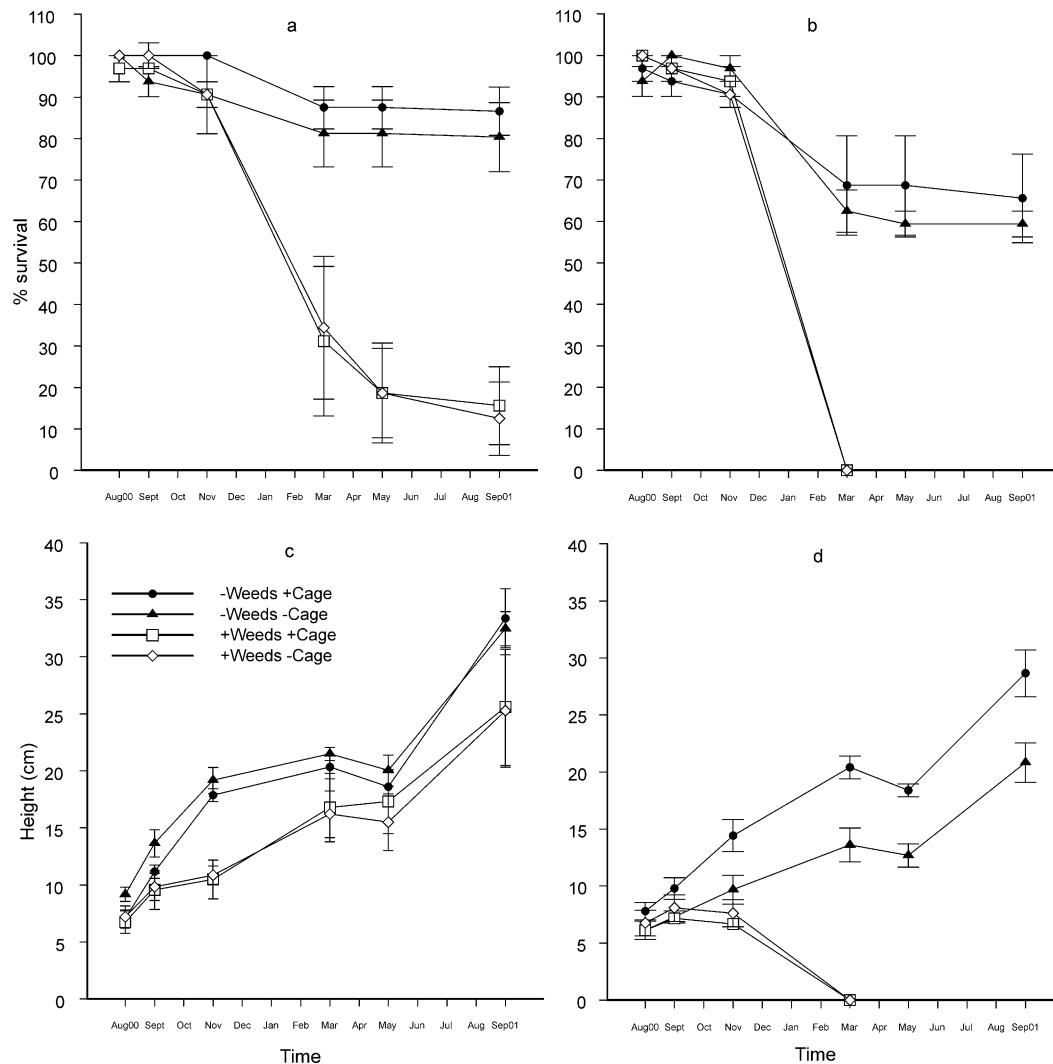
Fig. 7. Mean (±SE) survival of transplanted *Acacia aprica* seedlings in (a) population 3 and (b) population 5 and mean (± SE) growth of transplanted seedlings in (c) population 3 and (d) population 5 in weeded and unweeded plots with and without grazing exclosures.

many taxa being restricted to the first winter following fire (Cowling and Lamont, 1987; Enright and Lamont, 1989).

