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Population Structure, Flowering and Seed Production in the Endangered Whibley Wattle, *Acacia whibleyana* (Leguminosae: Mimosoideae)

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Abstract: *Acacia whibleyana* (Whibley wattle) is a nationally endangered wattle, endemic to the near-coastal region around Tumby Bay on the Eyre Peninsula in South Australia. Two distinct sub-populations, referred to as the Quarry and the Salt-lake populations, each contained plants growing on roadsides and in scrub fragments. Marked differences were observed in the population size structure between the two populations. The absence of juveniles on roadsides in both populations signaled potential limitations to natural recruitment. Studies of reproductive biology of scrub plants over two years (1996-1997) indicated that between 1.1% (Salt-lake) and 6.9% (Quarry) of *A. whibleyana* inflorescences produced fruit. Each infructescence produced an average of 1.2–1.8 pods, although up to 10 pods per infructescence were observed at the Quarry scrub in 1996. Each pod contained 4–6 seed on average, with a viability of 85%. Plants at the Salt-lake scrub generally set less fruit, produced fewer pods per infructescence, and had lower seed numbers per pod when compared with Quarry plants, differences attributable to the superior vigor of Quarry plants. *A. whibleyana* seeds were dispersed by ants attracted by the lipid-rich aril. The soil seed bank had a patchy distribution across both sites possibly due to seed concentrating in the vicinity of ant nests. We concluded that the reproductive attributes studied were unlikely to constrain natural recruitment of *A. whibleyana* as both populations were capable of producing viable seed over the two years of this study.

Keywords: Demography, rare, reproduction, seed bank, seed dispersal, South Australia, threatened plant.

INTRODUCTION

Whibley wattle, *Acacia whibleyana* R.S. Cowan & Maslin (Leguminosae: Mimosoideae: subgenus *Phyllodineae*: section *Plurinerves*) is a nationally endangered shrub with an extremely restricted distribution near Tumby Bay on south-eastern Eyre Peninsula, South Australia. Until the early 1990s, it was only known from a single population of less than 50 plants growing on road verges in a very localized agricultural area [1]. In the mid 1990s, extensive surveys around the region revealed the existence of two disjunct populations (Salt-lake and Quarry populations) about 15 km apart [2]. The majority of plants were mature individuals and there appeared to be little evidence of regeneration. The area had been extensively cleared leading to fragmentation and modification of natural ecosystems, with the only remaining suitable habitat to be found in small native remnants on road reserves or verges and on private land. A recent survey recorded 98 and 255 plants at the Salt-lake and Quarry respectively [3], 16% occurring on roadsides, 67% in scrub sites, and the remainder on farm land.

The paucity of *A. whibleyana* juveniles in these fragmented populations suggested recruitment limitations resulting from either constriction in supply of the natural seed

pool, and/or combined effects of natural field conditions (microsite, predation/grazing, competition, edaphic factors) on germination and growth. In this study we analyzed the effects of the former, namely limitations in seed supply. Seed limitations may occur at the level of seed set, maturation or dispersal [4]. The scattered nature of these small, fragmented subpopulations suggests that cross-fertilization may be restricted, potentially leading to in-breeding and population decline. Habitat fragmentation has a major negative influence on pollination and plant reproduction generally [5, 6] and for several species of *Acacia* specifically [7-10]. A few studies have also looked at the effect of fragmentation on seed dispersal, but these have mostly been restricted to tropical forest species [11 and references therein, 12]. Clearly, without ongoing recruitment of new individuals of *A. whibleyana*, these few remaining populations will be lost as mature plants die.

This paper reports on the results of investigations to evaluate and compare seed production of *A. whibleyana* at its two population centers by examining flowering, seed set, seed dispersal and the soil seed bank. The demographic structure of populations was quantified and the demographic stage structure between roadside and scrub sites at the two populations was compared. Our aim was to estimate past recruitment trends and to determine whether seed supply was a limitation to regeneration.

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MATERIALS AND METHODS

Study Species

A. whibleyana is a dense shrub, growing to 2.5 metres high and 4 metres across [13]. Phyllodes are elliptic to oblanceolate, asymmetric, and terminate in a rostriform tip. The plant is inconspicuous during most of the year, but very visible when flowering between August and September. Globular, bright golden heads (2.5–3 mm diameter) cover the plant during this time, and fruits mature between December and January.

Study Sites

Studies were performed at the two population centres for *A. whibleyana*, referred to as the Salt-lake scrub (Lat: 34°27.079'S; Long: 136°02.144'E, Altitude 10 m) and Quarry scrub (Lat: 34°19.270'S; Long: 136°02.984'E, Altitude 150 m) populations. The Salt-lake scrub consisted of a small (~ 0.8 ha) triangle of land forming part of a road intersection. The site was fenced prior to commencement of the study to prevent entry of vehicular traffic and to exclude rabbits and stock, although no evidence of herbivory was observed on translocated or wild plants at either site. Native vegetation was dominated by *Pittosporum angustifolium*, *Melaleuca acuminata*, *Enchylaena tomentosa*, *Lasiopetalum baueri* and a ground flora of samphires. Parts of the site were infested with weeds, including *Asparagus asparagoides*, *Lycium ferocissimum*, *Oxalis pes-caprae*, *Avena barbata* and *Lolium rigidum*.

The Quarry scrub, as the name suggests, was centred in and around a disused roadside quarry (~ 0.3 ha) in the hills overlooking Tumby Bay. Associated vegetation included *Eucalyptus peninsularis* – *E. pileata* – *E. dumosa* complex, together with *P. angustifolium*, *Acacia cupularis* and *A. rupicola*. Weeds near the road verge included *Avena bar-*

bata, *Bromus* spp., *Lycium ferocissimum*, *Asparagus asparagoides*, *Marrubium vulgare*, *Asphodelus fistulosus* and *Hordeum leporinum*.

