

Reproductive potential of *Acacia* species in the central wheatbelt: variation between years

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SUMMARY

In a study at Sandford Rocks Nature Reserve aimed at discovering how rainfall variation between years affects reproductive potential in *Acacia* species, the effect of phyllode number and branch position in the crown and seed quality were investigated. High rainfall in 1999 allowed heavier fruiting. More inflorescences set pods and more pods were produced. In 2000, pod yields were reduced by drought. The extent of flowering depends on good winter rainfall and fruit production depends on moisture availability in spring. Although all species suffered from drought in 2000, there were differences in their degree of susceptibility: *A. fauntleroyi*, *A. neurophylla*, *A. acuminata* and *A. steedmanii* were the least affected whereas *A. stereophylla* failed to develop pods; *A. hemiteles* did not flower, and less than 1% of inflorescences developed a pod in both *A. saligna* and *A. lasiocalyx*.

Late spring frost in 1998 limited seed development. All species produced few seed; many pods were empty; many immature and infected seed were found; and there was poor germination. Of 13 species, only three had more than 40% germination. In six species there was no germination, while all others had less than 30% germination.

Plants bearing more phyllodes had more flowers and fruits, and fewer inflorescences dried off. Generally, branches in the upper part of the crown initiated more inflorescences. In some species there were more pods in central parts of the crown. The difference in the form or architecture of branches among species presumably affected resource partitioning and consequently reproductive potential.

INTRODUCTION

The genus *Acacia*, with some 1165 taxa, is represented in most habitats of Australia (Maslin 2001). It dominates the woody vegetation of the arid and semi-arid regions and is well represented in more mesic environments. In Western Australia, Sandford Rocks Nature Reserve (SRNR; 31°18'S, 118°42'E), contains a complex mosaic of exposed granite rock, with surrounding shrublands and woodlands. The reserve has an area of 805.9 ha, consisting of granite outcrops, thickets and woodlands. Westonia experiences a Mediterranean climate with summer maximum temperatures ranging from 35–40°C and winter temperatures of 15–20°C (Beard 1979). The mean annual rainfall is 324 mm, most falling between May and August. Important floristic components of the vegetation are eucalypts, wattles, *Melaleuca* and grasses. Wattles are locally abundant, generally grow in mixed-species assemblages and clearly play important ecological roles. In three years of observations (1998–2000), most wattles flowered in July to September and produced seed in December. An exception was *Acacia jennerae* which flowered in March 1999 and 2000.

Reproductive potential or capacity of a plant is of practical concern in plant conservation as it often has an

impact on management and recovery strategies. An upper limit to the number of pods that can be produced by *Acacia* during a reproductive episode is set by the number of inflorescences and the number of flowers per inflorescence. Similarly, an upper limit to the number of seeds is set by the number of ovules within the flowers. Reproduction is dependent on the number of inflorescences, the number of pollinated flowers, the number of fertilised ovules, the extent of pod and seed predation, weather conditions and the ability of the maternal parent to provide resources for development.

Factors that may reduce reproduction include a short growing season, low or high temperature, low nutrient and moisture availability, herbivory, humidity, wind at the time of pollination, competition, disease and scarcity of pollinators. Reproduction may vary within a reproductive episode due to weather conditions. Late spring frost, winter cold and drought have been proposed as causing fluctuations in reproduction. These factors may reduce the possibility of flowering and seed set.

Plants are usually depicted as accumulating resources and allocating them to growth, maintenance and reproduction (Willson 1972). The resources needed for reproduction come from several sources. Inorganic nutrients and water move into fruits *via* the xylem while

carbohydrates and recycled nutrients from vegetative organs enter fruits from the phloem (Kozłowski 1971). Leaves donate carbohydrates and nutrients to fruits (Hocking and Pate 1977). Fruits can potentially attract resources from leaves a metre or more away but the tendency is for resources to flow into fruits from the nearest leaves (Mooney 1972). Consequently, in terms of assimilates provided by leaves each inflorescence and its adjacent leaves can be considered as an independent unit (Harper and White 1974).

The resources available to a given flower or fruit depend on the total resources of the individual or branches and the number of reproductive structures drawing upon those resources. Plants match reproductive output to resources available by flower and juvenile fruit abscission (Stephenson 1981). Many species commonly produce mature fruits from only a small portion of the flowers (Stephenson 1979). These species regularly abort flowers and immature fruits. *Acacia* species seem to be included in this category.

A 3-year study was conducted to investigate the potential for natural regeneration of *Acacia* species present at SRNR. In spring 1998, frost occurred while most *Acacia* species were in the reproductive phase. Understanding its effect on *Acacia* reproduction is of particular interest. The following questions were addressed: What proportion of inflorescences initiated result in formation of pods? Does any temporal variation in pod production occur from year to year? Does late spring frost affect seeds produced? Do the number of phyllodes per branch and the position of branches affect reproduction?

METHODS

The study was conducted between December 1998 and December 2000. In 1999-2000, eight *Acacia* species were examined: *A. acuminata*, *A. fauntleroyi*, *A. hemiteles*, *A. lasiocalyx*, *A. neurophylla*, *A. saligna*, *A. steedmanii* and *A. stereophylla*. For each species one to three representative plants in reproductive mode were selected for study. The plants were mature but of unknown age. Most were 2-3 m tall, size varying from 1-1.5 m for *A. hemiteles* to 3-4 m for *A. lasiocalyx*. Sets of 15-35 branches per plant were labelled. Plants were selected depending on the availability of flowering individuals in the area and time in the field. Position of branches was divided subjectively as top (distal), middle (central) or lower (basal) part of the plant crown. Parameters recorded were number of phyllodes and inflorescences per branch. After all pods had matured (or nearly so), plants were re-measured. Calculations were made of the number of inflorescences that set pods and number of pods per inflorescence.

