THE POPULATION BIOLOGY OF THE GAZETTED RARE SPECIES, *BANKSIA CUNEATA*, ON A ROADSIDE NEAR QUAIRADING

by

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NOTE: a management plan (in association with David Coates) and report on extinction risks (in association with Mark Burgman) based on much of the information given here are at present in preparation.

Abstract

Banksia cuneata is a large floriferous shrub or tree confined to seven small populations in the wheatbelt of Western Australia. The stand at the study site consisted of groups of even-aged, fire-sensitive plants, suggesting recruitment is usually dependent on recurrent fire. Following a four year juvenile period, annual fruit set increased exponentially, yielding 11,700 two-seeded follicles per plant over the subsequent 19 years. Two major constraints restricted the number of seeds available for the next generation: low fruit set relative to flower production (1.5%), and decay of canopy-held follicles and seeds after ten years. Herbivory of reproductive parts was absent, with minor abortion, senescence and pre-fire release of seeds. Most of the 17,100 viable canopy-stored seeds in the 23 year old cohort were released within 24 hours of a hot autumn fire, whereas wet-dry cycles were required following milder fires. Less than 5% of seeds germinated and only 0.1% of these survived the first summer drought. Seedlings transplanted to moister sites and/or watered regularly over summer were much larger and more likely to survive to the next winter than the controls. It is concluded that population numbers are not limited by the size and dynamics of the canopy seed bank but by the weather pattern following fire-induced seed release.

Introduction

The effective management of species targeted for conservation rests upon knowledge of those processes affecting population dynamics and geographic distribution (WHITSON and MASSEY 1981; MAIN 1982; LEIGH et al. 1984). This paper presents results of a population biology study of *Banksia cuneata* A.S. George, a rare and endangered species in the wheatbelt of south-western Australia (TAYLOR and HOPPER 1988).

B. cuneata is a shrub or tree to 5 m tall and 7 m wide which produces numerous flower heads at the tips of the current year's branches. Only 340 adult plants are known in seven populations located in the Quairading/Brookton Shires, about 180 km east of Perth, Western Australia. The study sought to determine if the size and structure of a roadside population were limited by the reproductive biology of this species as reflected in the dynamics of the canopy seed bank with increasing plant age. The role of fire and moisture/drought in seed release and seedling establishment were of particular interest, as these have been shown to be crucial to the recruitment of more widespread *Banksia* species in fire-prone mediterranean regions (COWLING and LAMONT 1987; LAMONT and BARKER 1988; ENRIGHT and LAMONT 1989). It was hypothesised that rarity in this species was due to poor seed production, frequent fire, and/or poor seedling recruitment in response to summer drought.

Materials and Methods

STUDY SITE

The study area was located 180 km east of Perth, Western Australia, 32°01'S, 117°25'E (CONNELL et al. 1988). The population investigated occurred on a road verge and covered 1.74 ha (two adjacent strips 650 m long and 12-15 m wide). *B. cuneata* dominated the 4-5 m stratum with occasional plants of *B. prionotes* and *Xylomelum angustifolium*. Nomenclature follows GREEN (1981). A 1-2 m shrub stratum contained mainly *Eremaea pauciflora, Leptospermum erubescens* and *Casuarina campestris*. The herb layer contained perennial graminoids and annual weeds. Beyond the road verge lay extensive areas cleared for dryland farming. The soil was deep yellow sand (Quailing depositional surface) derived from laterite (MULCAHY and HINGSTON 1961). The climate in the region is a dry, warm mediterranean type (BEARD 1980). Average annual rainfall at Quairading, 10 km west, is 347 ± 87(sd) mm with effective rainfall occurring from May to September (Australian Bureau of Meteorology records). Mean maximum and minimum monthly temperatures are 34.1 C and 6.1 C respectively. The rainfall for 1987 was 296 mm and that for 1988 was 399 mm.

AGE STRUCTURE AND CANOPY SEED STORE

All plants in the population were examined in February 1987 and June 1989. Their dimensions were assessed and ages determined from their stem branching pattern (LAMONT 1985). If they were dead, the likely cause was noted, as was the presence of dead major branches. Five representative 23 year old trees were harvested in April 1987 and transported to Curtin University to quantify the canopy-stored seed bank by assessing the cones, follicles and seeds. The numbers of cones (rachises bearing woody follicles) of successive crop ages were obtained from four major branches arising near the base of each plant. Cones on remaining limbs were counted and their age structure determined by ratio.

The numbers of follicles on all cones were counted and classified as open (seeds released) or closed, fully developed or underdeveloped (seeds aborted) and intact or insect damaged.