In agricultural landscapes where most of the native vegetation has been cleared landscape fires may no longer develop because of fire suppression and low fuel loads in agricultural land. As a consequence, plants which occur in small fragments and which rely on fire for recruitment may have fewer opportunities for regeneration. In non-sprouters, if the fire interval exceeds the longevity of both the plants and the seed bank, local population decline and even extinctions are likely (Whelan, 1995; Bond and van Wilgen, 1996). In many *Acacia* species the most common environmental cue for breaking seed dormancy is fire (Auld and O'Connell, 1991). This study observed that fire resulted in the emergence of *A. cochlocarpa* spp. *cochlocarpa* seedlings from artificially created and natural seed banks. The proportion of seeds which emerged from the

artificially sown seed banks was 8%. Similarly the number of seedlings which emerged from the natural seedbank was relatively small compared to the estimates of seed bank size. There are a number of reasons for these results. Firstly, the fires were too hot and seeds were killed; secondly, the fires stimulated germination but there was considerable mortality between germination and emergence; and thirdly, the fires were not hot enough to stimulate germination. The latter seems the most likely explanation because fuel loads were low and the fires were small and undertaken in late autumn on a cool day. The fires were therefore likely to be less intense than might occur during summer when fires are most likely to occur naturally.

Acacia aprica and *A. cochlocarpa* ssp. *cochlocarpa* have similar germination physiologies under laboratory conditions (Yates unpublished data) with both taxa showing increased germination after seeds are exposed to heat. Clearly, fire is an important germination cue for
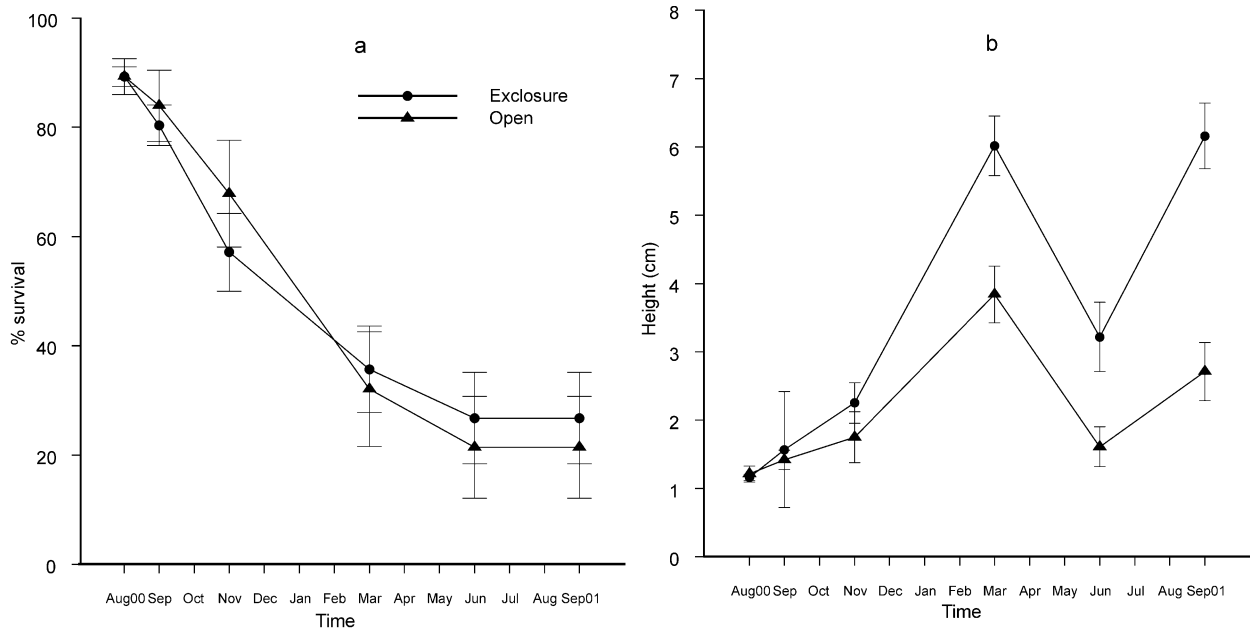
Fig. 8. (a) Mean (±SE) survival of transplanted *Acacia cochlocarpa* ssp. *cochlocarpa* seedlings and (b) growth of transplanted seedlings with and without grazing exclosures.

