Recruitment of *Banksia* spp. in an anthropogenically disturbed mediterranean climate type woodland in Western Australia

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DECLARATION

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which has been accepted for the award of any other degree or diploma of the university or other institute of higher learning, except where due acknowledgment has been made in the text.

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ABSTRACT

Introduction *Banksia* woodland is the characteristic mediterranean type vegetation of the sand plains of the Swan Coastal Plain in the Perth region of Western Australia. Once extensive in the past the woodlands are nowadays severely fragmented and threatened by a variety of perturbations including weeds, fire and seed predation. Conservation and management of the woodlands depends very much upon the knowledge of past land use, type of original vegetation, frequency and magnitude of significant disturbances and surrounding land-use.

The results of a long-term study in the Kings Park bushland, comparing vegetation differences between the 1939 and 1999, showed that there have been substantial changes in the composition and structure of the woodland. In term of tree species, the most significant trends have been a decrease in *Banksia spp.*

Aim The research reported in this thesis aims for an understanding of the features and different stages of *Banksia* spp. recruitment in an environment such as the Kings Park bushland urban remnant. The final objective of this study is to assess if recruitment of *Banksia* spp. is affected by the perturbations mentioned above, ultimately influencing bushland conservation.

Materials &Methods The study was conducted both in urban bushland and in suburban areas in the Perth region. Several of the experiments and investigations on some specific stages of recruitment also included other species dominant in the bushland. The stages of recruitment investigated are: seed production and dispersal, seed germination and seedling establishment, seed predation.

Results In the Perth region *B. attenuata* and *B. menziesii* have a small degree of serotiny, the two species release seeds at different times of the year - B. attenuata from Summer to Autumn and B. menziesii from Spring to Summer. In post- fire conditions seed release is more synchronised than for unburned trees but the amount of seed released depends on the timing of the fire. Fires in early Summer lead to mass release of *B. menziesii* seeds and destruction of immature seeds of *B. attenuata*. Later fires destroy *B. menziesii* seed that has been shed on to the soil but synchronises release of *B. attenuata* seed.

Of the investigated locations Kings Park, and Ridge State Forest, have higher level of pre-dispersal seed predation compared to other locations. The post-dispersal surveys and experiment, both in inter-fire and post-fire environment show that in Kings Park in Winter,

approximately 75% of the banksia seeds were consumed. Moreover, *Banksia* seed predation is not related to the density of seeds. Presence of leaf litter, weeds and plant material in the experimental unit reduced predation values. Most of the germination occurred on sandy soil, while presence of weeds and of a thick layer of leaf litter reduced germination numbers for the *Banksia* species. In post-fire conditions seedlings are also associated with "burn residuals" (accumulation of burned litter and ash). Most of the seeds that were sown in the soil and had germinated died.

Conclusion This project confirmed and quantified the decrease of banksia individuals (which until now was only assumed) over time and lack of their recruitment. Seed predation, both before and after seed release greatly affects banksia seed availability in Kings Park. Furthermore unfavourable sites for germination such as a thick layer of leaf litter and weeds are a great obstacle for establishment of large seeded species such as *Banksia*. Other dominant species, such as *Allocasuarina fraseriana*, *Acacia saligna* and *Dryandra sessilis*[1] on the contrary do not seem to reduce their recruitment potential as predation (or removal) is not conspicuous and the various substrata do not reduce the ratio between the number of germinants and seedlings that survive. In order to boost banksia recruitment a number of management actions could be taken. In particular weeds and thick layers of leaf litter must be removed and a sandy soil substratum should be arranged especially in the areas where, even in the presence of banksia trees, the number of seedlings is low. Predation must be reduced, in particular through removal of pests

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[1] *Dryandra sessilis* (Knight) is now known as *Banksia sessilis* (Knight) A.R.Mast & K.R.Thiele. See Mast and Thiele (2007). In this thesis, however, will be always used the term *Dryandra sessilis*

GENERAL SUMMARY OF THE DIFFERENT CHAPTERS OF THE THESIS

Banksia woodland is the characteristic vegetation of the sand plains in the Dry Mediterranean Bioclimatic Zone of Western Australia. It is widespread on the Swan Coastal Plain and is remarkably consistent, in terms of physiognomy and species composition. The region is distinguished by mediterranean climate with cool mild winters and hot dry summers.

Banksia woodland is dominated by small trees of about 6-10m among which *Banksia* spp. occur in abundance. *Banksia* woodlands comprise floristically rich and taxonomically diverse plant communities; the canopy comprises the dominants *Banksia attenuata* and *B. menziesii*, while *Allocasuarina fraseriana*, *Eucalyptus calophylla, E. marginata, Nuytsia floribunda* and other *Banksia* spp. occur, though less frequently, while *Banksia ilicifolia* is present in the wetter sites. The well developed evergreen sclerophyllous shrub understorey is dominated by the woody shrub families Myrtaceae, Ericaceae, Proteaceae and Fabaceae. Dominant herbaceous or woody-herbaceous elements are represented by members of the Anthericaceae, Stylidiaceae, Haemodoraceae, Xanthorrhoeaceae, Cyperaceae, Zamiaceae and Dasypogonaceae. These dominant families are also dominant taxa throughout the southwest so that *Banksia* woodlands are floristically representative of Western Australia's southwestern flora.

Well drained, deep, leached and nutrient poor quartz sands and quartz sand over limestone, form the characteristic edaphic habitat of *Banksia* woodland on the Swan Coastal Plain.

Banksia woodlands represent an ecosystem of serious conservation concern, while at the same time, are poorly studied and documented. Of greatest concern is the rate of the clearance and degradation of Banksia woodlands especially in urban and suburban areas. Essentially the once extensive Banksia woodlands on the Swan Coastal Plain are extensively fragmented with considerable reduction in the area they occupy.

Banksia woodland reserves i.e. areas that are not cleared for urban or other use, are threatened by a variety of perturbations, for which there is little research information available for managing the disturbance factors. Among the most important are:

Weeds

More than one hundred weed species have been recorded within *Banksia* woodland. *Banksia* woodland communities appear to be more susceptible to weed invasion than many other plant communities in the southwest of Western Australia and this may have led to habitat loss and biodiversity harm.

Fire

High intensity summer fires affect mediterranean climatic areas and the *Banksia* woodlands are no exception. The woodlands have been neglected in terms of the effects of fire. With recent urbanization and human population on the increase, the fire regime is likely to have been altered. Fire has the potential to promote weed invasion, which in turn, leads to an increase in flammability of the vegetation. Furthermore, frequent fires have the potential to eliminate species that rely on regeneration through seed production and subsequent seedling recruitment. On the other hand, fire can favour recruitment especially in fire-adapted vegetation.

Groundwater Extraction

The water resources on the Swan Coastal Plain are recharged directly from rainfall. The water is used by the Perth metropolitan region for a large range of purposes. Ground-water levels are generally at their lowest during autumn, prior to the first wet season rains.

Feral Animals

A variety of ‘introduced’ animals have become feral in *Banksia* woodland. These include rabbits, rodents, cats, foxes and dogs. The overgrazing and selective grazing of rabbits is a threat to the survival of some plant species while seed consumption by rodents reduces recruitment potential.

Climate changes

Since the 1980’s, there have been extended periods of below average annual rainfall and above average temperature. In the Perth district, between 1929 and 1999, annual precipitation decreased by about 15% while temperatures increased by about 1 °C.

Inter-Related Perturbations

A major problem in understanding the effects and relative importance of the various perturbations is that most of them are inter-related and indeed their effects may be synergistic. For example frequent fires combined with grazing and fragmentation will lead to degradation of the vegetation much faster than would be expected from the effects of the three disturbers measured in isolation. Indeed, the invasion of weeds is much faster in the presence of soil disturbance or frequent fires.

For all these reasons conservation and management of these habitats are a considerable challenge and depend very much upon the knowledge of past land use, type of original vegetation, frequency and magnitude of significant disturbances and surrounding land-use.

Degree of vegetation degradation is difficult to assess especially in the absence of long-term studies on the plant communities. Information of vegetation changes are difficult to obtain because changes in vegetation in response to management and natural perturbations are most likely to occur over many decades, beyond the average time of research projects.

In 1999 a fortuitous discovery in the Kings Park and Botanic Gardens archives of a 1939 map with the positions, along transects, of individual plants of 13 dominant native tree and shrubs species, occurring in a portion of the Kings Park bushland allowed the possibility of quantifying vegetational changes over time. The same transects were resurveyed with the aim to determine whether the composition and the structure of the vegetation had changed in 60 years.

Vegetation changes over time (chapter 2)

Results of the vegetation differences between the 1939 and the 1999 surveys showed that there have been substantial changes in the composition and structure of the woodland. In term of tree species, the most significant trends have been an increase in the density and relative frequency of *Allocasuarina fraseriana* and *Corymbia calophylla* and a decrease in the density and relative frequency of *Banksia attenuata* and *B. menziesii*. Furthermore *B. grandis* has become rare, while *B. ilicifolia* is almost locally extinct. As a consequence, the vegetation changed from open woodland dominated by *B. attenuata, A. fraseriana* and *B. menziesii* and to a lesser extent *Eucalyptus marginata* and *E. gomphocephala* to a more closed formation dominated by *A. fraseriana* with low stature eucalypts and an understorey dominated by *Dryandra sessilis* and *Acacia saligna*.

Sudden autumn death syndrome in banksia occurs in a small proportion of all size classes of *B. menziesii* and *B. attenuata* without any apparent prior decrease in plant health and changes in the micro-habitat would have distorted the natural recruitment pattern. The combination of plant death and lack of recruitment has been instrumental in the decline in banksia species in Kings Park

The causes of the changes outlined are complex and increasing drier climate or decline in groundwater levels may be implicated, but the changes are more likely due to a complex matrix of interactions between different factors, the more important being weed invasion biotic interactions and altered fire regimes.

The research reported in this thesis aims for a better understanding of the features and different stages of *Banksia* spp. recruitment in an environment such as the Kings Park bushland urban remnant. To have a better understanding of these processes the study was conducted both in urban bushland and in suburban areas outside the central Perth district.
All the sites (described in Chapter 1) were located within banksia woodland vegetation and occurred on the Swan Coastal Plain in the Perth Region.
The sites were:
1) urban remnant banksia woodland (Kings Park, Bold Park Bushland and Murdoch University bushland).
2) semi-pristine banksia woodlands (Jandakot Regional Park, Ridge State Forest).

Investigations in the different locations allowed comparisons within and between urban and suburban areas helping to better understand the recruitment pattern and the reasons which led to the vegetation changes in Kings Park.

The different stages of recruitment investigated and discussed in this thesis are: seed production and dispersal, seed germination and seedling establishment, seed predation. All these stages are crucial phases of the recruitment process. Several of the experiments and investigations on some specific stages of recruitment also included other species such as *A. fraseriana*, *D. sessilis*, *E. marginata*, *A. saligna*, and *A. pulchella*. Experiments in which other species were used included: seed bank germination trial, post-dispersal seed predation, and seed germination.
To test the hypotheses proposing a link among patterns of seed production and dispersal and seed predation with those of seedling recruitment a combination of surveys and experiments was undertaken.

Seed production and dispersal (chapter 3)
On the Swan Coastal Plain *B. attenuata* and *B. menziesii* have a small degree of serotiny, in particular the first can be considered weakly serotinous and the latter not serotinous at all. The seasonal monitoring both of seed production (from the inflorescence) and seed dispersal (when the woody follicles open) showed that the two species released seeds at different times of the year. *B. attenuata* from Summer to Autumn, and *B. menziesii* from Spring to Summer. Similar trends were detected in surveys undertaken in post-fire conditions. This difference favours the recruitment of the first species, especially in the presence of disturbance such as

frequent wildfires and severe seed predation. *B. attenuata* released over twice as many viable seeds compared to *B. menziesii*. Most of the seed released from the tree in inter-fire conditions are viable and germinants occurred beneath the tree canopy.

Seed predation (chapter 4)

One of the factors that can limit seedling recruitment is the predation of seeds both before or after dispersal from the mother plant. In this thesis, experiments and surveys were carried out with the intention of investigating type and extent of predation.

Pre-dispersal predation is responsible both for the consumption of seeds while they are on the infructescence protected by the woody follicles and for the 'snap' of the infructescence from the stem and consequent death of the seeds in the infructescence. Within the investigated locations Kings Park and Ridge State Forest have higher level of pre-dispersal predation than other areas examined. The post-dispersal seed predation study investigated the occurrence and the features of seed predation on several dominant tree and shrub species which compete in the woodland. Surveys and experiment, both in inter-fire and post-fire environment highlight the fact that when experimental units were unprotected from vertebrate predation, seeds removal levels were higher especially in Kings Park (and to a lesser degree in Bold Park) where, in Winter, approximately 75% of the banksia seeds were consumed. Moreover, *Banksia* seed predation occurred regardless of the number of seeds in the experimental unit highlighting the fact that predation is not related to the density of seeds.

Presence of leaf litter, weeds and plant material in the experimental unit reduced predation values.

No attempt was made to investigate the specific identity of the predator but observations, time of removal and specific 'bait-devices' helped to determine that 'hard beak' cockatoos may be considered responsible for pre-dispersal predation and rodents for post-dispersal predation. Invertebrates such as ants are likely to be responsible for post-dispersal predation/removal of the small seeded species.

Seed germination and seedling establishment (chapter 5)

The research in this chapter tried to assess the role of the germination process, of banksias and the other key species of the Kings Park bushland, in the changes of the bushland vegetation that were detected over 60 years.

In all the surveys and experiments the "germination behaviour" of *B attenuata, B. menziesii* and *B. grandis* were similar. *B. ilicifolia* displayed a comparable trend, only with lower germination values. Most of the germination occurred on sandy soil, while presence of weeds and of a thick layer of leaf litter reduced germination numbers for the *Banksia* species.

Also for the other investigated species recruitment is altered by the presence of weeds and of a thick layer of leaf litter. In the bushland, consequently, plant recruitment is associated with the different micro-site habitats in which seeds can germinate.

In all the surveys described in this chapter *Banksia* spp. germinate more on bare sandy soil, both after fire or in semi-natural unburned bushland.

In post-fire conditions seedlings are also associated with “burn residuals” (Lamont et al. 1993). In inter-fire conditions, on the other hand, most of the seedlings occur on sandy soil followed by substrata with native vegetation or mulch.

When *Banksia* seeds were added to different types of micro-site habitats results varied extremely according to the exclusion of vertebrate from the experimental units. Where vertebrate had access, banksia germinants were fewer compared to where vertebrate were excluded.

All the experiments, both in the greenhouse or in the bushland, showed that in the presence of soil moisture, seeds of *Banksia* spp. germinate starting from the third week. Thus the timing of seed release is of great importance as the longer the time spent in the soil seed bank (*Banksia* spp., however, belong to the transient soil seed bank) the more the seeds are exposed to predation, fire or other causes of death.

In a field experiment concluded after 3 years, most of the seeds that had been sown in the soil and had germinated had died. Recruitment occurred only in areas on sandy soils and with low competitions, of the 4,000 seeds sown just 47% germinated and only 2% of seedlings were still alive at the end of the experiment.

Final conclusion (chapter 6)

Conservation of banksia woodlands especially in urban and suburban remnants is a significant task both for environment managers and conservationists. Remnants make an essential contribution to biodiversity conservation, consequently preservation and enhancement of biodiversity in urban and suburban remnants become important especially considering that many of these areas are impacted by various types of non-natural disturbances and are isolated islands of vegetation.

This research, thanks to the re-surveying of vegetation transects undertaken 60 years before, had the capability to confirm and quantify the decrease of banksia species (which until now was only assumed).

Seed predation, both before and after seed release greatly affect banksia seed availability in Kings Park. Furthermore unfavourable sites for germination such as a thick layer of leaf litter and weeds are a great obstacle for establishment. The other dominant species, such as *A. fraseriana*, *A. saligna* and *D. sessilis* on the contrary do not seem to reduce their recruitment potential as predation (or removal) is not conspicuous and the various substrata do not reduce the ratio between the number of germinants and seedlings that survive. These small seeded species, furthermore, produce yearly many more seeds than do the *Banksia* spp. in relation to plant size.

In order to boost banksia recruitment different management actions could be taken. In particular weed and thick layers of leaf litter must be removed and a sandy soil substratum should be prepared especially in the areas where, even in the presence of banksia trees, the number of seedlings is low. Furthermore vertebrate predation must be reduced through capture or removal of pests such as rats. Considering the importance of the Kings Park feeding ground for the survival of cockatoos and the difficulty of moving the birds to areas of less conservation concern, the amount of seed predated by birds should be returned to the soil seed bank. These actions need to be carried out within the general management action plan and need to be monitored. Failure of banksia sapling recruitment could increase in the future and without proper management intervention, there may be local extirpation of some banksia species. Also dominant species under certain conditions of poor dispersal and recruitment may not be able to replace the dead old trees (especially *Banksia* spp. that have a relatively short life span) and the local isolated population may be in danger of collapse.

1 CHAPTER 1: BANKSIA WOODLANDS ON THE SWAN COASTAL PLAIN

1.1 **Introduction**

Banksia woodlands are such a familiar sight on the Swan Coastal Plain, including Perth, the capital city of Western Australia, that few people would consider these plant communities to be in need of attention. However, *Banksia* woodlands represent an ecosystem in need of serious conservation concern, while remaining poorly studied and documented. Of greatest concern is the rapid rate of clearance and degradation of *Banksia* woodlands. Essentially little remains of the once extensive *Banksia* woodlands from Jurien to Busselton, a distance of around 400 km (Fig. 1.1).

Of particular concern is that remnants, particularly in urban environments and those set aside for conservation, are vulnerable to inappropriate management practices and disturbance phenomena. Only 7% of the original 281,000 ha of *Banksia* woodlands are in Protected Areas (Hopper and Burbidge 1989). While some conservation reserves protect samples of *Banksia* woodland, not all floristic types of woodland are protected at present, nor are all the reserves large enough to be viable. Additionally, very little is known about the management needs of *Banksia* woodlands, especially in urban remnants; and still less is known of the restoration ecology and biology of most Banksia woodland species.

There are several factors that contribute to the sensitivity of Banksia woodland study sites, in particular: that they are located within a mediterranean biodiversity hotspot; globally, Mediterranean biomes are under the greatest threat from invasion (Sala, et al. 2000); mediterranean ecosystems with species fire-tolerant are susceptible to altered fire regimes (Richardson & Cowling 1992; Fisher et al. 2009; Crosti et al. 2010, see however Bradshow et al. 2011 on concept of plant traits adapted to fire in Mediterranean climates); the potential for altered fire regimes is greater in urban locations than in more remote sites; invaders in isolated locations such as Australian ecosystems lack most of their natural enemies (Callaway and Aschehoug 2000).

The aim of this chapter is to describe the characteristics of the studied region and of the *Banksia* woodland, while the following chapters will describe the changes in vegetation structure and species abundance in the Kings Park Banksia woodlands and to identify the reason behind the changes, using information taken from surveys and experiments performed at Kings Park and other sites on the Swan Coastal Plain both in urban remnants (Bold Park and Murdoch University bushland) and semi-pristine sites (Ridges State Forest and Jandakot R.P.) See annex I for all the different sites in the different locations.

1.1.1 Characteristics of Banksia Woodlands

Banksia woodland is the characteristic vegetation of the sandplains in the Dry Mediterranean Bioclimatic Zone of Western Australia. This Bioclimatic Zone corresponds to the Darling Botanical District in the southwest of Western Australia, and includes the Swan Coastal Plain, the Dandaragan Plateau and the Darling Scarp. The *Banksia* woodland vegetation differs from kwongan, which is the characteristic vegetation of the sandplains in the Extra-Dry Mediterranean Bioclimatic Zone by the presence of trees (Pate and Beard 1984).

