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SEED BIOLOGY AND SEED BANK DYNAMICS OF WESTERN AUSTRALIAN NATIVE PLANTS.

An understanding of both the seed biology and seed bank dynamics of any plant taxon or community is essential for the development of conservation and management protocols. This is especially important where regimes of disturbance (mechanical or fire) are used to maintain populations of reproductively mature plants.

The contribution of the soil seed bank in particular is often overlooked. Species richness estimates in communities do not usually taking into account those species that are represented only in the soil seed reserve. Likewise, the assessment of population status by individual plant census may be misleading, particularly where large and long-lived soil seed banks are maintained.

Factors such as the juvenile period, length of time before surviving individuals commence reproduction, levels of seed production and life span will influence the amount of seed available in the seed reserve. In Western Australia, research on the seed banks of native flora has largely focussed on serotinous species which maintain a store of canopy-held seed (Cowling & Lamont 1985; Cowling, Lamont & Pierce 1987; Enright & Lamont 1989b; Lamont 1988; Lamont & Barker 1988; Lamont & Barrett 1988; Lamont, Connell & Bergyl 1991; Lamont & van Leeuwen 1988; Witkowski, Lamont & Connell 1881). More recently attention has turned to the study of soil-stored seed banks (Meney *et al.* 1994, Vlahos & Bell 1986). This review, provides a summary of current knowledge on the location (plant, soil), extent, longevity, dispersal and turnover of seed banks for Western Australian plant taxa and communities. Aspects of individual species' seed biology are also discussed.

Two syndromes of seed release are recognised (Lamont, Le Maitre, Cowling & Enright 1991):

> **(i) release of seeds once mature**
> non-storage - no persistent seed store in the soil, with the seeds germinating during the first favourable period after release,
> soil storage - seeds persisting in or on the soil and successive seed crops accumulating to form a soil-stored seed bank.
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> **(ii) delayed release of mature seed (serotiny)** - release of mature seeds is delayed resulting in a build up of a canopy-stored seed bank. The term " bradyspory" is used in some literature to describe serotiny.

The maintenance of a persistent seed bank, either in the soil or canopy, offers an advantage over non-storage in that it enables populations to survive potentially destructive events such as fire and drought. Plants described as re-sprouters are capable of regenerating after fire or disturbance and so require only sufficient seed to off-set mortality of parent plants (Meney *et al.* 1994). Re-seeders on the other hand are killed by fire and disturbance and rely entirely on seed for their survival. In fire prone habitats they must accumulate a substantial soil-stored seed bank, produce large numbers of seed annually or release large numbers of canopy stored seeds in response to fire (Lamont & Barker 1988). Fire intervals need to be long enough to allow the plants to reach reproductive maturity and accumulate sufficient seed reserves. Exposure to spring fires prior to maturation of the seed crop may be especially damaging to reseeding species.

Reseeding species which do not maintain persistent seed stores and instead are dependent on annual inputs to the soil seed reserves for regeneration after disturbance may be susceptible to localised extinction, particularly where the interfire periods are short, the juvenile period is long or where plants are subjected to stresses such as drought or disease that may reduce their reproductive output (Meney *et al.* 1994).

CANOPY SEED STORAGE (SEROTINY)

Serontiny describes the condition where at least part of the previous seed crop is retained while the current seasons crop is mature (Lamont, Le Maitre, Cowling & Enright 1991). In serotinous species the seeds are stored in persistent, usually woody fruits and may be retained for one to many seasons. Seed release may occur spontaneously as the fruit ages, or synchronously in response to fire, drought or death of the plant or branches. The seed viability and duration of seed retention in some serotinous Western Australian species is compiled in Table 1.

Serotiny is characteristic of fire-prone, nutrient poor and seasonally dry sclerophyll habitats where interfire establishment of seedlings is unlikely (Lamont, Le Maitre, Cowling & Enright 1991). It is well developed in several Western Australian families, notably the Casuarinaceae (*Allocasuarina*, *Casuarina)*, Cupressaceae (*Actinostrobus, Callitris)*, Myrtaceae *(Agonis, Beaufortia, Callistemon, Calothamnus, Conothamnus, Eremaea, Eucalyptus, Leptospermum, Melaleuca, Phymatocarpus, Regelia)* and Proteaceae (*Banksia, Dryandra, Hakea, Isopogon, Lambertia, Petrophile, Strangea, Xylomelum*). Lamont, Le Maitre, Cowling and Enright (1991) review canopy seed storage in woody plants and discuss the adaptive significance of this storage syndrome.

The serotinous condition is not consistent within a genus, with different species varying greatly in their levels of seed retention. *Dryandra sessilis* for example lacks any form of seed storage, producing annual seed crops that are sufficient for regenerating dense stands after fire (Lamont, Le Maitre, Cowling & Enright 1991). *Leptospermum* includes species that are serotinous and others that are non-serotinous, the latter being hard seeded and forming a persistent soil seed bank (Keeley 1995).

Because of their reliance on seed for regeneration it would seem likely that serotiny be better represented in reseeder rather than resprouter species. This is only weakly supported in *Banksia* and there is no support in *Hakea* with 88% of both reseeding and resprouting species being serotinous (Lamont, Le Maitre, Cowling & Enright 1991). Bellairs and Bell (1990) found that for serotinous species in kwongan vegetation at Eneabba and Kulin, 32% were reseeding and 68% resprouting.

Reseeders reliance on seed is reflected in larger canopy seed reserves, as has been found in *Banksia* where reseeding species generally have larger viable canopy-stored seed crops than resprouting species (Table 2) (Cowling & Lamont 1987, Cowling *et al.* 1990, Lamont & Barker 1988, Lamont & van Leeuwen 1988). Evidence of this was reported in the northern sandplain near Eneabba where the two reseeding species, *B. hookeriana* and *B. leptophylla*, accumulated viable canopy stored seed banks ten to nearly 100 times larger than those for the co-occurring resprouting species *B. attenuata, B. candolleana* and *B. menziesii* (Enright and Lamont 1989b). At Mt. Adams, Cowling *et al.* (1987) recorded a higher mean number of canopy-stored viable seeds per plant, annual seed production per plant, proportion of cones which set seed and number of follicles per cone for the reseeding species *B. leptophylla* and *B. prionotes* than for the resprouting species *B. attenuata* and *B. menziesii*. In this study the seed bank of the serotinous *B. leptophylla* was 600 times greater than that of the weakly serotinous *B. menziesii*. *Banksia elegans*, a species which recovers from fire by resprouting from the stem and extensive suckering from lateral roots, rarely produces any seed despite prolific flowering (Lamont & Barrett 1988).

Table 1. Maximum duration of seed retention and viability in the first and final years before total pre-fire seed release or death for various taxa (taken from Lamont, Le Maitre, Cowling & Enright 1991).

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

*Maximum age of apparently viable seeds recorded (Cowling & Lamont 1985)

Bellairs and Bell (1990) reported that for members of the same genus, reseeding species tended to produce a greater number of canopy stored seeds per plant than resprouting members. Seed set was not necessarily low in resprouting species however, with *Allocasuarina acutivalvis*, *A. fraseriana*, *Calothamnus quadrifidus*, *Melaleuca acerosa*, and *M. tuberculata* all producing large numbers of canopy-stored seeds.

The frequency of fire has a major influence on the number of seeds that are available in the canopy seed reserve. In *Banksia,* many species take at least ten years to accumulate sufficient seed reserves (Cowling *et al.* 1987, Lamont & Barker 1988) and in some species, such as *B. grandis* and *B. tricuspis*, this period may be even longer (Abbott 1985, Lamont & van Leeuwen 1988). For reseeding species, fire intervals less than the period required for substantial seed production could result in local extinction.

Upper limits to fire intervals also need to be considered as reproductive output may decline in senescent stands. In *B. coccinea* for example, mortality increases dramatically in 15-20 year old stands. Since seeds on dead plants are soon released, fires at greater than 20 year intervals could be disastrous (Witkowski *et al.* 1991).

Several researchers have examined the influence of climate on canopy seed storage. Bellairs and Bell (1990) studied kwongan communities at Eneabba and Kulin and found that the size of the canopy seed reserve increased as average annual rainfall decreased, with seed production per plant higher at the more arid Kulin locality. In their study of wet sclerophyll forests Christensen and Kimber (1975) found that the proportion of species with canopy seed storage, rather than soil storage, increases in eucalypt forests as total rainfall and reliability decreases.