A. whibleyana plants were also found on roadsides in the vicinity of these two population centers. Roadsides were 5 m wide and generally more weedy than the spatially larger Salt-lake and Quarry scrub populations. No evidence of roadside management activities that may have been disruptive to roadside populations were observed during the study period.

Phenology, Growth and Population Structure

The annual cycle of growth, flowering and seed production in *A. whibleyana* was monitored over three years (1995–1997). Eleven plants representative of the size range of plants at the Salt-lake scrub site were selected. On regular visits (three per annum) to the site, each plant was measured in three dimensions (H = height, W1 = maximum width, W2 = orthogonal width) and the presence or absence of reproductive structures (buds, flowers, fruit) was recorded. Plant size-indices were calculated for each plant as $SI = (H+W1+W2)/3$ and means were plotted against time to show the seasonal pattern of growth. Annual rainfall at Tumby Bay (average annual rainfall = 338 mm) during the study period was 426 mm (1995), 325 mm (1996) and 309 mm (1997). Annual rainfall at Hillview (average annual rainfall = 366 mm) was 478 mm (1995), 397 mm (1996) and 359 mm (1997). These were the nearest weather stations to the Salt-lake and Quarry populations respectively, and monthly rainfall at these stations for 1996–1997 is shown in Fig. (1).

The plant size distribution of *A. whibleyana* populations was quantified in May 2007 by measuring all remnant wild plants at the Salt-lake and Quarry scrub sites and associated roadsides, and calculating their size indices as above. Data were tested for normality using residual plots, then subjected to analysis of variance (ANOVA) with habitat (scrub vs. roadside) nested within population (Salt-lake vs. Quarry).

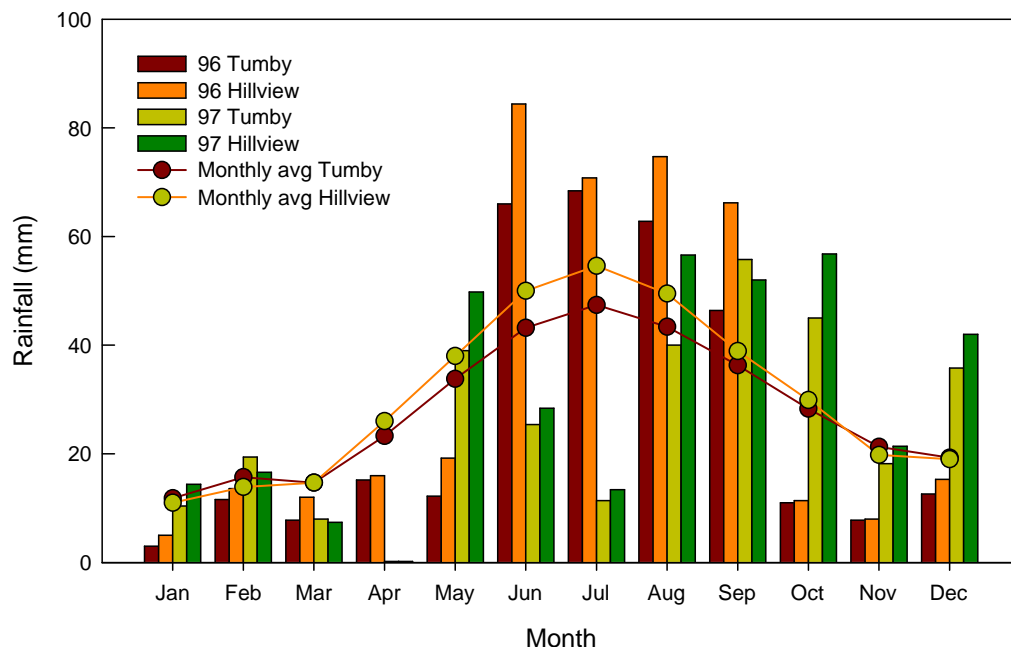


Fig. (1). Monthly rainfall for 1996–1997 and average monthly rainfall recorded at Tumby Bay and Hillview, the nearest weather stations to the study sites at Salt-lake and Quarry respectively.

Frequency histograms were plotted to compare plant size distribution between scrub and roadside plants at the two populations.

Flowering and Seed Production

Our terminology for floral structures will refer to the *inflorescence* as the single globular flower head (generally two per node for *A. whibleyana*), the *infructescence* as the structure made up of the inflorescence in fruit, and the *pod* as the legume or fruit of *Acacia*.

Experiments were set up at the Salt-lake and Quarry scrub sites to study seed production of open-pollinated flowers over two years (1996-1997). Early in flowering (before full-bloom), branchlets subtending clusters of flowers and buds were selected at random on flowering bushes (10 branchlets per plant). This was done on 17 September 1996 and again on 11 September 1997. Branchlets were tagged and labelled, and the total number of inflorescences (at all stages of maturity) distal to the tag were recorded. This was done on eight randomly selected plants at each site in 1996, and six randomly selected plants at each site in 1997. In both years, flowering was too prolific to allow accurate assessment of the number of inflorescences per plant or per unit area.

After pods had developed, but before dehiscence (14 November 1996, 18 November 1997), the numbers of infructescences, pods and seeds per pod on each branchlet were counted and the number of pods developing per infructescence was calculated. The proportion of infructescences to produce at least one pod was calculated using the formula

$$\% = (\text{number of infructescences/number of inflorescences}) \times 100.$$

Using the mean values for each plant as replicates, data were subjected to two-way ANOVA to determine the significance of site and year on flowering and seed production attributes.

