

Canopy-stored seed reserves (serotiny) in Cape Proteaceae

W.J. Bond

Saasveld Forest Research Centre, Private Bag X6531, George

Many species in several genera of Cape Proteaceae retain seeds in serotinous cones for a number of years after they have matured. This study is a report on the contribution of canopy-stored seeds to viable seed reserves. Cone retention patterns were censused for most of the common serotinous species in southern Cape fynbos and for *Protea nitida*, a non-serotinous species. Germination trials were conducted in an open nursery to determine age-related variation in seed viability. Significant numbers of viable seeds were stored for a year or more in all the serotinous species studied but the contribution of two-year and older cones was small in *Protea repens* and *Leucadendron conicum*.

These results suggest that seasonal variation in pre-burn seed reserves is not sufficient cause for recruitment failure in stands of serotinous Proteaceae burnt in winter or spring. Adaptive suites of characteristics associated with serotiny are described and contrasted with non-serotinous species of fynbos Proteaceae.

S. Afr. J. Bot. 1985, 51: 181–186

Baie spesies van verskeie genusse van die Kaapse Proteaceae behou sade in serotienstrukture (keëls) vir 'n aantal jare na volwassenheid. Hierdie studie is 'n verslag oor die bydrae van kroongestoorde sade tot lewenskragtige saadreserwes. Die patroon van keëldragingpatrone was gemonitor vir die meer algemene serotienspesies in die suidelike Kaapse fynbos en vir *Protea nitida*, 'n nie-serotienspesie. Ontkiemingstoetse was onderneem in 'n kwekery om verwantskap tussen ouderdom en die saad se lewenskragtigheid te bepaal. 'n Betekenisvolle getal lewenskragtige sade is in die keëls van al die bestudeerde serotienspesies gevind maar die bydrae van die twee jaar en ouer keëls was klein in die geval van *Protea repens* en *Leucadendron conicum*.

Die resultate dui daarop dat die seisoenale variasie in die saadreserwes voor 'n brand nie 'n betekenisvolle oorsaak vir die mislukking in die herwinning van serotien-Proteaceae gedurende die winter of lente is nie. Aanpassings of kenmerke geassosieer met serotien word bespreek en gekontrasteer teenoor nie-serotienspesies van die fynbos-Proteaceae.

S.-Afr. Tydskr. Plantk. 1985, 51: 181–186

Keywords: Fynbos, Proteaceae, seed, serotiny, southern Cape

W.J. Bond

Present address: Department of Biology, UCLA, Los Angeles, CA 90024, United States of America

Accepted 31 January 1985

Introduction

Nutrient-poor soils in mediterranean regions of Australia, California and the Mediterranean basin all share a group of woody species which survive fire from seed reserves stored in the canopy of the plant (Trabaud 1980; Vogl *et al.* 1977; Gill 1975, 1981; Naveh 1974). Seeds are stored in woody structures ('cones') for several years. This delayed release of mature seed is known as serotiny. All cones open after fire, releasing large numbers of seed simultaneously which then germinate in the following year or sometimes two (Warren & Fordham 1974; Gill 1975, 1981; Perry & Lotan 1979; Givnish 1981). Serotiny permits both accumulation of seed reserves in the canopy of the plant and fire-induced seed release at a time when predation and competition are reduced and resource levels are high.

Several Cape fynbos families have serotinous members, including Proteaceae (*Protea*, *Leucadendron*, *Aulax*), Cupressaceae (*Widdringtonia*), Ericaceae (*Erica sessiliflora*), Asteraceae (*Phaenocoma*, *Helipterum*) and Bruniaceae (*Brunia*, *Berzelia*, *Nebelia*) (Williams 1972; Van der Merwe 1966; Kruger 1977, 1983; Rourke 1980). However, there is disagreement on whether delayed seed release leads to an accumulation of seed reserves on the plant. Van Staden (1978) observed a reduction in *Protea neriifolia* seed viability from 86% in eight-month-old seed to 40% in one-year-old seed and commented that serotiny 'apparently serves no useful purpose as these seeds deteriorate and start losing viability'. The question is important to understand fire survival of serotinous Proteaceae. Jordaan (1949, 1965, 1981) suggested that a fire season could strongly depress seedling recruitment of some Proteaceae if 'dangerously' timed fires caused the release of an immature seed crop. The achenes of several *Protea* species take six months or more to mature so that the 'dangerous' period may be appreciable. This argument assumes that negligible quantities of seed are stored from one flowering season to the next, either in the soil or in the canopy.