both taxa and factor driving population dynamics. Fire killed adult plants in *A. cochlocarpa* ssp. *cochlocarpa* and *A. aprica* is likely to respond in a similar way given that it is predominantly single-stemmed and does not have a lignotuber. In non-sprouting species that rely on post-fire germination to persist, fire intervals which exceed the life expectancy of the species may result in localised population decline (Burgman and Lamont, 1992). Unfortunately the fire histories of the sites are unknown. Nevertheless reduced fire frequency since fragmentation could be responsible for population decline but other site specific factors such as weeds and grazing may affect the establishment of seedlings following fire and cannot be ruled out. Both weeds and grazing have been shown to be important factors limiting seedling emergence and survival in *Acacia* species elsewhere in Australia (Auld, 1995; Jusaitis and Sorensen, 1998). Populations of both taxa occur on disturbed road verges where weeds and grazing vertebrates such as rabbits and kangaroos occur. For *A. aprica* invasive weeds were abundant in three of the four populations while invasive weeds were less of a problem in *A. cochlocarpa* ssp. *cochlocarpa*.

The removal of annual weeds resulted in increased survival and growth of transplanted *A. aprica* seedlings. The mechanisms for this response are unknown but may be related to release from competition with weeds for resources such as nutrients and light (D'Antonio et al., 1998) and water (Eliason and Allen, 1997) and removal of allelopathic influences (Hobbs and Atkins, 1991). The exclusion of vertebrate grazing resulted in greater emergence of *A. cochlocarpa* ssp. *cochlocarpa* seedlings but all seedlings subsequently died from drought. The

exclusion of vertebrate grazing had no impact on survival of transplanted *A. aprica* or *A. cochlocarpa* ssp. *cochlocarpa* seedlings but did result in increased growth. In *A. aprica* this was more evident in population 5 than in population 3. These results suggest that in these extant populations grazing is not a major influence on seedling establishment but may affect growth in the first year. Experimental translocations currently being undertaken by the Western Australian Department of Conservation and Land Management to establish new populations of both species have, however, observed that grazing is having a significant impact on seedling survival and growth (Leonie Monks, personal communication). The impact of grazing on population growth may therefore be site specific.

In conclusion, the remaining populations of *A. aprica* and *A. cochlocarpa* ssp. *cochlocarpa* are all small ranging in size from several to 117 plants and appear to be declining with little regeneration occurring. All populations were capable of producing viable seeds but seed production varied considerably between years and between populations, however, no thresholds in seed production associated with population size were identified. The presence of a persistent soil seed reserve in both taxa may maintain population viability during years when seed production is low. The availability of viable seeds does not appear to be responsible for the absence of recruitment. Rather, factors associated with seed germination and seedling establishment (the regeneration niche) appear to be a more likely explanation of population decline. Both taxa are hard seeded and rely on fire-related germination cues to break dormancy. Since habitat fragmentation fires may no longer develop

in the landscape and opportunities for recruitment may therefore be less. Moreover, following seedling emergence annual weeds in particular and to a lesser extent vertebrate grazers result in high seedling mortality and reduced growth rates. Maintenance of stable populations of both species will therefore require in-situ management of the regeneration niche. This study has demonstrated that seedling establishment in the two taxa can be initiated through the careful use of fire to stimulate germination or by planting seedlings both in association with weed control. We suggest that the results of our study are relevant to other rare *Acacia* species and hard seeded legumes that also rely on fire for recruitment and which are restricted to isolated populations on road verges in southwest Western Australia.

Acknowledgements

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