Variation in the degree of serotiny over a climatic gradient was examined in *Banksia attenuata*, *B. menziesii* and *B. prionotes*. Cowling and Lamont (1985) observed that in these species a decrease in annual rainfall and increase in temperature paralleled a decrease in plant height and an increase in the degree of serotiny. They concluded that the degree of serotiny was related to the moisture availability and fire characteristics of the site. In the dry scrub-heath communities fire consumes the entire canopy of the *Banksia* species, promoting the release of seed and facilitating recruitment in an otherwise unreliable seedbed. In wetter woodland areas to the south, seeds are released spontaneously and site conditions are more suitable for recruitment in the interfire period (Cowling & Lamont 1985). Alternatively, it could be viewed that increased serotiny in drier areas may have developed to protect seeds in a habitat that is more likely to be burnt.

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Variation in the degree of serotiny with climate was supported in studies on both *B. cuneata* and *B. prionotes* by Fee *et al.* (1992). They found that the proportion of seed retained within the canopy was higher in the drier Quairading population (80.7%, 52% respectively) than in the southern, wetter Pingelly population (67.3%, 1.3%). The *B. cuneata* population at Quairading comprised only a few cohorts, indicating that population regeneration is linked to seed release and recruitment after disturbance events. There is a continuous variation in the age classes of *B. cuneata* in the Pingelly population, evidence that recruitment occurs after spontaneous release of seed in the interfire period.

Local site conditions influenced seed production (fruit set levels) in the Pingelly populations of *B. cuneata* and *B. prionotes*, with the mean number of total follicles per plant increasing with distance from a salt scald (Fee *et al.* 1992). Furthermore, in *B. cuneata*, seed viability (proportion of firm seeds) and germination potential (viable seeds capable of germination) decreased as soil salinity levels increased.

CANOPY SEED STORAGE IN BANKSIA SPECIES

Banksia has been the most intensely studied genus with regard to seed bank dynamics in Western Australia. Some general trends noted from the literature were that:-

- viability of fresh seed is highest for reseeder species and lowest for resprouter species (Cowling *et al.* 1987, Lamont & Barker 1988, Lamont 1988);
- the rate of decline in seed viability and pre-dispersal predation by insects were lowest in the most serotinous species (Cowling *et al.* 1987);
- most species suffered pre-dispersal insect predation of seed, with destruction of seed increasing markedly with cone age (Lamont & Barker 1988, Cowling *et al.* 1987, Witkowski *et al.* 1991);
- considerable site variability occurs within a given species in the level of pre-dispersal predation by insects (Scott 1982, Scott & Black 1981);

- birds contribute to flowerhead and seed destruction in many species (Cowling *et al.* 1987, Lamont and Barker 1988, Lamont & van Leeuwen 1988, Scott & Black 1981, Witkowski *et al.* 1991).

Table 2 provides a summary of data on the total viable seedbank, fire response syndrome and degree of serotiny for *Banksia* species for which major studies have been undertaken.
Need to follow up literature on road-edge effects (see references to follow-up).

Lamont, Connell & Bergyl (1991) investigated seed storage in a road verge population of the strongly serotinous, non-sprouting ***Banksia cuneata*** at Quairading. 23 year old plants accumulated large seed reserves, with a mean total of 17 100 viable canopy-stored seed. Seed production was exponential in this species, the current years crop contributing 41% of the total canopy seed reserve.

Fee *et al.* (1992) compared the canopy seed reserves in populations of *B. cuneata* at Quairading and Pingelly and found that the mean total number of follicles per plant (for plants of all ages) was lower at Quairading (1482) than at Pingelly (2180). This may be related to the different age structure of the populations (cohorts vs multi-aged) as plants in the Quairading population were observed to retain a higher proportion of seed in the canopy. Up to 26,000 follicles (not seed) were recorded within the canopy of one of the largest plants at Pingelly.

Unlike the Quairading population, inter-fire recruitment of seedlings appeared to be common in the wetter Pingelly population of *B. cuneata* (Fee *et al.* 1992). Lamont, Connell & Bergyl (1991) concluded that recruitment after fire in populations of *B. cuneata* was not limited by the size and dynamics of the seed bank but by the weather pattern, with a wet season necessary for successful recruitment after seed release.

The seed bank dynamics of the widespread ***Banksia prionotes*** was studied by Cowling *et al.* (1987) in scrub heath near Mt. Adams. Fifteen year old plants stored a mean total of 124 viable seeds, with cone and follicle production found to vary greatly between plants and between years. Weak serotiny was supported in the study with seed older than the current years crop comprising only 34% of the total viable seed bank.

Fee *et al.* (1992) compared canopy seed storage in *B. prionotes* populations at Quairading and Pingelly, where the mean total number of follicles per plant (of all ages) was 8450 and 3108 respectively. The canopy seed store was lower at Pingelly due to a large number of infertile cones per plant and high percentage of open follicles. Higher levels of serotiny were apparent at the drier Quairading site with plants retaining most of their seed. The amount of available seed was reduced in the Quairading population due to large scale insect damage (Fee *et al.* 1992).

Collins and Spice (1986) studied the pollination biology in a population of *B. prionotes* at Wongamine Nature Reserve north east of Perth and recorded a mean of 30.3 follicles per cone (based on data from all cones). This compares well with data from Mt Adams

Table 2. Comparisons of total viable canopy-stored seed bank, fire response syndrome and degree of serontiny of banksias in south-western Australia.

	Plant age / time since last fire	Total no. of viable seeds per plant	Fire response	Degree of serotiny	Reference
Banksia attenuata	15	56[A] 47[B]	resprouter	strong	[A]Cowling *et al.* 1987, [B]Enright & Lamont 1989b
B. baxteri	15	80	seeder	strong	Witkowski *et al.* 1991
B. brownii	12# 25#	67 233	seeder		Galea & Lamont 1993
B. burdettii	15	456	seeder	strong	Lamont & Barker 1988
B. candolleana	15	32	resprouter	strong	Enright & Lamont 1989b
B. coccinea	15	69	seeder	weak	Witkowski *et al.* 1991
B. cuneata	15	968	seeder	strong	Lamont *et al.* 1991
B. elegans	16	<1	resprouter	strong	Lamont & Barrett 1988
B. hookeriana	15	371	seeder	strong	Enright & Lamont 1989b
B.leptophylla	15	1344[A] 276[B]	seeder	strong	[A]Cowling *et al.* 1987, [B]Enright & Lamont 1989b
B.menziesii	15	2[A] 5[B]	resprouter	weak	[A]Cowling *et al.* 1987, [B]Enright & Lamont 1989b
B. prionotes	15	124	seeder	weak	Cowling *et al.* 1987
B.speciosa	15	147	seeder	strong	Witkowski *et al.* 1991
B. tricuspis	18	84	reprouter	weak	Lamont & van Leeuwen1988

#modal age of plants in population

where 32.2 follicles per cone (from all cones) and 27.1 follicles per fertile cone were recorded (Cowling *et al.* 1987, Enright and Lamont 1989a).

Banksia tricuspis a weakly serotinous, resprouting species restricted to the Mt. Lesueur area stored a mean total of 84 viable seeds per adult plant 18 years after fire (Lamont and van Leeuwen 1988). This was almost entirely accounted for by the size of the crops for the last 3 years, with spontaneous release of seed and senescence of retained seed increasing sharply in the fourth and subsequent years. The greatest impact on seed production in *B. tricuspis* was found to be due not to poor flowering but to the failure of most plants to set fruit. This was largely attributable to invasion of the rachis by moth larvae and subsequent destruction of the inflorescences by larval-seeking cockatoos. Lamont and van Leeuwen (1988) observed that 89% of flowerheads were destroyed in this way and calculated that the amount of mature seeds would be four times greater if it were not for feeding by these animals.

Spontaneously released seed was found to be ineffective for recruitment in *B. tricuspis*, with seedlings only establishing in the period immediately after fire (Lamont and van Leeuwen 1988). Too frequent fires are likely to have a serious impact on populations as seedlings are slow to mature and take more than 20 years to develop fire resistance. In a population burnt by wildfire, 80% of 17 year old plants which had failed to set any seed were killed.

Witkowski *et al.* (1991) studied the seed bank dynamics in three co-occurring reseeding species of the southern coastal shrublands and observed that the build up of a viable seed bank with time occurred at a slower rate than for non-sprouting *Banksia* species of the northern sandplain. In ***Banksia coccinea*** reproductive output declined after peak seed production at 16 years. This was a result of sharply decreasing cone fertility (percentage of fertile cones) with plant age and increasing mortality in 15-20 year old stands. The mean number of viable seeds stored per plant was 51 in the 10 year old stand and 67 in the 21 year old stand, with the mean annual seed production not varying significantly between the two groups.

