

## Canopy Seed Storage in Woody Plants

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## I. Abstract

The retention of seeds in the plant canopy for one to 30 years or more is termed serotiny. It is well represented floristically and physiognomically in fire-prone, nutrient-poor and seasonally-dry sclerophyll vegetation in Australia, and to a lesser extent, South Africa followed by North America. While the seed-storing structures vary greatly, all will release their propagules following exposure to the heat of a fire (pyriscence). This phenomenon can be contrasted with seed release at maturity (non-storage) and soil storage of seeds. Although the evolutionary requirements for serotiny are clear, its adaptive advantages over other seed storage syndromes are largely the subject of conjecture in the absence of comparative experiments. Nine hypotheses were assessed here. Canopy storage maximises the quantity of seeds available for the next post-fire generation (unlike non-storage). Synchronized post-fire release satiates post-dispersal granivores (unlike non-storage and soil storage) and ensures arrival on a seed bed conducive to seedling recruitment (unlike non-storage). Canopy stored seeds are better insulated from the heat of a fire than non-stored, and probably soil-stored, seeds. Fluctuating annual seed crops, the opportunity for post-fire wind-dispersal, the possible advantages of dense stands of adults, short lifespan of the dispersed seeds and their optimal location in the soil for germination have only a limited role in explaining the advantages of serotiny. It is concluded that canopy seed storage is favoured in regions where seed production is restricted and inter-fire establishment and maturation are unlikely. In addition, these regions have a reliable seasonal rainfall and are subjected to intense fires at intervals occurring within the reproductive lifespan of the species.

## Abstrakt

Das Speichern von Samen für ein bis zu 30 Jahren im Blattwerk der Pflanzen bezeichnet man als 'Serotiny.' Es ist in zu Bränden neigenden, nährstoffarmen und periodisch trockenen Hartlaub-Vegetationen in Australien und in geringerem Ausmaß in Nordamerika und Südafrika häufig vertreten. Obwohl die Samenspeicherungsstrukturen stark variieren, werden alle ihre Brutkörper frei, nachdem sie der Hitze von Feuer ausgesetzt waren (pyriscene). Dieses Phänomen steht im Gegensatz zur Samenfreigabe bei Reife (Nicht-Lagerung) und Bodenlagerung. Obwohl die Entwicklungsvoraussetzungen für 'Serotiny' bekannt sind, ist die Überlegenheit gegenüber anderen Samenspeicherungserscheinungsbildern aufgrund der Anpassungsfähigkeit, größtenteils Gegenstand von Vermutungen, da es vergleichende Experimente nicht gibt. Neun Hypothesen wurden hier bewertet. Blattwerkspeicherung maximiert die Menge des zur Verfügung stehenden Samens für die nächste Generation nach einem Feuer (im Gegensatz zur Nicht-Lagerung). Gleichzeitige Abgabe nach einem Feuer übersättigt die Körnerfresser (im Gegensatz zur Nicht-Lagerung und Bodenlagerung) und sichert so ein Auftreffen auf dem Saatbeet, dieses ist für die Sämlingverstärkung von Nutzen. Samen welche im Blattwerk gelagert sind, sind besser gegen die Hitze des Feuers geschützt als nichtgespeicherte Samen und wahrscheinlich auch als bodengelagerte Samen. Schwankende jährliche Samenausbeute, die größere Möglichkeit für Ausbreitung durch den Wind, die möglichen Vorteile durch dichteres Zusammenstehen von älteren Pflanzen, kurze Lebensspanne von verstreuten Samen und die für die Keimung optimale Lage im Boden spielen nur eine begrenzte Rolle in der Erklärung der Vorteile der 'Serotiny'. Es wird daher geschlossen, daß Blatt-

werksamenspeicherung in Regionen unwahrscheinlicher Zwischenfeuer-Etablierung und Reifung bevorzugt wird. Weiterhin haben diese Regionen einen verlässlichen saisonalen Regenfall und sind Gegenstand ausgedehnter Brände, die in Intervallen innerhalb der Fortpflanzungslebensspanne der Spezies auftreten.

## II. Introduction

Many species in the sclerophyllous shrublands and woodlands of Australia and South Africa and the coniferous forests of North America retain their seeds in persistent cones or fruits. Research on canopy seed storage in North American conifers dates back to the nineteenth century (e.g., Engelmann, 1880). More recently, intensive studies on canopy seed storage in flowering plants, especially the Proteaceae in Australia and southern Africa, have been carried out. In this review, we synthesize the world literature on delayed seed release and assess ideas about its evolution and ecological significance. We conclude that it is no coincidence that this curious phenomenon is widespread in regions with strongly seasonal climates, poor soils and recurrent fires.

Firstly, we review the descriptive terms that are currently in use and provide information on the geographic distribution of the taxa involved and the structures retaining seeds. We examine the role of fire in seed release. We then assess nine hypotheses about the function of canopy seed storage and draw conclusions about the evolution and significance of canopy-stored seed banks. Comparisons are made with the two possible alternative fates of seeds: release of short-lived seeds once mature (no seed storage) and soil storage of long-lived seeds. Our review is confined to shrubs and trees in temperate climates, although canopy seed storage is also a feature of some annuals, shrubs and succulents in deserts of the USA and southern Africa (Van der Pijl, 1969) where irregular rainfall may act as the cue for seed release (Hoffman & Cowling, 1987; Ihlenfeldt, 1971).

## III. Concepts and Terminology

Various terms have been used to describe the delayed release of mature seeds from the plant canopy. The term 'serotiny' is universal in the North American and South African literature while 'bradyspory' is sometimes used in Australia as well. Serotiny is derived from the Latin adjective *serotinus* meaning late in occurrence (Stearn, 1973). Michaux (1803) was the first to associate the term serotiny with the delayed opening of cones in his diagnosis for *Pinus serotina*. Engelmann (1880) described serotiny as the retention of seeds in temporarily or permanently-closed cones. Shaw (1914) also used the term for cones with intermittent release of seeds during dry sunny weather or those requiring heat to separate the scales. Although not specifically implied in the roots of the word, the concept of serotiny appears to have been confined historically to delayed seed release rather than to delay in other plant functions. In North America, serotiny is now often used to describe cones which require fire heat to release their seeds (e.g., Givnish, 1981; Perry & Lotan, 1979).

In an appendix to the third edition of his dictionary, Jackson (1916) cited Ulrich's definition of 'bradyspore' as a "plant which disperses its seeds slowly." It is derived from *brady*, Greek for slow, and *spory*, Latin for spore-like propagules. Van der Pijl (1969) used the term to describe the condition where seeds were not released on reaching maturity. His examples included *Pinus* and *Callistemon* as well as some

Mesembryanthemaceae. Specht (1979), however, used bradyspory to refer to fruits which release their seeds only in response to fire. Both serotiny and bradyspory have, therefore, been applied in a broader or different sense than used originally.

In this review we propose the following definitions: Historical and current use of the terms bradyspory and serotiny treats them as synonymous, making one redundant. We reject bradyspory in favour of serotiny, its predecessor by over 100 years. Since fire is only one of several possible ways (e.g., the passage of time; plant or branch death) of terminating canopy seed storage, we support the original concept emphasizing the length of seed retention rather than the process of release. We define *serotiny* as canopy seed storage, where at least part of previous seed crops is retained when the current season's crop is mature (Le Maitre, 1984). *Degree of serotiny* becomes the extent to which viable seeds are retained with increasing age of the fruit or cone (Cowling & Lamont, 1985a). Plants are either non-serotinous, weakly serotinous (most seeds released within a few years) or strongly serotinous (most seeds still retained after a few years). In deference to the general term for release of seeds, dehiscence, we introduce the term *pyriscence* (after *pyr*, Greek for fire and *hiscere*, Latin for gape) to describe the induction of seed release by fire. Most seed-storing structures will be facultatively pyriscent (as noted above) but some will be obligately pyriscent where most will *only* open in response to fire, otherwise they finally disintegrate unopened.

We recognise two contrasting syndromes of seed release:

1. The seed is released as soon as it is mature (non-serotinous). There are two sub-groups within this syndrome. In the first there is no persistent seed store in the soil. The seeds germinate during the first favorable period after release. In the second, at least some of the seeds persist in or on the soil and successive seed crops accumulate to form a soil-stored seed bank. There are numerous papers on the biology of soil-stored seeds (see reviews by Harper, 1977; Koller, 1973; Mott & Groves, 1981). Mechanisms for maintaining viability and breaking dormancy of soil-stored seeds in fire-prone environments have received considerable attention (Brits, 1987; Gill, 1981b; Keeley, 1987).
2. The release of mature seeds is delayed, resulting in the build-up of a canopy-stored seed bank. In species with canopy seed storage, conditions are not conducive to germination while the seeds remain in the closed fruit or cone. The seeds are short-lived after release and will germinate during the first favorable period (Cowling & Lamont, 1987).

#### IV. Requirements for the Evolution of Serotiny

Our starting point is that delayed seed release is an advanced condition over spontaneous release of seeds once they are mature. There are five conditions that must be satisfied for canopy seed storage to be a successful evolutionary option for a given species:

1. It must be phylogenetically possible to develop reproductive structures which can store and protect seeds from granivores, pathogens, rain and/or heat until the onset of seed release.
2. Canopy stored seeds must remain viable until the onset of conditions suitable for germination.

3. The operation of the seed release mechanism must be cued to the onset of conditions conducive to seedling establishment and recruitment.
4. The mean timing of the cue for seed release must occur within the mean reproductive lifespan of the species. This applies where viable seeds stored on a dead plant are unavailable for the next generation (Lamont & Barker, 1988), otherwise seed release can occur beyond the lifespan.
5. There must be the genetic capacity and sufficient opportunity to produce and store enough seed in the mean interval between cueing events to ensure population replacement in the next establishment phase.

These requirements, however, provide only the ingredients for change. They do not explain the adaptive advantages of canopy seed storage in the face of the possible alternatives, i.e., no seed storage and storage in the soil. Nor do they identify the environmental cue initiating seed release. We now show how these conditions are satisfied in practice and explore the major selective forces favoring the evolution of serotiny.

### V. Distribution and Genetics of Canopy Seed Storage

At least 530 serotinous species in 40 woody genera have been recorded (Table I). The true number of species is more than twice this, as most of the remaining 700 species in genera listed under the Myrtaceae are probably serotinous. In the Northern Hemisphere, canopy seed storage appears to be confined to three conifer families. In the Southern Hemisphere, serotiny occurs in the Cupressaceae and six families of dicotyledons: Casuarinaceae, Proteaceae, Myrtaceae, Asteraceae, Ericaceae and Bruniaceae (Table I). As incomplete as the data base is, the phenomenon is clearly best developed in Australia's sclerophyll vegetation. All seed-storing structures are pyriscent but obligate pyriscence has been poorly studied: it appears to be restricted to fewer than ten species in each of *Pinus*, *Cupressus* and *Banksia*. The seed-bearing structures in all other species either open with the passage of time or on death of the supporting stem as well as in response to fire. Among Northern Hemisphere flowering plants, *Platanus* (Plantanaceae), and *Cephalanthus* (Rubiaceae) show some tendency to retain seeds (Schopfmeier, 1974) but neither occurs in fire-prone environments.

Ecological research has centered on the coniferous forests of North America, the sclerophyllous shrublands of Cape Province, South Africa and the sclerophyllous woodlands and shrublands of Australia where serotinous species usually dominate the landscape. There is relatively little information on the coniferous forests of Europe and Asia where canopy seed storage has only been reported for a few conifers in the Mediterranean basin. Most information is available on *Pinus* (Northern Hemisphere) and the Proteaceae (Southern Hemisphere).

In conifers, the seed-bearing structure is a cone (strobilus) with the seeds located between woody scales around a central axis. In the Grevilleoideae, a sub-family of the Proteaceae, the seeds are retained in a woody follicle borne singly in some genera, e.g., *Hakea*, but aggregated around a bract-covered axis in others, e.g., *Banksia*. In the sub-family Proteoideae and family Casuarinaceae, the indehiscent fruits are packed between woody bracts. The involucre bracts completely surround the shallow cone in *Protea* (Rourke, 1980). In the Bruniaceae, bracts clasp the base of the persistent florets. The seeds of Myrtaceae (Leptospermoideae) are retained in woody capsules with apical valves which are borne singly, e.g., *Eucalyptus*, or aggregated, e.g., *Mela-*

TABLE I.

The taxonomic and geographic distributions of conifers and woody flowering plants with canopy-stored seeds (serotinous) and those whose seeds are usually only released by fire (obligately pyriscent). The remaining serotinous species are facultatively pyriscent. S Australia = Southern Australia.