Generally considered typical of the Swan Coastal Plain, one third of Banksia woodland occurs on the Dandaragan Plateau with minor occurrences in the Darling Scarp (Beard 1989) (Fig 1.1). However, it is on the Swan Coastal Plain that Banksia woodlands are most widespread and remarkably consistent, in terms of physiognomy and species composition. The woodlands occur over a distance of some 400km from the north to the south of the city of Perth in Western Australia bounded in the west by coastal vegetation bordering the Indian Ocean and in the east by the Darling Scarp.

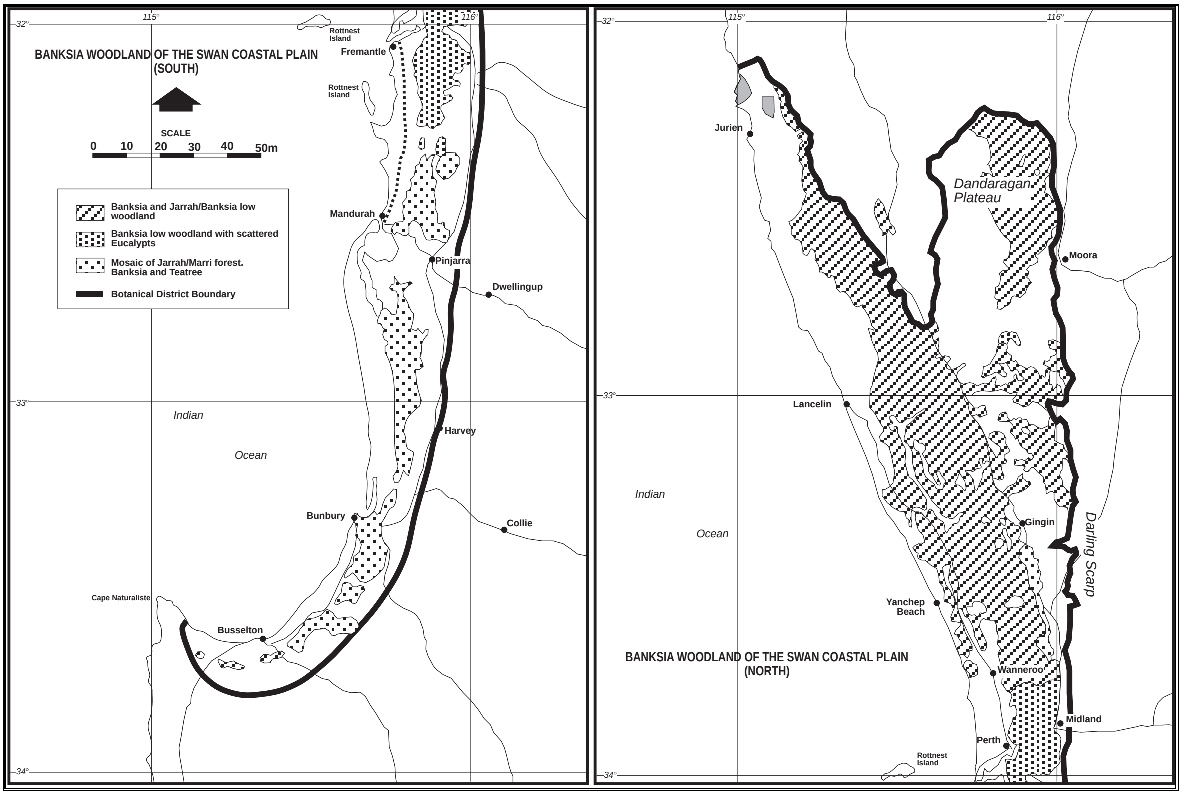

Fig. 1.1 Distribution and extent of *Banksia* woodlands on the Swan Coastal Plain, in the southwest of Western Australia (modified from Beard 1989).

A characteristic mediterranean climate of cool mild winters and hot dry summers is typical of this region. Annual rainfall averages 800mm, of which 80% falls between May and October (Dodd et al. 1984), leading to a pronounced summer drought between January and April when rainfall is sporadic or non-existent and soil moisture content is at its lowest. There has been a downward trend in annual rainfall levels since the 1910's (Froend et al. 1993; Yu et al. 1993; Tapp and Cramb 2000). Furthermore, since the 1980s, there have been extended periods of below average annual rainfall and above average temperatures. In the Perth district, between 1929 and 1999, annual precipitation decreased by about 15% while temperatures increased by about 1 °C (Crosti *et al*. 2006).

1.1.2 Flora of Banksia Woodlands

Banksia woodland (Banksia low woodland or low open forest) is dominated by small trees of about 6-10 metres (Powell 1990) among which *Banksia* spp. occur in abundance. There is an ecological similarity in the morphological characteristics of tree *Banksia* spp. (George 1987). The bark is very thick, dark and scaly; the leaves, 10-15cm long, are usually hard and rough, prominently toothed or lobed. While the leaves are large, they are relatively sparse on each shoot so that the crown is thin, branching is somewhat open and the tree bole is short in comparison with the canopy (Beard 1989).

The structure of *Banksia* woodlands resembles the physiognomy of thermophilous oak woodlands of the Mediterranean Basin (Beard 1989), which are part of the vegetation order Quercetalia-pubescentis (Br.-Bl. (1931) -1932) which comprises deciduous and evergreen woodland species. *Banksia* woodlands comprise floristically rich and taxonomically diverse plant communities and many are shared with the adjacent kwongan plant communities, 250km north on the Swan Coastal Plain (Dodd and Griffin 1989) Such is the resemblance between the plant communities that in some areas *Banksia* woodland can be considered kwongan with a *Banksia* overstorey. The dominant canopy species are *Banksia attenuata* and *B. menziesii*. However, *Allocasuarina fraseriana, Eucalyptus todtiana, Nuytsia floribunda* and other *Banksia* spp. occur, though less frequently; *B. littoralis* is present in seasonally wet sites (Beard 1989; Dodd and Griffin 1989). In the southern parts of the Swan Coastal Plain, *Eucalyptus calophylla* and *E. marginata* together with *A. fraseriana* are present and eventually dominate the upper layer. Flats and swamps support myrtaceous shrub communities in which *Eucalyptus rudis, Melaleuca rhaphiophylla* and *M. preissiana* occur (Havel 1968; Beard 1979; Heddle et al. 1980; Groom et al. 2000).

The well-developed evergreen sclerophyllous shrub understorey is dominated by the woody shrub families Myrtaceae (*Eremaea, Melaleuca, Scholtzia*), Ericaceae (*Astroloma, Leucopogon*), Proteaceae (*Adenanthos, Stirlingia*) and Fabaceae (*Acacia*, *Jacksonia, Daviesia*). Dominant herbaceous or woody-herbaceous elements are represented by members of the Anthericaceae (*Laxmannia, Thysanotus*), Stylidiaceae (*Stylidium*), Haemodoraceae (*Anigozanthos, Conostylis*), Xanthorrhoeaceae (*Xanthorrhoea*), Cyperaceae (*Lepidosperma, Mesomelaena*), Zamiaceae (*Macrozamia*) and Dasypogonaceae (*Dasypogon, Lomandra*) (Rokich 1999). These prominent families are also dominant taxa throughout the southwest. *Banksia* woodlands are therefore representative of Western Australia's southwestern flora.

The woodland understorey, unlike the canopy, shows a high degree of variation in composition. The lack of floristic uniformity in understorey composition has led to the division of Banksia woodlands into a number of floristic types. For example, Havel (1968) defined several floristic types of *Banksia* woodland just in the northern part of the Swan Coastal Plain alone, which reflected differences in a range of environmental variables, of which edaphic factors were the most important drivers of species composition.

1.1.3 The Soil System

Well drained (dry), deep, leached and nutrient poor quartz sands, which do not limit root penetration, form the characteristic edaphic habitat of *Banksia* woodland, and these occur principally on the Swan Coastal Plain (Fig. 1.2). Within the Plain communities, there is low scale edaphic variability in topography, soil depth, moisture characteristics (including depth to water table), degree of leaching and of soil nutrients (Beard 1989).

The Swan Coastal Plain consists of a series of geomorphic elements (Woolnough 1920) occurring parallel to the coastline; the Ridge Hill Shelf, the Pinjarra Plain and three coastal dune systems whose soils are at different stages of leaching and soil formation (Mattiske and Associates 1995). These geomorphic elements are formed almost entirely from either fluviatile or aeolian depositional material (McArthur and Bettenay 1960).

The Ridge Hill Shelf is the most easterly feature of the plain and occurs as a series of Pleistocene laterites and sands at the base of the Darling Scarp (McArthur and Bettenay 1960; McArthur 1991). To the west is the relatively flat Pinjarra Plain, formed from fluvial soils (Mattiske and Associates 1995).

To the west of the Pinjarra Plain is the Bassendean dune system, representing a Pleistocene accumulation of beach sands along an old coastline. This dune system consists of degraded aeolian landforms with either yellow or white quartz sand underlying slightly leached grey quartz sands, virtually devoid of nutrients (McArthur and Bettenay 1960). All these soils generally overlie a hard pan -B horizon-, composed of varying amounts of organic matter and iron and aluminium oxides (Bettenay 1984).

The Spearwood dune system is to the west of the Bassendean sands. These dunes are generally higher and more pronounced than the Bassendean dune system, and originated during the late Pleistocene, and consist of variable depths of siliceous and calcareous, brown and yellow leached sands of medium to coarse grained subangular to subrounded particles over a core of aeolianite - the Tamala Limestone (McArthur and Bettenay 1974; Gozzard and Mouritz 1989; McArthur 1991). Tamala limestone is made up of white to pale-yellow, grey, calcareous fragmented skeletal material with variable amounts of quartz sand (Smith 1985). Three soil associations occur on the Spearwood Dune System - Karrakatta, Cottesloe, and Yoongarillup soils (Semeniuk and Glassford 1989).

Further west, between the Spearwood dune system and the coast, lies the third and youngest of the three dune systems, the Quindalup Dune system. This comprises Holocene calcareous coastal dunes (McArthur and Bettenay 1960).

All three dune systems are chemically infertile, particularly low in phosphorus, potassium, iron and most other minerals. The physical nature of the soils leads to low water holding capacity and resultant plant moisture stresses during the dry summer months, representing a key limiting factor in plant growth. In contrast, the swamps are very poorly drained with about one metre of surface sand over an almost impermeable organic hard pan; they are generally saturated with water for up to nine months.

Fig. 1.2 Soil systems of the Perth region (McArthur and Bettenay 1974)

1.1.3.1 Soils as a Basis for Habitats of Banksia Woodlands

Havel's (1968) study of the vegetation on the Swan Coastal Plain defined seven floristic types of *Banksia* woodland, reflected differences in topography and soil depth, water drainage status and degree of soil leaching. Other factors that may determine variations in habitats and understorey assemblages in *Banksia* woodland include: location within dune or interdune; organic soil development; kaolin content; iron-mineral content; thickness of bleached soil; moisture content; subsurface stratigraphic or pedogenic features, particularly for their influence on soil hydrology; and retention of water and nutrients (Semeniuk and Glassford 1989). Some vegetation studies have identified habitats within *Banksia* woodland to various levels of detail, in terms of a number of these edaphic factors (Heddle *et al*. 1980, Cresswell and Bridgewater 1985). For example, Cresswell and Bridgewater (1985) related vegetation associations to locations on dune crests (tops), slopes and swales, an approach that identifies habitat location within the undulating topography.

1.2 Vegetation Changes in Banksia Woodlands

Before analysing the changes in species abundance and population structure of major tree species over time (chapter 2) and the relationship of the detected changes with *Banksia* recruitment (following chapters) some general comments are offered, regarding major disturbances and perturbations like weeds, fire, fragmentation and other factors in banksia-eucalypt-casuarina woodland communities and their ecological impacts. This will help to explain the pressures currently exerted on Kings Park and, in particular, on the two main investigated species (*B. attenuata* and *B. menziesii*).

1.2.1 Impacts within Banksia Woodland

Because of their location close to Perth and surrounding urban areas, *Banksia* woodlands are rapidly being destroyed for urban, agricultural and industrial development. By 1986 an estimated 55% of the 281,000 ha of *Banksia* woodland on the Bassendean and Spearwood dune systems alone had been almost entirely cleared of native vegetation (Hopper and Burbidge 1989). In addition, *Banksia* woodland reserves are threatened by a variety of perturbations, and there is little research information available for examining these disturbance factors. The more important are described below

1.2.1.1 Weeds

More than 100 species of weeds have been recorded within *Banksia* woodland (Bell *et al.* 1979; Milewski and Davidge 1981; Keighery 1989). *Banksia* woodland communities, according to some authors, appear to be more susceptible to weed invasion than any other plant community in the southwest of Western Australia; this has led to competition and subsequent elimination of some native species (Burbidge 1989).

Weed invasions do not normally occur in isolation. Disturbances or disruptions to the ecosystem generally precede them (Elton 1958). Ecosystems with high disturbance regimes, or multiple forms of disturbance, are particularly susceptible to environmental weeds (Amor and Piggin 1977; Fox and Fox 1986b; di Castri 1990; Westman 1990; Binggeli 1996, Crosti et al. 2010). According to Richardson and Pyšek (2006) biological invasions rise when both species and habitat are disrupted. Disturbances include cultivation, grazing by domestic and feral animals, the use of fertilisers, soil profile disruption or soil compaction by engineering works for roads and pipelines, road verge, altered water and nutrient cycle and, especially, disruption of natural fire regimes all contribute to the establishment of invasive alien species in new or temporarily "vacant niches".

As the disturbance regimes of nearly all ecosystems on earth are being altered through the influence of humans, increasing numbers of ecosystems are vulnerable to invasion by seedlings of environmental weeds (Richardson and Bond 1991). According to Sala et al. (2000), on a global scale, biotic introduction in mediterranean-type ecosystems is seen as one of the most important drivers of biodiversity change. These conclusions are particularly applicable to mediterranean-type ecosystems such as South-Western Australia, the Cape of South Africa and coastal California, where the impact of invasive species that have changed the assemblage, community structure and recruitment processes of native species is widely documented (van Wilgen & Richardson 1985; DiTomaso & Healy 2006; Fisher et al. 2009).

Through mass recruitment of seedlings, environmental weeds frequently produce permanent changes in community structure, function and composition by suppressing or killing native plants. Weeds compete with native vegetation for limited resources such as light, space, nutrients, and moisture (Williams and West 2000). Environmental weeds can also inhibit growth of native species, for example *Schinus terebinifolia*, which occurs in the region*,* by the production of allelopathic substances (Fox and Adamson 1979; Gordon 1998; Florence 1996).

1.2.1.2 Fire

High intensity summer fires typically affect mediterranean climatic areas. All *Banksia* woodlands are subject to fires. Indeed, Gill (1975) suggests that recurrent fire is an integral feature of sclerophyll communities in all mediterranean climates

In *Banksia-Eucalyptus-Allocasuarina* plant communities periodic mass seedling recruitment following fire is well documented (Hobbs and Atkins 1990) together with the failure of seedlings to establish during inter-fire periods.

These two life history characteristics, mass seedling recruitment following fire and the failure of seedlings to establish during inter-fire periods, have been linked to two main factors – mass propagule production and production of favourable establishment conditions. Synchronous mass release of canopy stored seed following fire (O'Dowd and Gill 1984; Burrows et al. 1990; Davies and Myerscough 1991) leads to a temporary satiation of seed harvesters and the production of a temporary soil seed reserve (O'Dowd and Gill 1984; Andersen and Yen 1985; Wellington and Noble 1985b; Andersen 1988, 1989). That is, the more massive the seed release following fire, the greater the likelihood that some seeds will reach safe sites for germination. Seeds of many species with soil-stored seeds are cued to germinate by heat and/or smoke (Dixon et al. 1995a; Crosti et al. 2006).

Secondly fire also increases the abundance of safe sites for seed germination and seedling establishment, in part encompassed by the term 'ash-bed effect' (Pryor 1963; Wellington and Noble 1985a; Enright and Lamont 1989). Fire increases the number of safe sites in many ways:-

- By improving the nutrient status of the soil through an increase of the available nitrogen and phosphorus (Humphreys and Lambert 1965; O'Dowd and Gill 1984; Attiwill and Leeper 1987; Tomkins et al. 1991; Bauhus et al. 1993; Chambers and Attiwill 1994). These particular nutrients are often in low concentrations in Western Australian soils. The nutrients are released during intense fires when nutrients in the soil, leaf litter layer and some above-ground biotic components are mineralised (Grove et al. 1986). Although this increase in nutrient availability is only temporary, it plays an important role in facilitating seedling survival and growth and the recovery of tree canopies following fire. It is important to consider, however, that nitrogen is readily volatized at temperatures that can be easily reached during a wildfire and that ashes can be blown clear during a fire by turbulences and convection and thus lost from the site of the fire.

- In the oligotrophic ecosystems of Western Australia, species have developed strategies such as rapid regeneration, growth and uptake after fire, evergreenness and symbiotic nitrogen fixation, which minimize relative nutrient loss after fire (Boerner 1982). Ash content of plant material however, increases the availability of nutrients in the surface soil, assisting seedling nutrient acquisition.
- Fire can destroy 'biological opposition' to recruitment, such as soil and litter microorganisms, pathogens and herbivores that inhibit seedling survival and growth (Renbuss et al. 1973; Whelan and Main 1979; Bell and Williams 1997). Before these agents recover from the fire, seedlings may grow to such a state where the biological opposition is no longer effective in preventing successful recruitment (Whelan et al. 1980).
- Fire alters soil characteristics such as reducing the bulk density, increasing water infiltration and increasing water availability (Hatch 1960; Loneragan and Loneragan 1964).
- Fire removes competition from surrounding vegetation for limited resources such as light, nutrients and water (Wellington and Noble 1985b; Bond and van Wilgen 1996).

These factors can result in the mass recruitment of seedlings on ash beds and sparse recruitment off ash beds.

The success of the recruitment process, though, is not determined by fire alone. It is driven by a combination of factors including timing and intensity of fire, amount of canopy or soil-stored seed, abundance of seed predators, herbivores and competitors, and rainfall events (O'Dowd and Gill 1984; Wellington and Noble 1985a). Therefore, a recruitment event may only occur a number of times within the lifespan of a particular population. In *B. attenuata*, a weakly serotinous species in the Perth area (see Chapter 3), the coincidence of fire and above average rainfall years suitable for seedling establishment may only occur a few times in the life span of an individual (Enright and Lamont 1992).

However, even when recruitment is successful after fire, survival of seedlings remains very low. Recruitment is dependent on the number of seedlings that initially become established. Where only a few seedlings recruit, it is likely that no seedlings will survive (Curtis 1990).

The fire regime, which is made up of frequency, severity and seasonality, to which populations are adapted (*sensu latu*), varies across Australia (Gill 1997). Sudden changes in fire regimes can be a negative influence, disrupting native populations by affecting normal reproductive and regenerative processes, which can lead to a decrease in biodiversity (Hobbs 1987; Saunders et al. 1991; Hobbs and Huenneke 1992).