Seed storage increases exponentially in strongly serotinous ***Banksia baxteri*** and ***Banksia speciosa*** and had not reached its peak in the 21 year old stand (Witkowski *et al.* 1991). The percentage of fertile cones increased with plant age in *B. baxteri*, unlike *B. coccinea* and *B. speciosa* where cone fertility declined and remained unchanged with age respectively. The mean number of viable seeds stored per plant for *B. baxteri* was 12 in 10 year old plants and 581 in 21 year old plants. In *B. speciosa* the mean number of viable seeds per plant was 27 in 10 year old plants and 906 in 21 year old plants (Witkowski *et al.* 1991). Spontaneous release of seed results in the inter-fire recruitment of *B. coccinea* seedlings, however this does not occur every year and is likely to be related to favourable environmental conditions (Witkowski *et al.* 1991).

Galea & Lamont (1993) studied seed storage and release in living and dead plants of ***Banksia brownii***, a rare south coastal species threatened by dieback disease (*Phytophthora cinnamomi*). Populations at Millbrook Reserve, South Sister Reserve and Mt Hassell differed in the average number of viable seeds on living (66.9, 232.9 & 5.8 respectively) and dead (7.7, 87.7 & 2.9) plants, the reduced seed store in dead plants being the result of high levels of follicle dehiscence and fewer viable seeds per cone. The number of follicle per cone (mean ~ 24) did not differ significantly between the live and dead plants.

The effect of small population size on reproductive output in *B. brownii* was evident in the Mt Hassell population, where there was an average of only 2 fertile cones per plant (modal age 11 years), compared with 46 at South Sister (modal age 25 years) and 7 at Millbrook (modal age 12 years) (Galea & Lamont 1993). The large difference in number of fertile cones in the later two populations is likely to be the result of age difference, with plants at South Sister more than double the age of those at Millbrook. Collins *et al.* (1994) recorded a mean of 36.36 follicles per fertile cone in *B. brownii* populations studied at Millbrook and South Sister. They observed that fruiting success (ie. the percentage of inflorescences that set fruit) was not related to the number of inflorescences per tree but appeared to be dependent on inflorescence length.

Rees and Collins (1994) demonstrated that a positive linear relationship exists between plant biovolume and both inflorescence and infructescence (cone) production in two populations of ***Banksia verticillata*** near Albany. Approximately 40% of the inflorescences set fruit, with the mean number of follicles per cone ranging from 67.7 to 95.8 over two years and the two study sites. Monks *et al.* (1994) observed that *B. verticillata* plants growing on the margins of granite rocks had a greater (although not significantly different) number of fertile cones per plant, possibly as a result of increased access to moisture and nutrient resources. Rees and Collins (1994) estimated that viable seed production per *B. verticillata* plant during 1993 was 149 at Stony Hill and 299 at Newhills. The age of the populations was not determined and the total viable seed stores are likely to be much greater.

Banksia goodii is a strongly serotinous, clonal species that resprouts vigorously after fire. The majority of populations in its restricted range north of Albany are road verge remnants that have produced few or no seed over many years. Lamont, Whitten, Witkowski & Abbott (1993) compared the road verge and non-road verge populations of *B. goodii* where the mean number of plants per population was 7.8 and 163.3 respectively. While plants in both groups produced a similar total number of cones, the percentage of fertile cones was over five times less in the road verge populations. This resulted in a much lower mean seed production per plant (3.6 seed for road verge populations; 29.2 for non-road verge populations).

There was no significant difference in environmental attributes between road verge and non-road verge sites to account for the varying levels of seed production in *B. goodii*. Lamont, Klinkhamer & Witkowski (1993) suggest that low seed production in small populations of *B. goodii* is due not to inadequate pollinator visits, but to increasing pollen transfer between related individuals, resulting in an increased fraction of infertile cones or plants.

Lamont, Klinkhamer & Witkowski (1993) calculated that seed production becomes zero for population covering an area of less than $54m^2$, which is equivalent to about 6 plants. The effects of population size on seed production were present over the whole range of population sizes, indicating that even in large populations seed production may still not be at a maximum.

Comparing seed storage in three of the larger populations with the closely related and co-occurring *B. gardneri* found that *B. goodii* is not less fertile than its more widespread relative. The mean total number of viable seeds stored per plant ranged from 19.4 to 50.8 in *B. goodii* and from 4.0 to 24.4 in *B. gardneri* (Lamont, Whitten, Witkowski & Abbott 1993).

Banksia elegans reproduces vegetatively after fire by extensive suckering from its lateral roots (George 1981). It appears to rely little on seed for regeneration with no seedling recruitment observed in the populations studied west of Eneabba (Lamont 1988, Lamont & Barrett 1988). Individuals were found to be extremely infertile despite prolific flowering, producing an average of only one viable seed between four adult plants in a sixteen year period since the last fire (Lamont & Barrett 1988). More than 90% of the plants did not produce any seeds during this time.

A three fold increase in the number of *B. elegans* plants recorded after fire was due entirely to suckering from the lateral roots. Lamont (1988) concluded that vegetative reproduction is a nutrient conserving alternative to sexual reproduction in an environment where seedling establishment probably occurs only during periods of exceptional wet.

Lamont & Barker (1988) investigated the seed bank dynamics in ***Banksia burdettii*** a fire sensitive shrub restricted to the northern sandplains. Seed crops were slow to accumulate in this species as most individuals did not reach reproductive maturity until the sixth year after emergence. Plants produced an average of less than one cone in the first five years of flowering, increasing to 67 cones per plant by the 13th flowering year.

Despite this initially slow seed production *B. burdettii* had one of the largest seed banks (excluding *B. cuneata* and *B. leptophylla*) for plants of comparable age (Table 2). In sixteen year old vegetation in Watheroo National Park plants stored a mean total of 832 viable seeds (Lamont & Barker 1988). This large seed store is attributable to its escalating seed production with plant age and to strong serotiny, where at least 96% of the viable seed in any year remains stored on the plant.

In a study near Eneabba, Enright and Lamont (1989b) observed that the fire sensitive ***Banksia hookeriana*** had the highest seed availability of several associated *Bankisa* species (*B. leptophylla, B. attenuata, B. menziesii, B. candolleana*). Fifteen-year-old plants stored a mean total of 362-380 viable seeds (Enright & Lamont 1989b). Fertile cones averaged 11.4 follicles which is comparable to the 11.7 follicles per fertile cone recorded in plants near Mt Adams (Enright & Lamont 1989a). A mean of 12.2 intact (but not necessarily viable) seed per cone was recorded in shrubland at another study near Mt Adams (Lamont, Witkowski & Enright 1993).

Cowling, Lamont and Pierce (1987) observed considerable variation in cone and follicle production between plants and between years in a study of ***Banksia attenuata***, and several other *Banksia* species, near Mt Adams. They recorded a mean total of 56 viable canopy stored seed for fifteen year old plants. This compares well with the results recorded for fifteen year old plants at Eneabba where the mean total number of viable seeds ranged from 36-58 (Enright & Lamont 1989b). Follicle per fertile cone production was 3.6 and 5.8 at the two sites respectively.

In other studies based near Mt Adams *B. attenuata* plants produced a mean of 9.8 follicles per fertile cone (Enright & Lamont 1989a) and 11.7 intact (but not necessarily viable) seed per cone (Lamont, Witkowski & Enright 1993). Extreme serotiny was recorded for plants near Mt Adams, with seed older than the current years crop comprising 80% of the total viable seed bank (Cowling, Lamont & Pierce 1987). Cowling and Lamont (1985) reported seed storage in cones for up to 17 years in northern populations.

Further south, Lewis and Bell (1981) determined a mean of 13.3 follicles per cone at Cannington, although they do not specify if the data was collected from all or only fertile cones. Whelan and Burbidge (1980) recorded a mean of 11.3 follicles per fertile cone at Jandakot, noting that most of the inflorescences in the population had set fruit. At Jandakot and Cannington, Scott (1982) recorded a mean of 8.7 follicles per cone, based on data from all cones.

In their study on predation of *B. attenuata* fruits at Jandakot, Scott and Black (1981) found that trees in both low and high intensity burn areas had more than four times as many follicles per tree (180.9 and 207.0 respectively) as those in an unburnt area (43.5). Scott (1980) reported explosive seed production in *B. attenuata* in the second year following fires and the breaking of drought.