Taxon	Number of Species			Distribution	Source
	Examined	Serotinous	Pyriscent (obligate)		
<b>GYMNOSPERMAE</b>					
<b>Cupressaceae</b>					
<i>Actinostrobus</i>	3	3	0	SW Australia	Lamont unpubl.
<i>Callitris</i>	10	10	0	Australia	Lamont unpubl., Hardy 1926
<i>Cupressus</i>	25	23?	4?	N America, Europe	Dallimore & Jackson 1966, Vogl et al. 1977
<i>Tetraclinis</i>	1	1	-	Mediterranean Europe	Dallimore & Jackson 1966
<i>Widdringtonia</i>	3	3	0	S Africa to Malawi	Le Maitre unpubl.
<b>Pinaceae</b>					
<i>Picea</i>	17	1	-	N America, N Europe	Safford 1974
<i>Pinus</i>	95	22	6	N Hemisphere, widespread	Krugman & Jenkinson 1974
<b>Taxodiaceae</b>					
<i>Sequoiadendron</i>	1	1	0	California	Boe 1974
<b>ANGIOSPERMAE - DICOTYLEDONAE</b>					
<b>Asteraceae</b>					
<i>Helipterum</i>	15	1+	0	S Africa, Aust.	Bond 1985
<i>Phaenocoma</i>	1	1	0	SW Cape	Bond 1985

*leuca*. In *Erica sessiliflora*, the calyx becomes fleshy and encloses the capsule (Baker & Oliver, 1967).

The genetic basis of the clinal variation in the degree of serotiny in certain banksias (Cowling & Lamont, 1985a) has not been investigated, but the variation is apparently

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 Bruniaceae

<i>Berzelia</i>	12	12	0	Cape	Le Maitre unpubl.
<i>Brunia</i>	7	7	0	SW Cape	Le Maitre unpubl.
<i>Nebelia</i>	6	6	0	SW Cape	Le Maitre unpubl.

## Casuarinaceae

<i>Casuarina</i>	28	21	-	Australia	Ladd 1989.
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## Ericaceae

<i>Erica</i>	c.650	1	0	Africa, Europe	Baker & Oliver 1967
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## Myrtaceae - Leptospermoideae

<i>Agonis</i>	6	6	0	SW Australia	Lamont unpubl.
<i>Beaufortia</i>	2	2	0	SW Australia	Lamont unpubl.
<i>Callistemon</i>	5	5	-	S Australia	Lamont unpubl., Hardy 1926
<i>Calothamnus</i>	5	5	-	SW Australia	Lamont unpubl.
<i>Conothamnus</i>	2	2	-	SW Australia	Lamont unpubl.
<i>Eremaea</i>	6	6	-	SW Australia	Lamont unpubl.
<i>Eucalyptus</i>	104	97	-	Australasia	Boland et al. 1980 Lamont unpubl., Hardy 1926
<i>Kunzea</i>	3	3	-	Australia	Lamont unpubl.
<i>Leptospermum</i>	5	5	0	Australia	Lamont unpubl.
<i>Melaleuca</i>	15	15	-	Australia	Lamont unpubl., Hardy 1926
<i>Phymatocarpus</i>	1	1	-	SW Australia	Lamont unpubl.
<i>Regelia</i>	2	2	0	Australia	Lamont unpubl.
<i>Tristania</i>	1	1	-	Australia	Lamont unpubl.

## Proteaceae

<i>Aulax</i>	3	3	0	SW Cape	Rourke 1987
<i>Banksia</i>	75	70	5+	Australia	George 1981, Lamont unpubl.
<i>Dryandra</i>	34	30	-	SW Australia	S Connell, unpubl.
<i>Hakea</i>	77	65	-	Australia	Lamont unpubl., Hardy 1926
<i>Isopogon</i>	1	1	-	S Australia	Hardy 1926
<i>Lambertia</i>	2	2	0	S Australia	Lamont unpubl.
<i>Leucadendron</i>	81	41	0	S Africa	Williams 1972
<i>Petrophile</i>	6	6	-	Australia	Lamont unpubl., Bradstock 1985
<i>Protea</i>	115	42	0	Africa	Rourke 1980
<i>Strangea</i>	1	1	0	Australia	Lamont unpubl.
<i>Xylomelum</i>	3	3	0	S Australia	Lamont unpubl.

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continuous. This differs from pines where individual trees carry either mainly serotinous or non-serotinous cones (Crossley, 1956; Givnish, 1981; Ledig & Little, 1979). Teich (1970) concluded that serotiny in *Pinus banksiana* and *P. contorta* could be explained by a single gene with two alleles. There was some support for heterozygotes

TABLE II.

Maximum duration of seed retention and viability in the first and final years before total pre-fire seed release or death for various taxa.

Species	Duration (years)	Seed viability (%)		Source
		Year 1	Final	
<i>Actinostrobus arenarius</i>	6	83	7	Lamont unpubl.
<i>Banksia attenuata</i>	7-9 (17 <sup>*</sup> )	75	51	Cowling et al. 1987
<i>B. baxteri</i>	9-10	100	100	H King unpubl.
<i>B. burdettii</i>	9-12	100	65	Lamont & Barker 1988
<i>B. coccinea</i>	10-11	100	75	H King unpubl.
<i>B. cuneata</i>	12 (15 <sup>*</sup> )	97	50	Lamont et al. 1991
<i>B. hookeriana</i>	11-14	90	50	Enright unpubl.
<i>B. leptophylla</i>	10-12	96	65	Cowling et al. 1987
<i>B. menziesii</i>	7-9 (11 <sup>*</sup> )	11	7	Cowling et al. 1987
<i>B. prionotes</i>	7-9 (12 <sup>*</sup> )	76	40	Cowling et al. 1987
<i>B. speciosa</i>	11-12	100	50	H King unpubl.
<i>B. tricuspis</i>	4-( $<15$ )	100	18	Lamont & van Leeuwen 1988
<i>Hakea undulata</i>	7	-	-	Lamont unpubl.
<i>H. sericea</i>	8+	99	c.90	D Richardson unpubl.
<i>H. gibbosa</i>	8+	97	c.90	D Richardson unpubl.
<i>H. suaveolens</i>	5+	93	c.90	D Richardson unpubl.
<i>H. salicifolia</i>	15	97	c.0	D Richardson unpubl.
<i>Picea mariana</i>	5 (15 <sup>*</sup> )	50	15	Viereck 1983
<i>Pinus attenuata</i>	20+	-	-	McMaster & Zedler 1981



<i>P. banksiana</i>	20+ (25*)	-	50	Cayford & McRae 1983
<i>P. contorta</i>	30	-	-	Heinselmann 1981
<i>P. coulteri</i>	24-26	-	-	Borchert 1985
<i>P. muricata</i>	20+	-	-	McMaster & Zedler 1981
<i>P. pungens</i>	11	42	22	Barden 1979
<i>P. torreyana</i>	13	77	20	McMaster & Zedler 1981
<i>Protea neriifolia</i>	7	94	-	Le Maitre 1990
<i>Widdringtonia nodiflora</i>	7	-	-	Le Maitre unpubl.
<i>W. cedarbergensis</i>	7	-	-	W Bond unpubl.

\* Maximum age of apparently viable seeds recorded (Cowling & Lamont, 1985a; Fowells, 1965; Snyder et al., 1985).

with incomplete dominance whose expression was related to the position of the tree in the environmental gradient. Rudolph et al. (1959) considered serotiny in *P. banksiana* was the recessive condition of a multi-gene trait. Clearly, much more remains to be known about the genetic versus environmental control of serotiny within species. In both of the above species, the proportion of serotinous cones per crop increases with age of individual plants (Critchfield, 1985; Crossley, 1956). Unlike pines, as far as is known, no flowering plants vary in degree of serotiny per crop year over their lifespan.

## VI. Seed Longevity and Fire-cued Release

As the seed-bearing structures age, an increasing proportion of seeds is released spontaneously (Cowling & Lamont, 1985a). This is enhanced by exposure to the sun or high ambient temperatures (Fowells, 1965). Longevity of the canopy-stored seeds has received some study (Table II). Seeds retained in pines may remain viable for up to 20–30 years, while a small proportion may reach 10 to 15 years in banksias. Viable seeds have been extracted from 150 year old cones embedded in the trunks of *Pinus contorta* (Mills, 1915). Death of the parent plant, or shoot supporting the fruit or cone, results in general seed release, e.g., *Hakea*, or sometimes in a negligible increase, e.g., *Banksia burdettii* (Lamont & Barker, 1988).

Provided the heat generated is high enough (Enright & Lamont, 1989a) but insufficient to destroy the fruits or cones (Lamont & Barker, 1988), fire will always stimulate the release of mature seeds (pyrisence as proposed here). In conifers, heat melts the resins which bind the apophyses of the cone scales (Ahlgren, 1974; Shaw, 1914). Cones of *Pinus banksiana* will open at temperatures of 93 to 700°C (Beaufait, 1960). The minimum melting point of the resin in *P. rigida* is 42°C, with a mean of 57°C (Ledig & Little, 1979). Wardrop (1983) noted that resins binding the cell walls

in the abscission layer of *Banksia* follicles melt when heated. The follicle ruptures when the reflexing tension in the valves, due to desiccation, exceeds the bond strength in the abscission layer (Gill, 1976). A minimum of two minutes at 100–300°C to a maximum of 350–600°C may be required for follicle rupture in banksias (Enright & Lamont, 1989a; Lamont, 1988). The results are consistent with higher melting points recorded in strongly serotinous fruits.

The heat produced by combustion of the old florets retained around the follicles is sufficient to induce fruit opening in serotinous *Banksia* and *Dryandra* species (Lamont & Cowling, 1984). The florets are usually deciduous in non-serotinous species only. Prolific seed release within a stand generally only occurs after fire when most of the mature plants, or at least the outer branches of resprouting species, are killed.

If fire is the most effective cue for seed release and subsequent seedling recruitment, it would be expected that serotiny is best developed among woody species most affected by fire. It follows that shorter plants or those whose canopy reaches the ground, where even the mildest of fires will burn the aerial parts, should be more serotinous than taller plants with elevated canopies (Givnish, 1981; Muir & Lotan, 1985). This is well supported by the phenotypic variation in three *Banksia* species along a climatic gradient (Cowling & Lamont, 1985a), where the degree of serotiny increased with decreasing plant height. Two of the species are weakly serotinous trees under more mesic conditions and recover epicormically from fire. Under more xeric conditions, the highly serotinous shrubs are killed to ground level and recover from the lignotuber.

In winter-rainfall *Protea*, 10% of rhizomatous species are serotinous, whereas 90% of shrub species are serotinous (Le Maitre, 1987). However, most of the creeping proteas grow in rocky areas insulated from fire. This apparent exception to the hypothesis contrasts with banksias, where all rhizomatous and shrub species are serotinous, but only 40% of the tree species are (collated from George, 1981). On a regional level, where shorter vegetation is more fire-prone, the proportion of species with canopy seed storage is higher (Christensen & Kimber, 1975; Cogbill, 1985; Givnish, 1981; Kilgore, 1981; Westman & Whittaker, 1975). A reduction in nutrient and/or water availability may increase the understory canopy cover by reduction in the tree cover and retard litter breakdown. Further reductions in resources could reverse these trends, decreasing flammability and the opportunity for fire-cued seed release.

Species killed by fire are completely dependent on seedlings for restoration of the population. Thus, it would be expected that non-sprouters (fire-sensitive) are more likely to be serotinous than fire-tolerant resprouters (Bond, 1985; Zammit, 1986). This is generally supported in *Protea*, with 81% of non-sprouters serotinous and only 17% of resprouters serotinous (collated from Rourke, 1980). The hypothesis is only weakly supported in *Banksia* (Lamont et al., 1985). There is no support in *Hakea* with 88% of both non-sprouting and resprouting species serotinous (Lamont, unpubl. data), although non-sprouting populations of *H. sericea* (*sensu lato*) are strongly serotinous and resprouting populations are weakly serotinous (M. Gill, pers. comm.). It is not supported in *Leucadendron* (Lamont et al., 1985), although most non-serotinous species accumulate soil-stored seed banks instead (Bond, 1985). It is possible that, as many resprouters produce so few seeds throughout their lifecycle, there is as much selection pressure for serotiny on them as for non-sprouters (Lamont, 1988; Enright & Lamont, 1989b).