It is difficult to make generalisations regarding the fire history in Australia before and after the arrival of Europeans (Adamson and Fox 1982), although information gathered from historical records, fire scars on trees and the quantity of charcoal washed into lakes suggests that the fire regime in many banksia woodlands has changed since the arrival of Europeans (Norton 1997; Abbott 2003). Many native woodland areas were burnt for a variety of reasons including promoting grasses for consumption by livestock and to assist with clearing (Norton 1997). Disrupted fire regimes and broad scale clearing for extensive agriculture and urbanisation, among other factors, have led to native ecosystems in Australia becoming increasingly fragmented and disturbed.

1.2.1.3 Weeds and fire

There is often a direct association between disturbances such as fire, weed invasiveness and the degree of invasion (Amor and Piggin 1977; Kruger et al. 1989; Hobbs 1989; Rejmánek 1989; Hobbs and Huenneke 1992; Fisher et al. 2009). Fire is frequently considered a determining factor in increasing the likelihood of weed invasion of native vegetation in southwestern Australia (Bridgewater and Backshall 1981). There are two major effects of fire that can be distinguished. Firstly, fire can be a major catalyst for promoting a life cycle stage for environmental weeds by, for example, providing specific microsite conditions adequate for germination and establishment such as temporarily increasing irradiance and nutrient availability (Richardson and Bond 1991). In short, disturbance releases resources (Fox and Fox 1986a). Secondly, fire can lead to a reduction of biotic pressures including competition and herbivory, thus indirectly influencing the community's susceptibility to invasion (Bridgewater and Backshall 1981; Rejmánek 1989; Hobbs and Atkins 1990; Richardson and Bond 1991; Gentle and Duggin 1997). Therefore, in the wake of a fire, the remaining biodiversity depends on the ability of native species to recover (homeostasis of pristine and semi-pristine habitats, and their capacity to resist invasions by alien species).

The disturbance patch model (Hobbs 1989) summarises how fire can create opportunities not only for the recruitment of native plants, but also for environmental weeds by providing a patch in which colonization and invasion can occur. The disruption of competitive interactions and/or increases in available resources creates a patch within which an irruption of invasive species can occur, so long as propagules are available. A change in fire frequency from that which was normal for a plant community may also encourage weed invasion. The invasion of fynbos in South Africa by Western Australian natives such as *Acacia cyclops* (Trabaud 1990) and *A. saligna* (Holmes et al. 1997), for example, has been linked to a higher than average fire frequency in the area.

1.2.1.4 Groundwater Extraction

Underlying the Swan Coastal Plain to depths of 14m are large ground-water resources (Kite and Webster 1989). These systems are directly renewed by rainfall. The water is used by the Perth metropolitan region for a large range of purposes, namely private domestic irrigation, parks and gardens, public water supplies, horticulture, industrial and commercial purposes. In addition, the demands on the limited water resources in the vicinity of the metropolitan region surrounding Perth are increasing (Mattiske and Associates 1995) with the potential to greatly impact on wetlands and *Banksia* woodlands. Together with a decrease in rainfall there is a move from high water-use species towards drought tolerant species (Mattiske and Associates 1995).

Ground-water levels are generally lowest at the beginning of autumn, prior to the first seasonal rains. It is during this time that widespread death of mature *Banksia* trees has been observed in recent years. The term, ‘Banksia Autumn Death Syndrome’ is used to describe deaths where the reason is unknown, although it may be due to depleted groundwater levels and/or physiological problems linked to a depressed water table.

1.2.1.5 Disease

Phytophthora cinnamomi, an introduced fungus responsible for up to 20% of plant deaths in native ecosystems in Western Australia (Wills 1993), is now a major disease of *Banksia* woodland species. The fungus destroys most of the over-storey and shrub layers in affected areas (Podger 1972) and has become a major factor affecting the function of *Banksia* communities.

1.2.1.6 Feral Animals

A variety of ‘introduced’ animals have become feral in *Banksia* woodland. These include rabbits, rodents, cats, foxes and dogs. The overgrazing and predation by rabbits and rodents adversely affects particular species, while predation by cats, foxes and dogs is eliminating some native animals (Burbidge 1989).

1.2.1.7 Recreation

The *Banksia* woodland community of Perth's Swan Coastal Plain is a delicately balanced environment, far less able to withstand the impact of long-term urbanisation than the urban bushland in most other Australian capital cities (Poole 1989). Human use can lead to degradation of the communities within *Banksia* woodland, particularly from off-road vehicle usage, walking trails and rubbish dumping, one of the major sources for weed introduction (Burbidge 1989).

1.2.1.8 Fragmentation

In landscape ecology, fragmentation is the isolation of natural ecosystems by the creation of islands of habitats embedded in a different dominant habitat or matrix (Pickett and Thompson 1978; Noss and Csuti 1997). The main causes of fragmentation include urbanisation, agriculture and the establishment of exotic tree species (Gill and Williams 1996). Fragmentation is not only a type of disturbance that threatens an individual system (Piqueray et al. 2011), but landscape level disturbance that results in the rearrangement of the landscape matrix (Hobbs and Huenneke 1992).

Fragmentation can significantly alter natural disturbance regimes and the spread of disturbances, such as fire, across the landscape (Hobbs 1987; Yates et al. 1994b). Remnants are particularly susceptible to altered fire regimes. Populations within small remnants are subject to fluctuations and random events such as fire, whereas an increased area permits larger populations, thereby reducing the probability of extinction (Pickett and Thompson 1978; Saunders et al. 1991).

In addition, the problems caused by the fragmentation process can include the restriction or obstruction of the population processes of pollination and dispersal, which can restrict flow of genetic material (Hobbs and Hopkins 1990; Yates and Hobbs 1997; Yates et al. 2007). Thus, fragmented ecosystems may contain smaller populations, have lower levels of resilience, lower genetic diversity and higher rates of extinction. Urban areas can support a large number of exotic species, particularly predators (Malcom *et al.* 1996) that consume native fauna (Brunner *et al.* 1991). The presence of skilful predators can strongly effect the reproduction process of *Banksia spp*. as many are pollinated by small vertebrates.

Fragmented systems are highly vulnerable to environmental weed invasion (Hobbs et al. 1993), especially in an urban context. Firstly, they have high levels of exposure to invasive propagules from the high number of visitors entering the system, such as the Kings Park banksia woodland, (Adair 1995). Secondly, native systems that are fragmented by urban development have high edge to area ratios and are therefore more susceptible to invasion from neighbouring properties (Rose 1997). The effect of urban development can increase the total soil phosphorus of remnant bushlands; this can decrease the abundance of species naturally occurring on low nutrient soils, and increase the abundance of species adapted to higher nutrient levels (Clements 1983). Finally weeds can change the nutrient status of a fragmented system to the disadvantage of many native species (Fisher et al. 2006)

1.2.2 Inter-Related Perturbations

In addition to these perturbations being *Banksia* woodland neglected areas of research, a major problem in understanding the effects and relative importance of the various perturbations is that most are inter-related; indeed, their effects may be synergistic. For example frequent fires combined with seed predation will lead to degradation of the vegetation much faster than would be expected from the effects of the two disturbers measured in isolation (Burbidge 1989). Indeed, the invasion of weeds is much faster in the presence of soil disturbance or frequent fires (Baird 1977; Bridgewater and Backshall 1981; Fisher et al. 2009).

1.3 The locations of the study

For the aim of this study, surveys and experiments were mainly undertaken in Kings Park but also in other locations. All the sites were within banksia woodland on the Swan Coastal Plain in the Perth Region (Fig. 1.3).

The other sites were located in:

1) urban remnants of banksia woodland (Bold Park Bushland and Murdoch University bushland).

2) suburban semi-pristine banksia woodlands (Jandakot Regional Park, Ridge State Forest).

1.3.1 Kings Park Bushland (KP)

Kings Park and Botanic Gardens (400ha) is located approximately 1.5km west southwest from the Perth Central Business District, Western Australia (31^o57’53 S; 115°49’46 E). It comprises two sections, the parklands and Botanic Gardens, and the bushland. The bushland is a relatively large (267ha) and highly disturbed remnant of native vegetation and is an isolated bushland in the city of Perth (Wills et al. 1998); the Swan River lies to the east and south, with urban development to the west and north. The Kings Park bushland has significant conservation values and is an important component of the nature reserve system on the Swan Coastal Plain (DCE 1981).

Kings Park is located in a dry Mediterranean bioclimatic zone; characterised by warm to hot, dry summers and mild, wet winters (McArthur 1957; Beard 1989). The annual mean rainfall is 821.8mm, 80% of which occurs between May and October over winter (Beard 1990; Bureau of Meteorology 2001). A dry period extends from mid-October to the end of March, a length of 5.3 mostly dry months (Beard 1979). Mean daily maximum air temperature ranges from 31°C in February to 18°C in July with an annual average of 23.6°C. Water is usually available to deep-rooted species as the groundwater table in Kings Park ranges from 10 to 60m below ground level.

Kings Park is situated in the central part of the coastal belt of the Swan Coastal Plain, primarily on the Spearwood Dune System (McArthur and Bettenay 1960) on the Karrakatta soil association. It is located within the Drummond Botanical Subdistrict (Beard 1967) with native vegetation made up of mixed *Banksia-Eucalyptus-Allocasuarina* open woodland. The dominant species are *B. attenuata, B. menziesii*, *B. grandis*, *Allocasuarina fraseriana, E. gomphocephala, E. marginata* with a sparse understorey of small trees and large shrubs consisting mainly of wattle (*Acacia cyanophylla, A. saligna, A. pulchella*) and *Xanthorrhoea preissii* (Beard 1967). Two other species of *Banksia* occur in Kings Park: *B. ilicifolia* and *B. prionotes.* The shrub and understorey layers are dominated by 17 species of the family Mimosaceae (A*cacia*), 32 species of Fabaceae (*Bossiaea, Daviesia, Hardenbergia, Hovea, Jacksonia, Kennedia, and Oxylobium*), 27 species of Myrtaceae (*Calytrix, Hypocalymma, Kunzea, Melaleuca,* and *Verticordia spp.*), 26 species of Proteaceae (*Adenanthos, Dryandra, Grevillea, Hakea, Stirlingia*), 3 species of Dilleniaceae (*Hibbertia*) and 9 species of Goodeniaceae (*Scaevola*) (Bennett 1988).

1.3.1.1 Weeds in Kings Park

Since settlement by Europeans, disturbances in Kings Park have included logging, firewood collection, trampling by visitors, rubbish dumping, grazing, the introduction and cultivation of South African perennial Veldt grass (*Ehrharta calycina*), clearing, limestone quarrying, weed invasion, prescribed burning and summer wildfires. One of the most significant disturbance processes began with the felling of *E. marginata* for timber, which caused the canopy to be opened up especially at the end of the 19th century. The removal of the canopy of the main species increased light reaching ground level, which later stimulated understorey plants such as the invasive grass *Ehrharta calycina* (Baird 1977).

This increased the frequency and intensity of fires and established a cyclic degradation process of intense fires fuelled by high biomass production and further invasion. It is thought that as a result fire-sensitive, native species declined (Wycherly 1984). The high frequency of intense fires, as well as competition from the understorey containing weed species, also caused more damage to the native resident species (Baird 1977). Large areas of Kings Park are in relatively poor condition. In 1999, a survey conducted by Kings Park management suggested that 20% of the park was in ‘poor’ or ‘very poor’ condition.

The long history of disturbance in Kings Park has resulted in a severe environmental weed problem. Of the 465 plant species listed for Kings Park, 290 are native, 145 are exotic and 26 are native to other areas in Australia (Bennett 1988; Wycherly 1992). Some of the weed species have invaded the park from neighbouring properties, while others, such as *Eucalyptus cladocalyx* and *E. citriodora*, have been planted deliberately in Kings Park as part of ‘ornamental’ projects (Ruthrof et al. 2003).

Weed invasion progressively changes the floristic composition either through competing with the native flora or as a consequence of intensifying the grass/fire cycle (as in Hopkins et al 1989, D’Antonio and Vitousek 1992, Milberg and Lamont 1995; Rossiter et al. 2003). The introduced perennial grass *Ehrharta calycina* started to spread into the Kings Park bushland starting from the 1940s. The presence of this species has changed the cycle of regeneration after fires and made the survival of other species’ seedlings difficult (Baird 1977). However post-fire weed control has successfully reduced the number of weeds in the Park (Dixon *et al* 1995b).

Weeds that are still of concern in the Park are: *Eucalyptus cladocalyx, Brachychiton populneus, Buddleja madagascariensis, Solanum nigrum, Myrsiphyllum asparagoides, Gladiolus caryophyllaceus, Arctotheca calendula, Hypochaeris glabra, Sonchus oleraceus, Taraxacum officinalis, Urospermum picroides, Euphorbia peplus, Lupinus* spp., *Trifolium* spp., *Geranium molle, Oxalis pes-caprae*, *Bromus* spp., *Ehrharta calycina* and *Freesia* spp.

1.3.1.2 Fire in Kings Park

It is hypothesised that Kings Park may be experiencing ecosystem changes manifested by environmental weed invasion and native population loss due to fragmentation and an altered fire regime. Indeed, urban reserves, like Kings Park, represent an extreme form of fragmented system and are therefore difficult to manage (Hobbs and Hopkins 1990). Evidence suggests that the fire regime in Kings Park has changed since the settlement by Europeans almost 200 years ago (Dixon et al. 1995c). Prior to settlement, Aboriginal people used fire to provide favourable habitats for herbivores or increasing the local abundance of food plants (Bowman 1998). In Kings Park, the Nyungar people used fire regularly as a tool for hunting game (Dixon et al. 1995c). Following settlement, the development of the understorey after logging *E. marginata*, coupled with the decreased frequency of fire in the area around Kings Park, it is likely that the fires became more intense (Wycherley 1984). As a consequence of severe fires, the tree canopy, as well as seedlings, were damaged or killed (Wycherley 1984; Bell et al. 1992). The change in fire regime from frequent, patchy and low intensity fires during pre-colonisation times to larger scale, more intense landscape fires post-colonisation is likely to have occurred in much of the southwest of Western Australia (Bell et al. 1989; Burrows et al. 1990; Bowman 1998).

Kings Park has a reasonably complete fire record since 1944. During this period, four fire regimes have been implemented. Prescribed block burning (1944–1962), no burning (1963–1973), buffer strip burning (1974–1984) and integrated management (1985–). Results gathered regarding the total area burnt indicate that, despite the differing fire regimes, only a slightly greater area was burnt per year in wildfires; small confined wildfire events averaged 10 per dry season (September to May), and a major wildfire still occurred every 10 to 15 years (Dixon et al. 1995c). Between 8 and 45% of Kings Park was consumed during each of these major fires (Dixon et al. 1995c). Fires in the Park mainly fall into two groups; wildfires in mid-summer (January to February) and mild burns covering smaller areas in spring and autumn (Baird 1977). Records show that 48% of wildfires in Kings Park are due to arson (Dixon et al. 1995c). Two severe summer wildfires have occurred in Kings Park in the last two decades, the first in 1989, which burnt 45% of the bushland, and the second in 1996 which burnt 28% of the bushland (Bell et al. 1992). There is currently a management policy of no-burning in place for the park.

1.3.1.3 Fragmentation in Kings Park

The Kings Park bushland has not reduced in size over the last 60 years. Still, the area has become more isolated in the urban context, dramatically reducing its connections with similar natural environments. Urbanisation has negative effects, which are greater than those caused simply by habitat loss or degradation (Van den Berg et al. 2001). Isolated populations are more sensitive to disturbance. In Kings Park, following the devastating fire of 1989, the avifauna showed a slower recovery in contrast to other areas outside the city of Perth that were subjected to wildfires (Recher 1997).

1.3.2 The other Locations at which investigations were undertaken

1.3.2.1 Bold Park Bushland (BP) (31° 56’49 S; 115° 46’17 E)

Bold Park is a 437 hectare urban reserve, 8km from central Perth, Western Australia. Two major dune systems, Spearwood and Quindalup support 9 plant communities, with a total of 568 species, 336 native, 232 introduced (Barrett and Pin Tay 2005). The study was conducted in the *Banksia* woodland community, characterised by woodlands 6-8 metres tall of *Banksia attenuata* and *B. menziesii* (Proteaceae) with scattered emergent *Eucalyptus gomphocephala* over a well developed sclerophyllous shrub understorey and perennial herbs (Beard 1989). The dominant *Banksia* woodland community covers 58% of the Reserve. Mapping of introduced species within Bold Park in 1997 found *E. calycina* to be the most common introduced species, followed by *P. capitatum*. Moreover, virtually all banksia woodland communities were severely affected by introduced species with 81% of the Park being in Poor Condition (Botanic Gardens and Parks Authority 2000).

1.3.2.2 Murdoch University Bushland (Mu) (32°04’22 S; 115°50’04 E)

Located on the Spearwood dune system, most of the *Banksia–E. marginata* woodland vegetation present in the “Murdoch bushland” is in good condition.

1.3.2.3 Ridges State Forest (Rid) (31°22’00 S; 115°41’45 E)

The woodland is located approximately 80 km north of the city of Perth near to the city of Wanneroo and the study sites are located both side of Military road, on the Spearwood dune system.

The area has soils varying between deep sand and sand over limestone Karrakatta associations. Vegetation includes banksia woodland and heath with predominantly *Dryandra sessilis* (parrot bush) and *Hakea* spp.. Also *E. marginata* and *C. calophylla* woodland occur.

The woodland is divided by a few tracks and is relatively semi-natural. There are pine plantations along the north-eastern border of the area which host large cockatoo populations. There are also deposits of limestone, limesands, and diatomite, which are commercially quarried.

The main vegetation types are:

***Banskia Low* Woodland** This vegetation type consists of *Banksia attenuata, B. grandis, B. menziesii* and occasionally *B. ilicifolia, Allocasuarina fraseriana* and *Eucalyptus todtiana* (pricklybark).

***Banksia/Eucalyptus/Allocasuarina* Woodland.** This vegetation type is associated with the deeper soils on limestone and is common in Ridges State Forest. *Banksia menziesii, B. grandis, B. attenuata, Allocasuarina fraseriana* and *Eucalyptus todtiana* form a mixed overstorey. The understorey has a diversity of species.

Other species occurring are: *Banksia ilicifolia*, *Eucalyptus marginata*, *Nuytsia floribunda*. Understorey species include: *Xanthorrhoea preissii; Dryandra sessilis, Hakea trifurcata, Calothamnus sanguineus, Conospermum triplinervium*, *Hypocalymma angustifolium, Macrozamia riedlei; Petrophile macrostachya*; *Scholtzia involucrata*; *Astroloma xerophyllum, Eremaea pauciflora; Stirlingia latifolia; Synaphea polymorpha.*

In this location surveys and experiments were undertaken mainly in post-fire conditions. In this area fire was likely used by Aborigines as a tool in hunting and gathering. Little is known of the fire history of the Forest prior to 1970, when accurate records of fire were initiated as part of a regular fuel reduction burning program. Accidental or deliberate fires have also occurred. Winter is not normally associated with fires in the bush, but for the Department and Conservation and Land Management's (CALM) Perth District, it is the ideal time to use prescribed burning to reduce the threat of summer bushfires in the pine plantations and banksia woodlands in the Wanneroo region.

Of the three sites used for surveys and trials two experienced wildfire in summer.

1.3.2.4 Jandakot Regional Park (Jand) (32°12’19 S; 115°54’28 E)

Jandakot Regional Park is situated within the Perth area approximately 50 kilometres south of the city of Perth. The different sites where experiments and surveys were undertaken are located in the Park on the corner of Ankatell and Nicholson Roads.