The seed storage capacity of the strongly serotinous, non-sprouting ***Banksia leptophylla*** was found to vary considerably according to location. Near Mt Adams, Cowling *et al.* (1987) reported a mean total of 1344 viable seeds per 15 year old plant, much more than the 217-335 viable seeds stored for plants of the same age at Eneabba (Enright & Lamont 1989b). The number of follicles per fertile cone also differed markedly in separate studies with 25.2 and 69.7 recorded near Mt Adams (Cowling *et al.* 1987, Enright and Lamont 1989a) and 18.6 recorded at Eneabba (Enright & Lamont 1989b). Differences in the location and seasonal availability of resources may have contributed to this variation.

Resprouting ***Banksia menziesii*** stored a mean total of only 2 and 5 viable seeds per 15 year old plant in populations studied at Mt Adams and Eneabba respectively (Cowling *et al.* 1987, Enright & Lamont 1989b). Seeds were not retained in the canopy for many years, being released spontaneously during warm, dry conditions in late summer to early autumn. Near Mt Adams the current years crop accounted for 75% of the total viable seed bank (Cowling, Lamont & Pierce 1987).

In the north of its range the mean number of follicles per fertile cone was 8.5 and 2.9 near Mt Adams (Enright & Lamont 1989a, Cowling *et al.* 1987) and 2.85 at Eneabba (Enright & Lamont 1989b). In the Cannington and Jandakot areas means of 7.5 follicles per cone (not specified whether all or only fertile cones) (Lewis and Bell 1981), 4.2 follicles per cone (Scott 1982, based on data from all cones) and 3.9 follicles per fertile cone (Whelan and Burbidge 1980) were recorded.

The small size of the ***Banksia ilicifolia*** inflorescence is reflected in the low follicle set per cone. At Jandakot, Whelan and Burbidge (1980) recorded 1.1 follicles per fertile cone while at Jandakot and Cannington a mean of 1.3 follicles, based on data from all cones, was recorded (Scott 1982). In the former study a large proportion of the inflorescences in the population remained barren.

Banksia grandis resprouts after fire and is only weakly serotinous, releasing 90% of its seed within the first year (Abbott 1985). Seed production in this species was found to vary at different sites, with a mean of 92.4 and 50.0 follicles per fertile cone recorded in populations near Jandakot and Jarrahdale respectively (Whelan & Burbidge 1980, Abbott 1985). In a study located at Jandakot and Cannington, Scott (1982) recorded a mean of 88.0 follicles per cone, however this was based on data from all cones (ie. fertile and infertile). Abbott (1985) observed that only a portion of the inflorescences in *B. grandis* develop into fertile cones, with the number differing greatly between years.

Stock *et al.* (1989) investigated seed production in ***Banksia laricina***, a reseeding species restricted to the Moore River area. Plants produced an average of 26.5 seeds (not necessarily viable) in the seventh year after emergence, by which time most plants had reached reproductive maturity. The research indicated that *B. laricina* possessed the capacity to regulate its reproductive output according to the available resources, producing a few large, high quality seed suitable for long-term seedling survival.

In ***Banksia littoralis*** near Jandakot, Whelan and Burbidge (1980) recorded a mean of 67.7 follicles per fertile cone. Scott (1982) recorded a mean of 56.0 follicles per cones, based on data from all cones, from a sample of trees at Jandakot and Cannington. Also at Cannington, Lewis and Bell (1981) determined an average of 98.0 follicles per cone, however they do not specify whether this data was collected from fertile or both fertile and infertile cones.

Lewis and Bell (1981) recorded an average of 56.0 follicles per cone for ***Banksia telmatiaea*** at Kenwick, but do not specify whether the data was collected from all or only fertile cones. A mean of 29.5 follicles per cone (including data from all cones) was recorded for this species by Scott (1982) at Jandakot and Cannington.

The total seed store is low in the strongly serotinous, resprouting ***Banksia candolleana*** with fifteen year old plants near Eneabba storing a mean total of only 31-34 viable seeds (Enright & Lamont 1989b). The number of follicles per fertile cone is low with a mean of 1.9 recorded at both Eneabba and Mt Adams (Enright & Lamont 1989a, 1989b).

Other *Banksia* species for which the number of follicles per fertile cone have been recorded include *B. occidentalis* (58.1) at Cheyne Beach (Hopper 1980) and *B. grossa* (8.6) and *B. micrantha* (13.6) at Mt Lesueur (Enright & Lamont 1989a).

SEED PRODUCTION AND CANOPY SEED STORAGE - MISCELLANEOUS SPECIES

Bell *et al.* (1987a) studied seed production in *Hakea obliqua* and *Beaufortia elegans,* serotinous species that are killed by fire. The plants differed in their seeding strategies, *H. obliqua* producing few, relatively large seeds and *B. elegans* producing massive numbers of small seeds. In 11 year old vegetation *H. obliqua* had accumulated an average of 6 seeds per plant while *B. elegans* plants had stored more than 800 seed.

In *Petrophile drummondii* south of Dongara 21 year old plants produced a mean of 31.5 intact (but not necessarily viable) seed per cone (Lamont, Witkowski and Enright 1993).

Seed production in the rare *Eucalyptus rhodantha* of the northern wheatbelt has been assessed by several researchers (Sampson 1988, Southcott 1992, McNee 1989). Fruit set is low in this species, which unlike the majority of other eucalypts produces only a few large flowers and fruits per individual. Fire stimulates the synchronous release of seed, although fruits may open in the absence of fire. McNee (1989) observed that more than half of the fruit on a plant could open during a single year.

Sampson (1988) observed annual variation in fruit production in a small population of *E. rhodantha* at Watheroo, with means of 16.7 and 7.3 fruits per tree in two successive seasons. Productivity was found to vary between groups of trees in a larger nearby stand, with the mean number of fruits per tree 3.9 in area 1 and 6.1 in area 2. The mean number of seeds per fruit for the two groups was 23.7 and 58.4 respectively.

Southcott (1992) found that population size affected seed production in *E. rhodantha*, with the proportion of apparently viable seed per fruit (relative to the original number of ovules) lower in the smaller Three Springs stands (36.4% and 44.8 %) than in the larger Watheroo stands (62.6% and 52.6 %). A small population at Watheroo had a high proportion of viable seed per fruit (66.9%) which may be attributed to the abundance of pollinators and quality of pollen from nearby sources.

The mean number of apparently viable seeds stored per plant ranged from 130 in the smallest stand at Three Springs to 745 in one of the large stands at Watheroo (Southcott 1992). The number of canopy-stored seeds per plant was proportional to the total canopy volume, which varies greatly within a population. A very large plant at Three Springs stored 741 viable seeds. Sampson (1988) estimated a mean of 868.7 seeds per tree for a group of thirty plants in one of the large Watheroo populations.

Predation of buds by the bud weevil *Haplonyx maximus* was the major factor limiting seed production in *Eucalyptus rhodantha* (Southcott 1992). Some damage to the buds by the parrot *Barnardius zonarius* was also recorded.

Follow up Lee Sages report on Lambertia.

POST-DISPERSAL LONGEVITY OF CANOPY STORED SEED

Serotinous species tend to produce highly viable seed which, once released, are short-lived and germinate during the first favourable period (Bell *et al.* 1987b, Bell *et al.* 1993, Cowling & Lamont 1987, Wallace 1966). It is therefore essential for seed release in serotinous species to be followed by a reliable growing season, otherwise the seed will soon lose viability.

The longevity of released seeds is influenced by their location in the soil profile (ie. lying on soil surface, buried in soil or litter), with buried seed less likely to experience lethal temperatures and desiccation. Lamont, Witkowski and Enright (1993) observed that seeds of *Banksia attenuata* and *B. hookeriana* exposed on the soil surface over summer-autumn lost 2 - 3 times the viability of those buried. In a similar experiment on *B. hookeriana*, seeds buried in the soil over summer retained high viability at 81% while viability of seeds left on the soil surface fell to 2% (Enright & Lamont 1989b).

Lamont, Witkowski & Enright (1993) studied the effect of post-fire litter microsites on the distribution of seed and seedlings of serotinous species (*B. attenuata, B. hookeriana, Hakea polyanthema, Petrophile drummondii*) in sclerophyll shrubland south of Dongara. They found that more than 75% of seeds of all seeds released after fire fell or were dispersed by wind into the litter patches. The seeds remained equally viable in the litter and sand patches and had equally high levels of germination. Seedlings in the litter patches were less likely to survive than those in the sand due to high seedling density and intensified competition for water.