## VII. Evaluation of Hypotheses on the Function of Serotiny

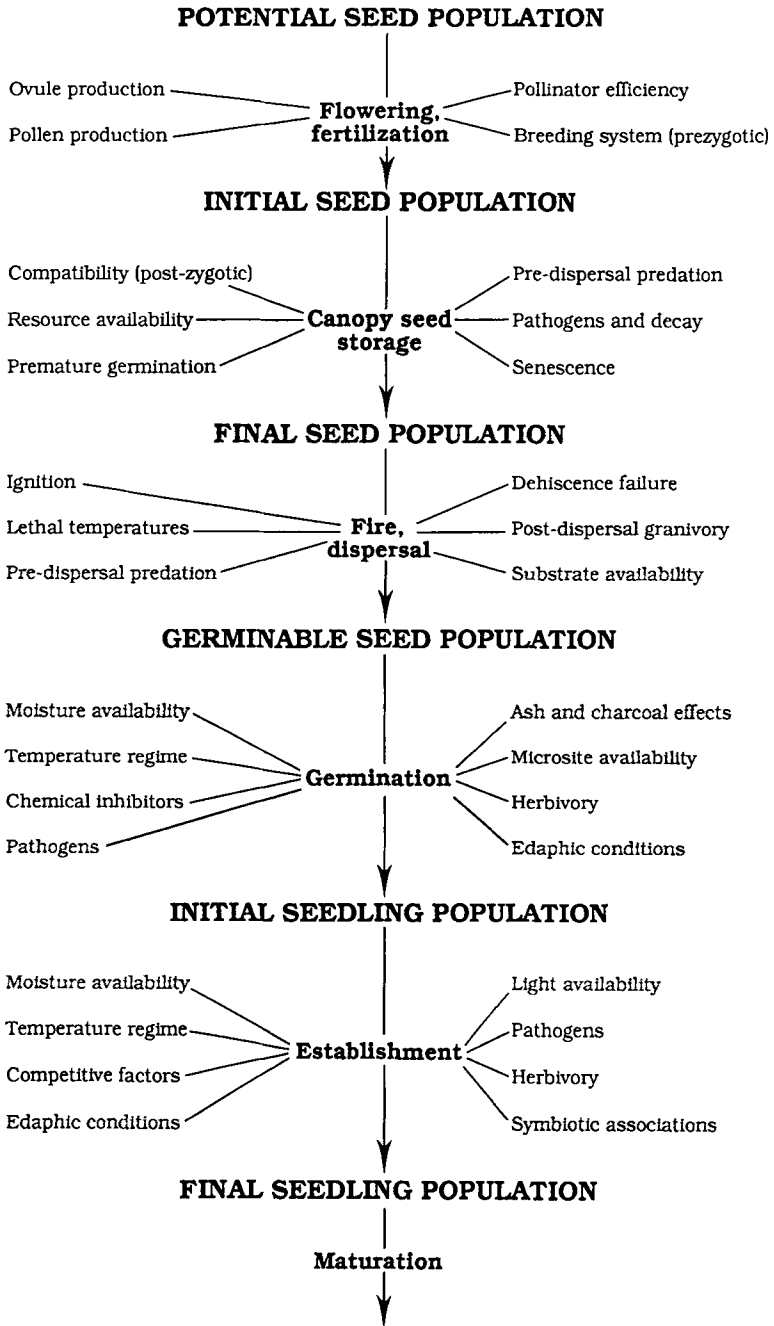
Canopy seed storage is one link in a chain of events connecting the potential seed bank in a stand of perennial plants with the final seedling population, after a major disturbance such as severe drought or fire (Fig. 1). Many internal (genetically controlled) and external (environmentally controlled) factors account for the fate of ovules, zygotes, seeds and seedlings (Lamont & Barrett, 1988). Any hypothesis which seeks to explain the role of serotiny in perpetuation of a species must address the constraints to seed availability at the time of seed release as well as constraints to seedling establishment and maturation following dispersal. While canopy seed storage has the potential to build-up the seed population until conditions are more suitable for seedling establishment, other factors come into operation to reduce the number stored (Fig. 1). If release can be delayed until the sum of the many constraints on germination and establishment is minimized, then storage will give that species an adaptive advantage. Furthermore, since the seed store may represent many years of sexual reproduction, genotypic variation should be maximized. This would provide more options under variable or changing post-fire conditions.

Here, we present nine hypotheses regarding the adaptive significance of canopy seed storage and evaluate them critically in terms of available data. As all serotinous structures in woody plants are most likely to open in response to heat (pyriscence), we concentrate on fire as the usual cue for seed release. The first four hypotheses contrast serotiny with non-storage of mature seeds, the next three contrast it with soil storage as well as non-storage, and the last two contrast serotiny with soil-storage only. The first three and the last two hypotheses assume that significant establishment is only possible after fire, while the last four attempt to explain why establishment is most likely after fire. The first three hypotheses and number five treat canopy seed storage as a means of maximizing the number of seeds available for the next generation. The last four hypotheses and the fourth regard canopy seed storage as a means of ensuring that the greatest proportion of released seeds germinate after fire.

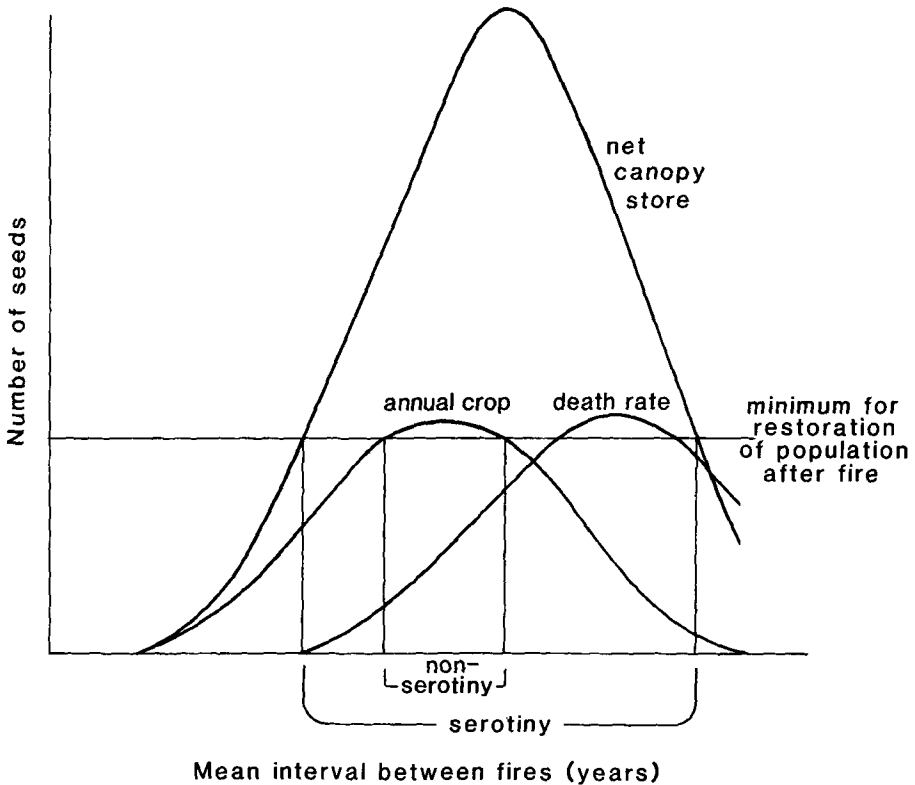
### A. HYPOTHESIS ONE

#### *Seed storage maximizes seed available for the next generation in fire-prone vegetation*

The question of fire regime needs to be addressed first. If fires usually occur at intervals within the reproductive lifespan of the species, then canopy seed storage (and soil storage) serve as devices for enhancing seed supply after fire (Fig. 2). Assuming that each canopy-stored seed survives only a quarter of the lifespan of the species, the maximum canopy seed storage would be almost three times the maximum annual crop. This maximum would be attained at about half the lifespan, somewhat older than the age for maximum annual seed production. For fire intervals near or exceeding the lifespan of the species, serotiny would still be beneficial if inter-fire establishment was not possible, but not if inter-fire establishment of non-stored seed was possible (Fig. 2). In addition, canopy seed storage on dead plants may be unavailable for the next generation, either because it is released spontaneously onto a hostile seed bed at plant death or the seed is destroyed when a fire does eventually occur (Lamont & Barker, 1988).



**Fig. 1.** The chain of events and associated constraints linking canopy seed storage with potential seed numbers and final seedling numbers in woody plants. The best hypotheses about the adaptive advantages of canopy seed storage will explain how it maximizes the recruitment of seedlings relative to seeds produced during the lifespan of the plant.



**Fig. 2.** Comparison of annual and cumulative viable seed crops, assuming the longevity of canopy-stored seeds is 25% of the lifespan of the species, in relation to time since the last fire. The minimum line for restoration of the population after fire, assuming inter-fire establishment is irrelevant, highlights how serotiny enables population restoration for a much greater range of fire intervals than if the species was non-serotinous.

The growth rates of any inter-fire recruits are usually slow and seed production poor or absent compared with the post-fire parents (authors' pers. obs.; Bradstock, 1985). Also, there may be insufficient time for inter-fire seedlings of some resprouting species to develop fire tolerance before the next fire as well (Bradstock & Myerscough, 1988; Lamont & van Leeuwen, 1988). In the early inter-fire period, existing plants of serotinous species would store progressively more seeds than the numbers provided annually by any later established plants of non-serotinous species. In the late inter-fire period, net canopy storage would drop but seedling additions to any non-serotinous population would have less time or access to sufficient resources to reach maturity before the next fire. We conclude that seed storage maximizes seed availability for the next generation, whether or not inter-fire establishment is possible.

Since canopy seed storage enables a greater number of seeds to be released following any fire that occurs within the reproductive lifespan of the species, the likelihood of exceeding the minimum required for restoration of the population is increased (Fig. 2). A major conclusion from this model is that serotiny enables the species to survive fires both more and less frequent than in the absence of a storage mechanism, agreeing

with McMaster and Zedler (1981). In the past, the restrictive nature of the fire regime conducive to serotiny has been emphasized (Bond, 1984; Givnish, 1981; Perry & Lotan, 1979). In fire-prone environments the reverse is true: canopy seed storage (and soil storage) greatly increases the fire resilience of the species (as distinct from that of the individual) and can be expected to widen the species' geographic range and buffer the effects of any changes in climate and fire regime.

It would be expected from this hypothesis that species with smaller annual crops would be more likely to be serotinous as they would have the most to gain from canopy seed storage. Within a genus, species with the lowest rate of seed production are among the most serotinous, many being obligately pyriscent, e.g., *Cupressus forbesii* (2–3 cones per 22 year old plant, Vogl et al., 1977), *Pinus contorta* ssp. *bolanderi* (Griffin & Critchfield, 1972), *Banksia elegans* (one follicle per 16 year post-fire ramet, Lamont, 1988; Lamont & Barrett, 1988), *Hakea megalosperma* (Lamont, unpubl. data). *Banksia* is the most intensely studied genus in this regard: the most fecund are often the most serotinous (Cowling et al., 1987; Enright & Lamont, 1989a, 1989b). But this is confounded by their differing responses to fire. We interpret weak serotiny in the resprouter *B. oblongifolia*, in contrast with the co-occurring, strongly serotinous obligate-seeder *B. ericifolia*, as signifying less reliance on seeds for survival rather than taking advantage of inter-fire opportunities for recruitment (Zammit & Westoby, 1987, 1988).

Another approach is to determine if environmental conditions that restrict seed production also favor canopy seed storage. Thus, we could predict that the shorter the recurrent fire interval (provided it exceeds the juvenile period), the more serotinous the component taxa. This is best studied at the within-species level, and in all cases it has been supported (Borchert, 1985; Cayford & McRae, 1983; Cowling & Lamont, 1985a; Givnish, 1981; Lotan, 1968). However, this is confounded by the fact that fire-prone habitats are more likely to possess poor growing conditions—extended drought, nutrient-impoverished or toxic soils, high plant density, sometimes low temperatures and seasonal waterlogging (Beadle, 1966; Givnish, 1981; Specht, 1979; Vogl et al., 1977; Westman & Whittaker, 1975; Zedler, 1986). Plants dwarfed in response to the restricted or unbalanced resources produce smaller seed crops are more fire-prone (Low & Lamont 1990; Mitchell & Coley 1987) and more likely to be serotinous (Table III). We can predict that sub-optimal growing conditions or high fire frequency alone will favor serotiny but the evidence is meagre by comparison with that for their apparent synergistic effect.

Granivory, decay and senescence can drive the seed bank towards zero, at which point any benefits of serotiny will cease (Bond, 1984, 1985; Lamont & Barker, 1988; Lamont et al., 1985; Myburgh et al., 1974; Van Staden, 1978; Cowling et al., 1987). There are usually lower levels of seed abortion and predation and higher levels of viability in canopy stored seeds among co-occurring species which are strongly serotinous (Cowling et al., 1987; Lamont et al., 1991; Zammit & Westoby, 1988) that are consistent with the present hypothesis. In some species, substantial release occurs spontaneously after only a short period of storage. This tends to occur in proteas in direct response to high pre-dispersal predation levels (Coetzee & Giliomee, 1987) and also in environments with milder climates and low risks of post-dispersal predation, where inter-fire establishment is more likely and fires are insufficiently intense to ensure seed release (Cowling & Lamont, 1985a; McMaster & Zedler, 1981). These examples show that maximizing seed storage may not be adaptive if the seed is poorly protected or fires do not guarantee seed release.