An alternative explanation for regeneration failure (Bond 1984) is based on the observation that seeds may lie dormant for a year or more after fire until the cool, moist conditions of winter. The dormant seeds would be exposed to predators or pathogens for long periods after a spring burn but only short periods after an autumn burn. Consequently, regeneration will be poor after spring and good after autumn fires. Predictions of regeneration success would depend on the timing of germination, not of flowering and seed maturation. The hypothesis also differs from Jordaan's in that fire season would have no consistent effect on recruitment where seed

predation is negligible, or where seeds have no (or brief) dormancy, for example on the cool, moist slopes of the southern coastal ranges.

This study reports the results of a general survey of serotiny in southern Cape Proteaceae. The purpose was to determine patterns of viable seed retention in woody infructescences and whether these might be consistent with phenological explanations of regeneration failure. The results are compared with serotinous species elsewhere and a suite of adaptive traits is described and contrasted with non-serotinous species in fynbos.

Methods

Populations of six *Protea* species and six *Leucadendron* species were surveyed in the vicinity of Swartberg Pass, Swartberg (33°20'S, 22°05'E) and Montagu Pass, Outeniquas, (33°50'S, 22°20'E) in the southern Cape, Republic of South Africa. Field work was conducted in April, 1982. Site and species details are shown in Table 1. All stands had a post-fire age between 18 and 30 years old.

Cone retention

Most of the *Protea* species had either just completed their flowering season, were in the middle of it or had just started flowering. The main *Leucadendron* flowering season is spring and early summer (September–November), about six months before the census. Twenty individuals of each species were randomly selected using the wandering quarter method (Catana 1963). *Protea* infructescences are woody capitula with a thick receptacle on which fruits (achenes) are attached and protected by bracts on the perimeter. *Leucadendron* heads develop into hard, woody cones with tightly adpressed scales. Both structures will be referred to as 'cones'. The number of flower heads or buds of the current flowering season were counted on each plant, or, in large plants with numerous heads, the tallest branch of each plant. Cones from the previous flowering season were counted on the same plants or branches. The age of these cones varied from nine months to twenty months depending on species and flowering season.

Ageing of cones by node counts or weathering patterns becomes unreliable after three or four years. All cones older than about two years were thus grouped as 'old'. Only cones which still retained seed and which were still living were counted. Cones from the one-year-old and two-year or older groups were collected for germination experiments.

Seed viability

Because of the variability of seed set in Proteaceae, cones were grouped in subsamples of five for seed counts in each species and age class. Each group of five cones was heated in an open, brown paper bag at 50°C for four hours to promote seed release. Between six and twenty subsamples were available in each cone age class and species. The number of filled seeds ('plump' to the touch) in each subsample were counted and the remainder discarded. Three replicates of 50 seeds from each of the young and old classes were planted in acid, mountain river sand in an open nursery on 12 May 1982. Seeds were planted at a depth of 10–20 mm. The three replicates of old and young seed were planted in adjacent rows. The number of germinating seeds, with emergent cotyledons, were counted twice weekly. At the end of the experiment the sand was sifted and the remaining seed was crushed to determine whether endosperm was present.

Results

Cone serotiny

In six of the species, the number of two-year or older cones exceeded the number of young (\pm one-year-old) cones (Table 2). *Protea lorifolia* had the greatest proportion of old cones (81% of total cone reserves) in this sample set. Serotiny was relatively weakly developed in *Protea repens* and *P. aurea* with two-year and older cones contributing less than half of the total cone reserves. *Leucadendron conicum* retained only 26% of its cone reserves for two years or more.