CANOPY- BORNE SEED STORES IN COMMUNITIES

Bellairs and Bell (1990) quantified the canopy-borne seed store in kwongan communities at Kulin (1121 seeds/m2) and Eneabba (305 seeds/m2) and in the forest understorey at Jarrahdale (7 seeds/m2). They found that the density of serotinous species contributing to the seed bank was greatest at Eneabba, however the level of seed production per plant was greater at Kulin, resulting in a greater canopy-borne seed density. *Beaufortia micrantha*, *Calothamnus quadrifidus*, *Allocasuarina campestris* and *Melaleuca scabra* were the major contributors to the canopy seed reserve at Kulin. At Eneabba, *Beaufortia bracteosa*, *B. elegans*, *Eremaea violacea* and *Melaleuca acerosa* dominated the seed reserve. *Banksia attenuata*, *B. menziesii*, *B. hookeriana* and *B. grossa* contributed significantly to plant density but little to the seed density. *Hakea undulata* and *Allocasuarina fraseriana* were the only serotinous species present in the open forest communities at Jarrahdale.Serotiny was not well developed in *A. fraseriana* with many of the fruits open.

SOIL STORED SEED BANKS

The soil-stored seed reserve refers to the viable seeds present in the soil and on its surface and is composed of seeds that are readily germinable and seeds that remain dormant for several years (Roberts 1981). Germination of soil stored seed varies depending on depth of burial, penetration of moisture, soil turnover, seasonal conditions and dormancy requirements. Dormant seeds often germinate in response to disturbances such as clearing or fire, giving seedlings a better chance of survival in an environment free from the competition of mature plants.

Like canopy storage, soil storage acts as a buffer against annual fluctuations in seed production. Soil storage has an advantage over canopy storage however, in that the seeds may remain dormant following seed release until conditions become suitable for germination (Lamont, Le Maitre, Cowling and Enright 1991).

Soil seed banks vary in the quantity and type of seeds they contain and can provide information on both the former and future vegetation composition of a site (Roberts 1981). Seed from early successional species may persist buried or dormant for decades after a different flora has developed above ground. In Western Australia such an example was provided by the leguminous species *Acacia pulchella*, *A. strigosa* and *Bossiaea aquifolium*, which regenerated in vast numbers after a fire in Dwellingup in 1961. These species formed only a minor component of the vegetation prior to the fire, indicating that the seed store must have developed during a period when they were more dominant (Shea *et al.* 1979).

The quantity of seed available in the soil reserve at a given time depends on factors such as seasonal or yearly fluctuations of species and seed production, germination, variable dormancy, destruction by parasites and predators, dispersal and death (Carroll & Ashton 1965, Howard & Ashton 1967).

Researchers in Western Australia have experienced difficulty in quantifying soil stored seed reserves due to a combination of factors including spatially and temporally patchy seed production and predation, uneven dispersal, extraction techniques and variable germination requirements (Bellairs & Bell 1990, Vlahos & Bell 1986). When analysing soil seed reserves in wet sclerophyll forest, Christensen and Kimber (1975) found that the small seed of Compositae and herb species were not able to be detected by sieving alone and the samples had to be subjected to conditions suitable for germination. Analysis of soil seed banks is further complicated by the inability of some seeds (eg. Restionaceae) to germinate under standard germination conditions (Meney & Dixon 1988).

Vlahos and Bell (1986) estimated a germinable soil seed store in northern jarrah forest communities ranging from 377 to 1579 seeds/m^2 (average 767 seeds/m^2). They recorded a total of 68 taxa of vascular plants, with the species richness ranging from 20-45 species per site. Annual species dominated the seed reserve (35% of total species and 63% of total germinable seeds), with *Styldium calcaratum*, *Waitzia paniculata* and *Hydrocotyle callicarpa* contributing the highest seed densities. Sub-shrubs, including *Stylidium brunonianum*, *Boronia viminea*, *Platysace compressa* and *Xanthosia* sp., comprised 24% of the species and 28% of the total seed reserve. Shrub species contributed 16% of the species and only 5% of the seed reserve and were dominated by those killed by fire and requiring seed for regeneration (*Trymalium ledifolium*, *Thomasia pauciflora*, *Gompholobium marginatum*, *G. capitatum*, *Kennedia prostrata*, *K. coccinea*, *Acacia pulchella)*.

The dominant tree species and species normally recovering after fire from epicormic buds were absent from the jarrah forest seed bank. Wallace (1966) reported that seeds of *E. marginata* are not stored in the soil but germinate soon after reaching the ground, developing into lignotuberous seedlings which remain suppressed until competition is reduced by disturbance.

In wet sclerophyll forest herbaceous species and the Compositae represented over half the total number of seeds present in soil samples (Christensen & Kimber 1975). Large seed reserves of prolifically seeding species such as *Acacia pulchella*, *A. strigosa*, *A. decipiens*, *A. urophylla* were also found.

In the jarrah forest communities only 11-29% of the existing flora was represented in the soil. This was due to a lack of woody shrub and tree seed in the seed bank, despite a dominance of these species in the mature vegetation (Vlahos & Bell 1986). A similar situation was reported in several Victorian communities where the dominant species (eg, *Eucalyptus*, *Antherosperma*, *Callitris* and the Proteaceae) were absent while herbs and grasses, many with minute seed, dominated the seed bank (Carroll & Ashton 1965). Likewise, Howard and Ashton (1967) found that in Snow Gum woodland (*Eucalyptus pauciflora*) a conspicuous number of species that are dominant or frequent (eg . *E. pauciflora*) were completely absent from soil samples. They also recorded species in high frequency in the soil that were absent or extremely rare in the stands. These species must have been present in high numbers previously or were efficiently dispersed from distant sites. Contrary to these observations Hodgkinson *et al.* (1980), in researching the seed reserve in *Eucalyptus populnea* woodland in central New South Wales, found that there were no seeds in the soil not present as plants in the community.

Meney *et al.* (1994) determined a total soil seed bank in kwongan vegetation (of unspecified age) at Eneabba of 1545.2 seeds/m^2. Of this total, 15.1% was contributed by members of the Restionaceae (*Ecdeiocolea monostachya*, *Lepidobolus chaetocephalus*, *Lepidoblus preissianus*, *Loxocarya 'semiplana'*, *Lyginia barbata*, *Restio 'sinosus'*) and 21.1% by members of the Epacridaceae (*Andersonia gracilis*, *Astroloma xerophyllum*, *Leucopogon striatus*, *Lysinema ciliatum*). The higher proportion of Epacridaceae seed was notable, given that the parent plant densities were one fifth that of the Restionaceae. Reseeders reliance on seed for regeneration was reflected in the composition of the seed bank, with reseeding members of these families comprising a substantially higher proportion of the total seed bank than resprouters. In the Restionaceae and Epacridaceae 90% of the seed entering the soil seed bank lost viability after one year (Meney *et al.* 1994), hence the actual viable seed store at this site may be significantly lower.

In research also near Eneabba, Bellairs (1992) determined a germinable seed density from topsoil in undisturbed vegetation of 143-171 seeds/m^2 [need to check methods used to determine germinable seed density by Bellairs - **read abstract only, check PhD**. If standard methods were used then seed that requires special germination techniques or conditions to overcome dormancy would not have been recorded eg. Restionaceae which do not respond to normal germination techniques and require embryo extraction]

In members of the Epacridaceae and Restionaceae germination is restricted to the occurrence of fire or disturbance so persistent soil seed banks would be expected to accumulate in the years between fires. This was not found to be the case in kwongan vegetation near Eneabba. Meney *et al.* (1994) found that after fire seedlings occurred in similar densities as the estimated annual germinable seed input and that in an unburnt site, the soil seed bank did not differ appreciably from the estimates of annual seed production, even though the soil would have received several years seed production of most species. The large loss of soil stored seeds each year was attributed to rapid deterioration and loss of germinability. Predation may also have contributed to seed losses although this was not assessed.

Research on the rare wheatbelt species *Grevillea scapigera* has shown that seed banks do not accumulate, with 80% of the seeds produced predated by insects (Dixon pers. comm.) The fate of the remaining 20% of seeds is not known at this stage. **[Need to follow up progress with this research.]**

SEED PRODUCTION IN NON-SEROTINOUS SPECIES

The quantity and viability of seed set by an individual plant varies depending on many factors including climate, fire, disease, pre-dispersal predation, age, pollinator activity and the size and structure of the population.

Viability (using the tetrazolium chloride method) and germination tests conducted by Bell *et al.* (1987b) on a range of non-leguminous jarrah forest understorey species indicated that a large proportion of species produced mostly inviable seed. Long-lived, resprouting species generally had the lowest viability percentages while species which regenerate from seed tended to produce more abundant seed and a higher proportion of viable seed.

In a later review, Bell *et al.* (1993) reported that there was no difference between the viability of seed for species in the seeder and resprouter categories. Comparing seed storage syndromes (ie. soil vs canopy storage) showed that species which disperse seed on ripening have a lower seed viability than serotinous species which invest considerable resources in providing protective fruit structures.