TABLE III.

Predicted relationships between serotiny, fire frequency and growing conditions for woody plants.

Ratio of fire interval to juvenile period	Optimal growing conditions	Sub-optimal growing conditions
High	Non-serotinous	Serotinous
Low	Serotinous	Serotinous

We have shown that no matter how frequent fire is, or how soon one year old seeds begin to be shed, seed storage will usually increase the number of propagules available for post-fire recruitment. But this assumes that there is no extra cost involved in storage. This extra cost (energy, nutrients, water) is likely to be associated with the additional structural protection, such as woody fruits and extra bonding material required against fire heat, the weather, pathogens and granivores, for prolonged canopy seed storage. For example, G. Scheid (in Zedler, 1986) found the cones of serotinous cypresses were woodier than non-serotinous species. This may ultimately be at the expense of size of the annual seed crop (Muir & Lotan, 1985). Linhart (1978) showed that, as scale thickness increased in three serotinous pines, percentage survival of seeds increased when cones were exposed to 250°C for 5 minutes. However, the number of seeds per cone decreased markedly, with some increase in cone weight. This is a clear example of the cost of canopy seed storage, but the gains arise from the extra protection against fire and granivorous squirrels (Elliott, 1974). There is also a small cost involved in production of the ant-attracting elaiosome of some soil-stored seeds (Majer & Lamont, 1985; Rice & Westoby, 1981).

S. Naser (pers. comm.) has found that follicle wall thickness in populations of *Hakea sericea* varies with length of the ovipositor of granivorous insects likely to be encountered within each population. There is some evidence that less fertile sites produce plants with larger follicles (Beadle, 1968; Gill & Naser, 1984) and these habitats are invariably more fire-prone, both conditions favoring serotiny (Hypothesis 4). This also implies that crop size is smaller, but it is not known if the larger fruits are more serotinous. There is no clear relationship between follicle size and degree of serotiny in *Banksia* (Enright & Lamont, 1989a) though fruit size alone is probably a poor index of the cost of serotiny. The mean follicle/seed weight ratio (a better index) of five strongly serotinous *Hakea* species was five times that of four co-occurring weakly serotinous species (Lamont & Cowling, unpubl. data). Since most of the mobile mineral nutrients are retranslocated from the fruit to the developing seed (Hocking, 1982; Kuo et al., 1982), any cost must reside with dry matter, poorly mobile ions and perhaps water. Large serotinous fruits may be a mechanism for maximizing the N and P content of seeds providing an adaptive advantage for seedling

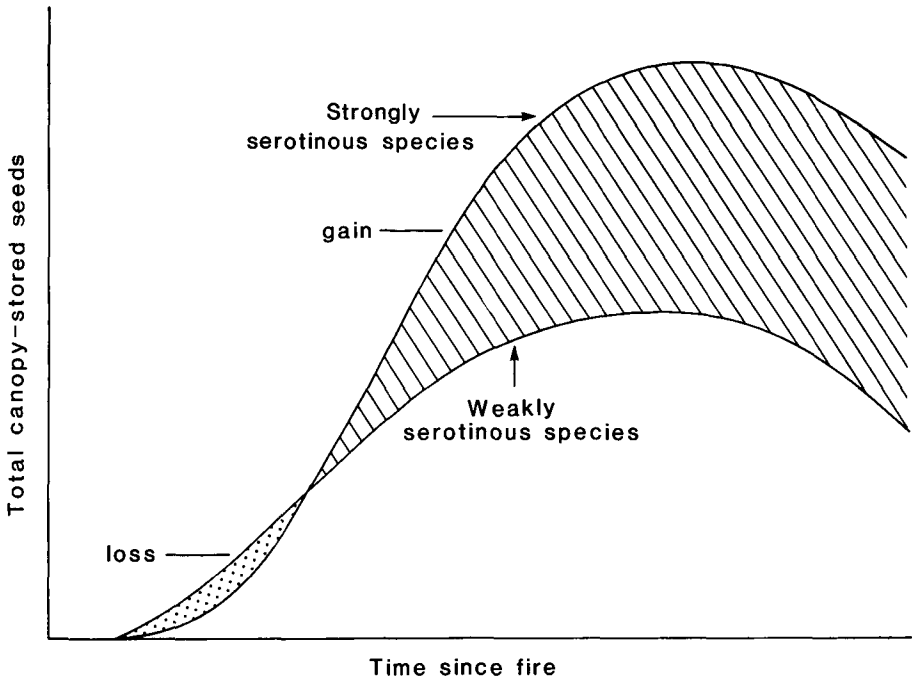


Fig. 3. Relative availability of canopy-stored seed over time on the assumption that the extra protection associated with strong serotiny is a resource cost compared with weak serotiny.

recruitment in impoverished soils (Lamont, unpubl. data) unrelated to protection from granivores (Midgley et al., 1991). In summary, once the minimum fire interval exceeds the juvenile period, serotiny *even at cost* becomes an increasing advantage, up to the time of plant death, in terms of increasing seeds available for the next generation (Fig. 3).

#### B. HYPOTHESIS TWO

##### *Seed storage dampens fluctuations in the annual seed crop ensuring adequate seedling establishment following fire*

It has been argued that canopy seed minimizes the problem of erratic flowering and coning, and years of drought-reduced seed production, through its additive effect (Gill, 1981c; McMaster & Zedler, 1981). Data on variations in degree of serotiny and extent of fluctuations in crop size compared with differences in range (reliability) about a given mean annual rainfall would be needed to test this hypothesis. Suitable data are not available.

This hypothesis is more easily tested by determining if serotinous species have greater crop fluctuations than those lacking seed storage. In collating data for 52 *Pinus* species, Strauss and Ledig (1985) found serotinous species were more likely to bear crops every year than non-serotinous species. Serotinous stands of *P. contorta* tend to produce constant seed crops whereas non-serotinous stands have wider fluctuations (Mowat, 1960; Smith, 1970). Cowling et al. (1987) were unable to demon-



strate a higher coefficient of variation (CV) in the annual seed crops of two serotinous *Banksia* species versus two non-serotinous species. The unusually high CV in cone production in *B. burdettii* (Lamont & Barker, 1988) was due to the exponential increase in cone production with plant age rather than marked annual fluctuations.

The reverse proposal, that highly serotinous species tend to develop widely ranging crop sizes, could also hold. Canopy seed storage favors the evolution of specialist pre-dispersal granivores (Myburgh et al., 1974; Scott, 1982). Crop fluctuations would limit population sizes of these specialist feeders, especially if they favored current season's crops (Forcella, 1980; Mattson, 1971; Schmidt et al., 1984; Scott, 1982). Much of our data, however, is consistent with post year-1 granivory (Cowling et al., 1987; Lamont & Barker, 1988; *B. prionotes* at Quairading, Western Australia, Lamont, unpubl. data) which greatly weakens this alternative view. Further, there are strategies other than crop fluctuations considered equally effective in limiting pre-dispersal seed losses, such as cone clustering in *Pinus contorta* (Smith, 1970) and variations in time of flowering in *Banksia* (Scott, 1982). Thus, there is at present no evidence to support the hypothesis that serotiny is specifically a response to, or cause of, unstable crop sizes.

### C. HYPOTHESIS THREE

#### *Serotiny maximizes seedling establishment because the biology of the species depends on dense monospecific stands*

This hypothesis proposes that there must be advantages in high plant density independent of promoting fire to ensure seed release (which is a consequence of canopy seed storage not a cause). For some pines with obligate pyriscence, dense stands suppress the understorey species so successfully that their post-fire seedlings need only compete with conspecifics (Bond, in press; Minnich, 1977; Vogl, 1973; Vogl et al., 1977). In contrast, the shrub/grass understorey that develops in more open stands is prone to more frequent fires than the seedling replacement capacity of these non-sprouting pines and they are eventually eliminated. However, in habitats with low rainfall, temperatures and/or nutrients, the vegetation becomes lower (pygmy forests) and the tree canopy and understorey merge, so that this distinction and the associated advantages no longer apply (Cayford & McRae, 1983; Heinselman, 1981; Kilgore, 1981; Westman & Whittaker, 1975).

Fires result in an improved environment for recruitment (Hypothesis 4) which may result in a selective advantage to species whose seedlings can benefit preferentially from these conditions. For example, the thicket-forming conifer, *Actinostrobus arenarius* (Table II), forms sharply-branched, impenetrable skeletons after fire that deter kangaroos from reaching the young seedlings which can only establish at this time (Lamont & Cowling, unpubl. data). The denser the thicket, the more effectively these herbivores are excluded. Since dense stands also inhibit inter-fire establishment, serotiny is an evolutionary consequence as well as the cause of the population structure of this species. The greater the biological advantages of high density and smaller the average annual seed crop, the greater the selective advantage of an increasing capacity for seed storage.

A simple test of the hypothesis is whether serotinous species routinely grow in dense monospecific stands. Examples among conifers supporting this hypothesis have already been cited (also see Schoenike, 1976) and Esler and Cowling (1990) provide

an example for a fynbos protea. However: (a) some densely-growing species lack any form of seed storage, e.g., *Dryandra sessilis*, in which annual crops are sufficient for forming dense stands after fire; (b) serotinous species are proportionately best represented in the species-rich scrub-heath with little species dominance in Australia and southern Africa (Lamont et al., 1977; Lamont et al., 1984; Taylor, 1978); (c) serotinous species may be well represented in open vegetation, e.g., sub-arctic woodlands of the serotinous *Picea mariana*, where fire is carried by a thick lichen mat which also inhibits inter-fire establishment (Black & Bliss, 1978); and (d) population density varies greatly at different sites and under different fire regimes (Bond et al., 1984; Cowling & Gxaba, 1990).

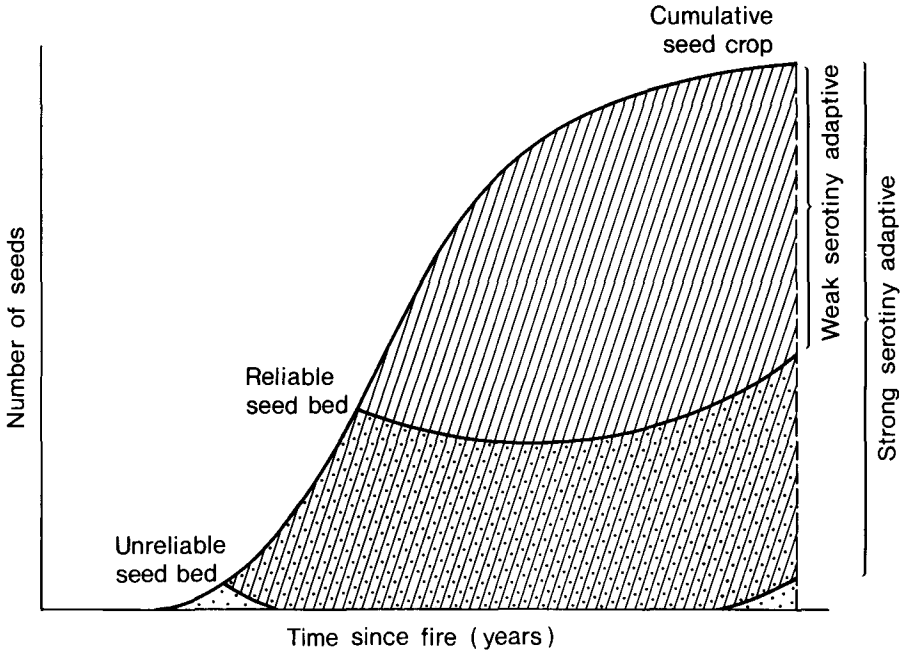
#### D. HYPOTHESIS FOUR

##### *Immediate post-fire release ensures seeds arrive on the optimal substrate for germination and establishment*

It is usually considered that the post-fire seed bed is favorable for germination and seedling growth on the following grounds: (a) litter removal enables seeds to reach the mineral soil; (b) nutrient, light and/or water availability are raised; (c) allelopathic substances are destroyed; (d) increased insolation at the soil surface raises soil temperatures; and (e) competitors, pathogens, granivores and/or herbivores are eliminated or reduced (Ashton, 1981; Ashton & Willis, 1982; Gill, 1981c; O'Dowd & Gill, 1984). All these changes, except (a), are also beneficial to soil-stored seeds, which are often cued to germinate *en masse* at the same time. Canopy storage in this case can be viewed as an alternative syndrome for taking advantage of the post-fire environment. The relative advantages of each syndrome are considered under Hypotheses 8 and 9 and in the Discussion.