In general, species from the dense vegetation of the cool, humid slopes of the Outeniqua Mountains had the weakest serotiny. Old cones contributed on average, only 42% of the total cone reserves in the four Outeniqua species, but 66%

Table 1 Species and site characteristics. Nomenclature follows Williams (1972) and Rourke (1980). Flowering seasons from the same sources and personal observations. Fire survival: S = seed (parents killed by fire), R = resprout (rootcrown sprouters or from epicormic buds). The age of 'one-year-old' cones is the time between the last flowering season and the census date. A = altitude, R = precipitation (from isohyet maps). Post-fire age was estimated by node counts

Species	Fire survival	Flowering season	'One-year' cone age (months)	Locality	A (m)	R (mm)	Age (y)
<i>Protea</i>							
<i>aurea</i> ssp. <i>aurea</i>	S	summer/autumn	12–16	Outeniquas	640	800	17
<i>eximia</i>	S	summer	17	Swartberg	1400	600	24
<i>lorifolia</i>	S	autumn/winter	11	Swartberg	1050	700	20
<i>nitida</i>	R	summer	15	Swartberg	950	550	8
<i>punctata</i>	S	autumn	12	Swartberg	1200	800	28
<i>repens</i>	S	autumn	12	Swartberg	1050	700	20
<i>Leucadendron</i>							
<i>album</i>	S	summer	17	Swartberg	1500	900	18
<i>conicum</i>	S	spring	18	Outeniquas	550	1000	18
<i>eucalyptifolium</i>	S	winter/spring	20	Outeniquas	600	1100	17
<i>rubrum</i>	S	spring	9	Swartberg	1100	750	20
<i>salignum</i>	R	winter/spring	9	Swartberg	1200	750	28
<i>uliginosum</i> ssp. <i>uliginosum</i>	S	spring	18	Outeniquas	550	1000	17

Table 2 The relative contribution of cones of different ages to total cone reserves. Only living cones, still containing seed, were counted. Buds or flowerheads of the current season (0), cones of the previous season (1) and cones two or more years old (2) were counted on 20 randomly selected plants of each species

Species	Mean number of cones (\pm S.E.M.)		
	0	1	2
<i>Protea</i>			
<i>aurea</i>	12,4 \pm 1,0	8,0 \pm 1,1	5,2 \pm 1,0
<i>eximia</i>	33,7 \pm 0,6	3,1 \pm 0,8	4,8 \pm 0,8
<i>lorifolia</i>	7,9 \pm 1,2	3,2 \pm 2,7	13,6 \pm 2,7
<i>nitida</i>	7,6 \pm 1,5	0,3 \pm 0,2	0,0
<i>punctata</i>	16,2 \pm 1,5	6,7 \pm 1,3	16,0 \pm 1,5
<i>repens</i>	18,4 \pm 3,2	11,4 \pm 2,2	8,8 \pm 1,9
<i>Leucadendron</i>			
<i>album</i>	7,1 \pm 1,8	13,4 \pm 1,2	27,3 \pm 3,7
<i>conicum</i>	6,4 \pm 1,1	7,3 \pm 1,0	2,6 \pm 1,1
<i>eucalyptifolium</i>	4,0 \pm 1,0	7,9 \pm 1,5	9,3 \pm 1,8
<i>rubrum</i>	8,9 \pm 1,5	4,5 \pm 1,0	12,1 \pm 1,7
<i>salignum</i>	14,3 \pm 2,0	10,7 \pm 1,8	4,5 \pm 1,0
<i>uliginosum</i>	17,8 \pm 3,0	15,9 \pm 2,6	15,3 \pm 2,5

in the six Swartberg species. However, these trends are partly a sampling artefact. 'One-year-old' cones from Outeniqua samples were generally six months older than Swartberg samples when censused because of differences in flowering season (Table 1).

Seeds

The number of filled seeds in subsamples of five cones in one-year-old and older age classes are listed in Table 3. Four of the five *Protea* species had significantly fewer full seed in the older age class than in the younger. In contrast, four of the five *Leucadendron* species showed no decline in seed number with cone age. *Leucadendron salignum*, which survives fire by resprouting, had a total of 322 filled seeds in 93 one-year-old cones (3,5 seeds/cone) compared with 99 full seeds in 51 older cones (1,9 seeds/cone). *Protea nitida* seeds were not counted because virtually none as old as one year could be found (Table 2).