The Jandakot Regional Park consists of a network of environmentally significant lands, comprising wetland and bushland systems. Although the Park is fragmented by rural and urban land uses, it is generally large enough to sustain diverse floral communities (Western Australian Planning Commission, 1995). The Park also serves to protect the underlying Jandakot Groundwater Mound, a significant source of water for the Perth metropolitan area. This rich diversity and complexity of ecosystems has very high conservation value because these ecosystems are now significantly cleared on the Swan Coastal Plain. The Bassendean and Spearwood Dune Systems, which underlies the Park, are characterised by low woodland of scattered trees, with dominant species being *Banksia attenuata*, *Banksia menziesii*, *Banksia ilicifolia*, *Eucalyptus todtiana* and *Nuytsia floribunda*, and with a dense understorey of sclerophyll shrubs.

Wetlands have formed in inter-dunal depressions where the underlying groundwater aquifer is present at, or close to, the surface. Surveys and experiment were undertaken in the Banksia woodland.

The main occurring tree species are: *Banksia attenuata*, *Banksia menziesii*, *Banksia ilicifolia*, *Allocasuarina fraseriana*, *Eucalyptus marginata*, *Nuytsia floribunda*. Understorey species include: *Daviesia quadrilatera*, *Pimelea sulphurea*, *Eremaea pauciflora*, *Jacksonia floribunda*, *Scholtzia involucrat*a, *Melaleuca scabra*, *Astroloma xerophyllum, Eremaea pauciflora, Stirlingia latifolia, Synaphea polymorpha, Xanthorrhoea preissii, Calothamnus sanguineus, Conospermum stoechadis* and *Hypocalymma angustifolium.*

For general view of the locations and sites (with local names) for each survey and experiment see annex I.

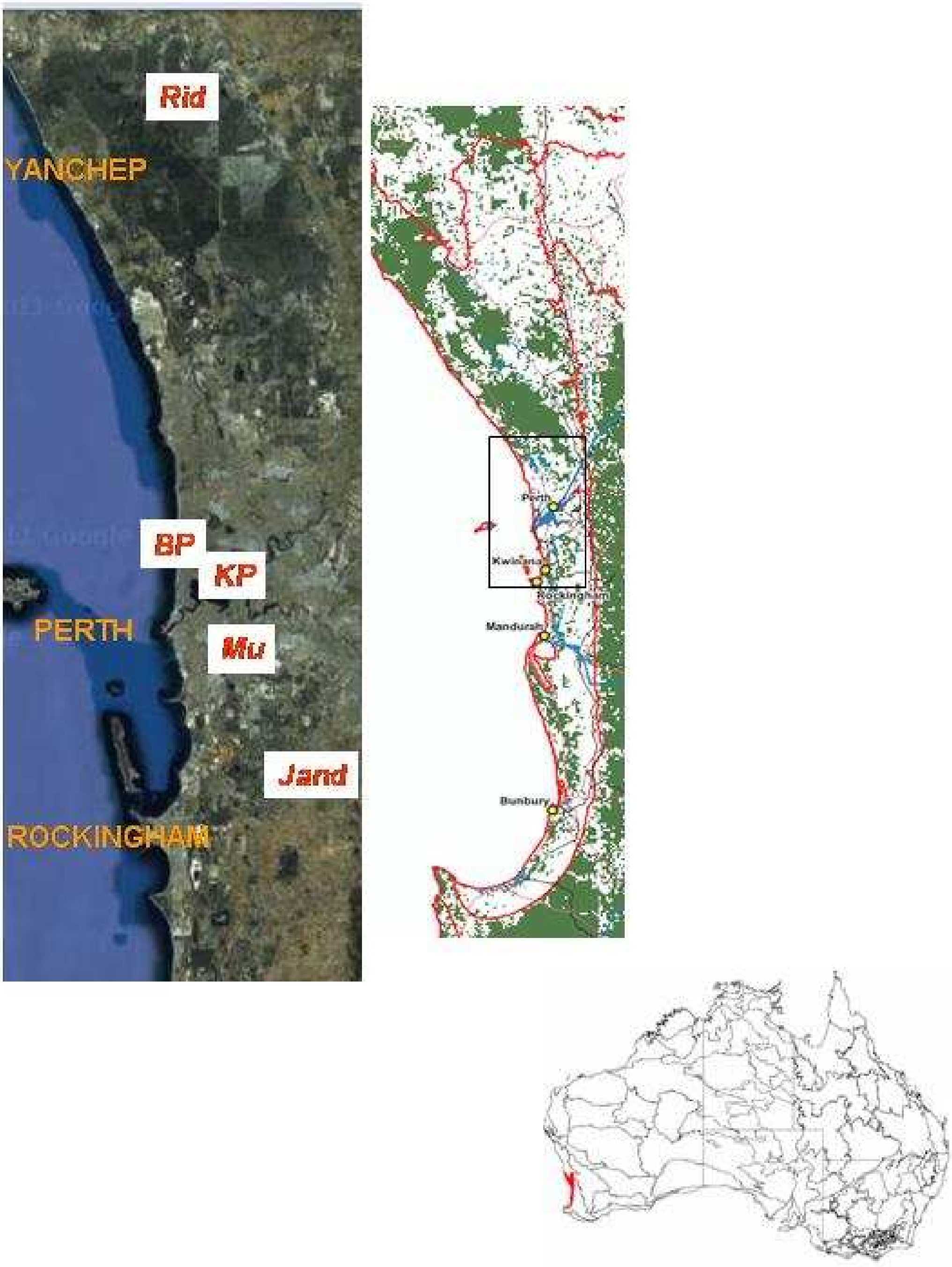

Fig. 1.3 The Australian continent and the Swan Coastal Plain. In the rectangular the Perth region where the investigated sites are located. KP=Kings Park; BP=Bold Park; Mu= Murdoch bushland; Rid= Ridges State Forest; Jand=Jandakot Regional Park.

1.4 The Investigated Species

Banksia attenuata and *B. menziesii* are the two main species investigated in this study, together with *B. grandis* and *B. ilicifolia*.

Surveys and experiments were also carried out on several other species occurring in the woodland at the other locations used for this study. These other species were investigated because they compete with *Banksia* spp. in the Kings Park bushlands. The species were *Eucalyptus marginata* (Jarrah)*,* and *Allocasuarina fraseriana* (casuarina) and the shrubs *Acacia saligna, Acacia pulchella and Dryandra sessilis.*

In chapter two, surveys were also undertaken on the following species: the medium-tall trees *E. gomphocephala* (Tuart) and *Corymbia calophylla* (Marri) and, the shrubs *A. cyclops, Conospermum triplinervium, Jacksonia furcellata* and *J. sternbergiana.*

For species complete description see annex II (plant nomenclature follows Paczkowska and Chapman 2000).

2 CHAPTER 2 THE VEGETATION CHANGES STUDY

2.1 Introduction
2.2 Aim
2.3 Materials and methods
2.3.1 The 1939 mapping
2.3.2 The 1999 re-surveying
2.4 Results
2.5 Discussion

2.1 Introduction

In some cities there are tracts of wild land that have been reserved as public open space. These are isolated islands of vegetation that had been widespread before urbanisation. These areas also serve as important cultural links to natural landscapes particularly as many city-based natural areas possess highly urbanised communities. Although often relatively small in area, urban remnants make an important contribution to biodiversity conservation as found for remnants in agricultural areas (Dilworth et al. 2000). In addition they provide a source of "natural" experience for city dwellers and for biodiversity maintenance (Miller 2006). In some cases these urban refuges acquire an iconic status and attract strong public attention, support and involvement e.g., Central Park (New York City), Gotteborg Botanic Garden (Sweden), the English Garden (Munich), Table Mountain (Cape Town), Riserva di Castel Porziano (Rome), Stanly Park (Vancouver) and Mt Coottha (Brisbane). In Perth, Kings Park bushland (Fig. 2.1) was set aside as a reserve in 1871 in the early stages of European colonization and enjoys a similar iconic status in Western Australia while being within the context of a global biodiversity hotspot (Myers et al. 2000).

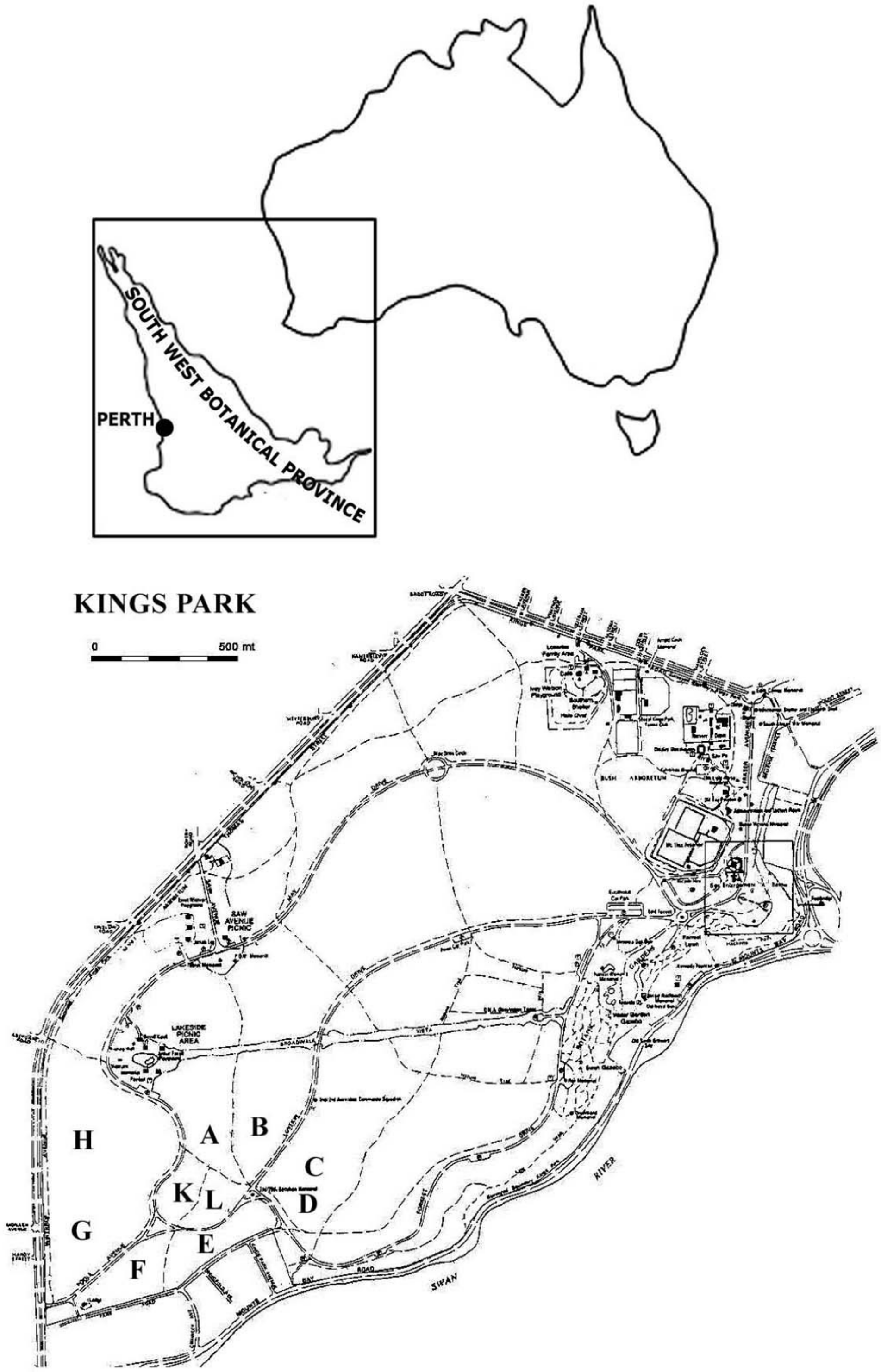

Fig. 2.1 Perth, Western Australia and location of the study plots in Kings Park. The Park is bordered by the Swan River to the south eastern side, Thomas Street on the north and Winthrop Drive on the western side.

Due to their urban context, biological isolation and high perimeter-area ratio, there are many threats to the persistence of species, which occur within such reserves. Management of these areas is, therefore, a considerable challenge and depends upon knowledge of past land-use, characteristics of the original vegetation, frequency and extent of significant disturbances and surrounding land-use.

Vegetation change in urban remnants can be usefully considered in a framework of "alternative states" as used in restoration ecology (Hobbs and Norton 1996; Suding *et al.* 2004). Although the vegetation of a remnant may not be considered as being highly degraded, changes in dominance, particularly in event-dependent systems, may result in changed structure and reproductive patterns which perpetuate different species from those originally present. Introduction of an aggressive weed would be one way of changing a system, if, for instance, weed proliferation made the vegetation more fire prone than it had been originally (examples in Suding *et al.* 2004). An understanding of the vegetation dynamics and the impact of past and current management on these dynamics is essential for successful conservation. However, this information is often difficult to obtain because changes in vegetation in response to management are most likely to occur over many decades, beyond the average time of research careers and most research project fundings. The century to decadal time scale that is the important period for urban reserves seems to have been a "blind spot" in vegetation studies (Bowman 2002).

In the absence of accurate long-term records of species abundance and distribution, attempts to monitor vegetation change have been based on short-term vegetation processes (Lunt 2002), proxy measures such as pollen analysis (Newsome and Pickett 1993), dietary analysis of herbivores from faecal deposits (Witt *et al.* 2000), tree ring analysis (Motta *et al.* 2002) and ethnographical records such as vegetation notes, postcards and photographs (Debussche *et al.* 1999). These techniques, while useful in the absence of long-term quantitative data, are limited in their ability to describe historical vegetation change because of variability between species in pollen production, difficulties in taxonomic identification, selective foraging and the descriptive nature of many historical documents, often with substantial bias by the observers. There is a lack of historical quantitative monitoring of vegetation through direct observation for most landscapes.

Historically, where fixed point, long-term monitoring stands have been established and subsequently re-surveyed, significant changes in the composition and structure of vegetation have been noted (Withers and Ashton 1977; Kirkpatrick 1986; Leendertse *et al.* 1997; Lunt

1998a,b; Nygaard and Odegaard 1999; Fisher et al. 2009) and possible causes linked to management activities have been suggested. For example, in remnant coastal woodland in Victoria, Withers and Ashton (1977) documented a change in succession from open woodland dominated by *Eucalyptus* species to a closed scrub dominated by *Allocasuarina* species. Withers and Ashton (1977) attributed this change to over 90 years exclusion of fire and predicted complete dominance of *Allocasuarina littoralis* and extinction of *Eucalyptus ovata* if environmental conditions remained similar. Lunt (1998b) resurveyed Withers and Ashton's stands 25 years after they were established and confirmed these authors' predictions, observing an increase in the density of *A. littoralis* and a decline in *E. ovata*. Lunt (1998a), using historical records, documented the chronology of different land uses in the woodlands for a 200 year period and confirmed the Withers and Ashton hypothesis that the most likely cause of change in the vegetation was the active exclusion of fire from the ecosystem.

The studies by these authors demonstrate that the combination of long-term vegetation monitoring, use of historical documents, and empirical/experimental studies of plant species demography can detect and determine the causes of vegetation change and loss of biodiversity associated with management. Long-term monitoring of fixed point or historically established stands has much to offer natural resource managers and where possible, existing stands should be re-surveyed to enable detection of any changes in the integrity of the biosystem.

In 1939, the locations of individual plants of 13 native tree and shrub species, occurring in a portion of the Kings Park bushland, were mapped along 126 transects. The map, with included notes, was fortuitously found in the Kings Park and Botanic Gardens archives in 1999. Resurveys of the same transects were undertaken in the same year. The species monitored in this study represent the predominant biomass contributors and may compose upwards of 70% of the total phytomass of the bushland. Dominant plant species can impact the rest of the plant community (Specht and Specht 1989) and as most of ecosystem properties, and associated changes, are likely to be detected in the plant biomass (Grime 1998), it is expected that the composition and the structure of the predominant species will reflect these changes.

2.2 Aim

The main aim of this thesis is to investigate the reason behind the vegetation changes in the urban bushland remnant within the protected area of Kings Park. In particular it investigates if the recruitment process may be responsible for the changes and/or if the changes have affected the recruitment process itself accelerating the vegetation changes.

In this preliminary study, by resurveying the transects in 1999 I intended to determine whether the composition and structure of the vegetation had changed in the intervening 60 years. Using information about the biology of the dominant species from this and other studies I aimed to explain how change had been instigated, how it had progressed through time and how management decisions have influenced change.

2.3 Materials and methods

Study area The Kings Park bushland is a 267 ha remnant of mixed *Eucalyptus-Banksia-Allocasuarina* woodland (Fig. 2.1) and in a global sense it is remarkable for its size and proximity to a capital city. The Park is isolated from other native vegetation by urban development to the north and west and by the Swan River to the south and east. The bushland has a long history of disturbance and almost a third of recorded plant species are exotics (Bennett 1995). Despite this, Kings Park has significant conservation value and is an important component for the preservation of the biodiversity on the Swan Coastal Plain (Anonymous 2000).

Geomorphological features Kings Park is located on an ancient dune ridge. The soil consists of podzolised sands overlying limestone at depth. Within the Kings Park study sites there are slight edaphic variations in soil depth, degree of leaching and sand grain size with pH varying from slightly acidic to neutral (Bessell-Brown 1990). The sandy soils are highly deficient in available nutrients for plants (Pate and Beard 1984). The Swan Coastal Plain is underlain by an extensive groundwater system (Kite and Webster 1989), which in Kings Park, flows from the north-east towards the Swan River and varies in depth between 56 m and 8 m below the surface, with annual maximum variation in depth of approximately 0.5 - 1 m (Davies 1996).

2.3.1 The 1939 mapping

In 1939, the vegetation in a 60 ha portion of the south-western corner of Kings Park was mapped by Alison (M) Baird (University of Western Australia). Baird established 126 transects, in 10 alphabetically coded ‘plots’, located parallel to each other within each plot. Each plot was bounded by roads or/and tracks (Fig. 2.1). Transects were 6 m wide and varied in length from 36 m to 460 m; the differences in length were a consequence of the location of roads or tracks. In total, approximately 25.8 km of transects, covering an area of approximately 15.4 ha, were surveyed (Table 2.1). The distance between each contiguous transect was 25 metres in plots covering a relatively small area and 50 metres in larger plots. Within each transect, the position of all individuals greater than 183 cm high (6 feet) of 13 dominant species was mapped. The species were the medium-tall trees *Eucalyptus marginata* (Jarrah), *E. gomphocephala* (Tuart) and *Corymbia calophylla* (Marri); the medium-small trees *Allocasuarina fraseriana* (Casuarina), *Banksia attenuata, B. menziesii, B. grandis* and *B. ilicifolia*; and, the shrubs, *Acacia saligna, A. cyclops, Conospermum triplinervium, Dryandra sessilis* and *Jacksonia furcellata*. No information on abundance in 1939 of other species present in the Park is available.

2.3.2 The 1999 re-surveying

In 1999, the plots mapped by Baird were re-located and surveyed using the methods employed in 1939. In the 1939 map notes there was no indication of whether plants were single or multi-stemmed (*Allocasuarina fraseriana,* in particular, can commonly have a multi-stemmed habit). However, study species that produce stems from the primary root-stock do not produce suckers at a distance from the main stem so multi-stemmed individuals were scored as a single plant. The native shrubs *Acacia pulchella* and *Jacksonia sternbergiana* were not recorded in 1939 but occurred in sufficient abundance to be scored in the 1999 survey.

There was no significant change in geographic features of the study area in Kings Park during the 60 year study period. The location of roads and tracks remained unchanged together with the length of transects and surface area of the plots.