Seed storage becomes more adaptive as the likelihood of inter-fire establishment or seed production by later established plants decreases (Givnish, 1981; McMaster & Zedler, 1981). Cowling and Lamont (1985a) have used this argument to help explain why ecotypes of three *Banksia* species at the xeric end of a climatic gradient were the most serotinous. Where conditions are sometimes suitable for inter-fire establishment (tree-fall gaps, exceptionally wet years) some spontaneous seed release in any year will be beneficial (Borchert, 1985; McMaster & Zedler, 1981). Here, post-fire sibling competition is largely replaced by inter-fire adult-seedling competition. Crossley (1956) interpreted increase in degree of serotiny with age in *Pinus contorta* as an adaptive response to decreasing opportunity for seedling establishment as the canopy closed over.

If the habitat is marginal for the species, or its germination and growth attributes are weak, seed release coincident with conditions optimal for establishment will favor strong serotiny. Since released seeds usually lack dormancy, the risk for serotinous species is that conditions may still not be suitable for establishment after fire. Apart from sources of post-dispersal seed loss (Hypothesis 5), no constraint is more important for germination than soil moisture (Bradstock & Myerscough, 1981; Lamont et al., 1991). Soil-stored seeds simply delay germination if it is a dry year or germination is staggered depending on depth of burial and penetration of the wet front. This is only partly overcome in some serotinous species by prolonged seed release and delay in germination of some seeds until the second year (Cowling & Lamont, 1987; Thomas & Wein, 1985; Zammit, 1984). If the reliability of the seed bed is



**Fig. 4.** Model of the probability of seedling establishment in relation to time since fire, reliability of the seed bed and cumulative crop size. ▨ these seeds should be released at maturity as they will be converted to seedlings, depending on reliability of the seed bed; ▩ these should be retained in the canopy as they will be wasted if released before the next fire, depending on reliability of the seed bed.

critical, then seed availability can be modelled as in Figure 4. If inter-fire establishment is always possible, then it is most adaptive for species to be only weakly serotinous. If establishment is only possible one or two years after fire, then it is most adaptive to be strongly serotinous.

To what extent is inter-fire establishment usually possible among serotinous species? O'Dowd and Gill (1984) concluded that percentage germination of *Eucalyptus delegatensis* was greater in a burnt site but percentage survivorship and growth was lower than in an unburnt (inter-fire) site. On a number grounds (litter from the scorched canopy smothering the seedlings, the surface was drier, browsing damage increased 500 times) they considered the post-fire substrate was far from ideal. More seedlings established only after fire because many more seeds were available then. For *Banksia burdettii* sown in autumn, there was no difference in germination success or seedling height by spring between burnt and unburnt sites (Lamont & Barker, 1988, unpubl. data). However, by the following autumn, there were no survivors in the unburnt plot while 60% of the original seedlings survived in the burnt plot. Predation was negligible.

A study of the germination and establishment of four co-occurring banksias showed that the post-fire substrate is not necessarily ideal and that herbivory has a major effect on seedling survival (Cowling & Lamont, 1987). However, it was concluded that the effect of summer drought was more extreme in the unburnt site (no seedlings survived eventually) apparently due to competition for water with adult plants. Seeds

of five strongly serotinous *Banksia* species were sown in a 25 year old stand at Hopetoun, Western Australia and their fate compared with those sown in an adjacent stand burnt a month before (Lamont & Connell, unpubl. data). For the unburnt stand, germination was similar, but growth and survival were much lower and herbivory (by insects) was much greater than in the burnt stand. By the next autumn there were almost no seedlings in the unburnt stand, attributable to the lower levels of soil moisture and severe grazing.

The so-called 'ash bed effect' resulting from fire is equivocal: high nutrient-demanding species benefit greatly (Loneragan & Loneragan, 1964), low nutrient-demanding species may be unaffected or even suppressed by the greater supply of minerals (Barrow, 1977; Grundon, 1972; Ozanne & Specht, 1981; Siddiqi et al., 1976). Serotinous species can be placed in all three categories, although those benefiting most from soil nutrients for establishment usually have small seeds of low nutrient content, whether serotinous or not (Barrow, 1977). Givnish (1981) interpreted low nutrient supply in the 'pine barrens' in eastern USA as favoring canopy seed storage by serving to increase fire-proneness of the vegetation and thus ensure seed release in association with the expected nutrient enrichment of the post-fire seed bed. Because of the tendency for seeds to aggregate into litter sites after fire, this improves access to nutrients but increases competition for water (Enright & Lamont, 1989b). In summary, while post-fire conditions may not be ideal, they are usually more conducive to seedling recruitment than inter-fire conditions, especially in relation to water availability.

#### E. HYPOTHESIS FIVE

##### *Synchronized seed release leads to post-dispersal predator satiation which ensures seedling establishment*

This hypothesis is functionally analogous to mast-fruiting (Janzen, 1971, 1974; Salisbury, 1942; Waller, 1979), except that the cause is different. If prolific post-fire seed release via serotiny is an evolutionary response to post-dispersal predation, then the following conditions must be met (O'Dowd & Gill, 1984): (a) consumers of dispersed seeds should regulate the size of the seed pool available for the post-fire generation; (b) the annual seed pool available on the ground should fluctuate widely (low between fires, high immediately after fires) so as to regulate granivore numbers; (c) cued seed release must be synchronized in time and space; (d) mass release must result in sufficient seed escaping from granivores to ensure parent replacement. Although not considered by O'Dowd and Gill (1984), a parallel set of arguments should hold for seedlings and their herbivores.

Since predator numbers are dependent on the availability of seeds or seedlings in the previous season, the greater the variation between years, as ensured by post-fire seed release, the greater the chance of seedlings continuing into the second year. Serotiny should operate on two such fronts in addressing this hypothesis. Firstly, it reduces the size of resident predator populations between fires by minimizing food available; secondly, it overwhelms the resident predators (if they survive the fire) and immigrants with excess food immediately after fire (Fig. 5). Usually the second point is made in the literature, but not the first. Figure 5 shows how there is more to be gained in post-dispersal predator population control if serotiny should develop in species which have reliable (or steadily increasing) annual seed crops than those

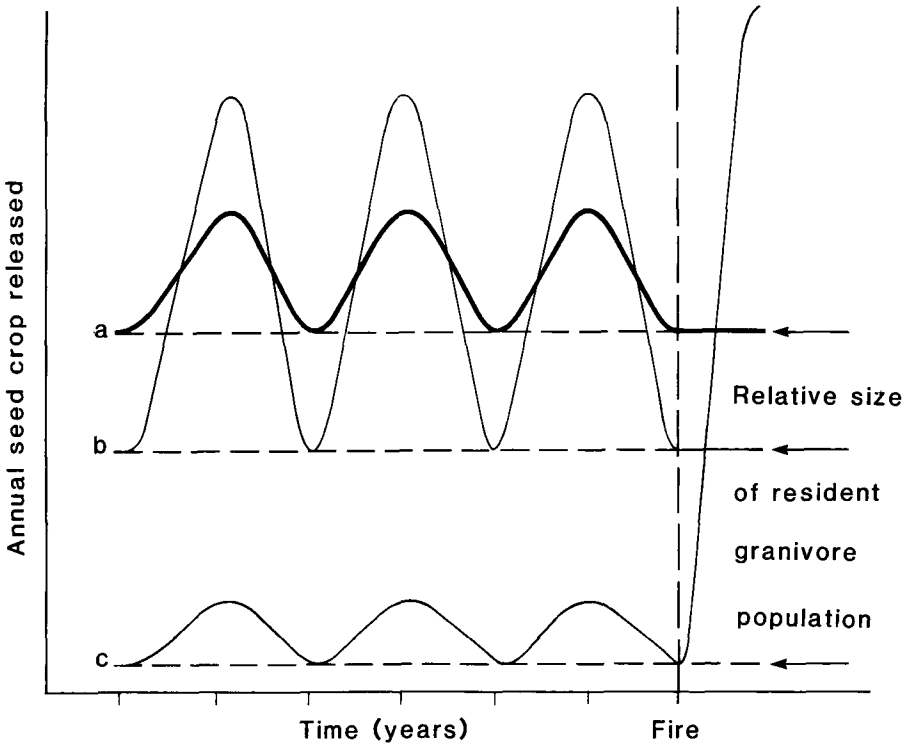


Fig. 5. Model of the effect on relative size of resident post-dispersal granivore populations on variations in size of the annual seed crop released. a) non-serotinous species with small fluctuations about the mean; b) non-serotinous species with wide fluctuations; c) strongly serotinous species with seed release largely restricted to the immediate post-fire period.

with widely fluctuating crops. This assumes stored seeds are well protected from pre-dispersal granivores, otherwise the reverse argument may hold (Muir & Lotan, 1985).

This hypothesis was supported on all four grounds above for seeds of a eucalypt by O'Dowd and Gill (1984), who contrasted it with site improvement (the previous hypothesis). Consumption of dispersed seeds and seedlings can have a major impact on recruitment, although strongly serotinous species are no more susceptible than non- or weakly serotinous species in this respect (Bond, 1984; Bond et al., 1984; Cowling & Lamont, 1987). We have found varying levels of *Banksia* seedling herbivory in burnt sites, depending on species, fire season, geographic location and extent of the fire (Cowling & Lamont, 1987; Enright & Lamont, 1989b; Lamont et al., 1991, unpubl. data). Herbivory in unburnt sites has varied even more, sometimes fully accounting for seedling death, especially in food-rich experimental plots, to negligible levels (Lamont & Barker, 1988, unpubl. data). At both burnt and unburnt sites, water availability during summer invariably proved to have more control over recruitment than herbivory.

Since predator numbers are dependent on the availability of seeds or seedlings in the previous season, the greater the variation between years, the greater the chance of some seeds and seedlings escaping in the long-term. On this basis, species that are

tied to a fairly constant or steadily increasing crop output should be highly serotinous in the presence of specialist post-dispersal predators. This ensures maximum differences between fire and non-fire years (Fig. 5). Species with wide fluctuations in their annual crops also benefit from canopy seed storage as this further enhances the potential difference between pre- and post-fire seed release. However, a prerequisite is that the seeds are well protected from pre-dispersal granivores. For species that cannot protect their seeds from pre-dispersal granivores, soil storage (with its requirement for some mechanism of escape from post-dispersal granivores) may be an evolutionary option. However, the type of storage is a generic trait in all but *Leucadendron*, suggesting phylogenetic constraints may override the possible evolutionary responses. Clearly, canopy seed storage is more effective than soil storage in maximizing the fluctuations in the annual on-ground seed pool. Both, however, have the capacity to swamp the site with seedlings after fire, depending on its intensity and extent.

Lamont et al. (1985) concluded that the apparent higher levels of soil storage (granivore avoidance) in the Cape of South Africa compared with temperate Australia could be attributed ultimately to the greater number of granivorous rodents there (Fox et al., 1985). It follows from the granivore satiation hypothesis that the degree of serotiny should also be higher in the Cape, but that is not so (Lamont et al., 1985).

Another potential problem with the hypothesis, as outlined in Figure 6, is that the timing of fires may be just as relevant in determining the extent of exposure to predators as the size of the stored crop. Spring fires may lead to much lower establishment levels than autumn fires (Bond, 1984; Bond et al., 1984; Cowling & Lamont, 1987; Midgley, 1989; Van Wilgen & Viviers, 1985). Thus, the within-year timing of seed release may be taken out of the evolutionary control of serotinous (pyriscent) species as it depends on the vagaries of fire. As spontaneous seed release is essentially a desiccation phenomenon, summer or autumn dispersal can be expected in non-serotinous species (Cowling & Lamont, 1987). If the primary function of serotiny is to minimize post-dispersal granivory, then it should occur in climates that favor seed release at or just before the onset of optimal conditions for germination and establishment. This will be early spring in cold climates, and late autumn in warm, mediterranean climates. This is the most fire-prone period in mediterranean climates where serotiny is also best represented. However, actual exposure is dependent on the opportunity for burial in 'safe sites' (Enright & Lamont, 1989b) as hazards for unburied seeds include lethal surface temperatures in warm climates as well as granivory (Cowling & Lamont, 1987). Mechanisms for delaying seed release after fire until the first winter rains have evolved in some serotinous species in mediterranean Australia (Cowling & Lamont, 1985b; Lamont & Barker, 1988).