In December 1998, pods were harvested to investigate the production capacity of 13 species (six of the eight listed above, plus a further seven: see legend to Fig. 4 for names). Number of seeds and aborted or diseased seeds per pod and dimensions of pods (weight and/or length) were recorded. Seeds were then germinated to obtain

percentage germination. Number of aborted seeds was determined by counting both empty locules and locules containing aborted seeds. Aborted seeds were seeds that started to develop but died before full maturation. Aborted seed were easily discriminated from the other categories by their size and texture. In this study an empty locule was considered as an aborted seed.

Analysis of variance was conducted to test whether reproductive characteristics differ between branch position. Tukey's family error rate was used to detect any significant difference between means for different positions. The relationships between the number of inflorescences initiated, pods set, pods matured and number of pods per inflorescence and the number of phyllodes were assessed using linear regression with number of phyllodes as predictor variables ($P < 0.05$). The relationships between the number of seeds and aborted seeds per pod; and the dimensions of pods were also analysed with regression in the same manner.

RESULTS

Comparison of reproductive characteristics in different years

All species sampled were flowering together in the period July-December. However, species differed slightly in the optimum time of flowering. They may share common pollinators and partition time to optimise pollinator availability. The flowering sequence among the eight species, based on percentage of open inflorescences and sizes of initial pods, was *A. fauntleroyi*, *A. acuminata*, *A. steedmanii*, *A. hemiteles*, *A. neurophylla*, *A. lasiocalyx*, *A. stereophylla* and *A. saligna*.

Reproductive success of each species was calculated based on the relative number of pods produced, number of pods per inflorescence and number of inflorescences initiated that produced a mature pod (b, c, d respectively in Fig. 1). This procedure gave these three characters sets of values totalling 100 and in sum the reproduction success criterion (RSC) had a maximum value of 300. Based on the percentage of inflorescences that set pods (d), the numbers of pods produced (b) and the number of pods per inflorescence (c), reproduction varied considerably among species and between years. Reproduction was better in 1999 than in 2000 (Fig. 1). More inflorescences set pods (d), more pods were produced (b) and there were more pods per inflorescence in 1999 (c).

Of the 8 species studied in 1999, the best reproduction (RSC) was attained by *A. neurophylla*, followed by *A. stereophylla* and *A. fauntleroyi* (Table 1). The poorest reproducers were *A. steedmanii*, followed by *A. lasiocalyx* and *A. saligna*. In the year 2000, the best reproduction was in *A. fauntleroyi*, followed by *A. neurophylla* and *A. acuminata*. The poorest reproduction was in *A. stereophylla*, followed by *A. lasiocalyx* and *A. saligna*, and *A. hemiteles* failed to flower.

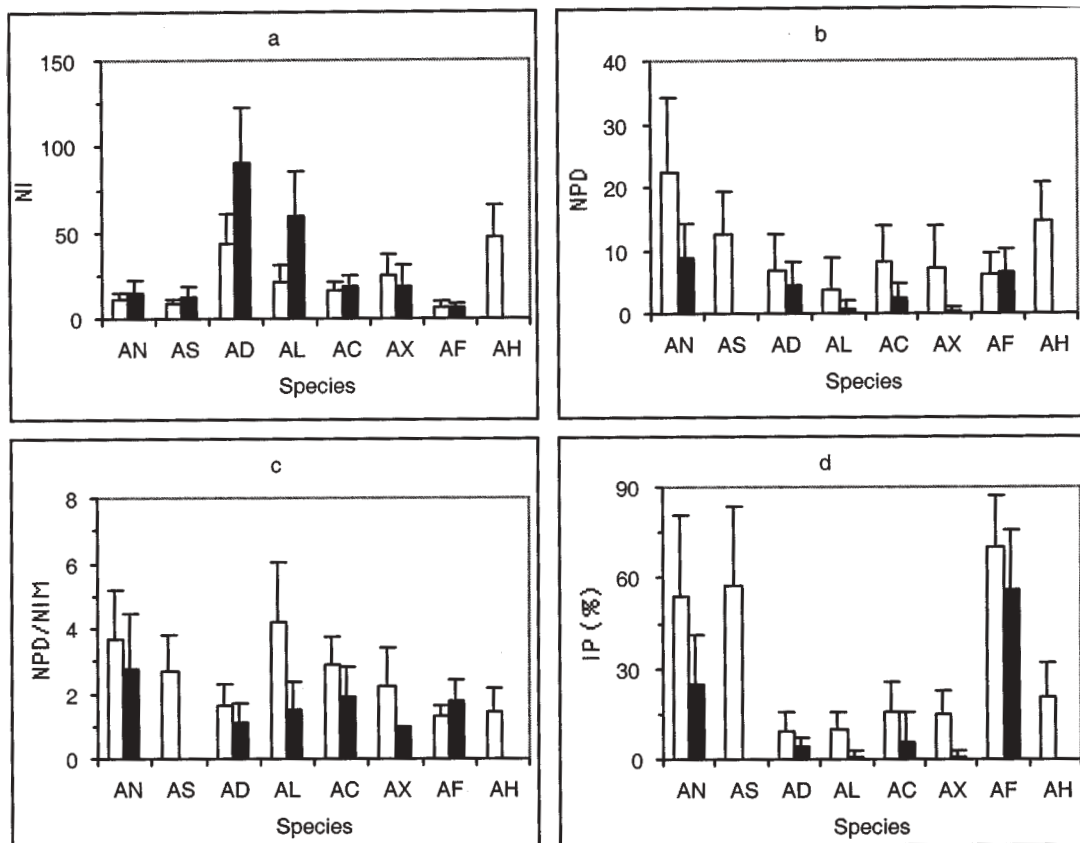


Figure 1. Comparison of *Acacia* reproductive characteristics in 1999 (white columns) and 2000 (black columns); error bars are shown. a, number of inflorescences initiated (NI); b, number of pods produced (NPD); c, number of mature pods per inflorescence (NPD/NIM); d, percentage of inflorescences that set pods (IP%). Species: AN = *A. neurophylla*; AS = *A. stereophylla*; AD = *A. steedmanii*; AL = *A. saligna*; AC = *A. acuminata*; AX = *A. lasiocalyx*; AF = *A. fauntleroyi*; AH = *A. hemiteles*.