Seed germinability following dormancy release by immersion of seed in boiling water for 30 seconds, was tested by incubating seeds from the Salt-lake population in petri dishes at 20°C in darkness. Dishes were irrigated with distilled water (3 replicates of 20 seeds each), and germinants were recorded and removed at frequent intervals over 12 weeks of incubation.

Seed Dispersal

This experiment monitored the removal of seeds using a baiting technique based on that outlined by Andersen and Ashton [14]. Seeds (20/rep) were placed onto the upper surface of plastic petri dish lids (90 mm diameter), either loosely or set onto a layer of lanolin smeared over the lids. The lanolin treatment was designed to prevent ant removal of seed. Lids were pressed into the soil so that the top surface was flush with the soil surface. Two sets of treatment pairs were set up, with one set being covered with inverted wire mesh cages (450 × 450 × 100 mm high) to prevent seed removal by birds, rodents or mammals. The experiment was set up along ant trails in relatively weed-free areas at both the Salt-lake and Quarry scrub sites in February 1997, and was replicated three times at each site. Seed numbers were monitored 24 and 48 hours after the experiment was set up. Three-way ANOVA was used to determine the significance

of site, caging and lanolin on the proportion of seed remaining after 48 h.

Soil Seed Bank

In order to estimate the size of the soil seed bank of *A. whibleyana*, a soil corer (Hamilton Treeplanter manufactured by Arborline, Victoria) was used to collect soil samples from around mature plants at both the Salt-lake and Quarry scrub sites. Cylindrical cores were 60 mm in diameter and 90 mm high, giving a surface area of 28.3 cm² and a volume of 255 cm³. Eight cores were collected from each of four sites at each population in February, 1997 (64 samples), after seeds produced from the previous flowering had dispersed. A further ten cores from each of five (not necessarily the same) sites at each population were collected in July, 1997 (100 samples). Soil cores were returned to the laboratory in labelled calico bags.

Air-dried soil samples were sieved using a series of laboratory sieves (1700, 1000, 500 μm aperture wire mesh) to fraction off seed in the normal size range for *A. whibleyana*. Collected seeds were soaked in initially off-boiling water overnight, then germinated in trays of potting soil to confirm their identity. Soil retained in 1000 and 500 μm sieves was similarly treated with off-boiling water until cooled, then spread over a layer of potting soil in shallow trays, covered with the soil fraction that passed through all the sieves, then covered with a thin layer of vermiculite. Trays were held outdoors under irrigation and emerging seedlings were monitored for three months.

Seed numbers per unit area were calculated from the seed data from each soil core, and results were analysed using one-way ANOVA to examine the effect of site on the soil seed bank.

Data Analysis

Statistical analyses were performed using the GenStat[®] (Fifth Edition, Release 4.2) statistical software package.

RESULTS

Phenology, Growth and Population Structure

A. whibleyana plants in the Salt-lake scrub grew gradually over the period of assessment: plants with an initial average height of 575 mm grew an average of 143 mm (25% increase) over 3 years. While growth of some plants appeared to be continuous and gradual, other plants showed definite growth flushes between late spring and early autumn. This coincided with the period between floral senescence and the appearance of next season's floral buds. Flower buds were evident on Salt-lake plants from late May and early June. Flowering commenced in early August, reaching full bloom by early to mid September. By October, flowers had largely senesced, and legumes were beginning to form. Fruits matured over December and January, dehiscing naturally when dry. Floral development of Quarry plants followed a little behind that of Salt-lake plants, with full bloom occurring in mid September. This slight delay could be a response to altitude or microclimatic differences between the two sites.

Flowers were produced at the nodes on the previous season's growth. As plants matured and became bushier, the

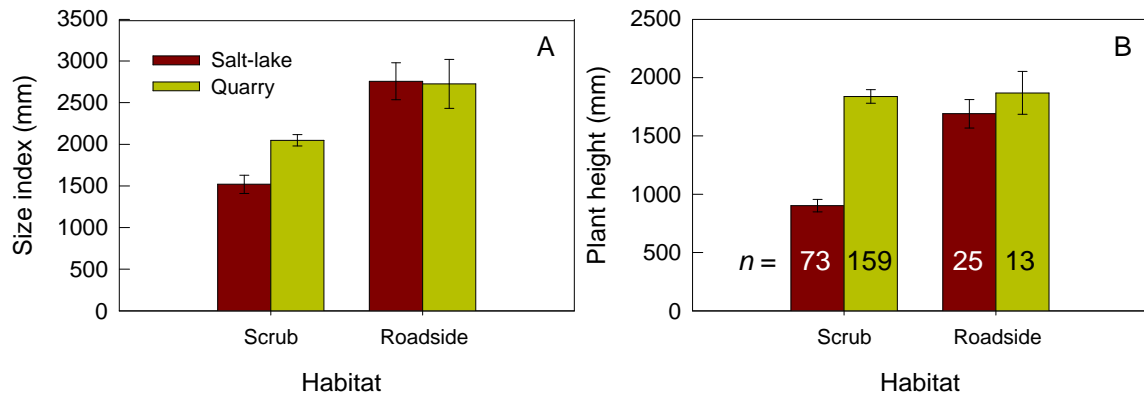


Fig. (2). Mean (\pm SE) size index (A) and height (B) of *Acacia whibleyana* plants growing in scrub or roadside habitats in the Salt-lake and Quarry populations as measured in May 2007. The numerals (n) represent the number of observations in each category (apply to both graphs).

annual growth per stem decreased, becoming restricted to the outer extremities of the canopy. As a result, flower and fruit production per stem declined with age.