Seed viability

Observations of seedling emergence continued until October 1982. However, more than 90% of all seedlings in all species had emerged by the end of July 1982. The number of seedlings recorded from old cone seeds was more or less the same or exceeded young cone seeds for all the *Protea* species except *P. repens* (Table 3). Among the *Leucadendron* species, however, there was a decline in seedling number from old cone seeds in four of the six species (Table 3). *L. album*, a high altitude species, typically has low germination percentages at lower elevations (unpublished observations). Too few seeds of this species germinated to confidently detect a decline in seed germination in older cones.

Changes in seed viability were assessed by calculating germination percentages as a proportion of filled seed only. Viability was comparably high from both old and young *Protea* seed, except for *P. repens* whose viability declined with age. Differences between young and old *Leucadendron* seed were not consistent between species, sometimes being higher and sometimes lower (Table 3).

Table 3 Number of filled ('plump') seeds and their viability in cones of different ages. n = number of subsamples of five cones each. \bar{x} = mean number of seeds per subsample (\pm S.E.M.). Germination = seeds germinated/all seeds and seedlings counted at the end of the experiment. Viability = seeds germinated/(seeds germinated + seeds with developed embryos only). Statistical significance was calculated by *t* test for seed numbers and Fishers Exact Test for germination and viability (***) = $p < 0,001$; ** = $p < 0,01$; * = $p < 0,05$)

Species	Cone age (y)		\bar{x} seeds per 5 cones	Germination %	Viability %
	n				
<i>Protea</i>					
<i>aurea</i>	1	20	27,8 \pm 3,4 **	79,4	100
	2	19	15,9 \pm 2,1	87,2	97,6
<i>eximia</i>	1	10	26,6 \pm 6,2	26,4	100
	2	7	30,1 \pm 9,0	59,1***	99,0
<i>lorifolia</i>	1	10	129,5 \pm 18,9	40,0	100
	2	10	34,9 \pm 5,4 ***	39,8	100
<i>punctata</i>	1	20	52,9 \pm 3,5	88,5	97,1
	2	20	29,5 \pm 3,1 ***	84,5	94,7
<i>repens</i>	1	20	23,0 \pm 5,0	15,8	58,1
	2	20	9,0 \pm 4,4 *	4,7*	22,2*
<i>Leucadendron</i>					
<i>album</i>	1	14	137,8 \pm 7,0	7,1	11,1
	2	20	152,0 \pm 6,2	5,6	12,2
<i>conicum</i>	1	15	40,1 \pm 4,9	24,0	32,3
	2	10	38,3 \pm 7,0	16,0	70,0***
<i>eucalyptifolium</i>	1	20	127,6 \pm 7,4	40,0	64,1
	2	20	110,6 \pm 8,1	44,6	72,9
<i>rubrum</i>	1	20	87,0 \pm 3,6	74,3	85,6
	2	16	36,3 \pm 5,2 ***	35,0***	62,5***
<i>uliginosum</i>	1	20	120,7 \pm 4,3	26,5	40,4
	2	20	136,1 \pm 5,4 *	11,8**	17,9**

The viable seed bank

The above data are summarized in Table 4 to show the contribution of serotinous cones to seed reserves. The table does not include seeds produced in the current flowering season. These would have been negligible in all of the *Protea* species (except *P. aurea*) and in *Leucadendron rubrum* which were flowering or in bud at the time of the survey (Table 1). The youngest cones of the remaining *Leucadendron* species, however, probably contained significant numbers of mature seed.

Of the ten species in the table, all held viable seeds in serotinous cones from the previous season. Seeds from earlier seasons contributed over half of the total reserves in five species; between 25 and 50% in three species and less than 25% in *Protea repens* and *Leucadendron conicum*.

All the species listed in Table 4 are killed by fire, all regenerate only from seed and all maintain viable seed reserves for at least a year. *Protea nitida*, however, survives fire either by resprouting from a lignotuber or, when mature, by resisting fire heat with its thick, protective bark. This species is not serotinous. Seeds are released less than a year after flowering with less than 4% of the cones retaining seed for as long as a year (Table 2).