TABLE 1
Reproduction success criterion (RSC) and its components for each of eight *Acacia* species (1999, 2000).

SPECIES	1999				2000			
	NPD	NPD/NI	IP	RSC	NPD	NPD/NI	IP	RSC
<i>A. neurophylla</i>	27.45	18.84	21.31	67.58	38.64	27.18	27.05	92.87
<i>A. stereophylla</i>	15.41	13.73	22.73	51.87	0.00	0.00	0.00	0.00
<i>A. steedmanii</i>	8.48	5.67	3.57	17.72	19.43	11.01	4.49	34.93
<i>A. saligna</i>	4.39	21.49	4.02	29.91	2.27	14.98	0.71	17.96
<i>A. acuminata</i>	9.82	14.75	6.26	30.83	10.47	19.15	6.51	36.13
<i>A. lasiocalyx</i>	8.85	11.28	5.92	26.06	0.85	9.92	0.62	11.39
<i>A. fauntleroyi</i>	7.54	6.74	27.96	42.24	28.34	17.76	60.62	106.72
<i>A. hemiteles</i>	18.07	7.50	8.22	33.79	*	*	*	*
SUM	100	100	100	300	100	100	100	300

NPD = Mean number of pods produced per branch; NI = number of inflorescences; IP = total of inflorescences that set pods; RSC = reproduction success criterion; * = no flowers in 2000.

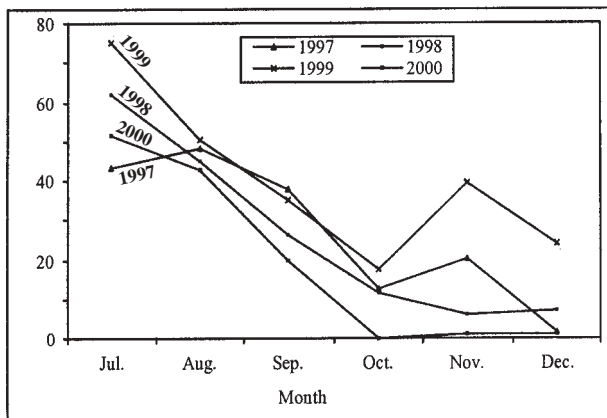


Figure 2. Monthly rainfall at Westonia during the reproduction season (July-December) 1997-2000.

Reproductive success is presumed to have been affected by lack of rain in 2000 from September onwards (Fig. 2). Between July and November 1999, approximately the period of inflorescence initiation to pod development and seed set, 335.3 mm of rainfall fell over 50 days compared with only 117.1 mm over 39 days in 2000. There was no rain in October 2000 at the time of pod development. It is of interest that the rainfall in 1999 was the heaviest recorded at Westonia (total: 597.3 mm).

Although all species suffered from drought in 2000, there were differences in the degree of susceptibility. Of the species studied, *A. fauntleroyi*, *A. neurophylla*, *A. acuminata* and *A. steedmanii* were the least affected by lack of rain in 2000. *Acacia stereophylla* was severely affected and failed to develop pods; *A. hemiteles* did not flower and less than 1% of inflorescences developed a pod in *A. saligna* and *A. lasiocalyx*.

Of all species studied in 1999, *A. neurophylla* attained the best reproduction. This species produced most pods and most pods per inflorescence. Some 39% of inflorescences initiated developed a pod; there were 15.5 pods per branch and 3.2 pods per inflorescence. Although growing in a well-drained sandy soil, the plants were not severely affected by the lack of rain in 2000. Only a small population of this species was observed. As seedlings were present, it may be assumed that there were no barriers to recruitment of new seedlings.

The second greatest number of pods produced was in *A. fauntleroyi*. A mean of 63% of those inflorescences initiated developed a pod, with 6.3 pods per branch and 1.6 pods per inflorescence. Reproduction in *A. fauntleroyi* was not severely affected by the lack of rain in 2000, presumably because the species is early flowering and plants had developed pods before severe drought had set in by October-November 2000. This species grows at the apron around the edges of granite rocks. Although it produced many pods and seeds, seedlings were rarely found in the field.

At SRNR, two varieties of *A. acuminata* occur: terete and broad phyllode types. The taxon studied was that with

terete phyllodes. Of all inflorescences initiated, 11% developed a pod with 5.2 pods per branch and 2.4 pods per inflorescence. Of the *Acacia* species at SRNR, *A. acuminata* has the largest population and the widest distribution. It is generally found in moister sites, which may explain why it was less severely affected by drought. The species has good recruitment; many seedlings were observed.

In *A. lasiocalyx*, of all inflorescences initiated, 8% developed a pod with 3.7 pods per branch and 1.6 pods per inflorescence. This species was also drought-affected in 2000 with only 0.6% of inflorescences initiated developing a pod, compared to 15% in 1999. This species grows in clefts among granite rocks and no seedlings were found. However, some saplings were found, suggesting that seedling establishment does occur regularly.

Acacia steedmanii initiated 67 inflorescences per branch (more than all other species), but from all inflorescences initiated only 6.6% developed a pod, with 5.6 pods per branch and 1.1 pods per inflorescence. This species was less severely affected by drought in 2000, perhaps because it flowers earlier. Plants developed pods during the severe drought in October-November 2000, thus it can be said that drought only slightly affected pod development. This species occurs in small numbers and, over 3 years of observations, seedlings or small plants (< 1 m) were never encountered in the field.

In *A. saligna*, of inflorescences initiated, 5.4% developed a pod with 2.1 pods per branch and 2.9 pods per inflorescence. This was lower compared to *A. saligna* at the Field Trial Area, Curtin University of Technology (MLG, pers. obs.) where 12.5% of inflorescences initiated developed a pod and there were 12 pods per inflorescence. This species also suffered from drought in 2000 as 10% of inflorescences initiated developed a pod in 1999 but only 0.7% did so in 2000. Although only a few pods were produced by *A. saligna*, the plants have quite good recruitment and many seedlings were found in the field.