The size of *A. whibleyana* plants varied significantly between the two populations ($P = 0.02$) with Quarry plants being larger on average than Salt-lake plants (Fig. 2A). The effects of habitat within population were also significant ($P < 0.001$, l.s.d._{0.05} = 521). Roadside plants did not differ in size between Quarry and Salt-lake sites, but were significantly larger than scrub plants. Plants in the Quarry scrub were larger than those from the Salt-lake scrub. They also differed in growth habit – plants at the Quarry scrub were taller and tending upright, while those at the Salt-lake scrub were half their height and more shrubby (Fig. 2B).

Frequency histograms revealed that scrub plants at both populations centres tended towards a smaller size distribution than corresponding roadside plants (Fig. 3). Roadside habitats had a higher proportion of very large plants (SI > 3000 mm) and a lower proportion of small plants (SI < 1000 mm) than scrub habitats. No plants with size indices less than 1000 mm were observed on Quarry roadsides. The majority of wattles in the Salt-lake scrub fell within the size index range 0 – 2500 mm, while most Quarry scrub plants were between 1501 and 3500 mm.

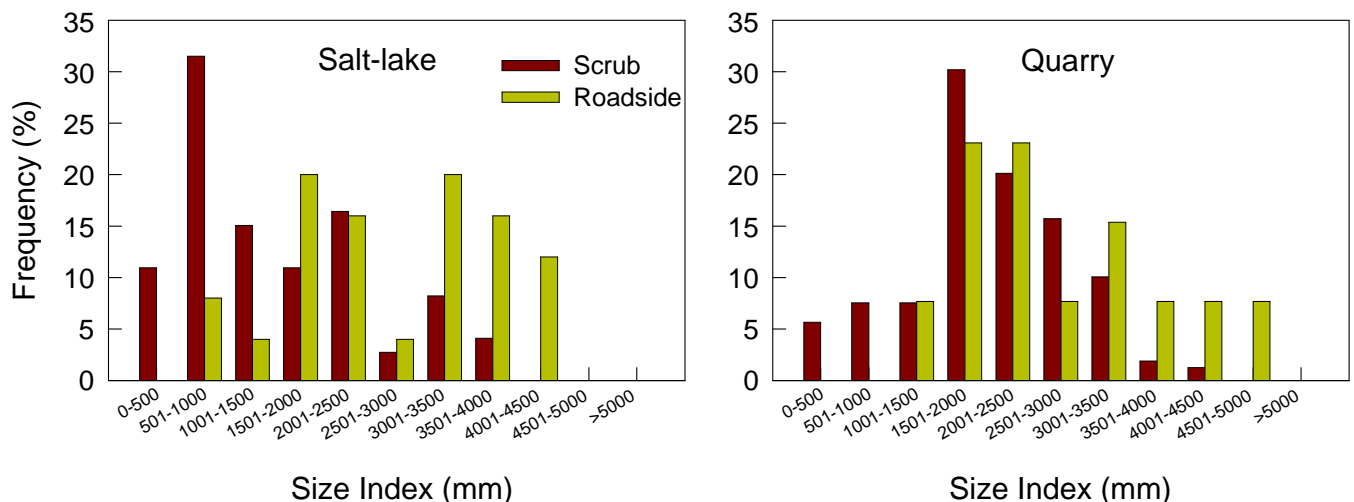


Fig. (3). Comparison of size class distribution of wild *A. whibleyana* plants growing in scrub or on roadsides at the Salt-lake (upper graph) and Quarry (lower graph) sites.

Flowering and Seed Production

Flowering and fruit production varied significantly between the two study sites. Quarry plants appeared more fecund in terms of overall flower and fruit production. Numbers of infructescences, pods and seeds produced per branchlet, pods per infructescence, seeds per pod, and the proportion of inflorescences to produce pods, were all significantly higher at the Quarry population (Table 1).

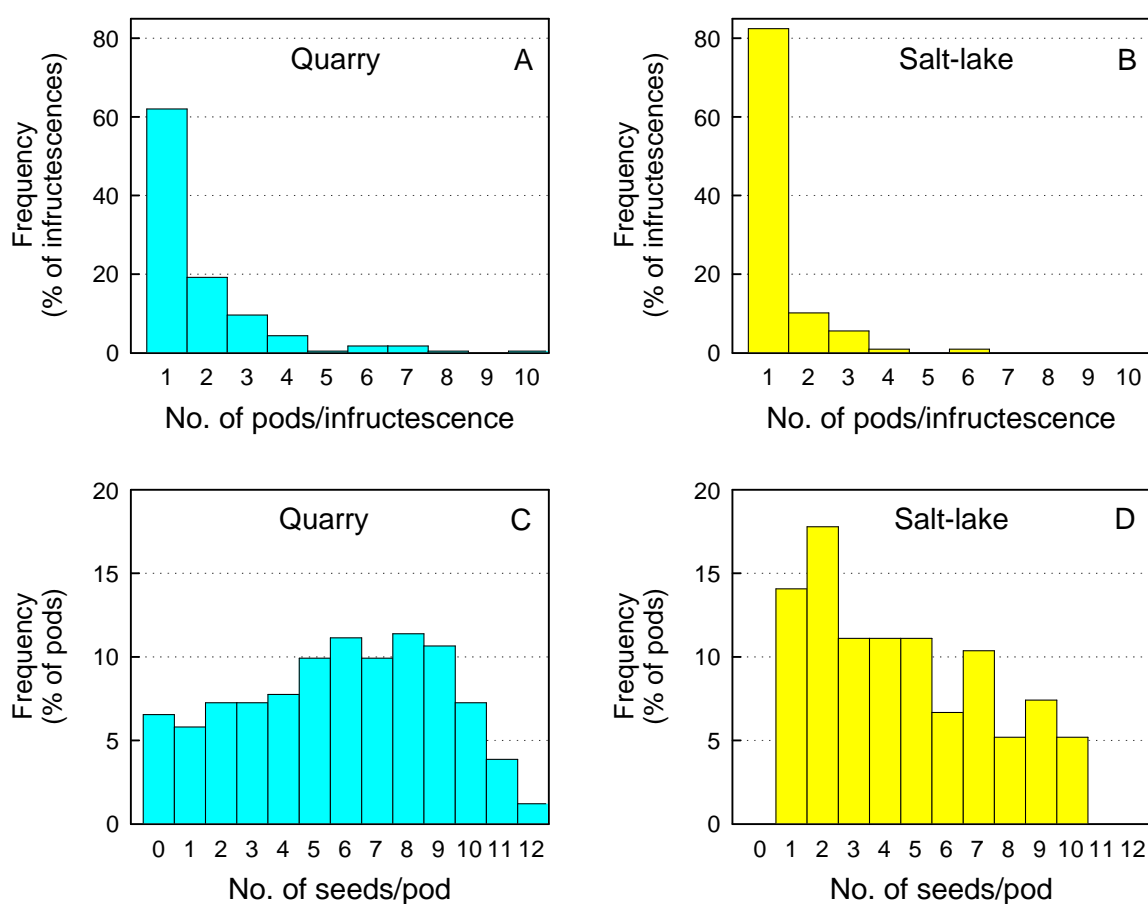
Differences across years were less significant. The number of inflorescences produced per branchlet was higher in 1997, but pod and seed production both declined when compared with the previous year (Table 1). In 1996, the majority of infructescences at each site subtended a single pod (Fig. 4A, B). However, multi-fruited infructescences (2–8 pods/infructescence) were more frequent on Quarry plants (38%) than on Salt-lake plants (18%), indicating a higher rate of successful pollination at the former site.