Follicles were obtained from one to ten year-old cones from the five plants for seed viability tests. They were heated over a gas flame to facilitate seed release. Seeds were classified as firm or aborted (after LAMONT and BARKER 1988) and intact or insect damaged. One hundred firm, intact seeds from each year were placed in moistened petri dishes and germination followed for 30 days at 15 C to determine their viability (LAMONT and VAN LEEUWEN 1988). Seed condition and release from dead but unburnt branches versus living branches were estimated as follows. Representative unburnt branches were tagged on five plants killed by an experimental fire in May 1987 (see below). Eleven months after the fire, 1,000 follicles were removed from these branches, aged and the number of follicles open and viability of mature seeds in each age class determined as before. Living branches were collected at the same time and 10,000 follicles assigned in the same way. Best fit linear and non-linear regressions and coefficients of variation were determined for the whole plant year-by-year data (after LAMONT and BARKER 1988). To obtain relative fruit set, counts of the number of florets were made on five flower heads from each of ten plants in September 1987.

EXPERIMENTAL FIRES AND SEED RELEASE

That part of the stand from which the five trees had been removed in April was burnt in May 1987 by a hot fire that consumed most of the leaves of all 18 *B. cuneata* plants present. The follicles were inspected for seed release over the next 24 h. In order to follow germination and seedling fate, 25 plots, each 2 x 2 m, were placed randomly in a 150 x 14.5 m area burnt by the fire. The numbers of living and dead seedlings in these plots and unburnt area were tagged and counted at 1-2 monthly intervals over the next 10 mo. The numbers of live and dead adults and seedlings in the burnt and unburnt areas were monitored for a further 16 mo.

To study the mechanics of seed release after fire, two branches were harvested from each of three unburnt plants at the study site. A branch from each tree was sprayed lightly with kerosine and ignited. Distances between the tips of the valves and between the wing tips of the separator (which secures the seeds in place, GEORGE 1981) of 100 follicles were measured. Half were dipped in tap water for 1 min at 4 d intervals over 10 d. The controls and treated follicles were then re-measured and numbers of released seeds noted. Weather was sunny throughout (early winter) with an average minimum temperature of 6 C and maximum of 21 C.

SEEDLING FIELD TRIAL

As results for the first year indicated that water availability limited seedling establishment, a field trial to confirm this was initiated the following year. In May 1988, three week old germinants in 3 x 5 cm tubes of peat-sand were planted along two strips cleared of vegetation beside the previously burnt area. One strip contained six 1 x 1 m plots on a slight ridge (dry) and there were six in a depression which received run-off water (moist). Each plot contained 13 seedlings arranged in two concentric circles with one in the centre, providing a range of densities similar to those observed after the experimental fire. The outer plants were 50 cm apart and the inner plants 14 cm apart. Three adjacent plots in each strip were left unwatered while the other three each received 3 L tapwater once a week during late spring to the next autumn. The number surviving in each of the four treatments was noted after 12 months, the living plants harvested and their dry weights taken.

Results

In June 1989, the population at the study site consisted of 91 plants with a modal age of 25 years (52% of plants, fig. 1). Because of likely errors in ageing these plants (LAMONT 1985) those within $\pm$2-3 years of this age (65% of the population) can be considered the result of the one establishment event. These plants averaged a height of 4.0 $\pm$ 0.6(sd) m and width of 4.7 $\pm$ 1.3 m. The oldest plants were 31 years (12%) at a mean height of 4.9 $\pm$ 1.4 m and width 6.6 $\pm$ 1.8 m. These plants were confined to one section of the road verge and presumably arose from a previous event but escaped the more recent disturbance associated with the 25 year old plants. All the dead plants noted at the site before the experimental fire (13%) were in these two age classes. Death in half the plants was due to gradual splitting-off of all the major branches from near the base. Living plants $\geq$ 20 years old, especially if isolated, showed varying degrees of branch splitting. In the 25 year age class, 35% had major branches sheared off in recent years, while all 31 year old plants had broken branches. Death in the other half was due, directly or indirectly, to human interference. Younger plants were of varying ages