For *A. hemiteles*, reproduction in 1999 saw 48 inflorescences initiated per branch and 21% developed a pod; there were 14.7 pods per branch and 1.5 pods per inflorescence. Low rainfall in May-June 2000 may have inhibited flowering, or more rainfall may be needed to induce flowering. Only 22.5 mm of rain over 9 days occurred in May and June 2000 compared with 152 mm over 22 days in May and June 1999. *A. hemiteles* has a large population and wide distribution. It occurs as an understorey species in *Eucalyptus* woodland. Despite the large population, seedlings were very rarely found.

Acacia stereophylla initiated many inflorescences each year but very few pods and seeds were produced. Only in 1999 did plants produce many pods: 12.6 pods per branch and 57% of inflorescences initiated developed. However, most pods were empty or failed to develop seeds. This species has a localised distribution, occurring in bands at the edges of *Eucalyptus* woodland. Seedlings of this species were not observed in the field.

Effect of phyllode numbers and branch positions on reproductivity

Generally, higher numbers of phyllodes were associated with more inflorescences initiated and more inflorescences that set a pod ($P < 0.05$). Numbers of pods per inflorescence were generally not related to the number of phyllodes per branch (Table 2). The result suggest that inflorescence initiation and subsequent pod development are related to the number of phyllodes as donor of resources or affected by resource availability, while number of pods per inflorescence may be determined by hereditary factors. High numbers of inflorescences affected by phyllode numbers may be a reflection of inflorescence initiation in axils (angle between phyllode and stem).

Number of phyllodes per branch was much greater in *A. fauntleroyi* compared to other species (Fig. 3). All others had about the same number of phyllodes per branch, except for *A. stereophylla* and *A. steedmanii*. Branches in the distal position generally had slightly more phyllodes than those in the basal position, whereas differences between the basal and central positions were not markedly different.

In *A. neurophylla*, the number of inflorescences initiated was greater in the distal than in the basal parts of the crowns (Table 3). However, more inflorescences set pods and produced pods in the basal position than in the distal position of the crown. In *A. stereophylla*, the number of inflorescences initiated and pods produced were greater in the central position of crowns. It would appear that more pods and more pods per inflorescence may result when fewer inflorescences initiated result in pods, allowing more resources to be available for pod development.

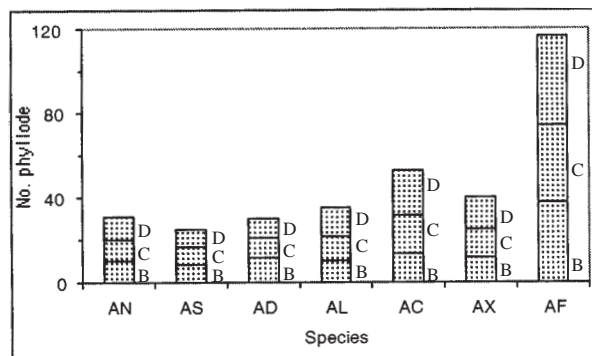


Figure 3. Mean number of phyllodes per branch of 7 *Acacia* species in basal (B), central (C) and distal (D) position of branches (combined 1999 and 2000). Species legend as in Figure 1.

TABLE 2

Significance values of linear regression between reproductive characters in 8 *Acacia* species (combined 1999 and 2000, except *A. stereophylla* and *A. hemiteles* 1999 only).

CHARACTERS/ SPECIES	AN	AS	AD	AL	AC	AX	AF	AH
NI Vs NP	<0.001	0.007	0.813	<0.001	0.008	<0.001	0.001	<0.001
NIM Vs NP	0.183	<0.001	0.042	0.070	0.754	0.245	0.089	0.092
NPD Vs NP	0.573	0.783	0.050	0.198	0.709	0.719	0.002	<0.001
NPD/NIM Vs NP	0.366	0.736	0.115	<0.001	0.238	0.204	0.011	0.310

NI = number of inflorescences initiated; NIM = number of inflorescences that set pods; NPD = number of pods produced; NPD/NIM = number of mature pods per inflorescence; NP = number of phyllodes. Species legend as in Figure 1.

In *A. steedmanii*, more inflorescences were initiated in the basal position, but pods produced did not differ among the branch positions. In *A. saligna*, more inflorescences and pods were produced in the distal position than in the basal position. In *A. acuminata*, slightly more inflorescences were initiated in the distal position than in the basal position but more inflorescences were produced and more pods set in the central position.

In *A. lasiocalyx*, the number of inflorescences initiated was greater in the distal position than in the basal position while the number of inflorescences that set a pod and the number of pods produced were greater in the central position of the plant. In *A. fauntleroyi*, the number of inflorescences initiated and pods produced were greater in the distal position than in the basal position. In general, the number of pods per inflorescence was not affected by position of branches.

Effect of frost and spring rain on reproductive characteristics

Seed and pod characteristics from pods collected in December 1998 suggest that late spring frost plus little rain in October-November 1998 (17.6 mm over 8 days) probably affected seed development. Most species produced low seed weight, many immature and infected seed, and germination was poor (Fig. 4). Many pods contained empty locules or locules that contained seeds that had started to develop but had died before maturation.

In *A. neurophylla* there was a mean of 1.4% diseased seeds and 8% immature seeds per pod. Mean seed weight was 4.33 ± 1.14 mg and 71% of these seeds germinated. *A. neurophylla* had 9.8 seeds per pod. The pods were 5 cm in length and weighed 54.4 mg. Larger numbers of seeds per pod were associated with longer, heavier pods and more immature seeds were found in these pods (Table 4), suggesting that competition for resources between seeds occurs.

Number of seeds per pod was not related to the number of seeds found to be infected. More immature seed was associated with lower pod weight, suggesting that some pods may have been unable to acquire sufficient resources.