In the following year, most infructescences again subtended a single pod (Fig. 5A, B). The proportions of multi-fruited infructescences were lower at both sites compared with the previous year, but plants at the Quarry site again had a higher proportion of multi-fruited infructescences (17%) than did those at the Salt-lake (12%).

Table 1. Flowering and Seed Production Attributes from Two Populations of *Acacia whibleyana* Measured in 1996 and 1997. Data are Presented as Averages of Individual Plant Means

Measurement	Salt-lake		Quarry		Significance ¹		
	1996	1997	1996	1997	Population	Year	Population x Year
No. inflorescences	46.4	51.2	48.0	56.5	ns	**	ns
No. infructescences	1.3	0.6	2.9	3.4	***	ns	ns
No. pods	1.7	0.7	5.1	4.4	***	**	ns
Pods/infructescence	1.3	1.2	1.8	1.4	**	ns	ns
No. seeds	7.7	2.6	29.7	24.6	***	*	ns
Seeds/pod	4.3	3.7	5.4	5.3	***	ns	ns
% inflorescences with pods	3.2	1.1	6.8	6.9	***	*	ns

¹ns, *, **, ***, within row differences non significant, or significant at $P = 0.05$, 0.01 or 0.001 respectively.

**Fig. (4).** Frequency distributions of pod number per infructescence for fruit-bearing peduncles (top), and seed number per pod (bottom) for *A. whibleyana* plants sampled at the Quarry (left) and Salt-lake (right) sites during fruit development in 1996.

Seed production per pod differed significantly between populations, but not years (Table 1). Mean values (over both years) of 4.0 and 5.35 seeds/pod at the Salt-lake and Quarry respectively, fail to realistically portray these differences. In 1996, a majority of Quarry pods (53%) contained between 5–9 seeds/pod, while a similar majority (54%) of Salt-lake pods developed only 1–4 seeds/pod (Fig. 4C, D). Over 5% of Quarry pods contained in excess of 11 seeds, but no similar pods were found at the Salt-lake. It was interesting to note that over 6% of Quarry pods were empty, either through

fruit having developed parthenocarpically (i.e., without seed set), or through seed abortion. This phenomenon was not observed with Salt-lake pods.

In 1997, the frequency distribution of Quarry pods differed in that a high 14.7% of pods had 2 seeds/pod, and considerably less empty pods (0.8%) developed than in the previous year (Fig. 5C). Nevertheless, 53% of pods (the same proportion as in the previous year) again contained between 5–9 seeds. At the Salt-lake, again the majority of pods (67.5%) contained between 1–4 seeds each (Fig. 5D).