Discussion

Results from this study show that cone serotiny in Proteaceae leads to the accumulation of viable seed reserves over several flowering seasons. For all the serotinous species studied,

Table 4 The contribution of serotinous cones to seed reserves. Seed reserves are calculated as mean number of cones per branch or plant (Table 2) × mean number of seeds per cone × % germination of seed in each cone age class (Table 3). The age class 0 (in parentheses) is an estimate of potential seed numbers from the current seasons crop calculated as mean number of flowerheads, buds and immature cones × number of seed in one-year-old cones × max. % germination in either 1 or 2+ -year-old seed (see text)

Species	Mean no. of seeds in age class			Proportional contribution to total reserves	
	0	1	2+	0:1&2+	2+:1&2+
<i>Protea</i>					
<i>aurea</i>	(60)	35,3	14,4	(1,2)	0,29
<i>eximia</i>	(106)	4,4	17,1	(4,9)	0,80
<i>lorifolia</i>	(82)	33,2	37,8	(1,2)	0,53
<i>punctata</i>	(151)	62,7	79,8	(1,1)	0,56
<i>repens</i>	(13)	8,3	0,7	(1,4)	0,08
<i>Leucadendron</i>					
<i>album</i>	(14)	26,2	46,5	(0,2)	0,64
<i>conicum</i>	(27)	14,1	3,2	(1,6)	0,19
<i>eucalyptifolium</i>	(46)	80,6	91,7	(0,3)	0,53
<i>rubrum</i>	(116)	58,2	30,7	(1,3)	0,35
<i>uliginosum</i>	(114)	101,7	49,1	(0,8)	0,33

recruitment after fire would not depend solely on the most recent cohort of seeds. Instead seed produced over several seasons would contribute to the new seedling population (Table 4). *Protea repens*, the species studied most intensively by Jordaan (1949, 1965) shows weak serotiny in comparison with other species. Yet even in this species, one-year-old cones with viable seed overlapped with new flowerheads (cf. *Protea nitida*, a non-serotinous species) so that ripe seed would be present at any fire season. Lombaard (1971) found similar patterns in detailed studies of seed storage in *P. repens* and *P. pulchella*.

Nevertheless, the youngest seed crop contributes substantially to total seed reserves (Table 4) so that the timing of fire in relation to flowering season and seed ripening may influence the number of seedlings — as suggested by Jordaan (1949). There are often 4–16 or more seedlings per parent after autumn burns compared with one seedling for every five or ten parents after spring burns (Bond, Vlok & Viviers 1984; Van Wilgen & Viviers 1984). To explain these patterns, the size of the current seed crop must be 10–100 times greater than all older seed reserves.

The potential contribution of the current season's crop of flowers to total seed reserves was approximated by taking the product of the number of flowerheads, buds and young cones (age class 0 in Table 2), number of plump seeds in one-year-old cones and the highest germination percentages from Table 3. The estimates (Table 4) are generous because they ignore losses of buds, flowerheads and fruits from abortion or predation by insects, rodents and baboons. Viability declines in some species as seeds age (*P. repens*, *L. uliginosum*, Table 3) so that germination percentages for these may be too low.

Results show that most species might double seed reserves, at best, from the worst to the best time of year (i.e. by adding current year's seed production to total seed reserves). *Protea eximia* would increase seeds five-fold in the (improbable) event that all its buds survived to produce mature fruit. Even with

100% viability (= 23 seeds in age class 0) *Protea repens* would, at best, increase seed reserves and therefore seedling numbers only three-fold. These differences are not sufficient to explain the observed variation in seedling numbers after different fire seasons. Seeds accumulated by serotiny should be adequate for good regeneration — if recruitment depended only on pre-burn reserves. I have suggested elsewhere that post-burn conditions are more important, since seed reserves can be decimated if the period after a fire and before germination is prolonged (Bond 1984).