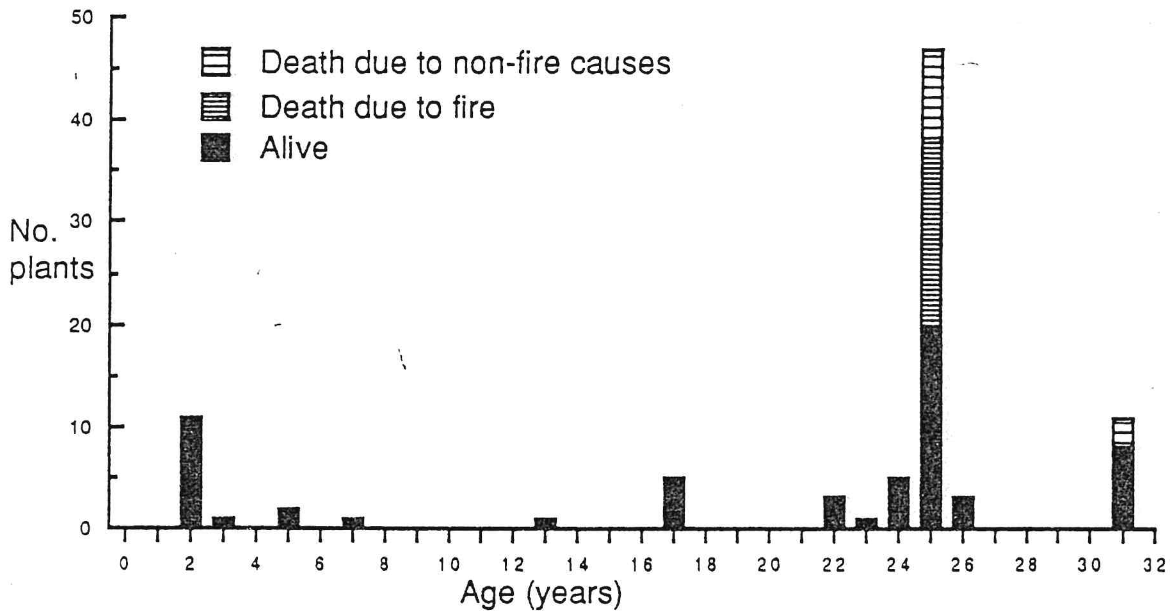

Fig. 1. Frequency of plants by age (estimated by branching pattern, Lamont 1985) in the study population two years after the experimental fire which burnt 18 adults.

and probably represented occasional establishment from seeds released from old dead plants (including the five at 17 years, with a mean height of 2.7 ± 0.6 m and width of 2.0 ± 1.0 m) as well as from living plants. As a result of the experimental fire two years before, 18 (all those burnt) of the 25 year old plants were dead and 11 post-fire seedlings had replaced them.

The age distribution of cones on 23 year old plants indicated that plants retained fruits up to 16 years, ie. produced by the plants at seven years (table 1). However, inspections of younger plants (more likely to retain their first fruits) showed they had flowered and fruited by five years. One plant appeared to first set fruit at three years. The number of flower heads produced annually increased exponentially to a mean of 3,359 in year 23 with a mean total of 11,463 over that time. Each head possessed 69 ± 7 florets (in the year of the study) with two ovules per floret. Overall, 53% of heads on the plant produced at least one follicle. There were 1.24 ± 0.42 follicles per cone in the year of the study, ie 1.79% of florets set fruit. There was an exponential decrease in number of cones with 0 to 8 follicles (table 2.). Sterile cones were more common than expected from the binomial distribution. Almost 93% of the fertile cones bore 1-3 follicles, with less bearing one, and more bearing ≥3, than expected by chance alone. There was a slight increase in fully-developed follicles and seeds with increase in number of follicles per cone. On a year-by-year basis, there were 1.04 ± 0.19 follicles per cone, yielding a total of 11,686 follicles per 23 year old plant (table 1). Assuming mean floret number per head remained stable, 1.5% of all florets produced over 18 years yielded fruits. While there was no trend in number of follicles per cone with crop age, the size of the follicle crop increased exponentially with plant age following the increase in cone numbers.

All cones and follicles showed negligible levels of insect damage. Table 3 shows 95% of the current season's follicles contained one (18%) or two (82%) mature seeds per follicle from the two ovules produced. There were more sterile and two-seeded fruits, and less one-seeded fruits, than expected from the binomial distribution. All sterile follicles were small or malformed but this was not due to insect damage. Overall, 3.6% of follicles held on the plant were sterile, with no trend between crop years.

Altogether, 3.3% of follicles were open at the time of harvest, with annual levels ranging from a mean of 1% in one year old fruits to 11-17% in years 10-12 (table 1). Years 13-18

TABLE 1

MEAN CONTRIBUTIONS OF VARIOUS REPRODUCTIVE ATTRIBUTES TO EACH AGE CLASS AND TOTAL VIABLE SEED STORE IN A 23 YEAR OLD STAND OF BANKSIA CUNEATA. THE SIGNIFICANCE OF REGRESSIONS FOR ATTRIBUTE VALUES VERSUS AGE ARE ALSO GIVEN. RESULTS ARE X ± SD FOR FIVE PLANTS. P = PROPORTION