Acacia steedmanii had 9.1 seeds per pod. The pods were 5.8 cm in length and weighed 120.7 mg. Mean seed weight was 3.64 ± 2.93 mg, which was considerably less

TABLE 3

Mean reproductive characters in basal (B), central (C) and distal (D) branch positions, for 7 *Acacia* species (combined 1999 and 2000). Entries with different letters in a column indicate a significant difference between the means using Tukey's family error rate; significance (*P*), * *P* = < 0.05, ns = not significant. PS = position (B: basal; C: central; D: distal); NI = mean number of inflorescences initiated; NPD = number of pods produced; I = inflorescences that set a pod. Species (SP) legend as in Figure 1.

SP	PS	NI	NPD	NPD /NIM	I (%)	SP	PS	NI	NPD	NPD /NIM	I (%)
AN	B	11.90b	20.25a	3.79	33.20a	AC	B	16.36	4.14b	1.12	6.7b
	C	11.91b	18.67a	3.95	18.51b		C	16.67	10.50a	1.66	20.7a
	D	14.85a	15.45b	2.69	17.82b		D	17.42	0.73c	0.83	4.6b
	<i>P</i>	*	*	ns	*		<i>P</i>	ns	*	ns	*
AS	B	9.36	14.90b	2.79b	23.41b	AX	B	12.50b	2.43	1.17	4.8b
	C	11.48	41.03a	9.32a	11.43c		C	18.90 a	4.19	1.06	8.2a
	D	10.74	13.00b	2.57b	34.55a		D	25.33a	3.35	0.83	4.2b
	<i>P</i>	ns	*	*	*		<i>P</i>	*	ns	ns	*
AD	B	94.50a	4.5	0.97	2.6	AF	B	9.94b	7.67c	2.53	18.4b
	C	70.40b	4.82	1.18	2.7		C	8.51b	10.20b	2.62	20.8b
	D	78.27b	5.56	1.46	2.7		D	14.75a	14.40a	3.08	38.3a
	<i>P</i>	*	ns	ns	ns		<i>P</i>	*	*	Ns	*
AL	B	34.04b	0.23b	0.29b	0.4b						
	C	44.13a	2.24a	1.05a	3.0a						
	D	48.05a	2.97a	2.69a	2.4a						
	<i>P</i>	*	*	*	*						

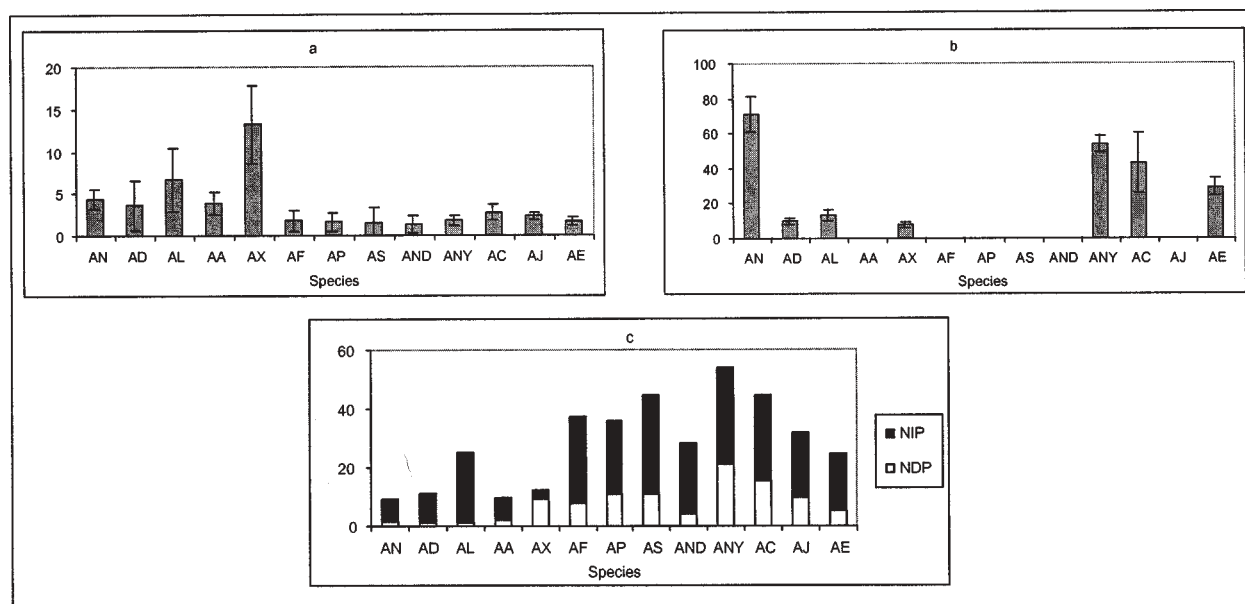


Figure 4. Seed characteristics of 13 species, from pods collected December 1998. a, mean seed weight ($n = 100$); b, germination percentage ($n = 4-8$, for replicates, 50 seeds per replicate); c, percentage of immature (NIP) and diseased seed (NDP). Species: AN = *A. neurophylla*; AD = *A. steedmanii*; AL = *A. saligna*; AA = *A. acuminata*; AX = *A. lasiocalyx*; AF = *A. fauntleroyi*; AP = *A. prainii*; AS = *A. sessilisipica*; AND = *A. densiflora*; ANY = *A. nyssophylla*; AC = *A. coolgardiensis*; AJ = *A. jibberdingensis*; AE = *A. cremophila*.

than the mean weight of seed collected in 1994 (12.01 ± 1.24 mg). Only 10% of the 1998 seeds germinated; this is much lower than the 83% germination obtained from seeds collected in 1994. There were 1.2% diseased seeds and 10% immature seeds per pod, giving 11.2% of seed aborted. Larger numbers of seeds per pod were associated with longer, heavier pods; immature seeds occurred in pods with larger numbers of seeds per pod.

Acacia saligna had 6.2 seeds per pod. The pods weighed 76.8 mg. There were some 1.2% diseased and 24.1% immature seeds per pod. Mean seed weight was 6.64 ± 3.79 mg. Some 13.3% of seeds germinated. Larger numbers of seeds per pod were associated with heavier pods. At SRNR many mature plants of *A. saligna* were infected by the rust fungus, *Uromycladium tepperianum*.