Table 2.1 General attributes of the plots where transects were located in 1939 and resurveyed in 1999 in Kings Park. S=surveyed plots, N=number of transects, F=number of extensive wildfires in the 60 years period.

Plots	S (ha)	N	F
A	0.53	7	1
B	0.65	7	1
C	0.7	9	2
D	1.4	6	2
E	1.6	29	0
F	1.4	18	0
G	0.9	8	1
H	6.7	26	1
K	1.1	7	1
L	0.4	9	1
TOT	15.4	126	2

Climate for the 20 year periods prior to the 1939 and 1999 vegetation surveys

Perth has a mediterranean-type climate with cool moist winters and warm dry summers (Fig. 2.2). Climatological data for the twenty-year periods prior to the 1939 and 1999 surveys were taken from the Australian Commonwealth Bureau of Meteorology's climate archive of records from the nearest weather station to the study area. From 1992, data were recorded from a new station located approx. 6 km north-east of the original station. Consequently, based on the proportion between the long-term record averages (47 years) of the two different stations, data from 1992 to 1999 were adjusted on a monthly basis.

Climate for the 20-year periods prior to 1939 and 1999 was compared and mean air temperature, annual precipitation and hours of sunshine during 1920-1939 and 1980-1999 are shown in Table 2.2.

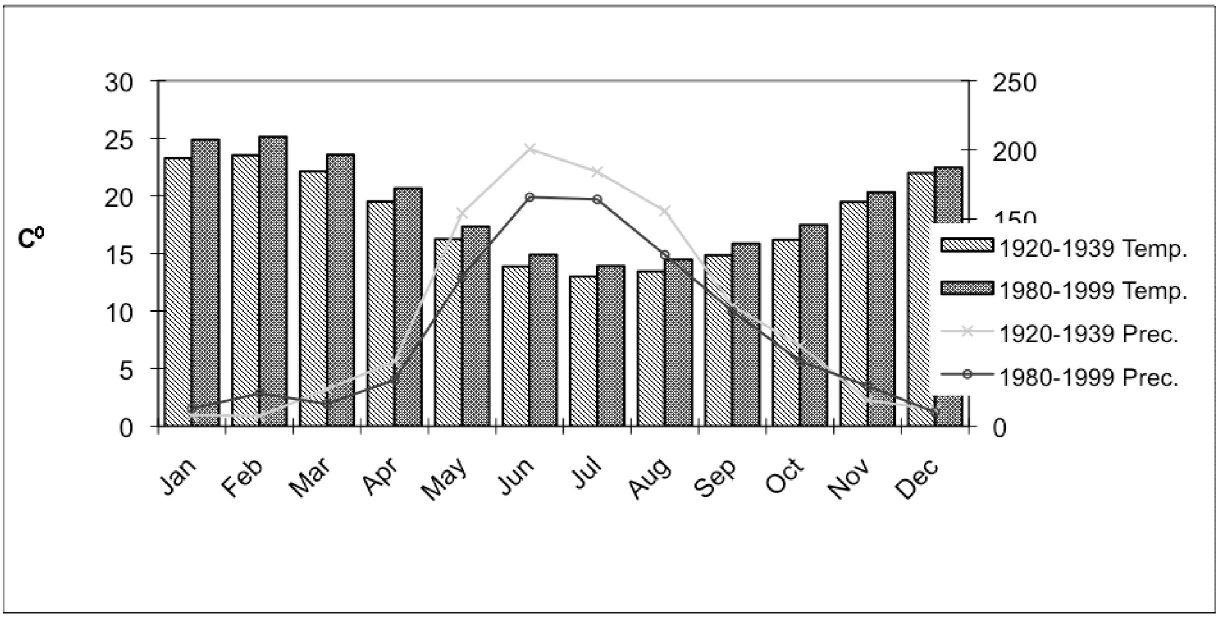

Fig. 2.2 Thermopluviogram data taken from the nearest weather station to the study area, averages of temperature and precipitation from the 20 year periods before 1939 and 1999. The temperature bar chart and precipitation lines show this is a typical mediterranean climatic regime.

Table 2.2 Climate in the study area, for the 20 year periods prior to 1939 and 1999; Mx=mean maximum air temperature, Mn= mean minimum air temperature, Dm=absolute mean, P=Precipitation, S=Bright sunshine.

	Averages					Averages				
	1920-39				1930-39	1980-99				1980-99
	Temperature (^{0}C)					Temperature (^{0}C)				
	Mx	Mn	Dm	P mm	S hrs/day	Mx	Mn	Dm	P mm	S hrs/day
Winter	17.6	9.3	13.4			18.6	10.2	14.4		
Summer	28.8	17.0	22.9			29.7	18.6	24.2		
Ann. mean			18.1		8.1			19.2		8.6
Total				960					817	

Fire history Historical fire maps and recent geographic data files were examined to investigate the fire pattern in the study site.

Statistical analysis

Descriptive: In each of the 126 transects, the densities of the 13 species from the 1939 and 1999 surveys were calculated as the total number of individual plants divided by the area of the transect and expressed as plants ha^{-1}. The relative frequency of the 13 species was also calculated.

Analytical

Univariate. For each species, the two sets of data (the densities in the 126 transects in 1939 and 1999) were compared (for each transect, the density of each species 'before' and 'after' the 60 years) using the Paired Two Tailed *T*-Test, the null hypothesis being that there was no difference between the two sets. Each transect was considered as an independent sampling station. The Paired *T*-Test assumes that paired differences are normally distributed. For some species data were not normally distributed (for those species which were not common in 1939). Consequently differences in the densities were also tested with a non-parametric test, the One Sample Sign Test that does not assume the form of the data apart from a large number of paired observations; the null hypothesis being that there were equal numbers of positive and negative differences of the densities observed. A conservative level of significance was chosen and temporal changes were considered significant if $P < 0.01$.

Multivariate. The abundances of the 13 species in the 10 plots at the two times were analysed using ordination. A community data matrix was created using 20 samples (the 10 plots in 1939 and in 1999) and the mean density of the 13 species in each plot. Mean density for each plot was calculated from the density of species in transects in each plot divided by the number of transects in the plot (Tables 2.3 and 2.4). The samples were ordinated using Non-Metric Multidimensional Scaling (NMDS) in two dimensions and with the Bray-Curtis distance function. NMDS is considered a robust ordination technique for indirect gradient analysis based on species composition representation. It was assumed that sample separation space is directly related to ecological dissimilarity so that examination of ecological change over time can be made from the display of samples in the ordination space.

2.4 Results

The composition and the structure of the *Eucalyptus-Allocasuarina-Banksia* woodland on the Kings Park study area in 1939 differed considerably from that in 1999 (Figs. 2.3 and 2.4). In the 60-year period the mean density of indigenous woody plants in the woodland more than doubled from 530 plants ha^{-1} to 1200 plants ha^{-1}. This increase in density was relatively uniform across all sites sampled, but was not uniform across species or life forms (Tables 2.3 and 2.4).

All tree species, except *Banksia* spp., showed significant increases in abundance (Tables 2.3 and 2.4). Compared with 1939, in 1999 there were twice as many *E. gomphocephala* and *E. marginata*, a 10-fold increase in *C. calophylla* and three times as many *A. fraseriana*. In contrast, there was a general decrease of a third in *Banksia* spp. abundance (Fig. 2.5). The decline of *Banksia* spp. however, was not uniform in all the plots of the study site (Table 2.3).

There was a significant increase in abundance of *A. saligna* and *D. sessilis* in 1999 compared with 1939 (Fig. 2.3; Table 2.4). In particular, *A. saligna* numbers increased approximately 60-fold while *D. sessilis* is now spread throughout most of the study plots, yet was infrequently encountered in the survey in 1939.

Table 2.3 Mean values of trees (hectare^{-1}) for transects within each plot and statistical significance, using t-test and sign test, based on paired comparison, between 1939 and 1999, of 126 transects; **=P<0.01, *** =P<0.001.

Sp.	***E. marginata***		***E. gomphocephala***		***C. calophylla***		***A. fraseriana***		***B. attenuata***		***B. menziesii***		***B. grandis***		***B. ilicifolia***	
	‘39	‘99	‘39	‘99	‘39	‘99	‘39	‘99	‘39	‘99	‘39	‘99	‘39	‘99	‘39	‘99
A	59.3	63.5	0	1.4	0	229.9	293.2	551.6	294.1	160.4	180.4	61.5	30.6	6.2	0	0
B	27.3	97.3	0	8.6	0	32.0	166	758	183.0	278.0	60	66	17.0	3.6	0	0
C	13.3	87.7	0	7.1	0	13.7	197.3	794.2	301.5	517.9	57.1	131.5	22.1	1.5	0	0
D	35.9	117.6	0.7	10.9	45.6	84.7	152.8	503.8	182.8	287.5	90.4	75.7	11.4	0.6	0	0
E	96.4	172.7	13.2	36.7	8.3	124.3	118.4	503.4	114.4	38.4	49.6	51.8	23.9	2.9	11.1	0
F	103.7	139.6	47.5	94.3	2.3	4.6	157.9	166.7	134.9	8.6	33.7	11.8	3.2	0	0	0
G	39.8	76.5	7.3	10.5	0	13.4	138.7	291.3	106.7	57.7	159.5	42.9	5.1	1.2	0	0
H	40.7	27.8	12.3	31.9	0.2	15.0	128.6	402.3	255.6	173.5	91.9	39.2	5.5	3.2	1.7	0.1
K	53.1	186.2	2.2	41.9	2.2	100.2	153.9	516.3	240.6	83.7	51.5	16.8	18.8	1.9	0	0
L	62.6	132.8	5.4	10.1	4.1	45.8	137.2	503.6	196.0	119.8	100.6	40.5	6.4	0	0	0
t-test	***		***		***		***		***		***		***		**	
sign test	***		***		***		***		***		***		***		***	

Table 2.4 Mean values of shrubs (hectare^{-1}) for transects within each plot and statistical significance, using t-test and sign test, based on paired comparison, between 1939 and 1999, of 126 transects; **=P<0.01, *** =P<0.001; ns =not significant.

Sp	*A. saligna*		*A. cyclops*		*D. sessilis*		*C. triplinervium*		*J. furcellata*	
	1939	1999	1939	1999	1939	1999	1939	1999	1939	1999
A	0	125.7	0	4.5	0	40.0	64.2	39.6	0	6.9
B	0	597.1	0	4.0	0	40.1	0	0	0	18.4
C	0	46.3	0	1.3	0	94.8	0	0	0	23.3
D	0	48.4	0	0.0	0	60.2	0	2	16.6	74.7
E	8	15.7	0	7.7	0.7	599.4	3.2	4.3	10.5	66.8
F	0	26.9	0	20.9	0	294.0	0	0	0	34.9
G	0	48.6	0	0.0	0	29.5	4.9	0	13.1	3.5
H	0	70.7	0.3	3.4	1.7	51.9	8.2	29.7	0	6.4
K	6.5	146.6	0	2.4	0	193.4	0	50.5	0	6.5
L	8.7	173.5	0.8	31.4	0.8	211.2	0.8	0	3.9	33.6
t-test	***		**		***		ns		***	
sign test	***		***		***		ns		***	

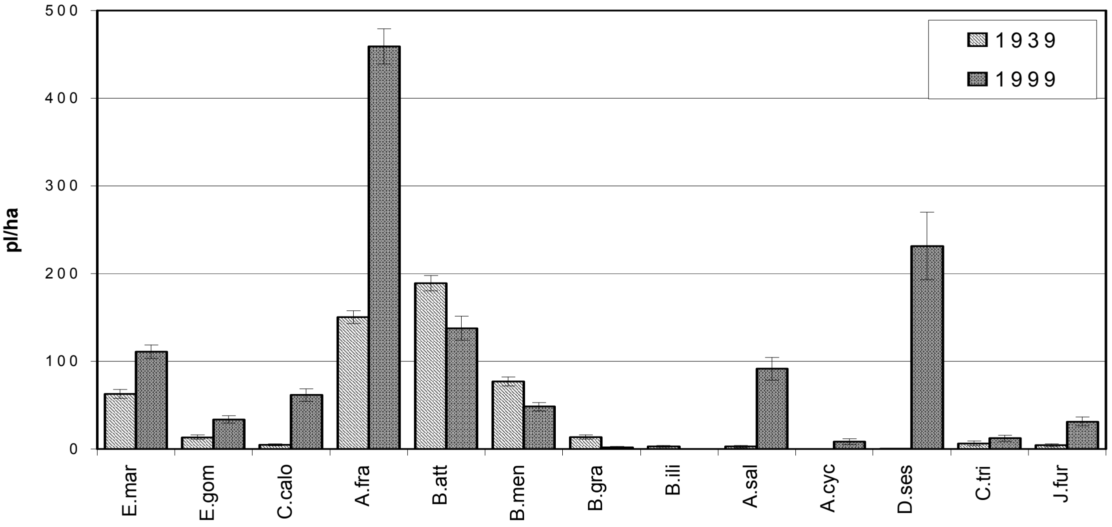

Fig. 2.3 Comparison between plant density of the selected study species (hectare^{-1}), in 1939 and 1999; mean ± 1SE based on 126 transects.

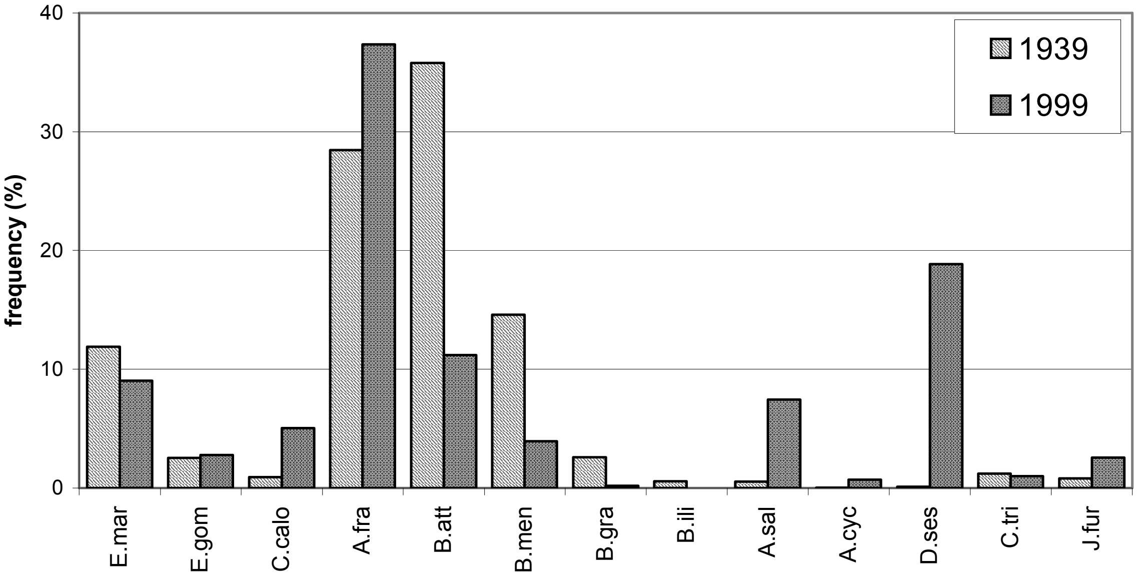

Fig. 2.4 Comparison between plant relative frequency of the selected study species, in 1939 and 1999.

Given such changes in the density of species, it is not surprising that the relative frequency of species in the woodland has also changed with the greatest change being in the *Banksia* species, from a relative frequency of 53% to 15%. *A. fraseriana* increased from 28% to 37%, while 'eucalypts' did not show any overall change. The shrub species, mainly due to proliferation of *A. saligna* and *D. sessilis* increased from 3% to 30%. For *C. triplinervium,* there was no evidence of any change in abundance.

The meteorological data showed that for both summer (December-February), winter (June – August) and over the whole year the temperatures in the period 1980 – 1999 were about 1^0 C higher than in the period 1920 - 1939. Mean rainfall for the 1920-39 period was 960 mm compared with 817 mm in the 1980-99 period. Mean hours/day of sunshine increased by more than 5% being 8.1 in the decade 1931 -1939 and 8.6 in the decade 1991-1999 (Table 2.2).

Fig. 2.5 Diagramatic representation of the structure of the Kings Park bushland: above 1939 and below 1999 Data were gathered from average values of the 10 plots

Fire records showed that over the 60 year period, two sites experienced two extensive fires, two sites were unburnt while the remainder experienced one extensive fire (Table 2.1); no extensive burns were reported for the 5 years prior to 1939.

Non-metric multidimensional scaling (stress = 0.07) confirmed an overall pattern of change in tree/shrubs between 1939 and 1999 as the two groups of samples are well separated on the ordination axes (Fig. 2.6), indicating a difference in the community composition, with a total separation of 1939 and 1999 plots. In particular the plots from 1939 clustered close together showing small difference in variability in the ordination, while 1999 samples were more dispersed showing a greater variability between them. The 1999 plots that had not experienced any extensive wildfire, E99 and F99, are displayed in the lower left corner of the ordination, while the plots which had experienced two wildfires, C99 and D99, are displayed diagonally opposite indicating substantial differences between them. These two plots (C and D) are close to plot B99, and are the plots where there was an increase or no decline of the two main *Banksia* spp. of the Park (Table 2.3). The smaller variability within the 1939 plots, compared to the 1999 plots, could be explained by lower tree densities and the absence of many shrubs in 1939.

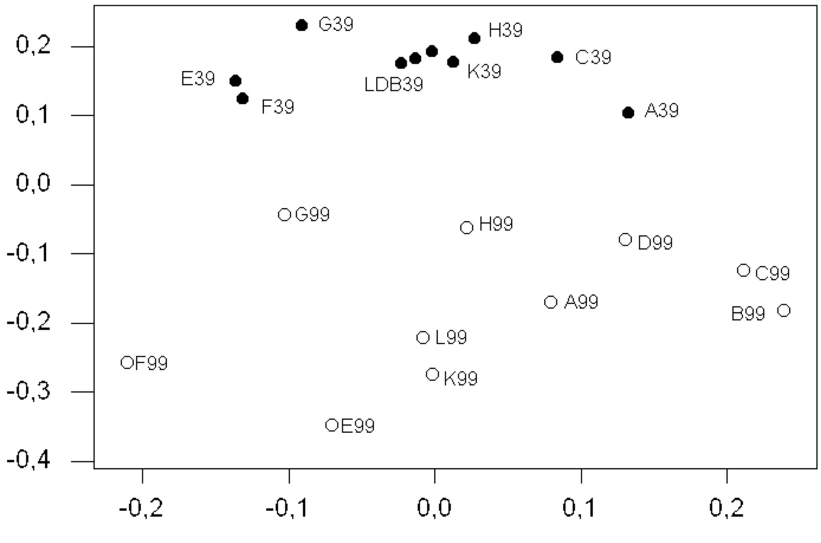

Fig. 2.6 Non-metric multidimensional scaling ordination of 1939 and 1999 plots. NMDS in two dimensions with Bray-Curtis distance, function Stress = 0.07. Letters indicate the plots

2.5 Discussion

There have been substantial changes in the composition and structure of the woodland in Kings Park between 1939 and 1999. While the changes reported here are only between two time points, concerns about vegetation changes (often referred to as decline) in Kings Park have been expressed since 1967 (Beard 1967, Seddon 1972). These authors attributed the decline to initial selective felling of the eucalypt overstorey that allowed more light into the understorey. This would have resulted in increased productivity in the understorey that in turn may have placed stress on the water relations of the overstorey plants leading to dieback of the larger trees due to drought stress or suppressed seedling recruitment.