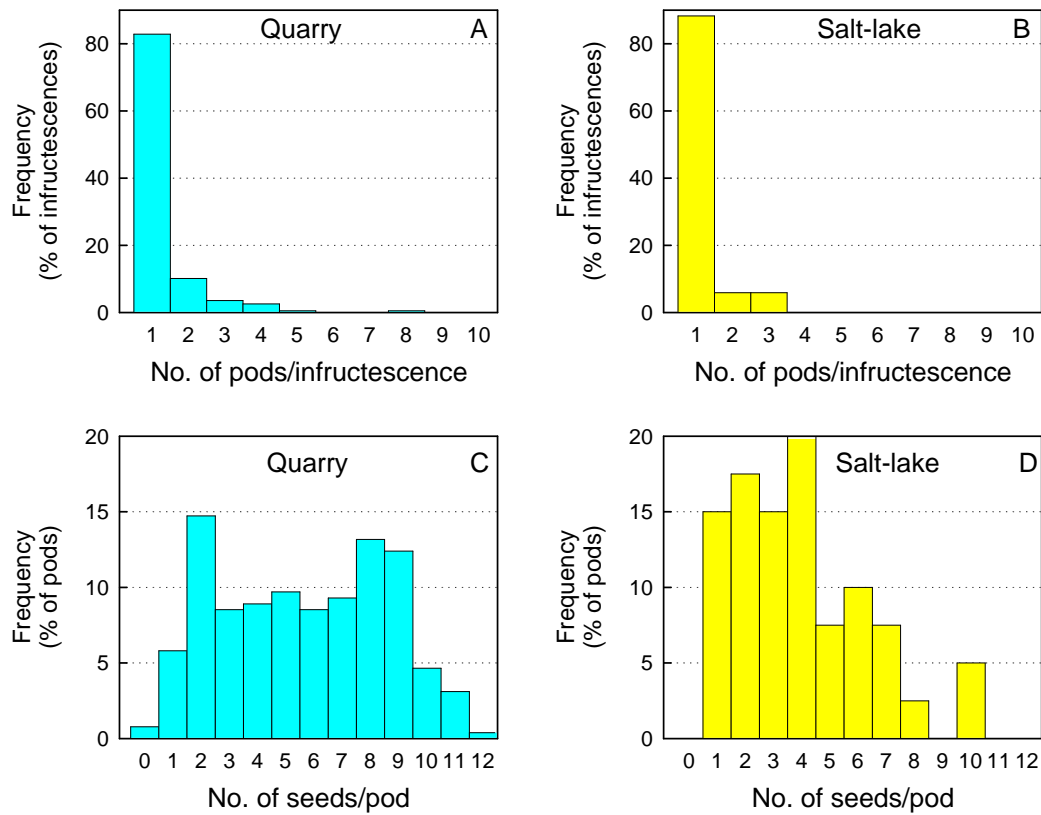


Fig. (5). Frequency distributions of pod number per infructescence for fruit-bearing peduncles (top), and seed number per pod (bottom) for *A. whibleyana* plants sampled at the Quarry (left) and Salt-lake (right) sites during fruit development in 1997.

No evidence of diseased or insect-damaged seeds was found when pods were opened. Seed germination tests resulted in an average of $85 \pm 12.6\%$ of seed germinating over 11 weeks.

Seed Dispersal

Small black ants at the Quarry scrub were observed removing loose seed almost immediately it was placed in position. In one replicate at the Salt-lake scrub, all loose seeds were removed by ants within 24 h.

ANOVA of baiting experiments revealed that significantly more seeds were removed from control petri dish lids than from those smeared with lanolin ($P < 0.001$). After 48 h of exposure, an average of 98% of seed remained on lanolin-covered lids, while 44% remained on control lids. No significant differences were observed between sites, or between covered and exposed treatments (Table 2). This suggested

that the rate of seed removal was similar at both sites, and that removal of seeds by rodents, birds or other larger vertebrates was non-significant.

The loss of a few seeds from lanolin-smearred lids under wire mesh cages suggests either the action of larger ants with the strength to remove seed from around the edges of lids, or perhaps the activity of small reptiles able to pass through the mesh, but expressing no further interest after initial sampling of the seed.

Soil Seed Bank

All viable *A. whibleyana* seed in soil cores was successfully fractioned off by sieving, as no further germinants were observed following incubation of sieved soil. Of the soil cores collected in February, only two samples from the Quarry contained seed (16 in one, 1 in the other). Of the Salt-lake cores, a single seed was found in one sample.

Table 2. Proportion of Seeds Remaining on Petri Dish Lids (Exposed or Covered by a Wire Mesh Cage) After Being Offered to Ants for 48 h. Site and Exposure Effects were Not Significant, the Lanolin Effect was Highly Significant ($P < 0.001$)

Site	Lanolin Treatment	Seeds Remaining After 48 Hours (%)	
		Exposed	Caged
Salt-lake	Lanolin	98.3	98.3
	Control	18.3	31.7
Quarry	Lanolin	98.3	96.7
	Control	65.0	61.7

At the later sampling date in July, four cores from the Quarry and five from the Salt-lake contained *A. whibleyana* seed. Average seed numbers (\pm SE) calculated for the Quarry and Salt-lake sites at this time were 42 (\pm 24) and 113 (\pm 53) seeds/m² respectively. Statistically, these figures were not significantly different due to the large variance between samples. The presence of seed in only a small proportion of soil cores at both sampling times suggested an extremely patchy distribution of seed across both sites.

DISCUSSION

Phenology, Growth and Population Structure

Studies on a range of acacias in the field have shown that flowering and fruiting are seasonal and dependent upon rain falling under particular temperature and/or photoperiodic conditions that are characteristic for each species [15]. For *A. whibleyana*, it appears that a growth flush is induced in response to the increasing temperatures and lengthening photoperiods of spring, and flowering occurs on that new growth in the following winter-spring, possibly triggered by autumnal rains. Flower production in acacias is generally confined to new shoots produced in the previous season and Southern Australian acacias typically flower between July – December, although species differ in their optimal flowering time [16]. Overall, the three years during which floral observations were made in this study were climatically rather average, although 1996 had an exceptionally wet winter and 1997 experienced above average rainfall in spring. Unseasonable or extreme climatic conditions are likely to seriously disturb the pattern of flowering and seed set [16, 17].

Assessment of the size distribution of *A. whibleyana* revealed significant differences between populations and habitats. Roadside plants were skewed towards larger demographic size classes than scrub plants, suggesting they may be older. However, size is not always an accurate determinant of plant age [18, 19]. Indeed, the larger size of Quarry scrub wattles compared to those in the Salt-lake scrub may well be attributable to the fact that many plants in the Quarry scrub were growing under eucalypt canopies, resulting in etiolated morphologies. Furthermore, natural size variation, competition in high density stands, microhabitats (soil, fertility, light factors), grazing and pathogen activity all contribute to influence plant size independently of age, making predictions of age from size in this species imprecise [20]. An alternative method of estimating plant age using basal stem diameter was impractical for this species due to impenetrable hemispherical canopies and multiple stems on most plants.