As immigration tends to offset any *in situ* dilution of predators after fire, the larger the burnt patches, the greater the likelihood of predator satiation. Whelan and Main (1979) showed insect herbivory decreased towards the center of a burnt patch in banksia woodlands. In addition, the larger the patch, the lower the density of seeds received from adjacent unburnt non-serotinous plants after the fire. It follows that serotiny should be best developed in those woody vegetation types which support extensive, non-patchy fires (Lamont et al., 1985). That this is often the case does not prove post-dispersal predation is always limiting, since the support as outlined here is variable.

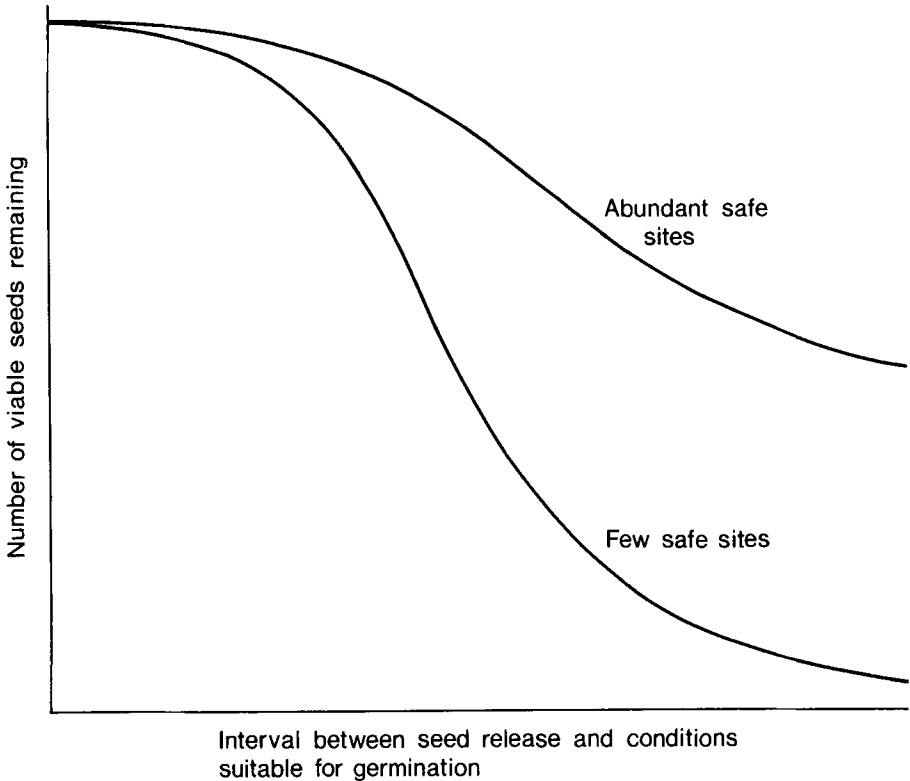


Fig. 6. The effect of time interval between seed release and conditions suitable for germination on seedling recruitment for a serotinous species as affected by the availability of 'safe sites' (protection from granivores, sunlight, desiccation, heat). Generalized from Enright and Lamont (1989b).

#### F. HYPOTHESIS SIX

*Seed release is delayed until conditions (post-fire)  
favor dispersal by wind*

Support for this hypothesis requires demonstration that: (a) wind dispersal is enhanced in the post-fire environment, (b) serotinous species are adapted for wind dispersal and (c) the extra distances increase the chances of seedling survival.

The distance diaspores travel is proportional to wind speed, which is affected by both windward and leeward obstacles (Lamont, 1985). Fire frees the canopy and ground of many obstacles to the passage of wind and seeds (Bond, 1988). The heat generated by the blackened soil surface following fire creates updraughts and small whirlwinds which may also carry and disperse diaspores (Le Maitre, pers. obs.). The significance of these observations must depend on serotinous species having well-developed structures for wind dispersal. This is supported in *Leucadendron*, where serotinous species have wings or parachutes and non-serotinous species are ant-

dispersed or have no dispersal mechanism (Bond, 1985; Williams 1972). All *Protea* species have long hairs which favor wind dispersal, although many lack canopy storage (Table I). In *P. burchellii*, the persistent style is burnt off by fire which enables the fruit to tumble along the ground more readily than those released in the absence of fire (Lamont, pers. obs.). Given a surface free of obstacles, Bond (1988) showed fruits of some *Protea* and *Leucadendron* species may be tumbled by the wind up to a distance of 100 m.

All species of *Banksia*, *Dryandra* and *Hakea* in the Proteaceae are prominently winged, whether highly serotinous or not. In some serotinous banksias (Section Abietinae), the wing is grasped by the separator as the means of pulling the seed out of the fruit and may rarely function in wind dispersal (Lamont, pers. obs.). Strictly non-serotinous Proteaceae produce air-buoyant seeds or fruits (e.g., *Grevillea*, *Serruria*) and/or attractants for ant or bird dispersers (e.g., *Leucospermum*, *Persoonia*) (Lamont et al., 1985). Seeds of pines lacking wings, on the other hand, are non-serotinous and primarily bird dispersed (Lanner, 1982).

The leptospermoid Myrtaceae have squat, angular seeds which provide little opportunity for wind-dispersal, whether serotinous or not. However, strong winds may be required to shake them from their capsules after fire (Cremer, 1966), as in *Leucadendron* (Williams, 1972), maximizing dispersal distances. The Myrtaceae are a striking exception to the rule that serotinous taxa are adapted for wind dispersal. Although many non-serotinous taxa are also wind dispersed, this does not refute the hypothesis. In fact, it might be expected that species with lower wind dispersability (e.g., larger diaspores) would be the serotinous ones, since wind dispersal is specifically facilitated in the post-fire environment. Van Leeuwen (unpubl. data) noted an inverse relationship between terminal velocity and seed size in the weakly serotinous *Banksia tricuspis*, i.e., larger seeds would disperse shorter distances. Some serotinous seeds are the largest in their genus or even sub-family (*Xylomelum angustifolium*, *Hakea platysperma*, *B. candolleana*). This would limit their dispersability, although they still have well-developed wings. However, there appears to be no relationship between follicle (seed?) size and degree of serotiny in *Banksia* species (Enright & Lamont, 1989a).

Few studies have been done on the likelihood of establishment relative to distance from the parent population. There may be no short-term gain in substantial departure from a fire-killed parent in a stable, favorable habitat, especially in the case of South African and Australian Proteaceae, many of which are extremely habitat specific (e.g., Lamont et al., 1989; Rourke, 1980). Furthermore, dispersal into the unburnt area is a waste of propagules given that inter-fire recruitment is seldom successful (Hypothesis 4). In a dissected landscape with fluctuating or deteriorating growing conditions and subject to extensive fire, there may be considerable long-term advantages in having sufficient dispersal capability to reach and pervade new habitats or localities where conspecifics were eliminated by previous fires (Cowling & Gxaba, 1990).

It is worth considering the inverse of this hypothesis, that high dispersability may be a *consequence* of serotiny. Wind dispersal enables the seed to escape the intense competition that otherwise results from synchronized seed release after fire, by reaching areas of lower density lacking conspecifics or perhaps even unburnt areas where inter-fire establishment and maturation are sometimes possible. However, efficient wind dispersal into post-fire litter sites may increase density-dependent mortality in serotinous species (Enright & Lamont, 1989b). In general, canopy-stored seeds appear



to be more dispersable than soil-stored seeds, but no more so than those with no storage.

#### G. HYPOTHESIS SEVEN

*Because seeds are short-lived after release, immediate post-fire dispersal ensures that the interval between release and optimal conditions for establishment is minimized*

Generally, the viability of canopy-stored seeds only drops markedly after release. Seeds of *Sequoiadendron sempervirens* which remain in full sunlight after release lose viability within 20 days (Wright & Bailey, 1979). Over the hot, dry summer, 100% of canopy-stored seeds of *Banksia hookeriana* remained viable; buried seeds were highly viable at 81% while seeds left on the soil surface fell to 2% (Enright & Lamont, 1989b). Dispersed seeds of other serotinous species usually lose viability within 12 months (Bond, 1985; Ledig & Little, 1979; Midgley et al., 1989; Van Staden, 1978). However, one prediction of this hypothesis is that released seeds of serotinous species should lose viability sooner than non-stored species. Seeds of *Banksia* species exposed on the soil over summer lost viability in versely proportional to their degree of serotiny in one study (Cowling & Lamont, 1987; Cowling et al., 1987) but there was no trend in the other (Enright & Lamont, 1989a, 1989b).

If inter-fire establishment is possible, the timing of release of non-serotinous seeds (usually late autumn in temperate climates) is likely to be more consistently suitable for germination (early winter) than for serotinous seeds released immediately after fire—which can occur at times of year other than late autumn. This problem is partly overcome in many banksias and related taxa with their wet-dry cycle requirement for seed release after fire (Cowling & Lamont, 1985b). This does not always ensure that seed release is delayed until late autumn (Cowling & Lamont, 1987; Enright & Lamont, 1989b). Where the suitability of post-fire conditions for establishment far outweigh inter-fire conditions (Hypotheses 3 and 4), serotiny results in release within 1–9 months of the start of the next growing season. The equivalent interval for non-stored seeds is similar. This interval may be too long for seeds exposed on the soil to high summer temperatures (Cowling & Lamont, 1987) or to large granivore populations (Bond, 1984), independent of longevity of the seeds under laboratory conditions. In addition, should it prove to be a dry year, conditions may still not be suitable for recruitment (Lamont et al., 1991; Le Maitre, 1988; Wellington & Noble, 1985a). The same constraints apply for seeds released at maturity.

Within the Proteaceae, there are clearly defined syndromes of serotiny coupled with wind dispersal and soft, short-lived seeds (once released) versus non-serotiny with ant dispersal and hard, long-lived seeds (Bond, 1985; Lamont et al., 1985; Majer & Lamont, 1985). Wind-dispersed diaspores have thin walls, independent of their degree of serotiny, in contrast to genera such as *Leucospermum* (Proteaceae) and *Acacia* (Mimosaceae) which have hard-coated diaspores stored in the soil. Poorly protected embryos are more prone to desiccation and are soon consumed by pathogens and granivores. Weiss (1984) found buried seeds of *Banksia integrifolia* were no longer viable after two years, whereas those of *Acacia longifolia* were still completely viable after three years. Serotiny prolongs the life of otherwise short-lived seeds. Hard dehiscent fruits and cones afford the same protection as hard testas,

although for a shorter time (Table II; Farrell & Ashton, 1978). Both syndromes ensure that seeds are exposed quickly to optimal establishment conditions after fire, although serotiny involves greater risk of failure (the next hypothesis).

#### H. HYPOTHESIS EIGHT

*Post-fire dispersal ensures seeds are ideally located in the soil to take advantage of growing-season rains*

This hypothesis has affinities with Hypothesis 4, but the comparison is with soil-stored seeds rather than with no storage. It is argued that wind blows the fire-released seeds into favorable microsites (Hypothesis 6)—often debris-filled depressions which are accessible to direct rain and run-off (Enright & Lamont, 1989b). Since the seeds lack any dormancy mechanism, germination begins after the first soaking rains. This contrasts with soil-stored seeds, whose depth may be beyond the critical heat-pulse generated by the fire (Shea et al., 1979) or post-fire temperature fluctuations (Brits, 1987), both of which may cue germination readiness, or the seed reserves may be exhausted before the germinants reach the soil surface (Auld, 1986). If rainfall is spasmodic or light, insufficient moisture may reach deeper seeds to initiate germination.

Soil-stored ('hard') seeds which do not germinate in the first year after fire may do so later if they are brought nearer to the surface later (wind, excavation by animals) or seasonal rainfall is higher. Released serotinous ('soft') seeds that do not germinate in the first year will be lost (heat, desiccation, granivory, decay). In this all or none situation, a dry post-fire year may mean local elimination (Bradstock & Myerscough, 1981; Lamont et al., 1991; Wellington & Noble, 1985a, 1985b). Where rainfall is erratic, soil-stored seeds are much less likely to be 'false cued' to germinate following fire than canopy-stored seeds (Fig. 7). Only when growing-season rainfall is reliable and substantial will fire-released seeds be consistently better placed than soil-stored seeds to take advantage of the opening-season rains. In such predictable climates there is no advantage in the 'bet-hedging' associated with soil storage.