Cone age (y)	Cones/ plant	x	Follicles/ cone	x	Zygotes/ follicle	x	Follicles closed(p)	x	Condition of seeds: Firm, intact (p)	x	Condition of seeds: Viable (p)	=	Total seed store
1	3,359±416		1.2±0.4		2		0.99±0.01		0.87		0.97		6,960±2,498
2	2,170±404		0.8±0.2		2		0.97±0.01		0.74		0.98		2,469±803
3	1,759±550		0.8±0.3		2		0.98±0.02		0.64		0.96		1,815±927
4	1,159±328		0.9±0.1		2		0.98±0.02		0.83		0.93		1,580±236
5	956±305		1.1±0.2		2		0.93±0.04		0.87		0.89		1,500±298
6	623±336		1.3±0.5		2		0.94±0.05		0.87		0.96		1,230±567
7	538±177		0.7±0.2		2		0.97±0.07		0.89		0.91		622±217
8	377±136		1.1±0.2		2		0.95±0.07		0.86		0.85		566±180
9	219±78		1.3±0.3		2		0.90±0.10		0.90		0.50		225±75
10	157±70		0.9±0.5		2		0.83±0.25		0.86		- ø		85±9#
11	77±43		1.0±0.3		2		0.89±0.16		0.88		- ø		35±2#
12	54±48		1.3±1.3		2		0.84±0.25		0.79		- ø		18±16#
13-18	15±7		0.4±0.4*		2		- *		- *		- *		0
19-23	0		-		-		-		-		-		0
Total	11,463±1,793		11,686±1,830		23,372		0.97		0.82		0.93		17,105±2,710
Regression	exp		-		-		lin		-		-		exp
r^2 (%)	97.7		-		-		73.9		-		-		92.2
P	<0.001		>0.05		-		<0.005		>0.05		>0.05		<0.001

* Follicles disintegrating
ø Insufficient seed available
\# Assumed 40, 30, 20% germination respectively (based on year 9 of 50%)

TABLE 2

DISTRIBUTION OF FOLLICLES PER CONE FOR THE CURRENT SEASON'S CROP AND ITS RELATIONSHIP WITH FOLLICLE DEVELOPMENT AND SEED VIABILITY. THE EXPECTED NUMBER IS BASED ON A BINOMIAL DISTRIBUTION WITH N = 69 (NUMBER OF FLORETS PER HEAD) AND p = 0.015 DERIVED FROM FRUIT SET IN THE SAMPLE RELATIVE TO FLORET NUMBER

Follicles per cone	Observed			Expected	Follicles fully developed (p)	Viable seeds (p)
	Number	%	%	%		
0	1,983	-	44.1	35.3	-	-
1	1,090	43.3	24.2	37.0	0.924	0.91
2	860	34.2	19.1	19.2	0.935	0.86
3	394	15.7	8.8	6.5	0.942	0.92
4	121	4.8	2.7	1.6	0.949	0.98
5+	52	2.1	2.1	0.4	0.981	1.00
	4,500	100.1	100.1	100.0		
Curve	exp				lin	lin
Test	$r^2 = 97.0$			$\chi^2 = 436.4$	$r^2 = 88.3$	$r^2 = 70.8$
P	<0.001			<0.001	<0.01	<0.05

TABLE 3

DISTRIBUTION OF MATURE SEEDS PER FOLLICLE FOR THE CURRENT SEASON'S CROP. THE EXPECTED NUMBER IS BASED ON A BINOMIAL DISTRIBUTION WITH N = 2 AND p = 0.8593 DERIVED FROM THE NUMBER OF MATURE VERSUS ABORTED SEEDS IN THE SAMPLE

Seeds per follicle	Observed			Expected
	Number	%	%	%
0	580*	-	5.4	2.0
1	1,848	18.3	17.3	24.2
2	8,263	81.7	77.3	73.8
	10,691	100.0	100.0	100.0

$\chi^2 = 953.6$, $P < 0.001$

*Follicles small or malformed

were not tabulated as sample sizes were small and many follicles were disintegrating. Degree of serotiny, calculated as the inverse of the slope (x 100) of the regression line between percentage of follicles closed and time (COWLING and LAMONT 1985a), was 76.7. Altogether, 82% of the seeds in unopened follicles reached maturity, with mean crops varying over 64-90% without any trend between years (table 1). There was little reduction in viability of mature seeds up to year 7 (overall 93% viable from the germination tests), declining to 50% by year 9 (table 1). The net result was a mean canopy-stored reserve of 17,105 viable seeds per 23 year old plant. One year old seeds contributed 41% of the reserve, decreasing exponentially to 0% by 13 years. This represents a mean of 1.49 viable seeds retained per cone produced over 18 years, and 1.46 viable seeds per fruit produced.

Table 4 shows an estimated 463,500 ovules per plant were produced in year 23. This was reduced immediately to 8,300 zygotes (assuming development of all follicles required fertilization of both ovules, since even sterile follicles always contain two well-formed seeds with papery embryos). Minor levels of seed abortion, loss of viability and dispersal would reduce the canopy store to 5,870 seeds after eight years. A sharp increase in senescence and dispersal would reduce this to almost zero by 13 years.

The May experimental fire resulted in combustion of all leaves (except some branches overhanging the fire break) and death of all *B. cuneata* plants. All follicles were scorched (except some overhanging the fire break) and the valves separated immediately. About 95% of seeds from scorched follicles were released within 3 h of the fire and the rest over the next two weeks. Most follicles on plants and branches already dead before the fire were incinerated and so released no seed. Some follicles on dead unburnt branches opened spontaneously over the next 11 months (25.2% vs 8.5% on living branches, $\chi^2 = 406.5$, $P < 0.001$), with some loss in viability of retained seeds (78.4% germination vs 95.5% on living branches, $\chi^2 = 744.3$, $P < 0.001$). Branches submitted to a mild burn resulted in rupture of all follicles but only in the treatment receiving wet-dry cycles did the separators recurve sufficiently to effect seed release (table 3).