Nevertheless, the absence of wattles in the 0 – 500 mm size index range on roadsides in both populations suggested a lack of recent recruitment in this habitat. The trend was particularly evident on Quarry roadsides where no plants fell in the size index range 0 – 1000 mm. However, small wattles within this size range were found in the scrub habitat in both populations. This difference in demographic structure is potentially due to the isolation of roadside fragments, many confined to a mere handful of plants, and the higher weed densities found on roadsides compared to scrub habitats. As a non-sprouting species, *A. whibleyana* relies on fire-stimulated germination to persist, and weeds were shown to significantly reduce its regenerative capacity from seed [3]. Habitat fragmentation and decline in population size can also

lead to negative effects on individual fitness, the so-called Allee effect [21-23].

Flowering and Seed Production

Data on fruit set of open pollinated flowers revealed that the average proportion of inflorescences producing fruit varied from 1.1 to 6.9%, with plants at the Quarry site tending towards the upper end of this spectrum (6.8–6.9%), and plants at the Salt-lake tending towards the lower end (1.1–3.2%). These results did not fluctuate widely between the two years of observation. Comparable figures of 5.5% for *A. tortilis* [24] and 9% for *A. nilotica* [25] have been reported. Fruit/flower ratios [24] and reproductive effort generally [17, 26] are reportedly low in most mimosoid legumes, possibly due to pollen limitations or environmental effects on ovule availability or seed set [17].

The average number of pods per infructescence (1.2–1.8) was of the same order of magnitude as comparable figures determined by Tybirk [24, 25] for *A. tortilis* (1.36) and *A. nilotica* (1.3). Seed yield per pod for *A. whibleyana* varied from zero to 12, averaging between 4–6 seeds/pod. Kenrick and Knox [26] recorded maximum seed numbers per pod of 12 and 13 respectively (averages 7.3 and 6.9 respectively) for *A. rigens* and *A. melanoxydon*, both also members of section *Plurinerves* to which *A. whibleyana* belongs. Variability in seed yield of pods may be attributed to genetic differences between individuals and populations, and possibly also to variability in pollen viability [24]. Viability of *A. whibleyana* seed was high, with 85% of seed germinating after scarification.

Seed yield per pod in multi-fruited infructescences was the same as that for single-fruited infructescences (data not shown), indicating that pod seed-number is not regulated by post-fertilisation seed abortion resulting from resource limitations in the infructescence. Tybirk [24] postulated that abortion of young pods seemed a more probable solution regulating limitations in resource availability for infructescences, branches or whole plants. Indeed, Morrison [see 26] reported high levels of fruit abortion in *A. suaveolens* during the first 5–8 weeks after fertilisation, the total duration of fruit development being 12 weeks.

The development of parthenocarpic fruit (pods without seed) at the Quarry site, but not at the Salt-lake site, was unusual, and apparently not an irregularity since it occurred in consecutive years. This discrepancy may be explained by the delayed development of plants at the Quarry compared with those at the Salt-lake. It is possible and likely that parthenocarpic pods are aborted at some stage during development before maturation. Fruit abortion was observed in *A. suaveolens* up to the eighth week of development [Morrison in 26]. Since pods in the present experiments were assessed 8–9 weeks after flowering (ie, pod development time was ostensibly less than eight weeks), and assuming later development at the Quarry site, it is possible that at the time of assessment, parthenocarpic pod abortion may have already occurred at the Salt-lake site, but not yet at the Quarry. Kenrick [17] observed that in most species of *Acacia*, pods containing low numbers of seed rarely reached maturity. Low pollen viability or unknown inhibitory factors during pollen tube growth and fertilisation have been suggested as possible explanations of seed failure or abortion [24]. Immature pods

without developed seed were also observed in *A. polyacantha*, *A. senegal*, and *A. ataxacantha*, but no explanation was given for this phenomenon [24]. Gaol and Fox [16] found that 9 out of 13 species of *Acacia* they examined had more than 20% of seed aborted and they attributed this to a late spring frost. New [27] found between 6 – 17% seed abortion in four bipinnate *Acacia* species, attributed to unknown causes. Some Australian acacias were subject to predispersal seed predation by weevils, but the proportion of seed attacked was rather low and attacked pods usually contained only one infested seed [27, 28]. Although the possibility of abortion due to oviposition into immature seeds could not be excluded, no obvious evidence of insect damage to pods or seeds was observed.

Inter-population variation was very significant for fruit set, pods per infructescence, and pod seed numbers in *A. whibleyana*. Generally, plants at the Quarry scrub produced a higher fruit set (proportion of infructescences/inflorences), more multi-fruited infructescences, and higher seed yields per pod than plants at the Salt-lake. Reasons for this are unclear, but may relate to the differences in plant habit and vigour between the populations – Quarry plants put on more annual growth and consequently flowered more profusely the following year (flowers are borne on the previous season's growth) than Salt-lake plants. Less plant competition, the higher altitude and rainfall at the Quarry site, and edaphic differences between the sites may also have been contributory factors. Spatial and temporal variability in environmental conditions between population sites can markedly affect population dynamics [29, and references therein]. It is possible that above average winter rainfall in 1996 contributed to the higher yield of pods and seeds observed in both populations of *A. whibleyana* that year. Yates and Broadhurst [30] found inter-population and annual variations in flowering intensity and success for two endangered Western Australian *Acacia* species, and generalised that for both rare and common acacias, seed production is likely to be limited by rainfall and resource availability.