In terms of tree species, the most significant trends have been an increase in the density and relative frequency of *A. fraseriana* and *C. calophylla* and a decrease in the density and relative frequency of *B. attenuata* and *B. menziesii* in most of the plots. Furthermore, *B. grandis* has become rare, while *B. ilicifolia,* which was infrequent in 1939, recorded only six times, is almost locally extinct and was recorded only once in the 1999 survey. *Eucalyptus gomphocephala* increased in density, between 1939 and 1999 but this has been due to increased numbers of saplings and decreased mature tree density indicating a change in the population age structure. As a consequence, the vegetation changed from open woodland dominated by *B. attenuata*, *A. fraseriana, B. menziesii*, and larger *E. marginata* and *E. gomphocephala* to a more closed formation, dominated by *A. fraseriana* with low stature eucalypts and an understorey dominated by *D. sessilis* and *A. saligna.*

Long-term transect studies (Recher and Serventy 1991) of the avifauna in the Park, encompassing surveys in the 1920s, 1950s and in 1986, showed that the changes in the abundance of some bird species also followed a long-term pattern. Changes in habitat structure and composition are sensitively detected by birds, with bird species capable of being used as indicators of changes and stress in urban ecosystems (Clergeau *et al*. 1998, Savard *et al*. 2000). From 1928 to 1986, there was significant change in the abundance of different bird species. Most of the bird species that decreased in number are ground foragers that require open vegetation, and are disadvantaged by increasing density of the understorey. The avifaunal studies provide independent verification that substantial structural vegetation changes have occurred in the bushland of Kings Park.

The causes of the changes outlined above are complex. An increasingly drier climate or decline in groundwater levels may be implicated, but the changes are more likely due to a complex matrix of interactions between different factors, the more important being abiotic and biotic interactions, weed invasion and altered fire regimes. In this scenario the banksia recruitment is investigated in this and in the following chapter

Precipitation and Hydrology Water availability plays a crucial role in plant survival especially in seasonally arid environments, where soils have low water holding capacity, such as the siliceous sands in Kings Park bushland. Between 1929 and 1999, annual precipitation decreased by about 15% and temperatures increased by about 10C. However, this is unlikely to be the cause of species changes in Kings Park as the ranges of all species extend into areas with much drier climates to the north and east of the Perth region.

Over the last 50 years utilization of the ground water under the Swan Coastal Plain has increased so decline in the water table under Kings Park may be involved in the decline of some species. However, a lowered water table is unlikely to be the culprit. In the Kings Park study site the average depth to the groundwater from the soil surface ranges from 8 m to 28 m (Davies 1996). *Banksia attenuata*, *B. menziesii* and *B. ilicifolia* have deeply penetrating tap roots (Dodd *et al.* 1989) and may draw water from the water table**.** However, Zencich et al. (2002) showed that for *B. ilicifolia* (the species that generally occurs in low points in the landscape) individuals growing three metres above the water table were not highly dependent on the ground water as they derived less than 40% of their water from this source. Davies (1996), predicted that the aquifer level within the study site varies seasonally by no more than 0.75 m. Thus, *Banksia* spp. are unlikely to be adversely impacted by such a relatively moderate change in groundwater level. Large scale pumping of the aquifer underlying Kings Park commenced in the 1960s (W. Kullmann, pers. comm.). Drawdown of the water table, of greater magnitude than the prediction assumed in 1996, may have occurred, especially in the surroundings of the extraction bores. However, in the study area no extraction bores were present within a kilometre. In addition the study plots are located in the area of Kings Park were the soil surface is closest to the water table thus, it is unlikely that generally lowered water tables could account for tree deaths over many years. The only record of death of banksias (*B. attenuata*) due to water table lowering by excessive extraction was from a site over 40 km north of Kings Park (Groom *et al.* 2000) but this was very localised and due to an exceptional combination of high summer temperatures and extreme water table draw down.

A manipulative experiment in the glasshouse undertaken within this study (see annex IV) investigated seedling growth of seven key species of the Kings Park *Banksia* woodland and tested if survival, root biomass and length could be related to rate of soil water lowering to different depths. *Acacia saligna* and *D. sessilis* seedlings may be less sensitive, compared to the other species, including banksias, to lower moisture availability due to their ability to increase root length under more rapidly drying soil conditions. Difference in root growth between the different species could help explain why seedlings of some species may not be performing as well now as they might have been under conditions of a slightly higher rainfall regime in the past.

Weeds The increased presence of weeds is commonly associated with fire (Milberg and Lamont, 1995). The introduced perennial grass *Ehrharta calycina* (Veldt grass) spread into Kings Park bushland from the 1940s and rapidly expanded across the entire Park (Baird 1977). This caused two major changes. Firstly, increased competition, especially for tree seedlings if they recruit in the interfire period. In situ manipulative trials and ex situ experiments in the glasshouse (better described in the following chapters of this thesis) showed that, of the dominant species in Kings Park, seedling emergence of Banksia spp. is reduced, compared to the other species, in the presence of weeds and leaf litter. Secondly an increase in grassy fuel loads leads to development of a grass/fire cycle, such as described for other grassy forests (Hopkins and Griffin 1989; D'Antonio and Vitousek 1992; Milberg and Lamont 1995), savannas (Bond et al. 2003) and shrubland (Keeley 2002). Controlled burning that was used between the late 1950s to 1989 would have exacerbated the fire cycle, changing the vegetation towards a grassy rather than a shrubby community. In Kings Park, the dense cover of weeds, particularly *E. calycina* altered the pattern of regeneration in tree seedlings primarily by decreasing seedling survival (Baird 1977). Thirdly high fire frequency can facilitate a change from resprouters to short lived weed seeder dominance and proliferation of *E. calycina* (Fisher et al. 2009). In addition to the weed species that have invaded the Park there are also trees such as *Eucalyptus cladocalyx*, *E. botryoides* and *E. citriodora* that have been planted for ornamental purposes. In particular *E cladocalyx* (sugar gum) can be considered an environmental weed that affects the recruitment of the once dominant E. gomphocephala and *E. marginata* (Ruthrof et al. 2003).

Fire Recurrent fires of uncertain frequency have been part of the Western Australian landscape for at least several million years (Hassell and Dodson 2003) and certainly since human arrival (Bowman 2003). Some studies suggest possible frequencies of 3 – 4 fires per decade in the Perth area before 1860 (Abbott 2003; Lamont et al. 2003). However these frequencies in the Perth area are unlikely, even under the most moderate fuel loads, as dominant understorey fire-sensitive species from the Restionaceae and Ericaceae occur in areas outside of Kings Park and require fire-free intervals of up to 15 years (Meney et al. 1994). From 1932 to 1962 there were prescribed burns of blocks of vegetation and, until 1984, burning along edges of tracks was routine in Kings Park (Wycherley 1983; Dixon et al. 1995c). The complete absence of fire-sensitive members of these two families in Kings Park bushland (Bennett and Dundas 1988), in contrast to other comparative bushland areas in the Perth region (Dixon et al. 1995c), points to an increase in fire frequency as being a probable factor in the absence of these fire sensitive species from Kings Park.

Changes in the frequency of species in any plant community are the result of mortality of adults and variation in recruitment. Beard's (1967) assessment of species change in Kings Park in the 1960s was that the eucalypt overstorey was deteriorating, eucalypt recruitment was not occurring and lower storey small trees, such as banksias, were increasing in frequency.

While the distribution of trees in Kings Park is patchy the key to understanding the changes through time is related to the balance between adult mortality and juvenile recruitment. In addition a focus on the interaction between competition and regeneration is necessary for an understanding of the future structure of forests influenced by fire (Wardell-Johnson 2000). The focal tree species of this study have diverse longevity, resistance to fire, propagule dispersal and competitive ability. All species can resprout after fire and are capable, to some degree, of establishing seedlings after fire (e.g., Fox and Curry 1979; Burrows and Wardell-Johnson 2003), but for some, seedling establishment is more favoured by severe fire, while for others establishment can occur between fires (Hobbs and Atkins 1990; Dixon and Barrett 2003).

Tuart, in particular, establishes well after a severe fire, as has been recorded in Kings Park in 1996 for an area separate from the survey sites and the historical disturbance regime of Kings Park, in particular the altered fire regime facilitated the invasion by *E. cladocalyx* (Ruthrof et al. 2003.). A severe fire will inflict extensive canopy damage which allows the development of saplings in a higher light intensity environment than would occur under a eucalypt canopy.

Tuart benefits from canopy clearance (Beard 1967) but as a sapling is the least fire resistant of the eucalypts in the Park (Burrows and Wardell-Johnson 2003) and will be disadvantaged by fires while still in the sapling stage. It is important to note that in the 1999 transects two of the three highest Tuart densities are in plots that have not been burnt in the last 60 years. Jarrah and Marri lignotuberous saplings and ground coppice are more fire resistant than Tuart but may take decades to transform into trees (Abbott and Loneragan 1984). However, as with Tuart, two of the three highest Jarrah and two of the four highest Marri densities are in the two, long unburnt transects, so a long period without fire appears to benefit all the eucalypts.

In 1967 Beard predicted that banksias would become more dominant in Kings Park as eucalypts declined. He felt that the scene had been set for banksia dominance in the 1920s when hot fires had damaged the eucalypts and allowed seedlings of the banksias and casuarina to establish prolifically. However compared to banksia, eucalypts live longer, produce more seeds that are less predated and in Kings Park potentially can recruit both in inter (if summer drought is not severe) and post fire periods.

Banksias establish well after fires (Abbott 1985a; Hobbs and Atkins 1990) and some of the lowest *B. menziesii* and *B. attenuata* densities are from transects which have had no fires, while the highest densities are in the two transects which have experienced two intense fires in the last 60 years. *Banksia attenuata* and *B. menziesii* are very fire resistant, both as adults and saplings, although saplings would be reduced back to lignotubers after each fire. In a survey in 1959 (Baird 1977) only 2% of *B. attenuata* saplings (n = 50) were killed after a severe fire (adult mortality was 4%, n = 158). While 25% of *B. menziesii* saplings died the sample size was only 4 and mortality of adults was low at 5% (n = 33). There were no individuals of either of the other banksia species in Baird's study. However *B. grandis* is much less fire resistant, as there was 25% mortality of adults in a mild fire near Dwellingup and a more severe fire would have killed most individuals (Abbott 1985a). The largest proportional reduction in *B. grandis* (except in plots which had very low numbers in 1939) was in the plots that had experienced 2 wild fires in the last 60 years. So increased fire severity could explain the decrease in this species.

Ending the control burning regime in the early 1960s would have allowed release of lignotuberous saplings of all species in the same way as "gullivers" in savannas escape the grass layer once fire is excluded (Bond and van Wilgen 1996). The generally higher density of eucalypts in the sites with no wild fires supports this. For Jarrah in the northern Jarrah forest seedling transformation to ground coppice stage (shoots up to 1 – 1.5m) takes from 15 – 20 years (Abbott and Loneragan 1984) so 60 years without fire would be sufficient time for eucalypts to move out of the ground coppice stage. Beard (1967) believed that the smaller trees in Kings Park were depriving the overstorey species of water – a type of competition. However in 1999 it was the banksia that were generally decreasing in density.

Casuarina has increased in all plots in 1999 but *B. attenuata* and *B. menziesii* have declined in all except three plots each. This decline in banksias in contrast to casuarina is likely due to severe post dispersal predation of banksia seeds in Kings Park combined with seasonal deaths of banksias. Post dispersal seed predation was examined as part of this overall study and was found to be much more severe for banksia seeds but not seeds of other species in Kings Park than in other similar Perth metropolitan areas. This would limit recruitment of banksia species.

"Sudden autumn death syndrome" in banksias occurs in a small proportion of all size classes of *B. menziesii* and *B. attenuata* in the autumn before the break of season, without any apparent prior decrease in plant health. The syndrome has been recognised for about 20 years by workers on the Swan Coastal Plain (Veneklaas, Lambers and Dixon unpublished data) but has not yet been definitely tied to any particular cause, although many have been investigated. That this syndrome has a longer history than 20 years is demonstrated by comments of earlier workers such as "the bush is full of dead individuals which have succumbed naturally, especially in summer" (Beard 1967 referring to banksias) and "the usual summer deaths" (Baird 1977, referring to banksia deaths not related to fire in Kings Park). The combination of death of plants and a lack of recruitment has been instrumental in the decline in banksia species density in Kings Park.

Allocasuarina fraseriana was projected as likely to become dominant in the Park (Main and Serventy 1957; Beard 1967) and this present study supports the prediction. The prominence of the species may be due to a combination of greater longevity than *Banksia* (Beard 1967), high resistance to fire (Ladd 1989), high level of fecundity, lack of seed dormancy and increased grass competition due to proliferation of Veldt grass in the understorey. In Kings Park, after severe wildfire in 1989, 82% of *A. fraseriana* but only 50% of banksias and eucalypts survived within sixteen months from the fire and surviving trees tended to be smaller than average (Bell *et al*. 1992). *Allocasuarina,* in general, is prominent in grassy forests (Withers and Ashton 1977; Kirkpatrick 1986; Lunt 1998a,b) and seems to be favoured by increased burning (Henderson and Keith 2002) with abundant seedling germination of *A. fraseriana* after fire in Kings Park (Baird 1977). However, as with the other tree species discontinuing control burning would have released the lignotuberous sapling bank from the ground layer to become young trees.

This study also found a marked change in species composition and abundance in the understorey. Population cycling is likely to be much faster and life spans much shorter for many of the shrub species and fire may play an influential role. Only one of the shrub species censused (*Jacksonia furcellata*) can resprout after fire. Almost all can establish without fire but benefit from disturbance and the two *Acacia*, in particular, regenerate prolifically following fire (Shea *et al*. 1979; Holmes and Cowling 1997; Tozer 1998). *Dryandra sessilis* is non-serotinous and shows weedy tendencies and it is notable that this species has its highest densities in vegetation patches that have been long unburnt. Population density may be related to how quickly recruits can invade burnt areas from unburnt patches so patchy control burns would benefit the species more than landscape scale fires. In contrast *A. saligna* is most abundant in patches which have experienced one fire and least abundant in the unburnt patches and this is related to its relatively short life span and a low likelihood of establishment in the absence of disturbance.

In the Kings Park bushland some species are clearly in danger of local extinction (*B. ilicifolia*) and even common species may be under threat. In the 1939 survey, in plot E, *Banksia ilicifolia* was detected, yet sixty years later, it had disappeared from the site. For *B. grandis,* in 1999 the density of the species in each plot was lower than that recorded for *B. ilicifolia* in 1939 in plot E (Table 3). Beard (1967) noted that *B. grandis* in his study area was also very sparse so the species may be at significant risk of extinction from Kings Park bushland.

In the last ten years management approaches in Kings Park have changed from those in earlier times. Controlled burning is no longer implemented, from 1989 post-fire herbicide programs have successfully reduced the number of weeds in the Park (Dixon *et al*. 1995c), and in areas with flora sensitive to water table draw down pumping wells have been removed. At present it is still too early to know if the latest management regime will result in a reversal of the *Banksia* decline. Certainly without management intervention, there may be local extirpation of a number of *Banksia* species and given their importance as nectar sources for local birdlife (Ramsey 1988; Phillips et al. 2010) there is a risk of broader ecological consequences of the decline.

This initial survey laid the ground work for the questions that needed to be examined to gain a clearer picture of the critical factors involved in the plant community changes in Kings Park. The important points to come from the survey were:

- Increase in *Allocasuarina casuarina* and some eucalypts
- Decrease in *Banksia* species
- Increase in understorey density

Clearly not all of these topics could be addressed in one PhD project. Aspects of tuart recruitment and status in Kings Park have been examined (Ruthroff 2003). Jarrah ecology has also been extensively studied (Abbott and Loneragan 1984; Stoneman et al. 1994; Stoneman and Whitford 1995) as it is a major commercial tree species. While marri and casuarina have been less well studied their increase in the park has been well established and there is information on establishment biology of the two species (Abbott 1984).

It was decided to concentrate on the reproduction and establishment of the *Banksia* species as this is the essential element of the banksia decline – why are adult *Banksia* species not being replaced? In addition recruitment of prominent understorey species was clearly an important part of the increasing understorey density, and relative competition with *Banksia* establishment, so that seeding and seedling attributes of key understorey species was also examined.

3 CHAPTER 3: SEED PRODUCTION AND DISPERSAL

3.1 Introduction

For sessile plants seeds represent the predominant mobile stage and dispersal is a crucial process for the dynamic and spatial pattern of the plant population especially in plants with a medium length life span. Seed dispersal is the movement of seeds away from the parent plant and determines the potential area of plant recruitment, whether the seedlings will have to compete with the parent plant or not and influences the genetic structure of a population. For these reasons investigating the different stages of seed dispersal is important to better understand the ecological range of the species in the community in which it occurs. Seed dispersal can be studied in different ways: following the fate of marked seeds (Turchin 1998), using genetic marker investigation (Ouborg 1999) or, as in this study, by investigating seed deposition and distance of seedling emergence from the original source (Wilson 1993).

Seeds awaiting the best conditions to germinate can be stored in different ways such as on the soil surface, in the soil and in the tree canopy – serotiny (Bond 1985, Lamont et al. 1985; Cowling et al. 2005). In mediterranean Western Australia, ideal germination conditions occur in autumn when the summer drought is over but weather is still warm and soil moisture level increases due to rainfall (Bell 2001). Serotiny can be defined as the retention of at least part of the seed crop on the plant in the presence of the succeeding crop. Based on the slope of the linear relationship between open fruits and crop age, we can distinguish different degrees of serotiny, from weak to strong (Lamont 1991). In parts of its distribution range *B. attenuata* is known to be highly serotinous while *B. menziesii* is moderately serotinous (Cowling and Lamont 1985).

The genus *Banksia* is distinguished by a woody infructescence with woody follicles, usually bearing two seeds, separated by a winged woody plate (separator). In many species the follicles are serotinous and seeds are released after fire (He et al. 2011) or following the death of the stem carrying the infructescence, while in other species (non-serotinous) seeds are released when the seeds/follicles are mature (Gill 1976, George 1981, Cowling and Lamont 1985). The eventual release of seeds generally involves a hygroscopic mechanism that is based on shrinkage of the separator due to desiccation, causing the seeds to move out of the follicle (Lamont 1991; Lamont et al. 1991). Canopy seed storage is associated with fire prone habitats as no other disturbance can create such a strong trigger for seed release and subsequent germination. In addition, however, Lamont (1991) and Groom and Lamont (1997) suggested the hypotheses that woody fruit could have evolved also for the protection of seeds from pre-dispersal predation (see also chapter 4 on seed predation). Serotinous species are abundant in the sclerophyll vegetation of Australia and South Africa which occurs in mediterranean-type climate. In this type of climate, the end of summer is the period when fires are most likely to occur. Such conditions are represented in Western Australia in areas south of the Capricorn Tropic. According to Lamont et al. (1998) more than 70% of the Proteaceae species in South Western Australia occur in such a fire-prone habitat. Seeds of serotinous species that have been shed must germinate as soon as moisture and temperature are suitable as seeds are not long-lived. Consequently, the timing of the seed release is crucial for the establishment of the species.