Serotiny in fynbos and elsewhere

Serotiny in southern Cape Proteaceae is comparatively weak. Seed is seldom stored for more than five or six years and fire is not essential for seed release. 'Short term' serotiny has also been reported for species of *Eucalyptus* (Cremer 1965; Ashton 1975) and several conifers e.g. *Pinus torreyana* (McMaster & Zedler 1982), *Picea mariana* (Damman 1964), *Cupressus* spp. (Vogl *et al.* 1977). In contrast, seeds of *Banksia*, *Hakea* and some conifers e.g. *Pinus attenuata* and *P. muricata*, are retained for a decade or more (Warren & Fordham 1974) and often require fire heat for seed release.

Although the incidence of serotiny has been related to fire frequency (Givnish 1981), the significance of variation in the duration of seed retention is not well understood. Many factors influence the size and age distribution of serotinous seed reserves, including weather conditions, pollinator activity, the age and density of a stand, flowerhead predation by rodents and baboons or seed predation by insects. It seems reasonable that stronger serotiny will evolve where the probability of seed production in any year is low or variable. However, geographic or ontogenetic trends in seed storage patterns have yet to be systematically studied.

Seed biology of Cape Proteaceae

Most fynbos Proteaceae appear to be either serotinous or myrmecochorous (i.e. their seeds are dispersed, but not eaten, by ants) (Bond & Slingsby 1983; Slingsby & Bond 1983). No species is both serotinous and myrmecochorous. Both traits are unusual in world vegetation, both serve the same ends — building of seed banks and reduction of seed predation. Pre-dispersal predation is reduced by woody bracts in serotinous species: post-dispersal predation is diminished by timing massed seed release when vertebrate predators are at low densities (Gill 1981; O'Dowd & Gill 1984). Myrmecochorous seed is hidden away from seed predators by ants. Seed reserves accumulate in the soil, not in the canopy.

Seed properties would be expected to differ between the two groups. Soil stored seed requires dormancy mechanisms which 'recognize' fire whereas cones fulfil this function in serotinous species. Consequently, soil stored seed should require special germination treatments in horticulture whereas serotinous seed would be expected to germinate readily if the planting season is suitable. The germination of soil stored seeds of species of *Leucospermum* (ant dispersed) and *Leucadendron* is usually very poor without pre-treatment in contrast to serotinous *Protea* spp. seed (Horn 1960; Brits & Van Niekerk 1976; Van Staden & Brown 1977). Soil stored seed would benefit by being thick-walled to resist predation and fungal decay whereas cones provide defences against predators in serotinous species and thick-walled seed would be an unnecessary additional cost. Soil stored seed should be long-lived whereas serotinous seeds may be either long-lived or short-lived after release from cones — short-lived if parental tissues alone give adequate pre-dispersal protection against

Table 5 The relationship between serotiny and seed dispersal structures in the genus *Leucadendron*, Proteaceae. Structures adapted to wind dispersal include wings, plumed perianths and dense, villous hairs enabling fruits to roll over the ground as in the genus *Protea*. Data ex Williams 1972; Slingsby & Bond 1983 and unpublished observations

Sub-section	No. of species	Serotiny	Fruit type	Probable dispersal agent
Non-serotinous				
<i>Villosa</i>	7	–	Nuts, villous or sparsely pubescent	Myrmecochory or wind
<i>Membranacea</i>	4	–	Nut	Myrmecochory?
<i>Carinata</i>	2	–	Nut	Myrmecochory
<i>Uniflora</i>	2	–	Nut	Myrmecochory
<i>Aliena</i>	2	–	Nut, shortly pubescent	Myrmecochory
<i>Cuneata</i>	3	–	Nut	Myrmecochory
<i>Nucifera</i>	16	–	Nut	None known
<i>Ventricosa</i>	4	±	Narrowly winged or ridged nut	Cones open after 1 year, seeds rattled free
<i>Trigona</i>	1	–	Trigonal nut	Wind?
Serotinous				
<i>Trigona</i>	7	+	Winged, trigonal or compressed	Wind
<i>Brunneobracteata</i>	1	+	Narrowly winged, compressed	Wind
<i>Alata</i>	18	+	Samara	Wind
<i>Compressa</i>	6	+	Samara	Wind
<i>Villosa</i>	4	+	Nut, long villous hairs	Wind — rolling over soil surface
<i>Nervosa</i>	1	+	As above	As above
<i>Leucadendron</i>	4	+	Nuts with persistent plumed perianth	Wind

decay, long-lived if they do not. There is field evidence for the considerable longevity of myrmecochorous seeds of *Orothamnus zeyheri* Papp and *Mimetes stokoei* Phill. & Hutch. (Rourke 1976; Boucher 1981). At least some serotinous *Protea* spp. seed is short-lived after release from cones, both in laboratory trials (Van Staden 1978) and in natural vegetation (Bond 1980).