In Western Australian species low seed viability has been recorded in **Chloanthaceae** (*Lachnostachys*), **Cupressaceae** (*Actinostrobus*), **Epacridaceae** (*Andersonia, Astroloma, Lysinema*), **Myrtaceae** (*Pileanthus, Calytrix, Darwinia, Scholtzia, Verticordia*), **Proteaceae** (*Petrophile, Conospermum, Grevillea, Stirlingia*), **Rutaceae** (*Boronia*) and **Thymeleaceae** (*Pimelea*) (Schatral & Osborne 1994, Sisteberio & Plummer 1994) although the value of such results will be dependent on the germination techniques employed. Schatral and Osborne (1994) observed that seed viability in *Darwinia speciosa*, *Conospermum triplinervium*, *Dryandra carlinoides*, *D. tridentata* and *Petrophile drummondii* varied with the year of collection.

Annual seedfall (seed/m^2) of some common woody seeder species in 3-5 year wet sclerophyll forest has been calculated by Christensen and Kimber (1975). Seedfall was greatest for *Acacia* species, ranging from 2 to 4630 seed/m^2. *Bossiaea linophylla* and *B. laidawiana* produced up to 118 seeds/m^2 and 48 seeds/m^2 respectively while *Trymalium spathulatum* produced only 4 seeds/m^2.

Seed production in the relatively short-lived *Acacia pulchella* var. *glaberrima* commences at 2 years, reaching a maximum of 12 000 seeds/plant/year at 3 or 4 years and declining to 2000 seeds/plant in the 13th year (Monk *et al.* 1981). Only a small proportion of shed seed accumulated in the soil under the canopy of currently alive plants, reaching a maximum of between 4000 and 5000 seeds in stands of 7 years and older. Heavy removal or predation of seeds by ants and birds must have occurred to account for the lower than predicted accumulation of seed in the soil.

The number of seeds (containing embryos) per culm (ie. the jointed stems bearing leaves, branchlets and spikelets) calculated for rush and sedge species at sites near Eneabba over several years were - *Ecdeiocolea monstachya* (1.0), *Lepidobolus chaetocephalus* (11.5, 18.2), *Lepidobolus preissianus* (4.0), *Loxocarya semiplana* (3.0), *Lyginia barbata* (1.3, 1.0), *Mesomelaena pseudostygia* (0.1), *Restio sinosus* (3.7, 1.4), *Restio* aff. *sphacelatus* (1.6) (Meney & Dixon 1988, Meney *et al.* 1994). Seed production in these species varies from year to year and is dependent on the extent of grazing and on seasonal factors. All species (*Ecdeiocolea monostachya*, *Lepidobolus chaetocephalus*, *Restio* aff. *sphacelatus*, *Mesomelaena pseudostygia*) examined by Meney and Dixon (1988) experienced some damage or removal of new shoots, floral structures and intact seed by insect larvae (Lepidopteran and less commonly Coleopteran) and by grazing kangaroos and rabbits. Loss to these factors was minor in *R.* aff. *sphacelatus* and *M. pseudostygia*.

Pate *et al.* (1985) studied the biology of fire ephemerals in sclerophyllous shrubland in the Jurien - Badgingarra region, concluding that fire ephemerals, especially those that set seed only once (monocarpic species), tend to produce a large number of small seeds with a poor nutrient content. These species maximise propagule output and rely on the ready nutrient supply of the ash bed after a fire. Reproductive output (seeds/plant/year) in the monocarpic species studied was 1477 (*Stipa elegantissima*), 1367 (*Athrixia asteroides*), 674 (*Waitzia suaveolens*), 552 (*Isotoma hypocrateriformis*), 490 (*Calandrinia corrigioloides*), 417 (*Podotheca gnaphalioides*), 157 (*Waitzia paniculata*) and 39 (*Trachymene cyanopetala)*. In the much larger polycarpic species, which reproduce several to many times after reaching maturity, *Gyrostemon ramulosus* produced 11860 and 21590 seed/plant in the 2nd and 3rd years respectively while the larger-seeded *Tersonia brevipes* produced only 500 seed/plant in the 2nd year and 900 seed/plant in the 3rd year.

A study on seed set in *Hibbertia* species (Schatral & Osborne 1994) found that considerable variation occurred between species, with the proportion of flowers setting seed almost 90% in *H. amplexicaulis*, about 30% in *H. commutata* and between 1.5% and 11% in *H. hypericoides*. The proportion of actually viable seed per flower was low for all species with *H. commutata* averaging 16-20 viable seeds/flower, *H. amplexicaulis*, *H. cuneiformis* and *H. huegelii* 7-10 viable seeds/flower and *H. hypericoides* less thas 1 viable seed/flower. Exclusion experiments showed that a lack of suitable pollinators may be the cause of low seed set observed in *H. hypericoides*. Insect predation had a significant impact on seed set in *Hibbertia* species with beetles causing serious damage to a high proportion of the flowers, and other insects (moths, wasps and weevils) damaging the maturing fruits and seeds. Seed viability of 45-60% was recorded by Schatral and Osborne (1994) for fresh *Hibbertia* seed.

Annual seed production (total seeds/m^2) calculated for Epacridaceae species (of unspecified age) in kwongan vegetation near Eneabba was 74 for *Andersonia gracilis*, 550 for *Astroloma xerophyllum*, 668 for *Leucopogon striatus* and 1052 for *Lysinema ciliatum* (Meney *et al.* 1994).

Geleznowia verrucosa, a species of the northern sandplains, produces abundant seed, up to 500 seed on a mature 30cm tall plant (Paynter & Dixon 1990).

Lamont (1982) observed that cultivated mature (4m) plants of *Grevillea leucopteris*, a species occurring from north of Moora to Kalbarri, produced an estimated 3000 to 5000 seed annually.

Research on the seed biology of several *Eremophila* species is underway **(follow up research by Guy Richmond**).

LOCATION OF SEED IN THE SOIL PROFILE

Seeds may enter the soil and be distributed through the soil profile by various means including percolating rain, falling down crevices, self-burial (eg. weedy species with hooks or awns), accumulation of leaf litter and soil, unintentional burial by animals (eg. earthworms, mammals) and harvesting activities (eg. ants) (Harper 1977, Howard & Ashton 1967).

On the whole, buried seeds last longer than seeds located in the surface layers which may germinate or perish more quickly (Ewart 1908). Burial may impose dormancy on seed, placing them in conditions of low oxygen, moisture and light where they do not germinate. Most deeply buried seeds appear not to germinate until, and if, they are returned to the surface and a large proportion of the seed bank probably decays *in situ* (Carroll & Ashton 1965). Burrowing animals, falling trees and soil erosion may bring up seed from deep in the soil profile.

The location of seed in the soil profile has been investigated in several Western Australian communities. Christensen and Kimber (1975) analysed the number and location (litter, 0-1cm, 1-2cm) of seeds in litter and soil under six to ten year old wet sclerophyll (Karri) forest. They found that most of the seed was located in the 0-1cm soil layer, followed by the litter layer. Small seeds that could only be detected through subjecting the soil to conditions suitable for germination dominated the 1-2cm soil layer. In the northern Jarrah forest the upper 10cm of topsoil contained significant stores of seed, with the majority found at 2-5cm depth (Grant and Bell 1994).

Monk *et al.* (1981) examined the location of *Acacia pulchella* var. *glaberrima* seed in the coastal sands in and around Perth. They recorded seed at depths up to 15cm, with the majority located within the top 3cm. For *Acacia pulchella* in upland jarrah forest sites, Shea *et al.* (1979) found that the majority of seed was located in the first 6cm of the soil. Observations of seed burial by ants found that *Grevillea leucopteris* seeds reached a storage depth of 1-9cm overnight (Lamont 1982).

These results from local research compare well with research on seed distribution in *Eucalyptus populnea* woodland in New South Wales where 78% of the soil stored seed was in the 0-1 cm layer, 22% in 1-4 cm and 0% in 4-10 cm (Hodgkinson *et al.* 1980). In

Snow Gum, (*Eucalyptus pauciflora*) woodlands Howard and Ashton (1967) estimated that 83% of the total seed to a depth of 17.5 cm was located in the top 2.5 cm. After fire in dry sclerophyll forest near Canberra, Purdie (1977) observed that most of the seeds that occurred in the litter layer were lost, particularly with high intensity fire, but that many seeds stored in the soil survived.