Following the May fire, there were on average 670 seedlings per (dead) parent after four relatively wet, cool winter months (fig. 2). As monthly rainfall fell and temperatures rose from

TABLE 4

SUMMARY OF EXPECTED FATES OF GENETS (OVULES THROUGH TO OLD SEEDS) PRODUCED BY A MEAN 23 YEAR OLD PLANT OF B. CUNEATA AT THE STUDY SITE, ASSUMING THE PLANT SURVIVES A FURTHER 13 YEARS. DERIVED FROM TABLES 1-3

		Net genets stored per plant		
Sequence of Events		Total		%
1.	3,359 flower heads per plant, 69 florets per head, 2 ovules per floret	463,542	ovules	100.00
2.	1.79% of florets set fruit	8,297	zygotes	1.79
3.	13.1% of zygotes abort	7,210	seeds	1.56
4.	97.5% viable, 2.0% dispersed in years 1 and 2	6,890	seeds	1.49
5.	94.5% viable, 0.0% dispersed in years 3 and 4	6,678	seeds	1.44
6.	92.5 % viable, 5.5% dispersed in years 5 and 6	6,169	seeds	1.33
7.	88.0% viable, 0.0% dispersed in years 7 and 8	5,869	seeds	1.27
8.	<50.0% viable, 8.5% dispersed in years 9 to 12	1,211	seeds	0.26
9.	Follicles disintegrating in years 13+	→ 0	seeds	→ 0.00

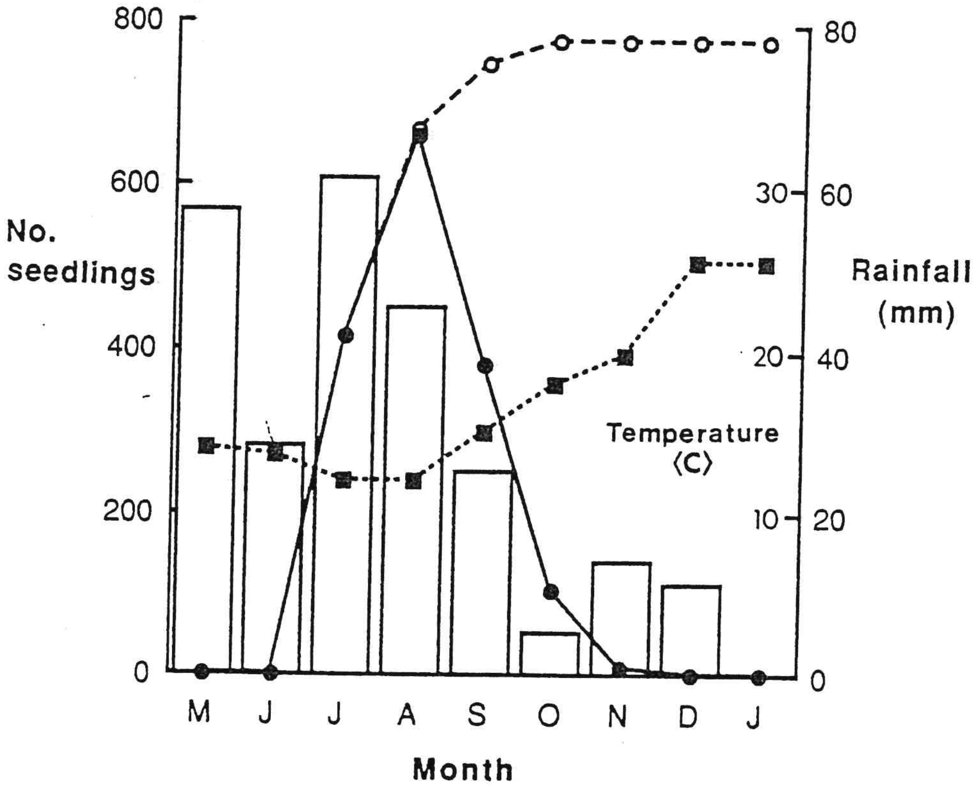

Fig. 2. Mean number of seedlings produced (o) and surviving (●) per parent plant following the May fire in relation to monthly rainfall (bars) and mean temperature (■). No seedlings were observed in the unburnt area during this time.