Bearing in mind that the dense profusion of flowering on each bush made assessment of total yield per plant impractical, the results of these studies suggest that neither flowering nor seed set are likely to limit recruitment of *A. whibleyana* at either population site. A similar conclusion was reached in studies of other rare *Acacia* species (e.g., *A. aprica*, *A. cochlocarpa*, *A. sciophanes*) for which factors associated with seed germination and seedling establishment provided a more likely explanation of population decline [30-32].

Seed Dispersal

Acacia whibleyana has a relatively small (2.5–3 mm long), arillate diaspore, which is shed following ripening. The aril is pale and off-white in colour. The seed-baiting experiment indicated that *A. whibleyana* is a myrmecochorous species – the majority of seeds were removed by ants within 48 h. The seed-removal trends over 24–48 h indicated that removal would continue until eventually all seeds were gone. Hughes and Westoby [33] showed that for *A. myrtifolia*, seed-removal over the first 12 h was representative of removal over longer time periods, as the removal rate remained fairly constant over 72 h of exposure. The fact that seed removal at the Salt-lake scrub occurred more rap-

idly than at the Quarry scrub suggested higher levels of ant activity at the former site compared with the latter.

There is some evidence that ant removal of seed is reduced as weediness increases due to changes to ground conditions (eg., litter development) and that ant diversity also declines under such conditions [34]. Thus seed dispersal at weedy roadside sites may well be less effective than that observed in this experiment, which was performed in relatively weed-free surroundings.

Soil Seed Bank

The soil seed density of *A. whibleyana* was at least an order of magnitude less than that of the weedy *A. saligna* growing in coastal New South Wales [35]. Several reasons may account for the relatively low numbers and patchy distribution of seed recovered in this experiment. Firstly, it is possible that the seed bank size was underestimated due to seed dispersal beyond the sampling domain. Ant dispersal of seed would suggest that the soil seed bank is concentrated in and around ant nests [36-38]. Dispersal distances of up to 180 m have been reported for ant-dispersed *Acacia* seed [39] and myrmecochorous species have been found buried at depths of up to 20 cm [40]. Our sampling procedure did not take this into account, since cores were sampled to a depth of only 9 cm from the immediate vicinity of *A. whibleyana* plants. Indeed, if the assumption is made that seed is removed by ants soon after dehiscence (most removal occurs within 10 days according to Andersen and Ashton [14]), then relatively low seed numbers would be expected from a February sampling. After arils are removed in ant nests, and seed returned to the surface for discarding, seed numbers in samples may be expected to increase (eg, by July). This was supported by the data. All *A. whibleyana* seeds extracted from soil cores were devoid of arils.

Secondly, some seed may remain in ant nests after aril removal because ants are unable to grip the smooth, round surface with their mandibles [41]. This hypothesis was not specifically tested for *A. whibleyana*, but the presence of a hard, smooth seed coat suggests that this option should not be excluded. The location of seeds within nests is usually advantageous in that such sites afford protection from the effects of fires and seed predators, and provide ideal nutrient-rich environments for germination to occur [38, 42, 43]. Burial of seed in the soil generally confers long-term persistence [44]. The ability to germinate and emerge from deep burial is dependent on seed size – at least one *Acacia* has shown the capacity to emerge from a depth of 15 cm [45].

Thirdly, seed predation can contribute to seed losses from the soil seed bank [46]. It is unlikely that harvester ants eat *A. whibleyana* seed because of the hard seed coat. However, wasps, weevils, birds and other vertebrates have been reported as predators of legume seeds [38, 47, 48]. Myrmecochory, as a trait favouring rapid seed removal immediately after maturation, has been implicated as an important factor in avoidance of seed predation [49, 50].

Seed losses in soil seed banks have also been attributed to rapid deterioration and loss of germinability of seed following dehiscence [51]. However, this is unlikely to apply to *A. whibleyana* seed, which retains viability for at least three years after harvest (Jusaitis, unpublished data) and further-

more, the viability of seed isolated from the soil seed bank was confirmed by germination tests.

CONCLUSIONS

Acacia whibleyana is an endangered wattle, extremely restricted in distribution, with a small, fragmented population and showing little sign of natural regeneration along roadsides. Our results suggest that reproductive attributes, including flowering, pollination, seed set and dispersal, and seed viability, are unlikely to constrain natural recruitment of *A. whibleyana*, as abundant viable seed was produced over the two years of this study. Although seed production varied somewhat from year to year and between populations, the presence of a persistent, viable soil seed store provided insurance against years of lean seed production. Rather than seed supply *per se*, factors associated with its germination and establishment were more likely determinants of regenerative capacity. An earlier study found that while 10% of sown seed (pretreated with off-boiling water) germinated and emerged in weed-free plots, only 5% emerged in weedy plots and only 0.7% remained four months after sowing [3]. The presence of annual weeds in most remnant populations of *A. whibleyana* presented a severe limitation to recruitment and establishment from seed, whether natural or translocated [3].

Although the current small, fragmented populations of *A. whibleyana* may persist for some time, they are unlikely to be sustainable in the long term without appropriate management intervention. Many acacias require both frequent and infrequent disturbance events of high intensity to re-establish their populations [52, 53]. Pollinator limitation is already a clear threat to several endangered acacias that are restricted to roadsides in Australia [7, 54]. Shrinking genetic variability in these small isolated populations may also contribute to longer term population decline [31]. Immediate management options include the use of translocations designed to rejuvenate, stabilize and interconnect roadside populations. However, the key to this species long-term persistence lies in facilitating its regenerative capacity by controlling annual weeds and providing periodic recruitment triggers to encourage establishment of new juveniles.

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