Seed shed and seedling production is often triggered by fire (Gill 1981). This is particularly the case for seeder species where adults do not survive fires, but it is also the case for many species which re-sprout after fire, particularly in southern hemisphere mediterraneoid areas, though recruitment in these species may be less than that of seeder species (Hanley & Lamont 2001). It has been suggested that sprouter species may be better adapted to dispersal away from their parents than seeder species as seeder seedlings do not have to compete with their parents after fire (Bond & Midgely 2003). Seedling regeneration has been considered a less vital link in the population biology of re-sprouters than for seeders. However most sprouters are not immortal and seedlings must be produced to maintain population viability. Sprouter seedling production has been much less studied than seeder regeneration but is essential for understanding the function of mediterranean-type systems where sprouters make up the predominant species group in a plant community. The sequence of the most likely time for fire at the end of Summer/start of Autumn followed by a relatively predictable wet season in late Autumn provides a generally reliable system for the regeneration of seedlings in a fire prone environment.

This chapter follows seed dispersal and production pattern starting from flowering phenology. Seed dispersal patterns are determined by the pattern of the adult plants, by their seed output and by their seed shadow. *Banksia attenuata* and *B. menziesii* were the two investigated species in this chapter.

Banksia seeds in the locations that were studied are unlikely to spread far from their original sources because the topography (flat) and geology (sand) of the landscape together with the flat shape of the seed, with no particular dispersal device, reduce the role of dispersal by abiotic agents such as wind, rain or water flow.

3.2 Aim

The aim of this study was to assess the magnitude of seed production (seed output); the seed set and spatial distribution of the seed flux (seed shadow), once seeds leave the source (fruit) both in inter-fire and post-fire conditions.

Different surveys were undertaken to assess whether *B. attenuata* and *B. menziesii* have the same:

1. seed production and dispersal;
2. time of seed release both in inter and post fire period;
3. degree of serotiny in the geographic region of the Swan Coastal Plain.

The number and distribution of germinant/seedling survival, micro-site limitation and distance of seedling emergence from the nearest potential source will be analysed and discussed in the next chapters.

3.3 Materials and methods

The species investigated in these surveys were: *B. attenuata* and *B. menziesii*.

Four different surveys were undertaken to assess the pattern, seasonality and magnitude of seed fall and dispersal.

1. Tagged inflorescence.
2. Seed traps in inter-fire period.
3. Seed traps in post-fire period.
4. Quadrats used to estimate the pattern of post-fire seed fall.

Surveys number 1 and 2 were undertaken in the following four locations: Kings Park, Bold Park, Jandakot R.P. and Ridges State Forest, while surveys number 3 and 4 were undertaken in an area of the Bold Park *Banksia* woodland where in Summer 2000/01 two sites experienced a devastating wildfire, once in early summer (December 2000) and once in late summer (February 2001).

When distribution of collected data did not satisfy the assumptions for parametric statistics (such as Anova or T-test) non-parametric statistics were used. The Kruskal-Wallis test was used to compare more than two groups. The Mann-Whitney U test was used to test two groups at a time and/or as a post hoc test; if the value of observations were the same in different groups, the outcomes were also displayed with the probability (P) adjusted for ties.

3.3.1 Tagged inflorescences

Banksia inflorescences were tagged and the development of follicles was followed through the years. In other surveys in this thesis, presented in the next chapter, the data collected from the tagged inflorescences were used to measure the level of predation on the 'cones'. In this chapter seed set and dispersal are examined.

The tagging of the inflorescence started in Summer 2000/2001 (January) and the scoring was recorded for 24 months until summer 2003. *Banksia* inflorescences and infructescences were scored in each season. The plants selected for labelling of the inflorescences were mature trees with more than five inflorescences. On each tree no more then 50% of inflorescences were randomly tagged. The height of the tagged 'cones' was less than four metres above the ground ("the height of the investigator on the metal ladder used to reach the inflorescences"). The number of trees and of tagged flowers varied between the four different locations (populations). In Kings Park and Bold Park four different sites were chosen while in the other locations only two sites were used for the investigation (Table 1).

Table 3.1 Sites in the different investigated locations (4 in KP and BP and 2 in Jand and Rid); number of trees (n=165) and number of tagged inflorescences (n=754) for each species. Names given to the sites are local names only: B. att = *Banksia attenuata*; B. menz = *Banksia menziesii*

Location	**Kings Park (KP)**							
site	Banksia site		Banksia site 1		Banksia (traps) site		Banksia (traps) site 1	
species	B. att	B. menz	B. att	B. menz	B. att	B. menz	B. att	B. menz
N. of trees	7	6	4	7	6	7	8	7
N.of labelled inflorescences	32	28	21	27	34	31	39	29

Location	**Bold Park (BP)**							
site	weed 1		weed next burn		low valley		high valley	
species	B. att	B. menz	B. att	B. menz	B. att	B. menz	B. att	B. menz
N. of trees	6	11	5	8	8	7	6	6
N. of labelled inflorescences	34	45	27	32	36	31	27	26

Location	**Jandakot R. P. (Jand)**				**Ridges State Forest (Rid)**				**Total**	
site	Plan next 10X10		Alex jeorgia site		4 banksia		caffeteria			
species	B. att	B. menz	B. att	B. menz	B. att	B. menz	B. att	B. menz	B. att	B. menz
N. of trees	8	9	6	7	7	6	6	6	77	88
N. of labelled inflorescences	33	43	32	30	37	27	30	23	382	372

The *Banksia* inflorescences were tagged with a small aluminium tag. Each season the development stage of the 'cones' and of the follicles was scored. 'Cones' were scored as undeveloped or developed. In the latter case follicles were additionally scored as open, closed or predated/damaged. If the 'cone' was missing, it was scored as fallen; according to the 'cone' stage recorded in the previous season, fallen cones were subsequently scored as 'fallen undeveloped' or 'fallen developed'.

Description of the 'cones' and follicles status:

- "Cones" were scored as developed if all the follicles present on the infructescence were of a woody structure, otherwise these were scored as undeveloped.

The status of the follicles was assigned to one of the following categories:

- <u>Open</u>: the follicle was open, even partially, with no sign of any damage.
- <u>Closed</u>: the follicle was closed, with no sign of damage.
- <u>Predated/damaged</u>: the follicles showed signs of predation or damage.

Graphs show the percentage of closed follicles of the tagged 'cones' during the season/years, and the number of fallen developed or undeveloped infructescences. Results are displayed as average of replicates for each single location and as average with all the locations grouped together. Furthermore graphs show percentage values of undeveloped, developed, and fallen inflorescences/infructescences two years after the start of the survey and the numbers of follicles, divided into three categories: open, closed and damaged/predated.

3.3.2 Seed traps

These surveys focus mainly on seed rain, which, according to Jensen (1998) is the release of seed from the parent plant once the seed is mature. Being able to assess the magnitude of seed rain is essential to assess the reproductive potential of a species. Page *et al.* (2002) review and evaluate different seed traps designed for 17 different seed rain studies. Loss of seeds, difficulty in isolating small seeds, the ineffectiveness for wind dispersed seeds, isolation from water and predation were the main problems identified in the review. In this study the seed trap was designed specifically for *Banksia* seeds, which fell directly from overhead vegetation. Each trap consisted of plastic cubic boxes of 25cmX25cmX25cm (with a surface opening of 0.0625 m^2, corresponding to 1/16 of m^2); to allow rainwater flow, the bottom of the boxes was drilled with one cm holes, which were overlaid with a metal fly net. A metal peg was inserted through one of the drilled halls to prevent the dislodgement of the box. In order to exclude seed predators, which through the predation study were revealed to be vertebrates, a device made with two layers of a 2 cm x 2 cm metal mesh (mesh size will pass banksia seeds easily) was placed on the top and inside the box. In Kings Park, where predation was found to be much more severe, and in Jandakot R.P., three extra boxes in each location, with metal mesh and 10 seeds placed inside were used to test the predator exclusion device in order to prove the reliability of the trial. The extra boxes were set within survey number 2 (inter-fire period) and displayed at a distance from tree canopy to avoid seed falling in the boxes. Seed were re-counted after 12 months.

With this type of design, the amount of seeds trapped is representative of the real seed rain values for the monitoring period. Seed rain reflects the reproductive potential of the investigated banksias, however it represents only one of the first stages of the reproductive cycle which ends with the establishment of the seedlings. Seed predation, micro-site limitation, grazing pressure, climatic conditions, periodic disturbance events are other important factors that would affect patterns of recruitment. Some of these factors are examined in other chapters of this thesis.

A total of 254 seed traps was used in these trials, 174 in survey 2 and 80 in survey 3.

3.3.2.1 Seed traps in inter-fire period

In each of the four locations chosen for this research two different areas were selected to undertake this specific survey; in each site 21 seed traps were purposely positioned: 16 equally distributed beneath randomly chosen mature *B. attenuata* and *B. menziesii* tree canopies of approximately similar size and five positioned in gaps more than three metres distant from a *Banksia* tree. In each site, the boxes were numbered and each box was considered as a replicate. Seeds trapped in the boxes were scored in each season for 24 months and a vitality test (cut test) was used each time to estimate the number of viable seeds trapped. The six extra boxes, placed in Kings Park and Jandakot R.P., used to test the reliability of the predation exclusion device were scored only once after 12 months year.

Graphs show seasonal seed fall, number of seeds m^{-2} $year^{-1}$ and percentage of seed set.

The Kruskal-Wallis test was used to test differences in seed fall during the four different seasons, while the Mann-Whitney U test was used to test differences in seed fall between the two species and between seed trap position (underneath the tree canopy and in the gap).

3.3.2.2 Seed traps in post-fire period

Seed rain in burnt vegetation Seed traps were placed in two different areas of Bold Park burnt respectively in December 2000 and February 2001.

In each of the two burnt areas two different sites were chosen; each site had 16 seed traps (boxes) equally distributed beneath *B. attenuata* and *B. menziesii*. The boxes had the same characteristics as those used in survey n° 2. The boxes were placed 3 weeks after the fire under trees with the crown still intact (seed release occurs some time after fire, not immediately). Boxes were examined every 3 weeks, starting from the sixth week since fire, for 4 months (30 weeks) and a vitality test (cut test) was used to estimate the number of viable trapped seeds. Line graphs show the mean number of seeds (± S.E.) trapped every three weeks

The mean number of seeds m^{-2} ± S.E. is shown in different graphs. For each species and fire period, the graphs display a different length of the survey:

A. Between the third and the ninth week (the week of the last seed fall of *Banksia menziesii*);

B. Between the third and the twenty-first week (the week of the last seed fall of *Banksia attenuata*);

C. Between the third and the thirtieth week (the week of the last scoring-at the end of the survey).

Kruskal-Wallis test and Mann-Whitney U test were used to test differences between species and fire periods.

3.3.3 Quadrats used to estimate post-fire seed fall

Seed shed onto the ground surface In order to examine the amount and pattern of seed released immediately after the passage of fires in the Bold Park *Banksia* woodland a specific survey was undertaken. In the burnt areas (in December 2000 and February 2001), at 40 randomly chosen metal pickets, of a pre-existing 50 metre X 50 metre grid, four 1x1metre plots of the soil surface were examined on the four points of the compass (N, S, E, W). All the seeds and the separators within a 1x1 metre plot in the $4m^2$ area were scored, for a total number of 160 replicates of one square metre. The bare sandy soil was sieved to search for all the seeds and separators present. The scoring was completed between the fifth and the sixth week after the fire.

According to the position of canopies occurring above it, each quadrat was assigned to one of the following categories:

a) Most (>50%) of the 1x1 metre plot was underneath the tree canopy of a *B. attenuata* (n=61);

b) most (>50%) of the 1x1 m plot was underneath the tree canopy of a B. menziesii (n=19);

c) most of the 1x1 m plot was not underneath a tree canopy but was within 3 m from the nearest canopy of a *B. attenuata* (n=32);

d) most of the 1x1 m plot was not underneath a tree canopy but was within 3 m from the nearest canopy of a *B. menziesii* (n=12);

e) most of the 1x1 m plot was distant over 3 metres from any *Banksia* canopy (n=16).

f) most of the 1x1 m plot was underneath a mixed canopy of *B. attenuata* and *B. menziesii* (n=12);

g) most of the 1x1 m plot was not underneath a tree canopy but was within 3 m of the nearest mixed canopy of *B. attenuata* and *B. menziesii* (n=8);

For the aim of the investigations discussed in this chapter, only the categories a, b, c, d, e were examined. For the categories f and g, it was difficult to assess to which tree species the canopy belonged.

3.4 Results

3.4.1 Tagged inflorescences

Inflorescences (referred to as cones in the following text) were initially tagged in Summer 2000/2001 (January) .

For *Banksia attenuata* from Spring 2001 to Autumn 2002 the percentage of closed (or undeveloped) follicles, across all locations, on developed cones declined from 88% to 37%. From Winter 2002 to Summer 2003 the percentage of closed follicles declined more gradually to 18% (Fig. 3.1). Most of the areas had similar trends with follicles that started opening after Spring 2001 (Fig. 3.2). The only exception was one of the four sites in Kings Park (Kpba) and one of the two sites in Ridges State Forest where follicles started opening after Summer 2002. For the same time period all the other sites had between 45-73% of the follicle closed.

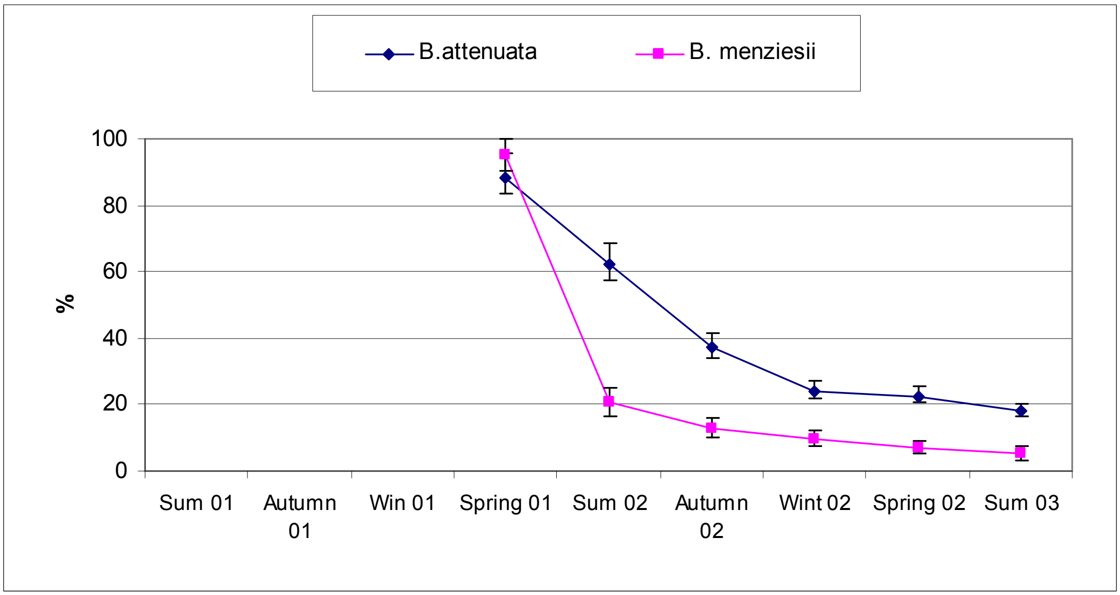

Fig. 3.1. *Banksia attenuata* and *B. menziesii* close follicles. Mean percentage for sites in the four locations.

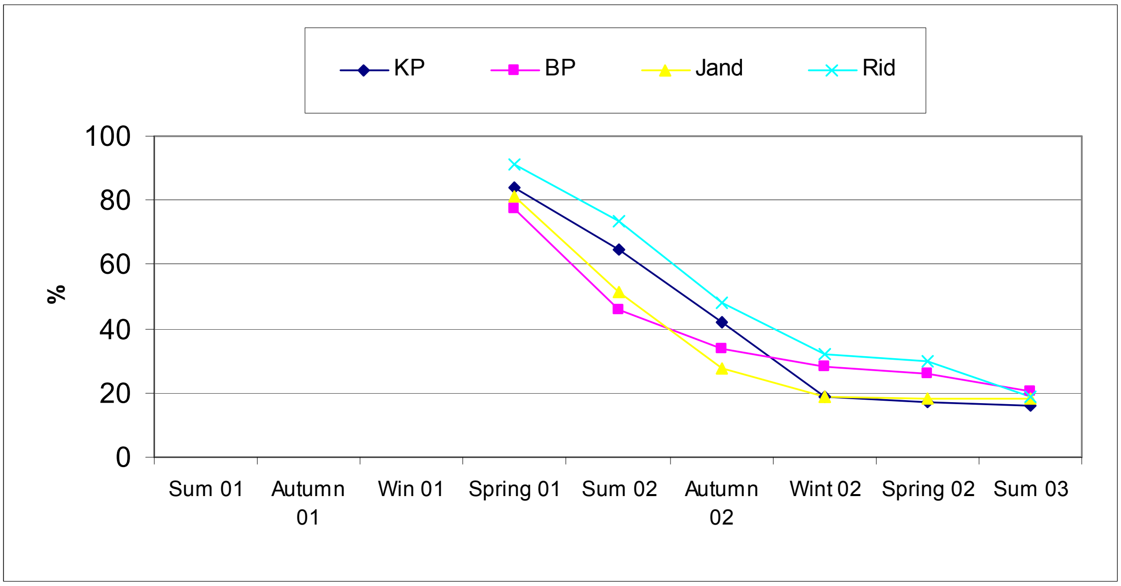

Fig. 3.2 *Banksia attenuata* closed follicles. Percentage for sites for each of the four locations.

For *Banksia menziesii* from Spring 2001 to Summer 2002 the percentage of closed follicles, across all locations, on developed cones, dropped rapidly, from 95% to 21% (Fig. 3.3). In Summer 2003, at the end of the experiment, only 8% of the follicles were closed. Most of the areas had similar trends with follicles that started opening after spring 2001 (Fig 3.4). At Jandakot R.P. the number of closed follicles was slightly lower than at the other locations.

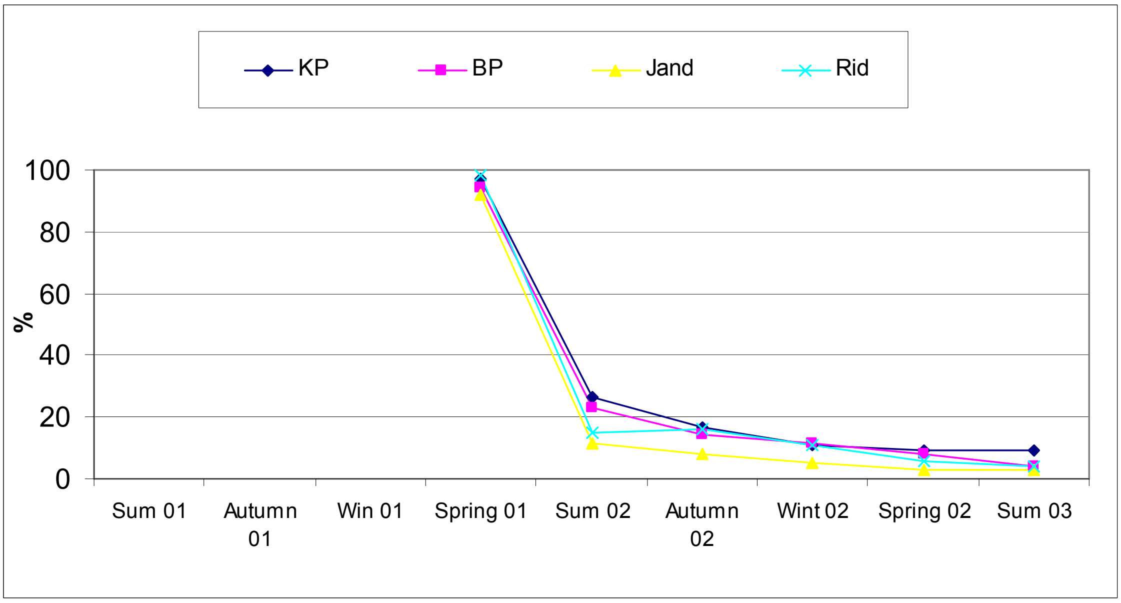

Fig. 3.3 *Banksia menziesii* close follicles. Percentage for sites for each of the four locations.