TABLE 5

EFFECT OF THREE WET-DRY CYCLES OVER 10 DAYS ON FOLLICLE OPENING AND SEED RELEASE. RESULTS ARE X ± SD FOR 50 FOLLICLES

		Follicle opening (mm)	Separator width*(mm)	Seeds released (%)
Control	- start/end	7.4 ± 1.3	4.2 ± 1.0	0
Treatment	- start	7.5 ± 1.5	4.3 ± 1.0	0
	- end	9.2 ± 1.1	11.1 ± 1.0	70
Test		t	t	χ^2
P		< 0.001	< 0.001	< 0.001

* Distance between wing tips of separator which levers seeds out of follicle.

August to November, seedlings increased by a further 100 but survivorship fell from 100% to 0.8%. A mean of 4.53% of the estimated canopy stored seeds that were released in response to the fire germinated. Seedlings in local depressions, particularly if shaded or among litter, were the last to die. By January, there were no survivors in the study plots and 11 over the entire area, i.e. 0.61 recruits per parent. These seedlings were located on the road shoulder bearing a 3 cm thick mulch of pisolitic laterite and survived over the next two years, when observations ceased.

The seedling field trial showed that survival and growth were much greater in the lower (moist depression) than higher (dry ridge) parts of the study site (table 6). Survival and growth were also much higher in the watered than unwatered treatments independent of position in the landscape. Survival and growth were by far the lowest in the unwatered treatment on the ridge.

Discussion

The disjunct age structure of the road verge population of *B. cuneata* is consistent with that of a species in which population regeneration is closely linked to major disturbance events. In this mediterranean climate region, the most likely cause is fire (COWLING and LAMONT 1987; LAMONT and BARKER 1988). The effects of the experimental fire and those apparently 25 and 31 years ago accounted for 89% of the population. Apart from fire and various minor anthropogenic causes in this vulnerable population (fertilizer toxicity, root damage, harvesting) gradual splitting off of major branches was a significant cause of death in older plants (> 20 years). Splitting was associated with the exponentially increasing cone weight and wind exposure. Occasional plants recruited over the last 17 years were the only departures from this pattern. These were restricted to the bare shoulder bounding the road, in the absence of which inter-fire establishment would have been negligible.

The juvenile non-reproductive period of *B. cuneata* is similar to other serotinous *Banksia* species killed by fire (GILL and MCMAHON 1986; COWLING and LAMONT 1987; VAN DER MOEZEL et al. 1987). This period represents a time when even-aged populations are susceptible to death through fire without regeneration. At the study site, the non-overlapping

TABLE 6

SURVIVAL AND SHOOT WEIGHT OF B. CUNEATA SEEDLINGS GROWN FOR 12 MONTHS AT THE STUDY SITE IN LOWER (DEPRESSION) AND HIGHER (RIDGE) PARTS OF THE LANDSCAPE AND UNWATERED OR WATERED ARTIFICIALLY AT WEEKLY INTERVALS OVER SPRING-AUTUMN. THERE WERE 13 SEEDLINGS IN 3 REPLICATES PER TREATMENT INITIALLY

		Treatment	
		Control	Watered
Survival (%)			
Site	Depression	79	97
	Ridge	41	74

For e ≡ 71, $\chi^2 = 8.24$ on 3 df, $P < 0.005$ (raw values used in test)
For independence, $\chi^2 = 0.99$ on 1 df, NS.

Shoot dry weight (g)

	Control	Watered
Depression	6.70 ± 0.78	7.26 ± 0.63
Ridge	1.75 ± 1.11	6.44 ± 0.82

2-way ANOVA : Treatment $P < 0.002$, site $P < 0.001$, interaction $P < 0.001$.

distribution of the two major age groups and an age difference similar to the length of the juvenile period indicate that they probably both arose from the same parent population that was burnt at different times. The dynamics of the seed bank of *B. cuneata* also shows many similarities to that found in reproductively-similar *Banksia* species (table 7; GILL and MCMAHON 1986; ZAMMIT and WESTOBY 1988).

The flower heads of both *B. cuneata* and its close relative *B. ilicifolia* undergo a colour change as they age (GEORGE 1981). LAMONT and COLLINS (1988) considered that colour change in *B. ilicifolia* optimised pollination efficiency by ensuring birds only visited heads with receptive stigmas. In the absence of pollinators, seed set was negligible. Seed set in *B. cuneata,* with 70% of its seed outcrossed at the study site (D. COATES, pers. comm.), must also be pollinator limited. Certainly, low percentage fruit set is the major constraint on seed reserves for the next generation (table 4). The isolation of the study population from other remnants of natural vegetation may result in irregular bird and insect visits. This could explain the higher levels of both cone sterility and cones with $\geq$3 follicles than expected by chance alone (table 2). In a similar way, varying quality of pollen received can explain the higher levels of sterile and fully fertile follicles than expected by chance alone (table 3). Inadequate nutrient supply per cone can be dismissed as limiting seed development as the proportion of viable seeds rose with increasing follicle number per cone. However, given adequate pollination, this may have been at the expense of seed set in nearby cones, but this idea was not tested.