TABLE 4

Significance values of linear regression between reproductive characters in 13 *Acacia* species (from pods collected in December 1998).

CHARACTER/SPECIES	AN	AD	AL	AA	AX	AF	AP
Length of pod vs no. seed/pod	+ < 0.001 *	+ < 0.001	NA	+ < 0.001	+ < 0.001	*	
Weight of pod vs no. seed/pod	+ < 0.001	+ < 0.001	+ < 0.001	+ < 0.001	+ 0.005	+ < 0.001	+ < 0.001
No. seeds immature/pod vs no. seed/pod	+ 0.047	+ 0.047	0 0.775	+ 0.022	+ 0.040	0 0.246	+ 0.002
Weight of pod vs no. seed immature/pod	- < 0.001	0 0.718	0 0.413	0 0.238	- 0.051	0 0.069	- 0.023
Weight of pods vs no. seed diseased/pod	0 0.577	0 0.898	0 0.752	0 0.150	0 0.751	0 0.744	0 0.230
No. seed diseased vs no. seeds immature	0 0.523	0 0.558	0 0.806	0 0.810	0 0.545	0 0.077	0 0.620
CHARACTER/SPECIES	AS	AND	ANY	AC	AJ	AE	
Length of pod vs no. seed/pod	*	*	*	*	*	+ 0.019	
Weight of pod vs no. seed/pod	+ < 0.001	+ < 0.001	0 0.808	+ < 0.001	+ < 0.001	+ < 0.001	
No. seed immature/pod vs no. seed/pod	0 0.702	+ 0.001	+ < 0.001	+ < 0.001	0 0.244	0 0.452	
Weight of pod vs no. seed immature/pod	- < 0.001	- 0.003	0 0.711	0 0.302	0 0.458	0 0.303	
Weight of pods vs no. seed diseased/pod	+ < 0.001	0 0.933	0 0.575	+ 0.0525	0 0.397	+ 0.053	
No. seed diseased vs no. seeds immature	+ 0.022	0 0.369	0 0.062	0 0.608	0 0.065	0 0.959	

Species legend as in Figure 4; $P < 0.05$ positive (+) or negative (-) relation; $P > 0.05$ no (0) relation; * = not available.

Acacia acuminata had 9.2 seeds per pod and the pods were 6.4 cm in length and weighed 69.6 mg. Mean seed weight was 3.85 ± 1.34 mg. This is less than half the weight of the seeds collected in 1996 (8.95 ± 0.23 mg). No seeds germinated, whereas 42.3% of 1996 seed germinated. There were 2.3% diseased and 7.5% immature seeds per pod. Larger numbers of seeds per pod were associated with longer, heavier pods; there were more immature and infected seeds with larger numbers of seeds per pod. Therefore competition for resources between seeds occurred. Infections in one seed may be associated with infection of more seed in the same pod.

Acacia lasiocalyx had 9.85 seeds per pod. The pods were 10.7 cm in length and weighed 171 mg. Mean seed weight was 13.21 ± 8.66 mg. Larger number of seeds per pod were associated with longer, heavier pods and more immature seeds were found in these pods. However it was also found that more immature seed were associated with lower pod weight. There were 9.3% diseased and 2.9% immature seeds per pod. Of the 13 *Acacia* species studied, *A. lasiocalyx* had the third largest number of seeds per pod; the heaviest seeds and pods; and the least number of immature seeds.

Acacia fauntleroyi had 10.2 seeds per pod and the pods weighed 144.3 mg. Mean seed weight was 1.78 ± 1.29 mg, much lighter than the weight of seeds collected in both 1996 (3.38 ± 1.54 mg) and 1999 (8.30 ± 2.00

mg). Seeds collected in 1998 were significantly lighter than 1996, and the 1996 seed lighter than 1999 (all $P < 0.001$). This species had the third highest number of immature seeds (30%). Larger numbers of seeds per pod were associated with heavier pods; and more immature seeds were associated with lighter pod weight. It was also found that more immature seeds were associated with more infected seeds. No seeds collected in 1998 germinated, while seeds collected in 1999 produced up to 100% germination.

Acacia prainii had 7.7 seeds per pod and the pods weighed 53 mg. Mean seed weight was 1.66 ± 1.08 mg, much lighter than the weight of seeds collected in 1996 (3.12 ± 1.26 mg) and 1999 (8.00 ± 3.40 mg). There were some 10.6% diseased and 25.3% immature seeds per pod, resulting in 35.9% of the seeds being aborted. Larger numbers of seeds per pod were associated with heavier pods and more of these seeds were immature. More immature seeds were associated with lower pod weight. There was no germination from seeds collected in 1998 whereas, of seeds collected in 1996, 52.3% germinated and up to 100% seed germination was recorded from seed collected in 1999. At SRNR, most mature plants of *A. prainii* become infected by the rust fungus (*Uromyces tepperianum*). Symptoms include a distinct lack of foliage and many brown, globose, corky galls on stems, phyllodes, peduncles and fruits. Some

inflorescences are also deformed, witches brooms develop and juvenile foliage is produced. The latter symptom suggests hormonal dysfunction (Berg 1977).

Acacia sessilispica had 6.4 seeds per pod and the pods weighed 12 mg. Mean seed weight was 1.46 ± 1.92 mg, much less than seed collected in 1996 (3.13 ± 0.83 mg). There were some 10.7% diseased and 33.8% immature seeds per pod resulting in 44.5% of seeds being aborted. Of all *Acacia* species investigated, *A. sessilispica* had the highest percentage of immature seeds and no seeds collected in 1998 germinated. Larger numbers of seeds per pod were associated with heavier pods. More immature seeds were associated with lower pod weight. More infected seeds were associated with heavier pods and more immature seeds with more infected seeds.