Ants transport seeds for short distances in fynbos (Bond & Slingsby 1983; Slingsby & Bond 1984). Serotinous species release their seed into areas where vegetative barriers to wind dispersal have been largely removed by fire. Seeds blown or rolled over the soil by wind after fire have the potential to move much greater distances than seeds dispersed between fires, whether transported by ants or not. One would therefore expect that the incidence of fruit structures adapted for wind dispersal would be higher in serotinous species than in non-serotinous plants which release seeds soon after they ripen. Table 5 compares serotiny and dispersal structures in different sections of the genus *Leucadendron*. Serotinous species generally have fruits with wings, feathery plumes or long hairs, similar to the genus *Protea*, which facilitate rolling over the soil surface (personal observations). In contrast, species which release seeds less than a year after flowering generally lack structures for wind dispersal.

Serotiny and myrmecochory appear to be associated with distinct, contrasting suites of physiological, morphological and ecological traits. If this is true, then studies of particular aspects of seed and seedling biology will profit greatly if viewed in the context of the biology of the plant in the field.

Acknowledgements

I thank Jan Vlok for vigorous criticism and assistance, with

R. America, in fieldwork and nursery experiments. J. Breytenbach, C. Biehl, R. Cowling, D. Le Maitre and J. Midgeley provided helpful discussion and comment. This work was supported by the conservation programme of the Directorate of Forestry, Department of Environment Affairs and is published with their permission.

References

- ASHTON, D.H. 1975. Studies of flowering behaviour in *Eucalyptus regnans* F. Muell. *Aust. J. Bot.* 23: 399–444.
- BOND, W.J. 1980. Fire and senescent fynbos in the Swartberg, southern Cape. *S. Afr. For. Jnl* 114: 68–71.
- BOND, W.J. 1984. Fire survival of Cape Proteaceae — influence of fire season and seed predators. *Vegetatio* 56: 65–74.
- BOND, W.J., VLOK, J. & VIVIERS, M. 1984. Variation in seedling recruitment of Cape Proteaceae after fire. *J. Ecol.* 72: 209–221.
- BOND, W.J. & SLINGSBY, P. 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S. Afr. J. Sci.* 79: 231–233.
- BOUCHER, C. 1981. Autecological and population studies of *Orothamnus zeyheri* in the Cape, South Africa. In: Biological aspects of rare plant conservation, ed. Synge, H. Wiley, New York.
- BRITS, G.J. & VAN NIEKERK, M.N. 1976. Opheffing van saadrus by *Leucospermum cordifolium* (Proteaceae). *Agroplantae* 8: 91–94.
- CATANA, A.J. 1963. The wandering quarter method for estimating population density. *Ecology* 44: 349–360.
- CREMER, K.W. 1965. How eucalypt fruits release their seed. *Aust. J. Bot.* 13: 11–16.
- DAMMAN, A.W.H. 1964. Some forest types of Central Newfoundland and their relation to environmental factors.