Once reproduction begins, a large canopy-stored seed bank accumulates. This is due to both exponentially increasing production over time and the exceptionally high degree of serotiny and viability of the seed (table 7). The retention of 74% of seeds produced over the last 12 years in a viable state was greater than for any other *Banksia* species (LAMONT and BARKER 1988). The seed bank is structurally different from other congeners as it arises from many hundreds of small cones which usually bear only one or two follicles. The total exceeds cone production by other non-sprouters (table 7, GILL and MCMAHON 1986) and resprouting banksias (ZAMMIT and WESTOBY 1987; ENRIGHT and LAMONT 1989) of similar age by one to two orders of magnitude. Total follicles per cone is higher in other

TABLE 7

QUANTITATIVE REPRODUCTIVE ATTRIBUTES OF B. CUNEATA COMPARED WITH FOUR MORE WIDESPREAD BANKSIA SPP. THAT ALSO STORE SEEDS ON THE PLANT, ARE KILLED BY FIRE AND OCCUR IN SOUTH-WESTERN AUSTRALIA : B. BURDETTII (LAMONT AND BARKER 1988), B. HOOKERIANA (ENRIGHT AND LAMONT 1989), B. LEPTOPHYLLA AND B. PRIONOTES (COWLING ET AL. 1987), THE LAST OCCURRING WITH B. CUNEATA. ALL RESULTS BASED ON 15 YEAR OLD PLANTS. MEANS ARE FOR ALL YEARS NOT WEIGHTED BY CROP SIZE PER YEAR

Attribute	*B. cuneata*	Other 4 *Banksia* spp.
Juvenile period (yr)	4	3-5
No. florets/head	69	350-1,431
Barren cones (1 year old) (%)	41	0-26
Fruit set (1 year old) (% florets)	1.8	0.7-4.7
Total no. cones/plant	>522	8-70
No. follicles/cone	1	8-32
Total no. follicles/plant	>588	254-1,318
Unopened follicles (%)	94	23-80
Degree of serotiny *	77	11-53
No. damaged follicles (%)	0	16-43
No. eaten seeds (%)	0	6-31
No. aborted seeds (%)	16	22-37
No. non-viable seeds (%)	14	3-14
No. viable seeds (%)	70	31-63
Total no. viable seeds stored/plant	968	124-1,344
Contribution year 1 seeds to total viable seeds (%)	41	8-66
Rate of seed release (%) ϕ	100	12-100
CV between no. cones/year (%)	89	29-111
CV between no. follicles/cone/year (%)	18	25-71
CV between no. mature seeds/follicle/year (%)	9	6-11
Annual no. cones vs age (best regression)	exp	ns-exp
Annual no. follicles/cone vs age	ns	ns
Annual no. follicles/cone vs annual no. cones	ns	ns-lin (-ve)
Seed viability vs age	ns	ns-lin (-ve)

* After COWLING and LAMONT (1985a)

ϕ Burnt cones submitted to regular wetting over 50 days.

species by an order of magnitude, except in some resprouters (table 7; ABBOTT 1985; LAMONT and BARRETT 1988; LAMONT and VAN LEEUWEN 1988; ENRIGHT and LAMONT 1989). This arrangement reduces the impact of cone sterility or loss but increases the likelihood of barren cones (table 7). It may also allow for a more even distribution of resources (sugar, minerals, water) to the developing fruits and seeds, as indicated by the high levels of follicle (96%) and seed (82%) maturation once development begins.

The seed bank of *B. cuneata* is also exceptional because cone damage and granivory losses were negligible (table 7). In other *Banksia* species, up to 70% of flower heads may be removed by larval-seeking birds (LAMONT and BARKER 1988; LAMONT and VAN LEEUWEN 1988), up to 80% of barren cones may have been tunnelled by insect larvae (ABBOTT 1985; ZAMMIT and HOOD 1986; LAMONT and BARRETT 1988), and up to 40% of seeds destroyed by insect larvae (ABBOTT 1985; ZAMMIT and HOOD 1986; LAMONT and BARKER 1988; LAMONT and VAN LEEUWEN 1988). *B. prionotes,* which occurs with *B. cuneata* at the study site, had 80% of its seeds eaten by bupestrid larvae (also see COWLING et al. 1987). The taxonomic and morphological partner of *B. cuneata, B. ilicifolia,* has over 20% of its flower heads destroyed by insects (SCOTT 1982). In *B. cuneata,* the fact that 47% of heads do not produce any follicles and 22% of fertile cones contain less than two mature seeds may deter egg-laying granivores over evolutionary time (also see LAMONT and BARRETT 1988). Alternatively, since many flower and seed predators are species specific (SCOTT 1982), the rarity and isolation of *B. cuneata* populations, in contrast to *B. ilicifolia,* may have made the study population inaccessible in the short term or not favoured the evolution of suitable insects in the long term, assuming that this species has always been rare. Not until year 9 was there a substantial fall in number of stored seeds and this was due to senescence and follicle decay rather than granivory.