Acacia densiflora had 5.7 seeds per pod and the pods weighed 21 mg. Mean seed weight was 1.30 ± 1.00 mg, much less than the weight of seeds collected in 1996 (2.84 ± 0.47 mg). There were some 4.0% diseased and 24.4% immature seeds per pod. Larger numbers of seeds per pod were associated with heavier pods and more immature seeds. More immature seeds were associated with lower pod weight. Seeds collected in 1998 did not germinate, whereas 65.3% of seeds collected in 1996 germinated.

Acacia nyssophylla had 10.6 seeds per pod and the pods weighed 50.7 mg. Mean seed weight was 1.78 ± 0.59 mg and 54% of seeds germinated. There were some 21.2% diseased and 32.6% immature seeds per pod. Of all *Acacia* species studied, *A. nyssophylla* had the greatest numbers of immature and infected seeds, with a total of 53.8% seeds aborted. Greater numbers of seeds per pod were associated with more immature seeds. More immature seeds were associated with more seeds being infected.

Acacia coolgardiensis had 8.5 seeds per pod and the pods weighed 35.3 mg. Mean seed weight was 2.76 ± 0.87 mg and 42.9% the seeds germinated. There were some 15.3% diseased and 29.1% immature seeds per pod. This species had the third highest number of immature seeds (44.4% of the seeds aborted). Greater numbers of seeds per pod were associated with heavier pods and more immature seeds. More seed infected was associated with heavier pods.

Acacia jibberdingensis had 7.5 seeds per pod and the pods weighed 19.9 mg. There were some 9.5% diseased and 22.5% immature seeds per pod. Mean seed weight was 2.29 ± 0.43 mg. There was no germination from seeds collected in 1998. Greater numbers of seeds per pod were associated with heavier pods and more immature seeds were associated with more infected seeds.

Acacia eremophila had 8.2 seeds per pod. The pods weighed 16.4 mg and they were 4.4 cm in length. Mean seed weight was 1.67 ± 0.52 mg and 29% of seeds germinated. There were some 5% diseased and 19.5% immature seeds per pod. Greater numbers of seeds per pod were associated with heavier and longer pods. More infected seeds were found to be associated with heavier pods.

DISCUSSION

Reproductive characteristics of *Acacia* species between years

A reproductive success criterion (RSC) of each *Acacia* species was calculated based on the relative numbers of pods produced, pods per inflorescence and inflorescences initiated that produced a mature pod. This procedure suggests that reproduction varies considerably among species and between years. Reproduction was better in 1999 than in 2000. It appears that good rainfall is an important requirement for flowering and is critical for good fruit set in many *Acacia*, since all species suffered from the drought of 2000 but produced good pod numbers in 1999. It seems that a wet winter is required to induce flowering (inflorescence formation) and that further rain is required after flowering to promote pod development and good seed. In the absence of the latter, a proportion of pods dry off without attaining good seed set.

Other studies, in a range of species, suggest that a general response of flowering to rainfall occurs. Morgan (1998) suggested that rainfall stress is an important overriding determinant of plant fecundity. Preece (1971) found that irrigation stimulates heavier flowering and fruiting in Mulga, *Acacia aneura*. Davies (1968) reported that rainfall stimulated flowering in arid zone species but that more rainfall was necessary for good seed. Porter (1978) found that cool, wet winters favour flower and bud formation in spring for *Eucalyptus sideroxylon*. For Myrtaceous species generally, Law *et al.* (2000) noted that high autumn rainfall is usually followed by prolific flowering in late spring. Pook, Gill & Moore (1997) found that flower buds and fruits of *Eucalyptus maculata* in southern N.S.W. were destroyed by severe drought.

In a comprehensive glasshouse study on faba bean (*Vicia faba*), Xia (1997) showed that water stress applied in the period between pod development and full pod maturation reduced seed yields by up to 45%, and water stress imposed after the flowering period reduced pod and seed number per plant up to 38%. That study showed that drought during pod-filling significantly reduces seed weight compared to the un-stressed control. According to Mwananwenge *et al.* (1999), the early podding stage of development is the most sensitive to water deficit in faba bean. Similarly Xia (1994) reduced pod set by imposing water deficits, particularly during the reproductive phase due to the abortion of flowers and small pods. The precise stage of generative development that is most sensitive to drought in *Acacia* awaits further investigation.

Although all wattle species suffered from the drought in 2000, there were differences in degree of susceptibility. *Acacia fauntleroyi*, *A. neurophylla*, *A. acuminata* and *A. steedmanii* were the least affected. Of these, *A. fauntleroyi*, *A. acuminata* and *A. steedmanii* may avoid

drought damage to some extent because they flower earlier. Only *A. neurophylla* seems to have considerable tolerance to drought. *A. stereophylla* was severely affected and failed to develop pods. The explanation for poor seed set, even in 1999, at the time of relatively heavy rain, is not known. It is possible that a combination of inadequate pollination and embryo abortion due to selfing may have affected seed quality, as the population size is relatively small. Species most affected by the severe drought of 2000 included, *A. hemiteles* which did not flower; only 0.6% and 0.7% of inflorescences developed a pod in *A. lasiocalyx* and *A. saligna* respectively. *Acacia hemiteles* may be especially drought-sensitive and it is likely that, for this species, a wet winter is necessary to produce new shoot growth. Observations in the field suggest that floral buds are produced only on new shoots.

Apart from *A. stereophylla*, there was no apparent effect of population size on seed set and pod development. In most species only small fractions of the inflorescences initiated developed to a pod. In *Acacia brachybotrya* (central N.S.W.), Cunningham (2000) found that habitat fragmentation was associated with a decline in pollination and subsequent fruit set. Low reproduction obtained in our study could be associated with the plants present being in fragmented habitats. The reserve is relatively small and surrounded by cleared farmland. Low seed production coupled with small population size may result in seed production falling below a threshold level necessary to maintain population size.

For species such as *A. steedmanii*, *A. fauntleroyi*, *A. neurophylla* and *A. lasiocalyx*, seed set appears sufficient to replace senescing adults but recruitment (seedling establishment) does not occur every year. These species had nil to very few seedlings in the field. Natural regeneration failure may be due to high seed predation, unsuitable seedbed and competition from established vegetation. From time to time some renewal probably results from natural regeneration after fires induced by lightning. In order to maintain these populations, it may be necessary to provide conditions advantageous to seedling recruitment as an important component of any conservation strategy; if not, local extinction of small populations may occur. An obvious artificial strategy is to burn small areas, in different places, from time to time.