There are no data available to substantiate this scenario. No study has compared the percentage germination of soil- and canopy-stored seeds from co-occurring species following fire. *Leucadendron* is a suitable genus as it contains both serotinous and ant-dispersed species (Bond, 1985; Midgley, 1987). The reliability of rainfall is a difficult concept as it is confounded with the yearly total, seasonal spread and likelihood of fire. The degree of serotiny of three *Banksia* species increased with decreasing annual rainfall and reliability (greater coefficient of variation) and increasing likelihood of fire, associated with a decrease in plant height (Cowling & Lamont, 1985a). However, Midgley (1987) has found that serotinous Proteaceae are most numerous in the wettest parts of the Cape of South Africa. Unlike Australia, where vegetation changes from a shrubland to an open woodland with increasing rainfall, Cape fynbos tends to develop a denser overstorey of proteaceous shrubs (Campbell & Werger, 1988; Specht & Moll, 1983). This makes conditions unsuitable for inter-fire establishment and thus serotiny/pyriscence is favored.

*Banksia cuneata*, on the verge of extinction, is fire-sensitive and obligately pyriscent. It occurs in land extensively cleared for agriculture that has experienced a downward trend in annual rainfall during the last 75 years (Pittock, 1988). Population

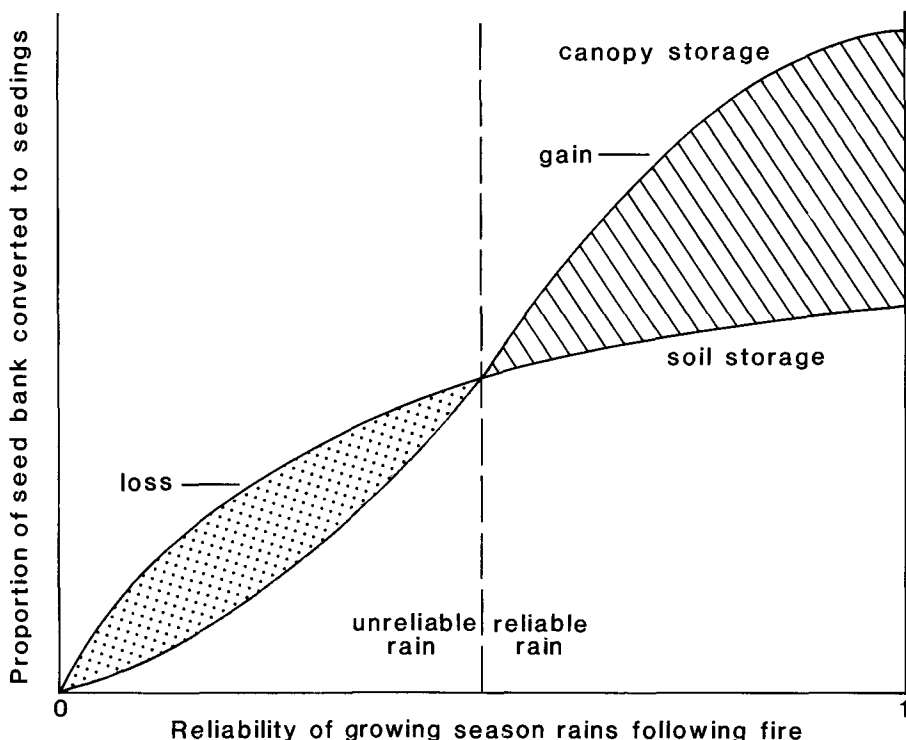
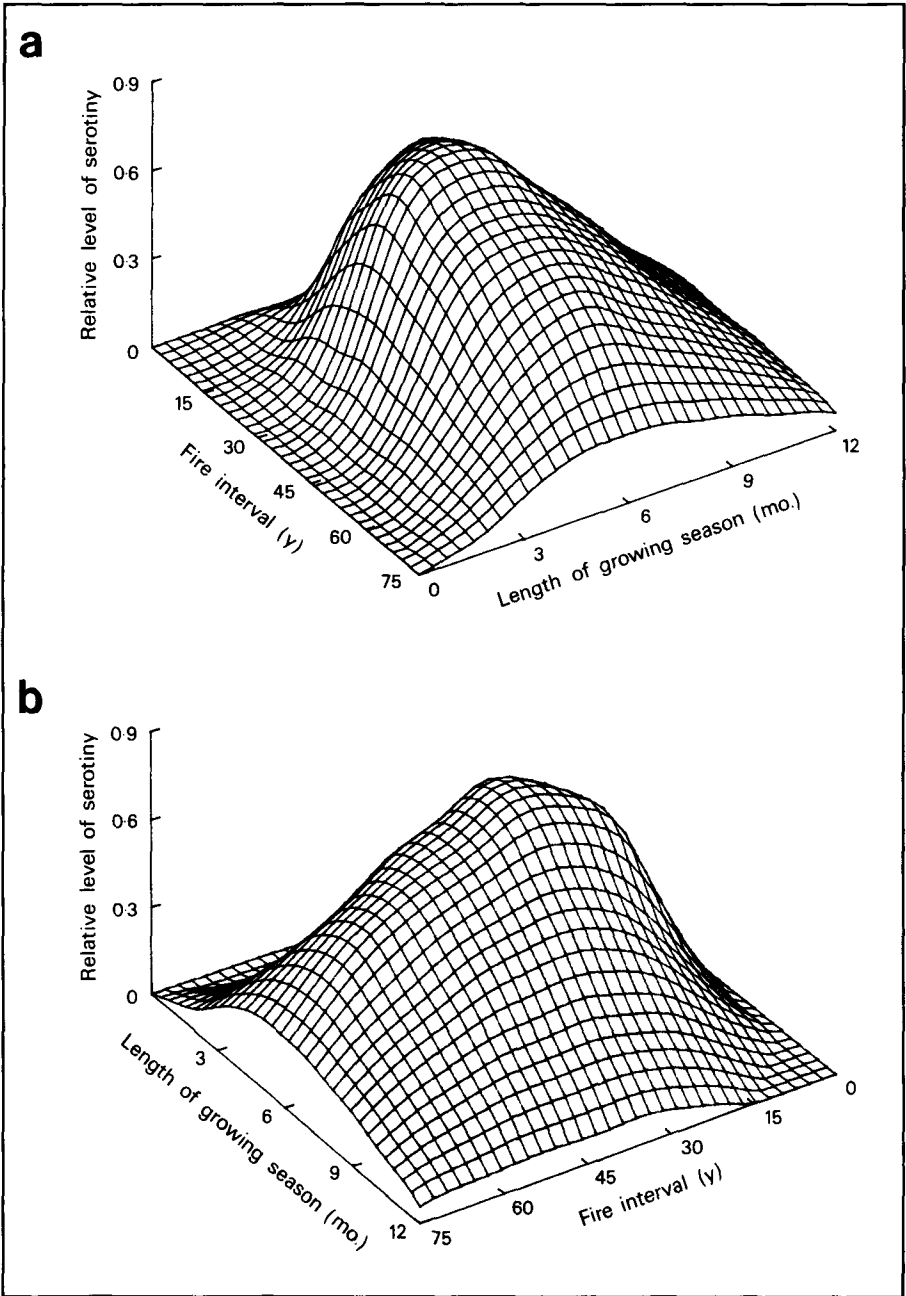


Fig. 7. Relationship between extent of seedling establishment from soil- and canopy-stored seeds with reliability of post-fire rainfall. The model assumes that the probability of fire is constant and canopy-released seeds are short-lived and more likely to germinate after rain than soil-stored seeds.

maintenance appears to require fire at 25–30 year intervals immediately followed by an exceptionally wet year (Lamont et al., 1991). Following an autumn fire during a year with rainfall 14% below the average for the last 15 years, 17,000 viable seeds were released per plant. Although 780 of these germinated, less than one seedling survived into the second year. There was no evidence of significant granivory or herbivory. Survival and growth were greatly increased by artificial watering and/or transplanting seedlings to moister depressions. With little opportunity for inter-fire establishment even in wetter years (negligible seed drop, other conditions unsuitable) and increasingly unreliable post-fire rain, the fate of this species appears sealed.

The proportion of species with canopy seed storage rather than soil storage increases in eucalypt forests as total rainfall and reliability decrease (Christensen & Kimber, 1975). It appears that fires are more frequent as well. Soil storage replaces canopy seed storage in semi-arid woody vegetation, especially those dominated by acacias (Davidson & Morton, 1984). Here, fires are probably too rare for fire-stimulated seed release and rainfall too unreliable to ensure survival of some seedlings after every fire. Figure 8 integrates the available data and expected trends in relation to both fire regime and annual rainfall. The model shows how it is possible to obtain opposite



**Fig. 8.** Two views of a 3-D model of the projected interaction between fire interval and mean length of the growing season in terms of their long-term effect on the proportion of woody species in the flora with canopy seed storage (the vertical dimension, arbitrary units) versus soil or no storage. Parts of the abscissa plane outside the 'dome' with zero canopy seed storage correspond to combinations of growing season and fire regime that are not possible. The model proposes that serotiny is best represented in climates with a short but reliable wet season and intermediate fire intervals relative to the mean lifespan of woody species in the flora.

trends in level of serotiny in the flora with increasing fire intervals and increasing rainfall. Canopy seed storage in woody plants should be rare when rainfall is either very low (unreliable) or high (reliable but non-seasonal) when fires are either frequent or rare. Serotiny should be best represented in temperate climates (reliable 4–6 month growing season) subject to fires at moderate intervals (say 20–30 years) relative to the mean reproductive lifespans of the component species. The soil storage graph would have a flatter 'dome' which would peak at a longer fire interval or closer to the mean lifespan of the species.

#### I. HYPOTHESIS NINE

##### *Canopy seed storage ensures minimal seed death from the fire required to create conditions suitable for germination*

The starting point for this hypothesis is that the post-fire seed bed is more conducive to seedling establishment than the pre-fire seed bed (Hypothesis 4). It proposes that seeds released before the fire are more exposed to lethal temperatures during the fire than canopy-stored seeds. It is necessary to show that canopy-stored seeds are less likely to experience lethal temperatures than seeds located on (non-stored) or in the soil. However, no data are available on temperatures reached by seeds during a fire within their storage structures.

There is no evidence of heat-death of canopy-stored seeds resulting from fire except on those rare occasions when old cones burn to ash (Beaufait, 1960; Lamont & Barker, 1988). All viability results for year one seed in Table II, except *Actinostrobos*, were based on seeds obtained after flaming the fruits and cones. Most seeds in thick-scaled (strongly serotinous) cones of three *Pinus* species survived at 250°C for 5 seconds in contrast with those in thin-scaled cones, while unprotected seeds all died at 115°C (Linhart, 1978). Reproductive structures of strongly serotinous species or populations require a higher temperature (Enright & Lamont, 1989a) or longer at a given temperature (Linhart, 1978) to open, which increases the likelihood of fire survival of the seeds compared with the weakly serotinous plants.

Following maximum temperatures near cones of up to 470°C, 78% of released seeds of *Banksia ericifolia* germinated, the same as for seeds removed from unburnt cones (Bradstock, 1985; Bradstock & Myerscough, 1981). Similar results were obtained for *B. serrata*, *Petrophile pulchella* and *Isopogon anemonifolius*. Even when cones of *Pinus banksiana* were exposed to 370–700°C for a few seconds, viability was maintained at 90% (Beaufait, 1960). M. Viviers and J. Midgley (pers. comm.) noted that percentage germination in *Leucadendron* species was even enhanced relative to controls when cones were exposed to temperatures up to 900°C for several seconds.

It is most unlikely that 'soft' seed lying on the soil surface or caught by litter would survive fire. Even the 'hard'-seeded *Acacia suaveolens* dies once temperatures reach 150°C (Auld, 1986). For a moderately intense fire, at least 33% of seeds buried at 10 mm died compared with no effect on those buried at 30 mm. Much depends on the usual location of the seeds in the soil profile, but few seedlings of *A. suaveolens* emerge from below 30 mm (also see Gill, 1981b; Shea et al., 1979). The hypothesis is clearly in need of some well-defined experiments, but present indications are that there is reasonable support for it.

## VIII. Discussion

### A. SEED STORAGE RELATIVE TO FIRE AND PLANT LIFESPAN

Canopy seed storage in woody plants is most closely associated with fire-prone habitats. No other disturbance/stress so effectively creates both a colonizing situation in otherwise stable woody vegetation and the cue for propagule release and germination. Prolonged summer drought is another candidate, but it is too much a matter of 'degree' to be the prime selective force and may herald a dry winter as well. The experience of drought stress varies between species and individuals, and drought-killed plants do not open up the habitat like fire so that the seed bed may remain hostile to seedling establishment. Post-fire showers can further refine the cueing of seed release to the start of the growing season in some species (Cowling & Lamont, 1985b; Vogl et al., 1977). The central place of fire explains why highly combustible vegetation-types or strata are more likely to contain serotinous species than more open or denser but less fire-prone communities (Fig. 8). In addition, the closer the mean fire interval is to just exceeding the reproductive maturity of a species, the greater the role of serotiny in maximizing the number of seeds available for the next generation.