As in other *Banksia* species (LAMONT and BARKER 1988), there was a progressive decrease in the coefficient of variation (CV) from that for the number of cones per year, follicles per cone per year to that for mature seeds per follicle per year (table 7). This reflects progressively less influence by annual growth and environmental fluctuations and greater internal control between cone, follicle and seed production.

Production of seeds was continuing to escalate at the time of harvest such that the seed crop in that year contributed 38% of all non-aborted seeds produced over the previous 18 years. In *B. ornata,* another serotinous non-sprouter, there was no indication of a plateauing in seed production until years 38-50 (GILL and MCMAHON 1986). In the absence of fire, reduction in reproductive output by *B. cuneata* is more likely to be caused by the shearing off of the large branches near the base of the plant, assisted by exposure to wind and the escalating weight of the fruits. If a major branch fell from a 23 year old plant, our data indicates up to 793 viable seeds would be released from it over the next year. Since dead branches are consumed by an intense fire, retained seed would not serve as a source of propagules for the next generation, as with *B. burdettii* (LAMONT and BARKER 1988). Up to 234 viable seeds would also be released from a living plant in the absence of branch loss. This contrasts with the 16,250 seeds estimated to have been released after the experimental fire.

Autumn-winter rains play a role in operating the seed release mechanism in unburnt or mildly scorched follicles (COWLING and LAMONT 1985b). As with *B. hookeriana* (ENRIGHT and LAMONT 1989), if the fire is sufficiently hot, the valves and separator spread enough to release the seed without a wet-dry cycle requirement. Rapid and complete unloading of the canopy-stored seeds normally ensures satiation of post-dispersal granivores and herbivores, provided the fire is widespread and the populations are large - neither of which can apply to this species or study site. It also favours early germination and maximises the length of the first growing season before the onset of the hot dry summer (COWLING and LAMONT 1987; ENRIGHT and LAMONT 1989). However, it increases the chance of establishment failure due to a 'false' start to the season. For example, 57 mm of rain in April 1975 at Quairading Post Office (10 km from the study site) was followed by only 20 mm in May; 134 mm in April-May 1984 was followed by 22 mm in June. If fires occur before or during summer, early release of seeds increases the chance of granivory or desiccation and heat death (COWLING and LAMONT 1987; ENRIGHT and LAMONT 1989).

Seeds released by living or dead branches during the inter-fire period rarely yielded seedlings - no new seedlings were observed in the unburnt part of the study population over three years and only five plants were recruited during the previous 16 years (fig. 1). Substantial germination and seedling establishment only occurred after fire, as found for other *Banksia* species (reviewed in COWLING et al. 1990). However, the level of germination and survival and seedlings recruited per parent was one to two orders of magnitude less than for other non-sprouting *Banksia* species in the region (COWLING and LAMONT 1987; LAMONT and BARKER 1988; ENRIGHT and LAMONT 1989) and even less than for some resprouters (LAMONT and VAN LEEUWEN 1988; LAMONT 1988; ENRIGHT and LAMONT 1989). There was no evidence of granivores (rodents, pigeons) and negligible consumption of seedlings by herbivores (rabbits, crickets, moth larvae) - contrast COWLING and LAMONT (1987). The study site was ≥150 km further inland than for previous parallel studies with a ≥ 65% lower mean annual rainfall and expected lower reliability, eg. 221 mm in 1980, 516 mm in 1983. The low June rain following the fire (fig. 2) illustrates the increased unreliability of the 'starting' rains as well as shortness of the growing season - no effective rain after September. The high density of seedlings in 'safe' litter sites would have exacerbated competition for water (ENRIGHT and LAMONT 1989).

The central role of water availability in seedling establishment was illustrated by a parallel drop in seedling numbers as monthly rainfall fell and temperatures rose during spring (fig. 2) and the reversal of this trend by artificial watering especially when located in inherently moister parts of the landscape (table 6). Earlier studies have used different approaches to demonstrate the importance of seedling drought tolerance versus moisture stress in accounting for the potential population size and distribution of other *Banksia* species (BRADSTOCK and MYERSCOUGH 1981; COWLING and LAMONT 1987; ENRIGHT and LAMONT 1989; LAMONT et al. 1989). Whether *B. cuneata* has special germination requirements under field conditions or is more sensitive to drought stress than other species requires further study. At present, population maintenance appears to rely on periodic fires at intervals of 20-30 years followed by unusually wet winter-summers. Since *B. cuneata* is killed by fire in a fire-prone landscape yet occurs in a climate with an unreliable rainfall, its conservation in the wild would appear to depend on both fire and water management, quite apart from minimising anthropogenic disturbances to the ecosystem. A management plan, including extinction scenarios, based on this work (BURGMAN and LAMONT, unpubl.) and its population genetics (HOPPER and COATES 1990) is currently in preparation.

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