The influence of burial depth on germination has been investigated in *Acacia pulchella* var. *glaberrima* by Monk *et al.* (1981). Seeds germinated successfully from depths up to 5.5cm after fire, whereas in laboratory trials buried seed emerged successfully from depths of 20cm. This suggests that penetration of the dormancy breaking heat from a fire, rather than depth of burial, determined whether the seed germinated.

Grant and Bell (1994) studied the germination of twelve jarrah forest species in controlled glass house experiments and found that while all species were capable of emerging from 2cm depth, four of the species (*Stylidium calcaratum*, *Chamaescilla corymbosa*, *Eucalyptus marginata* and *Xanthorrhoea gracilis*) were unable to emerge from 5cm depth. The leguminous species *Acacia pulchella*, *Bossiaea aquifolium* and *Kennedia coccinea* were capable of emerging from a burial depth of 15cm.

Floyd (1976) in his research in the wet sclerophyll forest of NSW, concluded that size of the seed determined the depth of successful germination. Small seeds such as those of *Dodonaea* emerged from a maximum depth of approximately 5 cm whereas the larger seeds of *Kennedia* germinated from depths of approximately 6.5 cm.

LONGEVITY OF SOIL STORED SEED

Harper (1977) has made several generalisations about seed longevity in the soil, claiming that long-lived seeds are characteristic of disturbed habitats, tend to be small in size and are often annuals or biennials. In his review on seed biology in the soil Cook (1980) concluded that selection for persistence and longevity favoured a decrease in seed size and a relative increase in seed coat thickness. In Australia long-lived seeds (eg. *Acacia*, *Hardenbergia* etc.) typically have hard, impermeable seed coats.

For the Western Australian flora information on the longevity of seed in the soil is lacking for all but a few species, however some assumptions can be made based on observations of abundant seedlings in areas that have been disturbed or burnt. Dependence on fire or disturbance to stimulate germination suggests that the seeds may be lying dormant in the soil, resulting in the accumulation of large, persistent seed reserves. Contradictory evidence to such a theory is provided by Meney *et al.* (1994) who observed that although recruitment occurs only after fire, persistent seed banks did not develop in the Epacridaceae and Restionaceae due to large annual losses in seed viability.

Longevity of seed in the soil may be particularly evident where a species formed only a minor component or was absent from the vegetation prior to fire or disturbance. Certainly species such as fire ephemerals (eg. Gyrostemonaceae), which usually complete their life cycle before the advent of another fire would require a seed bank of long lived seed (Pate *et al.* 1995). Seeds that fall into the mymecochorous category are also likely to be relatively long-lived as they have adapted to dispersal and usually burial by ants by providing an alternative food source in the elaiosome.

Families which show a germination response to fire or mechanical disturbance include **Papilionaceae** (*Bossiaea, Chorizema, Daviesia, Gastrolobium, Hovea, Jacksonia, Mirbelia*), **Mimosaceae** (*Acacia*), **Proteaceae** (*Grevillea, Adenanthos, Stirlingia, Persoonia*), **Rutaceae** (*Boronia, Geleznowia*), **Myoporaceae** (*Eremophila, Myoporum*), **Myrtaceae** (*Chamelaucium, Thryptomene*), **Haloragaceae** (*Haloragis, Gonocarpus*), **Haemadoraceae** (*Anigozanthos, Conostylis, Haemodorum*), **Chloanthaceae** *(Pityrodia*), **Xyridaceae** (*Xyris*), **Portulacaeceae** (*Rumicastrum*), **Solanaceae** (*Anthocercis*), **Sterculiaceae** (*Thomasia*), **Apiaceae** *(Trachymene, Actinotus*), **Pittosporaceae** (*Billardieria*), **Gyrostemonaceae** (*Gyrostemon*), **Antheriaceae** (*Sowerbaea, Laxmannia*), **Goodeniaceae** (*Leschenaultia*), ?**Lamiaceae** (*Hemigenia, Hemiandra*), **Stylidiaceae** (*Stylidium*), **Stackhousiaceae** (*Stackhousia, Tripterococcus*), **Rhamnaceae** (*Trymalium, ?Spyridium, ?Cryptandra)* (Beardsell *et al.* 1993, Beardsell & Richards 1987, Bell *et al.* 1993, Egerton-Warburton *et al.* 1994, Fox *et al.* 1987, Lamont 1982, Lamont and Grey 1984, Mollemans *et al.* 1993, Paynter & Dixon 1991, Robinson & Coates 1995, Shea *et al.* 1979).

Untreated seed from many of these genera show poor germination in the laboratory, indicating that some dormancy mechanism may be present and providing support for longevity (Taylor in Bell *et al.* 1993, Fox *et al.* 1987, Ewart 1925, Cochrane pers. comm.). **Need to follow up research on smoke - see Kingsley Dixon**.

Other genera showing poor germination in laboratory trials include **Iridaceae** (*Patersonia, Orthrosanthus*), **Violaceae** (*Hybanthus*), **Lobeliaceae** (*Isotoma, Lobelia*), **Tremandraceae** (*Tetratheca*), **Dasypogonaceae** (*Dasypogon, Lomandra*), **Dilleniaceae** (*Hibbertia*), **Myrtaceae** (*Verticordia, Pileanthus, Hypocalymma, Calytrix*) and **Proteaceae** (*Persoonia, Conospermum*) (Cochrane pers.comm., Taylor in Bell *et al.* 1993). Poor germination may be due to dormancy, suggesting long-lived seed, however it may also be due to a lack of viable seed, or to rapid loss of viability as is often the case in Ecdeiocoleaceae and Restionaceae (Meney *et al.* 1994). In some species, standard techniques are not successful in germinating viable seed and embryo extraction is required (Meney & Dixon 1988).

Ewart (1908) obtained data on the longevity of seed from a number of native species under storage conditions and while this does not accurately reflect longevity under natural conditions it provides an indication of the variation between different genera. He found that starchy seeds, as occur in members of the Leguminosae, tended to last longer than those that are oily, although many seeds containing appreciable quantities of oil (eg. Myrtaceae) were comparatively long-lived.

The Leguminosae featured as the most long-lived seeds in storage. Low levels of germination were recorded after varying periods - *Acacia* (68 years), *Bossiaea* (15 years), *Daviesia* (67 years), *Dillwynia* (32 years), *Gompholobium* (64 years), *Hardenbergia* (51 years), *Hovea* (105 years), *Jacksonia* (72 years), *Kennedia* (65 years), *Oxylobium* (63 years), *Pultenaea* (57 years). In the eastern Australian species, *Acacia mollissima* (now *A. mearnsii*) and *A. melanoxylon*, emergence of seedlings has been reported 60 years and 50 years after the last seed fall (Cambage 1926, Farrell & Ashton 1978).

Germination was recorded in *Eucalyptus* seed stored for 37 years, with most species tested showing reduced germination by 10-15 years (Ewart 1908). Under natural conditions *Eucalyptus* seed is generally not long-lived once released. Ewart (1925) reported that *Leptospermum* and *Callistemon* seed may remain germinable after storage for several years but that *Melaleuca* seed soon lose their viability. Keeley (1995) reports that some members of *Leptospermum* are hard-seeded and form a persistent seed bank.

Beardsell and Richards (1987) claim long periods of viability under natural conditions for seeds of most Myrtaceous plants and for woody coated seeds surrounded by fleshy fruits, such as those found in *Persoonia* and members of the Epacridaceae. Dunlop and Galloway (1983) report that in *Pittosporum phylliraeoides* (Pittosporaceae) the seed, which is ingested and dispersed by birds, loses its viability rapidly with time and weathering, and is unlikely to be maintained from season to season.

Research by Meney *et al.* (1994) on the seed bank patterns in Restionaceae and Epacridaceae in kwongan vegetation at Eneabba provided some information on seed longevity in these families. Excised embryo tests showed that seeds of Restionaceae collected from soil in unburnt vegetation had low levels of germinability, ranging from less than 20% for *Ecdeiocolea monostachya* to less than 5% for *Restio 'sinosus'*. This was considerably less than the germinability recorded for embyros from fresh seed - 88% in *E. monostachya* and 60% in *R. 'sinosus'*. A seed burial experiment (unpublished data in Meney *et al.* 1994) including *Ecdeiocolea monostachya*, *Astroloma xerophyllum* and *Lysinema ciliatum*, showed that 90-100% of seeds deteriorated within two years. Dixon and Meney (1994) report that for species in the Rutaceae, Epacridaceae, Cyperaceae and Restionaceae decline in the growth potential of embryos occurs as early as 1-3 years after collection and is independent of seed size, seed coat characteristics and habitat.