Seed storage (versus non-storage) so increases fitness in a fire-prone environment where inter-fire establishment or maturation is negligible as to be advantageous to both resprouters and non-sprouters (Table IV). Seed storage by both life forms will always result in greater availability of propagules for each recruitment event. As inherent seed production by resprouters may be several orders of magnitude less than for non-sprouters (Enright & Lamont, 1989b) and they must die eventually (vegetative reproduction is rare, Lamont, 1988), canopy seed storage is ultimately as important as for non-sprouters. Furthermore, seedlings of resprouters have longer juvenile periods than non-sprouters (Abbott, 1985; Lamont & van Leeuwen, 1988). With a fluctuating fire frequency, canopy seed storage among resprouters will compensate for losses in potential seed productivity following fires which killed seedlings before their juvenile period was complete.

On the other hand, pre-existing adults of resprouters will recover in habitats burnt so often that they generally do not allow seedlings of any woody growth form to reach maturity (grasslands, savannas). Here, seed storage is irrelevant and serotiny is unknown [e.g., *Pinus palustris* (Platt et al., 1988), summer rainfall proteas (Rourke, 1980)]. Establishment may depend on fire-protected pockets (bare ground, rock outcrops) with germination possible at any time. Alternatively, these species may be on the path to extinction with gradual attrition of old plants, vestiges of former times with fluctuating fire frequencies that allowed inter-fire or post-fire recruitment (Table IV; Beard, 1958).

The relative fire frequency that shaped the evolutionary development of a species is the only aspect of Table IV that cannot be observed directly. It is clear that species killed by fire are adapted to fire intervals which routinely exceed their juvenile period. Fire-tolerant species are adapted to fluctuating fire intervals that sometimes fall short of the juvenile periods (resprouting prevents local elimination) but usually exceed it (to restore seed levels which can eventually replace senescent plants). Species that are consistent with these categories abound in *Banksia* (e.g., Abbott, 1985; Cowling et al., 1987; Lamont & Barker, 1988; Lamont & van Leeuwen, 1988). The model requires testing and refining for other genera and regions.

TABLE IV.

Predicted Relationships between serotiny, fire sensitivity of adults, fire frequency and likelihood of inter-fire seedling establishment for woody plants

Ratio of fire interval to juvenile period	Inter-fire establishment possible	Inter-fire establishment unlikely
High	Non-serotinous, fire-sensitive	Serotinous, fire-sensitive
Low	Serotinous, fire-sensitive/tolerant	Serotinous, fire-tolerant

Mean fire intervals which exceed the mean lifespan of a species will not favor the evolution of serotiny/pyriscence when inter-fire establishment or maturation is not possible. Seeds retained on dead plants are unlikely to survive a fire (Lamont & Barker, 1988). In this case, short-lived species will be replaced by longer-lived serotinous species or their place will be taken by species with soil storage. Soil-stored seeds are longer-lived and more likely to survive fire once the parent is dead (Gill, 1981a, 1981c; Mott & Groves, 1981). Even if inter-fire establishment and maturation are possible, storage will maximize the seeds available for the next generation when fire occurs during a plant's lifespan. Some fire regimes and growth forms will foster incomplete serotiny with some inter-fire seedling establishment, but most seeds still released after fire. Most species with canopy seed storage have some spontaneous seed release. However, 'degree of serotiny' has received little formal treatment (cf. Cowling & Lamont, 1985a), so that the empirical subtleties of such relationships remain largely unexplored.

In summary, mean fire intervals that are shorter than the mean juvenile periods of both non-sprouting and resprouting species will lead to their eventual extinction. Longer-term survivors are non-serotinous resprouters, some of whose seeds may reach less fire-prone pockets. Mean fire intervals that fall within the reproductive lifespan of a species will always favor the development of canopy or soil seed storage. Fire intervals that are more likely to exceed the lifespan will favor soil storage.

#### B. RELATIVE IMPORTANCE OF THE POSSIBLE FUNCTIONS OF SEROTINY

On purely theoretical grounds, we have shown that any level of canopy seed storage which decreases the gap between the number of seeds available from the current crop and the minimum required for population restoration (Hypothesis 1) will provide

an advantage over non-storage. In addition, the accumulation of many seed crops should raise the genetic diversity of the offspring and hence the capacity to regenerate under a wide range of post-fire conditions. However, these do not explain the relative advantages of serotiny over soil-stored seeds. We have also argued that the multiple overlapping generations possible when inter-fire establishment and maturation are favored is a less efficient way of supplying seeds for the post-fire population. To some extent, inter-fire establishment (ignoring tree fall gaps) may only be possible because of inadequate seed supply immediately post-fire—a further case for serotiny if annual productivity has reached its evolutionary limit. However, were mass seed release to be followed by a poor growing season or some other cause of widespread seedling loss, subsequent seed release via incomplete serotiny might enable some amends to be made. A cost-benefit analysis of canopy seed storage in relation to these possibilities would prove enlightening, although the empirical base remains weak and the topic requires long-term studies.

The next major conclusion is that the immediate post-fire environment must, and does, favor seedling establishment more than the inter-fire period. The gains from serotiny compared with non-storage in terms of ultimate number of seedlings recruited per parent, are maximized when inter-fire establishment is not possible. The likely reasons are numerous, but the main ones are reduced competition with parents and other pre-fire plants, especially for water (Hypothesis 4), and predator satiation (Hypothesis 5).

But it is a two-edged sword. If conditions still prove to be unsuitable for recruitment, local elimination is inevitable, in the short-term for non-sprouters and long-term for resprouters. Here the 'bet-hedging' of soil storage can have an advantage over the all-or-none pattern of serotiny/pyriscence. If the season proves too dry for germination of heat-treated seeds the first year, they may remain dormant until conditions become suitable, though further decay and granivory can be expected. For serotiny to succeed as a means of maximizing the ratio of seedlings recruited to seeds released, it is essential that all fires be followed that year by a reliable growing season (Hypothesis 8). This is the third major point we make. Improvement of the seed bed is not enough; extensive seedling establishment must be guaranteed through substantial post-dispersal rain. When these conditions apply, serotiny has advantages over both non-storage and soil storage.

Seedling recruitment, even with serotiny, is most likely to prove inadequate for population replacement if fires occur:

- (a) too soon after seed production commences in the young stand;
- (b) in too small an area to satiate the post-dispersal granivores and herbivores;
- (c) at too low a temperature to release sufficient seeds (Lamont and Barker, 1988);
- (d) during a dry year (Lamont et al., 1991);
- (e) within the late senescent phase or death of the stand; and
- (f) at too long an interval before the onset of the next growing season (Bond et al., 1984).

These conditions will affect species without any seed storage even more than serotinous species. Recruitment of seedlings via soil storage will be similarly inhibited under conditions a–c above, but not under d–f. While fire temperatures are irrelevant to seed release for species with soil storage, the heat pulse may be insufficient to break dormancy of buried seeds, a prerequisite for germination of hard-seeded species



(Auld, 1986). Other species appear to rely on leachates from ash or charcoal to stimulate germination (Keeley, 1987) which again might prove insufficient following mild fires. Unlike canopy seed storage, however, all these seeds are given a second chance during subsequent (hotter) fires depending on their longevity.

Serotinous species usually have wind-dispersed seeds and their spread will be enhanced after fire (Hypothesis 6) which may have advantages for long-term survival. Closely-related, non-serotinous taxa are similarly adapted for wind dispersal, whereas soil-stored seeds are usually dispersed by less effective biotic agents. Again, serotinous seeds are short-lived, but so too are the equivalent non-serotinous seeds (Hypothesis 7). This contrasts with the hard, long-lived seeds which are adapted for soil storage. Seed attributes, therefore, may contribute to the adaptive value of serotiny when compared with soil storage but not with non-storage.

Occurrence in dense stands appears to have benefits for some serotinous species (Hypothesis 3), but the cases are too few (and potentially teleological) to provide a general case for the adaptive advantages of canopy seed storage. One of the surprising conclusions is that species with widely fluctuating annual seed crops are neither more likely to be serotinous, nor to benefit more from it (Hypothesis 2). Since canopy-stored seeds are rarely completely protected from granivores, species with widely varying annual crops would keep predator numbers low only when granivory was restricted to the current crop (Forcella, 1980). If the seeds are well protected, species with regular annual crops will benefit more from serotiny with respect to overwhelming post-dispersal granivores and herbivores (Hypothesis 5). Rapid seed maturation, hard seed coats and granivore avoidance through efficient burial by ants (Majer & Lamont, 1985) may minimize the incidence of granivory for soil-stored seeds.

There is good evidence that serotinous seeds are well-insulated from the heat of a fire compared with seeds at the soil surface, but there is insufficient evidence that this is more effective than for soil-stored seeds (Hypothesis 9). (This entire review has been limited by the lack of comparative experiments between the three seed storage syndromes.) If this hypothesis is true, serotiny should be best represented in regions with the more intense fires (supported by Christensen & Kimber, 1975). There are time and weight limits on how much protective covering can be added to ant-dispersed seeds (Lamont et al., 1985) which do not apply to serotinous seed-bearing structures. Protection from granivores and agents of decay, insulation from fire heat and efficient post-fire seed release are part of a suite of attributes which maximize the advantages of canopy seed storage.

### C. GEOGRAPHIC DISTRIBUTION OF SPECIES WITH CANOPY SEED STORAGE

The abundance of serotinous species in the sclerophyll vegetation of Australia, South Africa and North America can now be explained. All occur in fire-prone habitats with highly seasonal, usually mediterranean, climates. Low water availability over summer and the imminence of fire usually confine seedling recruitment to the reliably wet winter immediately following fire. The mean fire intervals are sufficient to allow substantial crop-bearing years in woody plants but do not exceed their potential lifespan (Fig. 2). Nevertheless, overall seed production is relatively low due to the environmental constraints on growth—summer drought, recurrent fire, nutrient-impooverished soils, high plant density, sometimes cold winters and toxic, shallow or seasonally-waterlogged soils (Givnish, 1981; Pate & Beard, 1984; Specht,

1979; Vogl et al., 1977; Westman & Whittaker, 1975). There is a tendency to produce larger, nutrient-rich seeds (and larger seed-bearing structures) under these conditions (Baker, 1972; Beadle, 1968; Esler et al., 1989; Kuo et al., 1982) which enhance seedling establishment. But this is at the expense of seed numbers (Harper, 1977), accelerating the adaptive push towards serotiny/pyriscence: 'survival of the fittest' resides with those species able to recruit (most) genets into the post-fire community. This is a question of seed quantity (the role of canopy seed storage) as well as quality (matching of the genotype to the constraints of its expected habitat). Because there is a further trade-off between resprouting ability and seed production (Enright & Lamont, 1989b), this argument also holds for resprouting species in these regions as well as those killed by fire. As already discussed, the above scenario does not exclude soil seed storage; these conditions are just not as optimal nor as advantageous for its development compared with canopy storage.

The phenomenon is possibly best represented in Australia, followed by South Africa, because of the vast areas, especially in Australia south of the Tropic of Capricorn, that conform with the description above. In particular, the incidence of serotiny (on both a relative floristic and physiognomic basis) increases across mediterranean regions of the three sub-continentals as the apparent availability of mineral nutrients decreases, based on comparative analyses of vegetation (Cowling & Campbell, 1980; Naveh & Whittaker, 1979), plants (Lamont, 1982; Lamont et al., 1985; Mooney, 1983; Rundel, 1988) and soils (Lindsay, 1985). The higher levels of sclerophylly and evergreenness in mediterranean Australia followed by South Africa, attest to their lower nutrient availability compared with other mediterranean regions (Monk, 1966; Mooney, 1983; Rundel 1988)—no deciduous (nutrient-rich) species is known to be serotinous.

Woody flowering plants have largely replaced conifers as dominants on the most inhospitable soils in Australia and South Africa, but not in North America (Bond, in press). This coincided with prodigious speciation of genera with canopy seed storage capabilities, especially in the Myrtaceae and Proteaceae in Australia (Table I). To what extent phylogenetic constraints have contributed to these contrasting trends remains an open question—at present, an ecological explanation appears adequate. Any tendency for lower productivity of the vegetation in the poorer soils of Australia and South Africa is offset by its high combustibility (Van Wilgen et al., 1990) and slow rates of litter decomposition (Low & Lamont, 1990). The greater longevity of serotinous pine seeds compared with species in Australia and South Africa (Table II) may in fact reflect a reduced expectation of fire in coniferous forests. A further reduction in seed production in southern Australia, due to the possible increased likelihood of fire, lower nutrient levels and larger seeds compared with South Africa (Lamont et al., 1985), consolidated the drift towards abundant canopy seed storage in this region.

### IX. Acknowledgments

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