- Forest Sci. Monogr.* 8. 62 pp.
- GILL, A.M. 1975. Fire and the Australian flora: A review. *Aust. For.* 38: 4–25.
- GILL, A.M. 1981. Fire adaptive traits of vascular plants. In: Fire regimes and ecosystem properties, eds Mooney, H.A. et al. USDA For. Serv. Gen. Tech. Rep. WO–26.
- GIVNISH, T.J. 1981. Serotiny, geography and fire in the pine barrens of New Jersey. *Evolution* 35: 101–123.
- HORN, W. 1962. Breeding research on South African plants: II. Fertility of Proteaceae. *Jl S. Afr. Bot.* 28: 259–268.
- JORDAAN, P.G. 1949. Aantekeninge oor die voortplanting en brandperiodes van *Protea mellifera* Thunb. *Jl S. Afr. Bot.* 15: 121–125.
- JORDAAN, P.G. 1965. Die invloed van 'n winterbrand op die voortplanting van vier soorte van die Proteaceae. *T. Natuurbew.* 5(27): 27–31.
- JORDAAN, P.G. 1981. The influence of a fire in April on the reproduction of three species of the Proteaceae. *Jl S. Afr. Bot.* 48: 1–4.
- KRUGER, F.J. 1977. Ecology of Cape fynbos in relation to fire. In: Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems, eds Mooney, H.A. & Conrad, C.E. USDA For. Serv. Gen. Tech. Rep. WO–3, pp. 230–244.
- KRUGER, F.J. 1983. Plant community diversity and dynamics in relation to fire. In: Mediterranean-type Ecosystems, eds Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. Ecological studies 43. Springer-Verlag, Berlin. pp. 446–472.
- LOMBAARD, H.B. 1971. 'n Ekologiese studie van aspekte van die generatiewe voortplanting van *Protea mellifera* en *Protea pulchella*. M.Sc. thesis, University of Stellenbosch.
- MCMASTER, G.S. & ZEDLER, P.H. 1981. Delayed seed dispersal in *Pinus torreyana* (Torrey pine). *Oecologia* 51: 62–66.
- NAVEH, Z. 1974. Effects of fire in the Mediterranean Region. In: Fire and Ecosystems, eds Kozlowski, T.T. & Ahlgren, C.E. Academic Press, New York. pp. 401–434.
- O'DOWD, D.J. & GILL, A.M. 1984. Predator satiation and site alteration following fire: Mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology* 65: 1052–1066.
- PERRY, D.A. & LOTAN, J.E. 1979. A model for fire selection in serotiny in lodgepole pine. *Evolution* 33: 958–968.
- ROURKE, J.P. 1976. Beyond redemption: The story of *Mimetes stokoei*. *Veld & Flora* 62: 12–16.
- ROURKE, J.P. 1980. The Proteas of southern Africa. Purnell, Cape Town.
- SLINGSBY, P. & BOND, W.J. 1983. Of ants and proteas. *Afr. Wild Life* 36(3): 104–107.
- SLINGSBY, P. & BOND, W.J. 1985. The influence of ants on the dispersal distance and seedling recruitment of *Leucospermum conocarpodendron* (L.) Buek. (Proteaceae). *S. Afr. J. Bot.* 51: 30–34.
- TRABAUD, L. 1980. Impact biologique et ecologique des feux de vegetation sur l'organisation, la structure et l'evolution de la vegetation des zones de Garrigues du Bas-Languedoc. CNRS, CEPE, Montpellier.
- VAN DER MERWE, P. 1966. Die flora van Swartboschkloof, Stellenbosch en die herstel van die soorte na 'n brand. *Annale Univ. Stellenbosch* Ser. A. (14), 42: 691–736.
- VAN STADEN, J. & BROWN, N.A.C. 1977. Studies on the germination of South African Proteaceae — a review. *Seed Sci. & Technol.* 5: 633–643.
- VAN STADEN, J. 1978. Seed viability in *Protea neriifolia*. I and II. *Agroplantae* 10: 65–72.
- VAN WILGEN, B.W. & VIVIERS, M. 1984. The effect of fire on serotinous Proteaceae in the western Cape and the implications for fynbos management. *S. Afr. For. Jnl* (in press).
- VOGL, R.J., ARMSTRONG, W.P., WHITE, K.L. & COLE, K.L. 1977. The closed-cone pines and cypresses. In: Terrestrial vegetation of California, eds Barbour, M. & Major, J. Wiley, New York. pp. 295–358.
- WARREN, R. & FORDHAM, A.J. 1974. The fire pines. *Arnoldia* 38: 1–11.
- WILLIAMS, I.J.M. 1972. A revision of the genus *Leucadendron* (Proteaceae). *Contr. Bol. Herb.* 3: 1–425.