Effect of phyllode and branch positions on reproductivity

The number of phyllodes per branch affected plant reproductivity. Plants bearing more phyllodes initiated more inflorescences; more inflorescences set pods; flowering was earlier; and fewer inflorescences dried off. These observations suggest that leaves/phyllodes donate carbohydrates (and nutrient) to fruits (Hocking and Pate 1977) and resources tend to flow into fruits from the nearest phyllodes (Mooney 1972). Preston (1999) noted that current assimilates flow from a source leaf into the

nearest most active sink that has a direct vascular connection to the source leaf (Watson and Casper 1984; Wardlaw 1990). Stephenson (1980) found that energy necessary to develop and mature fruits on Cigar Tree, *Catalpa speciosa*, comes from leaves on the same branch that bears an infructescence. Leaves are a source of carbohydrates that may be expended on flowering, whereas reproductive structures may be significant resource sinks (Stephenson, Devlin and Horton 1988). Therefore, in *Acacia* any damage to phyllodes caused by disease or herbivory could reduce primary resources and this would be reflected in reduced plant reproductivity.

Branch position also affected plant reproductivity. Generally, those branches in the upper part of the crown bear heavier inflorescences. However, the pods that develop in a particular species tend to be present in greater numbers at central parts of the crown. Generally, in *Acacia*, flower production is virtually confined to new shoots produced after the previous season. Only plants with abundant new shoots can bear many flowers. It is proposed that when lower parts of the crown initiate fewer new shoots than the upper parts, fewer flowers are initiated in the lower crown. More pods develop in the central than distal parts of the crown. Fewer inflorescences initiated in some species could result from smaller phyllodes at distal parts as they come from newer shoots. Furthermore, the difference in form or architecture of branches among the species may affect resource partitioning which in turn, reduces reproductive capacity (Lechowicz 1984).

In *Rosa × hybrida*, the stem is characterised by three distinct zones, one located at the base of the stem, one at the middle and one at the top (Erwin *et al.* 1997). Axillary shoots arising from each zone differ. The distal zone has higher axillary shoot and flower number. The axillary shoot number depends on mother shoot vigour, the presence or absence of leaves and the growth status of the remaining parts of the plant. Leaf removal decreases the flower number per mother stem. The removal of leaves also decreases the axillary shoot number. Defoliation may reduce carbon allocation to inflorescences immediately because it reduces photosynthesis.

Plant architecture may constrain flower production by limiting the number of meristems available for flowering. However, Preston (1999) noted that, although meristem number limits inflorescence number, inflorescence number does not necessarily limit flower or seed number. In compensation for limited number of inflorescences, individuals can increase the number of flowers or seeds produced by each inflorescence. Cunningham (2000) found that inflorescence production in the palm *Calyptrorhynchus ghiesbreghtiana* was correlated with trunk diameter and leaf area. A large leaf area and thick trunk may help a plant harvest light and store carbohydrates. Preston (1999) suggested that plant architecture also influences carbohydrate translocation patterns, and the location of the source leaf also significantly affects the pattern of carbohydrate translocation.

Effect of frost on reproductive characteristics

Of pods collected in 1998, all species produced apparently mature seed of low weight. There were many immature and diseased seeds and poor germination resulted. Many of the pods contained empty locules or locules that contained seeds that had started to develop but had died before full maturation. A late spring frost in 1998 is believed responsible for limited seed development. Of 13 species examined, 9 had more than 20% of seed produced aborted. Only *A. neurophylla*, *A. nyssophylla* and *A. coolgardiensis* had germination of more than 40%. *Acacia prainii*, *A. fauntleroyi*, *A. sessilispica*, *A. acuminata*, *A. jibberdingensis* and *A. densiflora* were severely affected, with no germination. All other species examined had less than 30% germination. Throughout the central wheatbelt, late spring frost in 1998 also caused much damage to crops.

All species produced many diseased seed. In some species, the number of immature seed was associated with number of infected seed. Damage to seed by frost may have provided foci for seed infection. A greater number of seeds per pod was associated with longer, heavier pods, suggesting that more resources were devoted to larger pods. As a greater number of seeds per pod was also associated with more immature seeds, there is an indication that competition occurs for resources within seeds in the pod. In some species, a greater number of diseased/infected seed per pod was associated with heavier pods, suggesting that in the case of infected seed/pods, plants devoted more resources as a response to infection stimuli.

The ecological and economic effects of frost are best known for crop plants. For native species such as *Acacia*, information is very limited. At the cellular level, frost can cause formation of ice crystals within or between cells. This can cause physical damage and trigger physiological problems through loss of solute. At the organ level, consequences of frost are primarily mediated through its effect on sensitive parts of plants. Reproductive organs of plants are usually most sensitive to frost (Sakai, Paton and Wardle 1981). Flowers and ovaries are often killed when older leaves are not affected, and frost damage can become a site for infection of buds or flower stalks. Inouye (2000) found that frost kills or damages flower buds and open flowers but causes minimal damage to leaves and stems in Aspen Sunflower, *Helianthella quinquenervis*, where late spring frosts kill some developing buds. Late frosts during spring are occasionally a principal cause of fruit mortality in Red Pine, *Pinus resinosa*. Trees located on lower ground lost all first year conelets to late spring frost, whereas trees on higher ground abscised conelets from only the lower part of their crowns (Hard 1963).

One possible effect of global climate change is that the frequency and distribution of frost events will change. Increased length of growing season in Europe is one indication of a change that may result in more frequent spring frost damage to plants (Menzel and Fabian 1999). A change in climate accompanied by an increase in the

frequency of late spring frost has been recorded previously in Virginia, U.S.A. (Inouye 2000). If global warming results in earlier flowering in temperate species, flowers might become more susceptible to frost damage.

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