Only a few specific examples of seed longevity can be cited for Western Australian species. Robinson & Coates (1994) observed seedlings of *Myoporum cordifolium* after disturbance of a mature woodland, estimated to be at least 30 years old, in which no parent plants were present. Since plants are short-lived (probably about 10 years) the seed must have survived in the soil for at least 20 years.

In a suburban garden in Victoria Park, seeds of Geraldton Wax (*Chamelaucium uncinatum*) germinated for a period up to 14 years after the removal of the original bush while seed of Hop Bush (*Dodonaea attenuata*) remained dormant in the soil for a period of at least 15 years (Perry 1973). In the Gnangara pine plantations Perry (1973) observed that seed of *Anigozanthos manglesii* must have remained in the soil without losing its viability for some 21 years.

Evidence that seeds of *Bossiaea laidlawiana* remain viable for several years was observed by Christensen and Kimber (1975) when the passage of a fire three years after the previous fire resulted in good germination of soil-stored seed. No additional *Bossiaea laidlawiana* seed had entered the soil reserve between fires, as mature plants were killed and the young plants had not produced any seed.

SEED DISPERSAL

Ants are known to predate seed, however they also play an important role in the dispersal of many Western Australian species. In the northern jarrah forest for example, Shea *et al.* (1979) observed that burial of leguminous seeds by ants had a pronounced effect on legume seed distribution, with distinct clumping of germinants around nests. Storage of seeds in the nest by ants offers several advantages, providing a favourable environment for germination, limiting predation and protecting against fire and desiccation (Berg 1975, Buckley 1982, Lamont 1982). In some instances burial may be a disadvantage, placing seed too deep for penetration of the dormancy breaking heat from a fire (Monk *et al.* 1981) or at a depth where seedlings are unable to reach the surface (Grant & Bell 1994).

Three general categories of seed removal by ants are recognised by Majer and Lamont (1985): (i) removal and predation of the seed (harvesting); (ii) nest decoration where the ant incorporates the diaspore into the nest structure and (iii) mymecochory, where the ant is attracted to an oil or fat bearing body (elaiosome) on the seed, eating this and leaving the seed intact, thus dispersing it away from the parent plant.

In the Australian flora myrmecochorous species are typically sclerophyllous shrubs often with explosive fruits that depend upon extreme desiccation for their dehiscence (Berg 1975). They are usually found in dry sclerophyllous forests, woodlands, heath and shrublands. Berg (1975) compiled a list of mymecochorous Australian species based on a review of literature and his research in the ACT, NSW and QLD. Local studies (Bell 1994, Lamont 1982, Lamont & Grey 1984, Majer 1982, Majer & Lamont 1985, Schatral *et al.* in press, Shea *et al.* 1979) substantiate observations of ants harvesting seed from local species.

Some of the more notable genera listed by Berg (1975), which also occur in Western Australian, include - *Acacia* (**Mimosaceae**), *Bossiaea*, *Brachysema*, *Daviesia*, *Dillwynia*, *Gastrolobium*, *Hardenbergia*, *Hovea*, *Kennedia*, *Pultenaea*, *Templetonia* (**Papilionaceae**), *Boronia*, *Phebalium* (**Rutaceae**), *Beyeria*, *Ricinocarpus* (**Euphorbiaceae**), *Cryptandra*, *Spyridium*, *Trymalium* (**Rhamnaceae**), *Lasiopetalum*, *Rulingia*, *Thomasia* (**Sterculiaceae**), *Goodenia*, *Velleia* (**Goodeniaceae**), *Hibbertia* (**Dilleniaceae**), *Boronia* (**Rutaceae**), *Tetratheca* (**Tremandraceae**), *Lepidosperma* (**Cyperaceae**), *Xanthosia* (**Apiaceae**), *Caesia*, *Johnsonia*, *Thysanotus* (**Liliaceae**), *Opercularia* (**Rubiaceae**) and *Gyrostemon* (**Gyrostemonaceae**). Myrmecochory may also occur in members of the **Lamiaceae** (*Hemiandra*, *Hemigenia*, *Microcorys*, *Westringia*) and the **Epacridaceae** (*Brachyloma*, *Monotoca*). The presence of an elaiosome has been reported in *Geleznowia* (**Rutaceae**) (Paynter & Dixon 1990) suggesting that ant harvesting of seed probably occurs. The seeds of *Eucalyptus* species lack an elaiosome but are collected in large quantities by ant species that are generally not regarded as harvester ants (ie. that use the endosperm and embryo for food).

In the Proteaceae harvesting of seed or fruit by ants has been reported in members of *Grevillea* and *Adenanthos*. These genera are characterised by rapid fruit maturation and spontaneous seed release and thus would benefit from the storage of seed in the soil (Majer & Lamont 1985). The apparent absence of seed harvesting by ants in other proteaceous genera such as *Hakea*, *Xylomelum* and *Banksia* may be attributed to their serotinous condition where seed is released into a suitable seedbed and germinates readily when exposed to correct conditions.

In *Grevillea* seed harvesting by ants has been recorded in *G. pteridifolia*, a widespread species of northern Western Australia, the Northern Territory and Queensland (Majer & Lamont 1985) and *G. leucopteris*, a more restricted species occurring in the Moora - Kalbarri area (Lamont 1982). Both species possess a brittle papery wing surrounding the seeds which is eaten by ants. Composition tests on the wing of *G. pteridifolia* have shown that like elaiosomes, the wing has a high lipid and protein content, making it an attractive food source (Majer & Lamont 1985). The elaiosome-bearing fruits of

Adenanthos cygnorum are collected by ants visiting the plant to feed on the extra-floral nectaries (Lamont & Grey 1984). Ants were observed transporting fruits of this species to nests up to 8m away.

Abbott and van Heurck (1985) studied the removal of seeds and fruit of the six commonest plant species in upland areas of the jarrah forest and found that the smallest seeds (*Eucalyptus marginata* and *Allocasuarina fraseriana*) were taken by insects, presumably ants, while the heavier seeds or fruits of *E. calophylla*, *Banksia grandis*, *Persoonia elliptica* and *P. longifolia* were taken more often by vertebrates, presumably small mammals.

Vertebrates are not considered to be important seed dispersal agents in Western Australian plant communities (Bell 1994). Some plants, however are specifically adapted to dispersal by birds and mammals and possess succulent, fleshy fruits. Families containing genera with succulent fruits include Chenopodiaceae, Epacridaceae, Goodeniaceae, Myoporaceae, Pittosporaceae, Proteaceae, Santalaceae, Solanaceae and Zygophyllaceae, although the character occurs consistently only in the Loranthaceae (Beadle 1981). Bird-attracting elaiosomes are found in some acacias (eg. *Acacia cyclops*) and are usually larger and more brightly coloured than the elaiosomes found on seed of myrmecochorous species.

Consumption of the fleshy fruit of *Persoonia elliptica* has been recorded by Abbott and van Heurck (1988) in Common Brushtail Possums, Western Brush Wallabies, Western Grey Kangaroos and Emus. In *P.elliptica*, seedlings are usually found far from fruiting trees, with rare recruitment from fruit falling beneath the canopy. This suggests that passage through the gut of vertebrates may be required to stimulate germination (Abbott & van Heurck 1988). Noble (1975) observed that germination of seed from the Nitre bush *Nitraria billardieri* (Zygophyllaceae) is promoted by passage through the gut of emus. *N. billardieri* seed was also recorded in the faeces of kangaroos, however they appear to be much less effective in facilitating germination.

Dunlop and Galloway (1983) found that birds were effective in dispersing seed of the Weeping Pittosporum (*Pittosporum phylliraeoides*), with seedlings located up to 73m from the nearest mature clump. Singing honeyeaters (*Meliphaga virescens*) were observed eating seeds from open fruits of *P. phylliraeoides* and were also found to feed on seed from the Ruby Saltbush, *Rhagodia baccata*. Emus have been recorded feeding on seeds and fruits from arid zone species of *Acacia*, *Santalum*, *Eremophila*, *Cassia*, *Solanum* and *Scaevola* (Davies 1976). They probably assist in the dispersal of at least some of these species. In Kings Park, Bobtail lizards have been seen eating the fleshy fruits of *Astroloma macrocalyx* (Fox *et al.* 1987).

Wind is known to be an active agent in the dispersal of species with winged (eg. *Allocasuarina* and *Hakea*) or hairy (eg. Compositae) fruits or seeds. In Western Australia, wind dispersal has been reported in *Nuytsia floribunda* and *Grevillea leucopteris* (Lamont 1985, Lamont 1982). Greatest dispersal in these species was found to occur in the direction of the prevailing south-westerly winds.

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