Comparison of the two species shows that by the first spring after flowering *B. menziesii* releases seed more rapidly than *B. attenuata* (Fig 3.1). However, seed set for *B. attenuata* starts in Summer and for *B. menziesii* in Winter so follicles of *B. menziesii* mature earlier in the following year than those of *B. attenuata*. Difference of percentage seed released between the two species by the first Summer after flowering is highly significant ($P<0.0001$) with *B. menziesii* having only 20% of the follicles still closed compared to 60% for *B. attenuata*.

After 24 month from the beginning of the survey, the mean number of follicles cone^{-1} for *B. attenuata* was 12.6 (± 0.7) of which 7.8 (± 0.26) were open, 2.2 (± 0.26) were closed and 2.4 (± 0.34) were damaged or predated (Fig. 3.5) with significant differences between the three groups (DF=2, H=12.78, P=0.002) There were significantly more open follicles *versus* the number of close and damaged/predated follicles ($P<0.001$) but there was no significant difference (P=0.092) between closed and damaged/predated follicles. Of the tagged inflorescences of *Banksia attenuata* (n=382) only 41% reached maturity and of these 11% fell, while of the 59% that did not reach maturity 7% fell to the ground (Fig. 3.6).

The average number of *B. menziesii* follicles cone^{-1} was 6.63 (± 0.36) of which 4.9 (± 0.36) were open, 0.4 (± 0.1) closed and 1.2 (± 0.2) damaged or predated (Fig. 3.7) and there was a significant difference between the three groups (DF=2, H=14.36, $P<0.001$). The Mann-Whitney U test between paired groups showed statistical differences between all groups ($P<0.01$). Of the tagged *B. menziesii* inflorescences (n=372) only 55% reached maturity and of these 10% fell while of the 45% that did not reach maturity only 6% fell on the ground (Fig. 3.8).

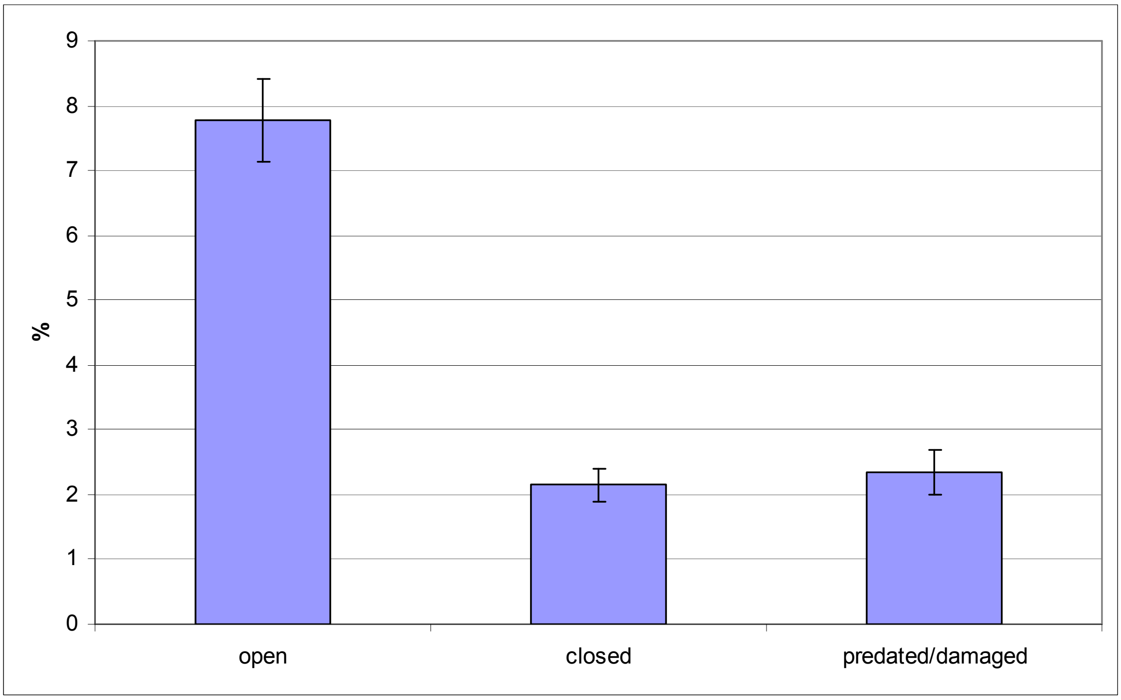

Fig. 3.4 *Banksia attenuata* mean of open, closed, predated/damaged follicles per cone after 24 month survey.

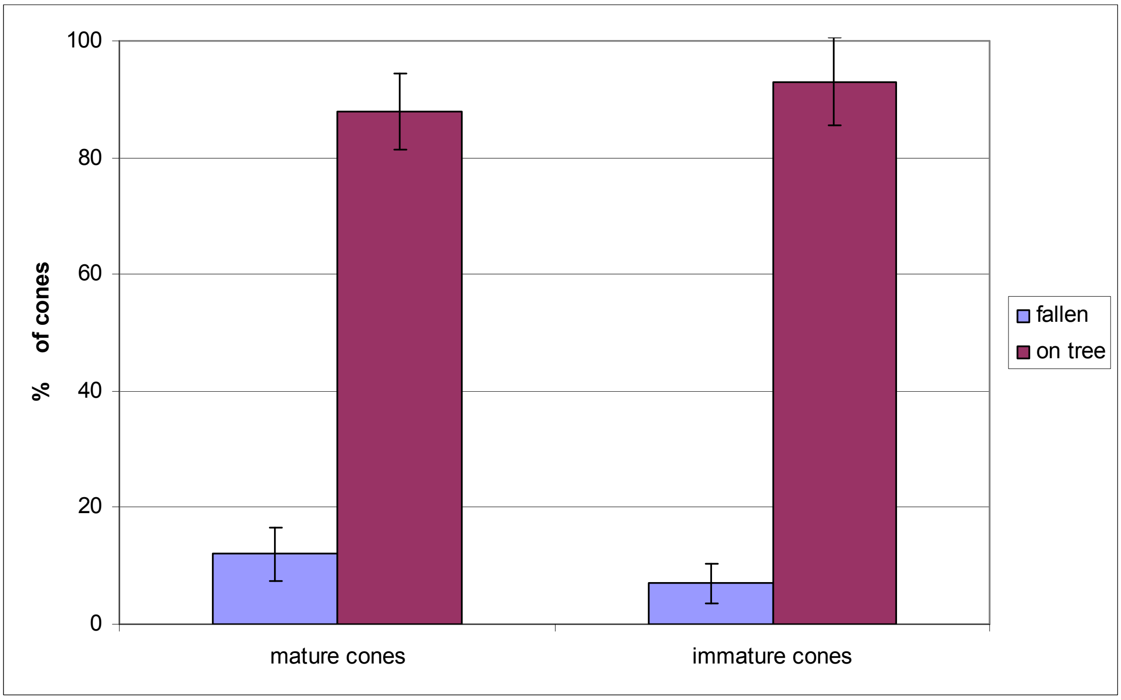

Fig. 3.5 *Banksia attenuata* mean percentage of developed and undeveloped cones, on the tree or fallen from the tree.

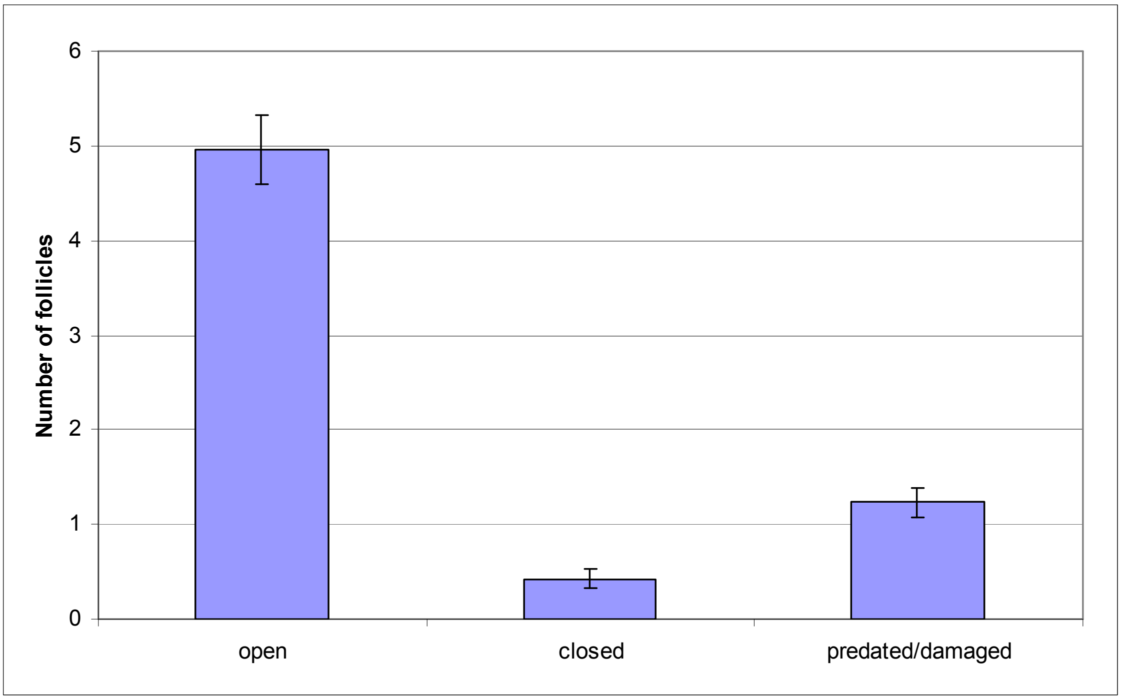

Fig. 3.6 *Banksia menziesii* mean number of open, close, predated/damaged follicles per cone.

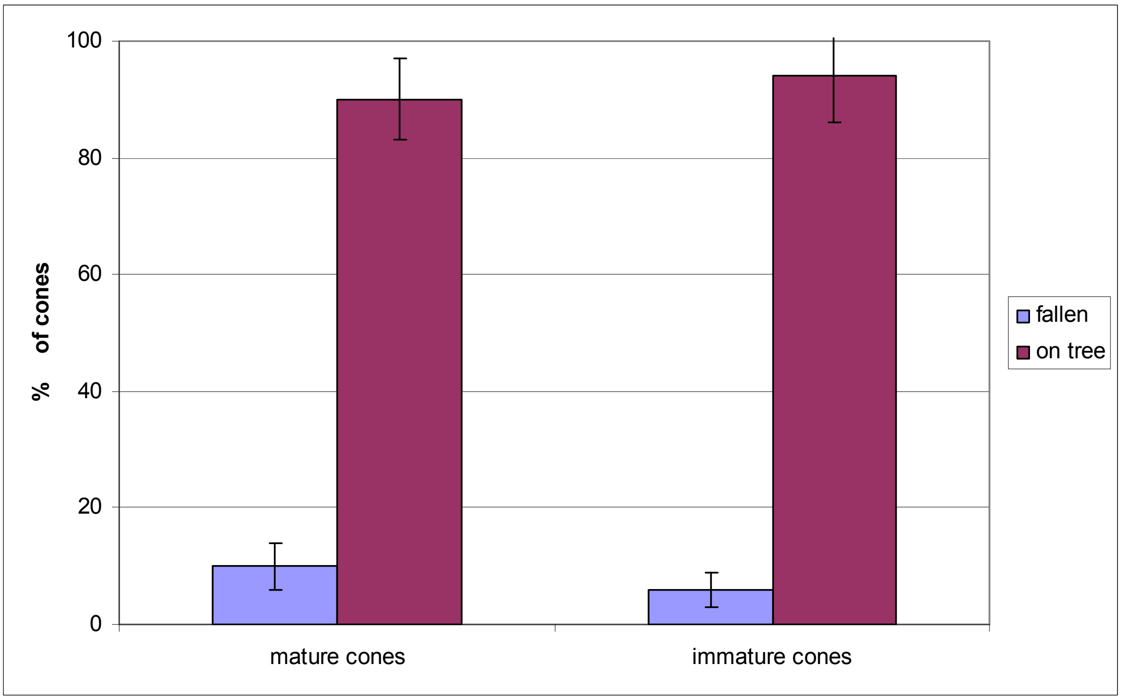

Fig. 3.7 Banksia *menziesii* mean percentage of developed and undeveloped cones, on the tree or fallen from the tree.

For developed infructescences, most of the fallen cones were missing in the period when follicles on the infructescences were still closed: until autumn 2002 for *B. attenuata* and Summer 2002 for *B. menziesii* (Figs. 3.9-3.16). The trend of fallen cones was similar for all the 4 investigated locations. However both in Kings Park and Ridges State Forest values of missing cones were higher compared to the other two sites (Figs. 3.10, 3.12, 3.14, 3.16).

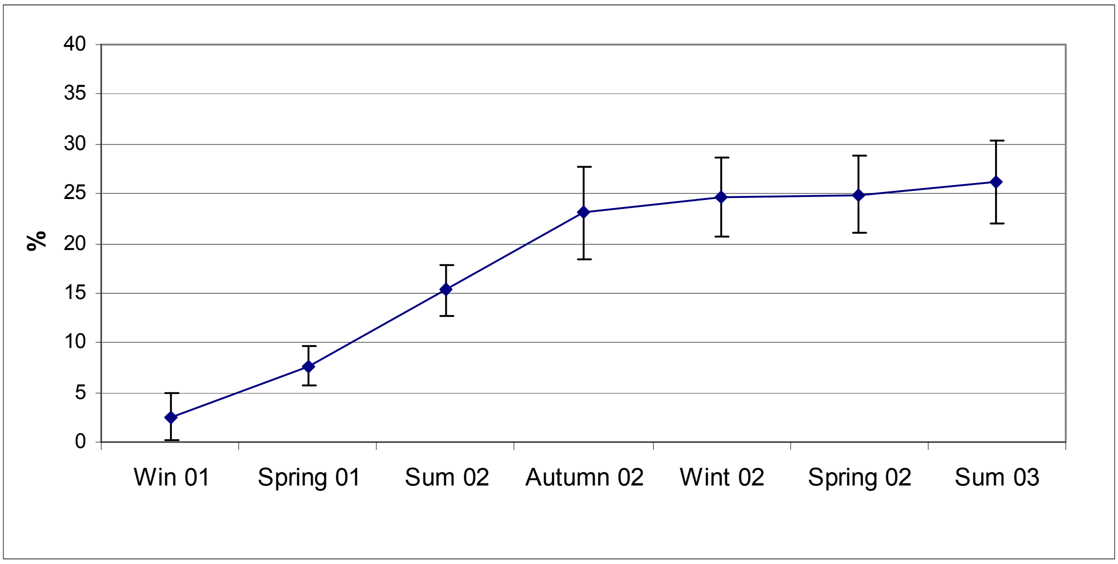

Fig. 3.8 *Banksia attenuata* developed fallen infructescences. Mean percentage for sites in the four locations.

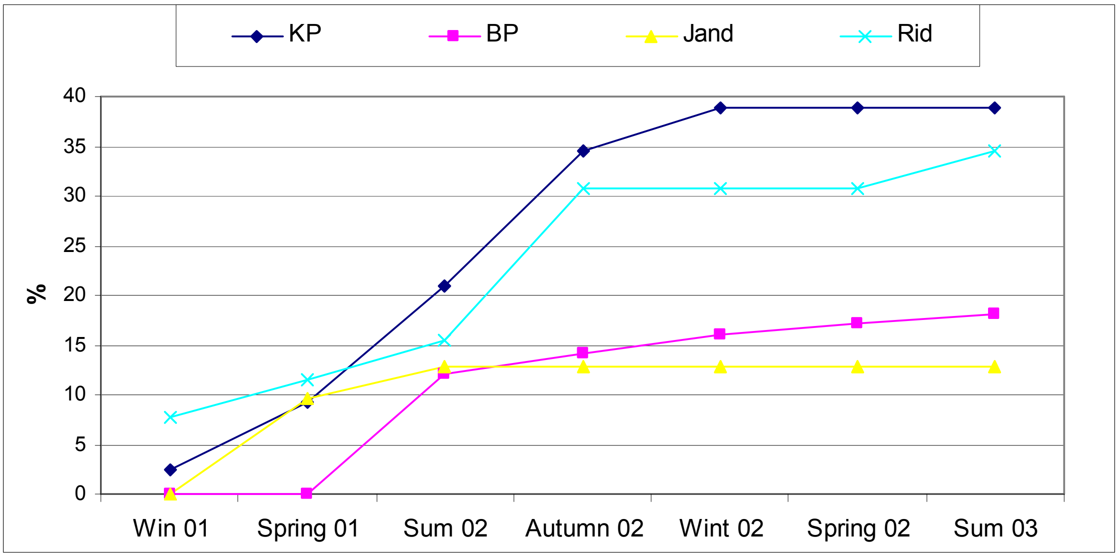

Fig. 3.9 *Banksia attenuata* developed fallen infructescences. Percentage for sites for each of the four locations.

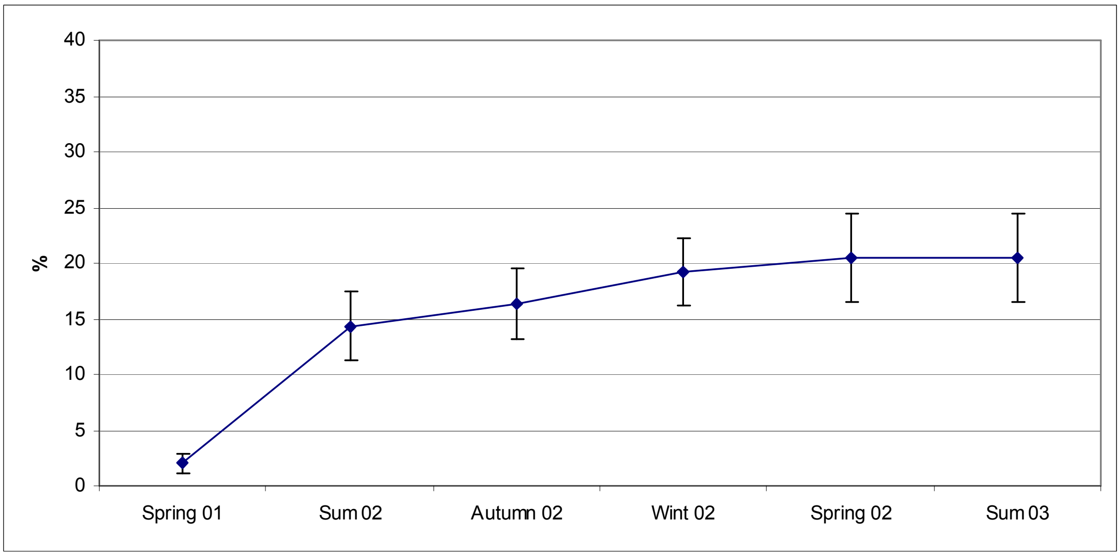

Fig. 3.10 *Banksia menziesii* developed fallen infructescences. Mean percentage for sites in the four locations.

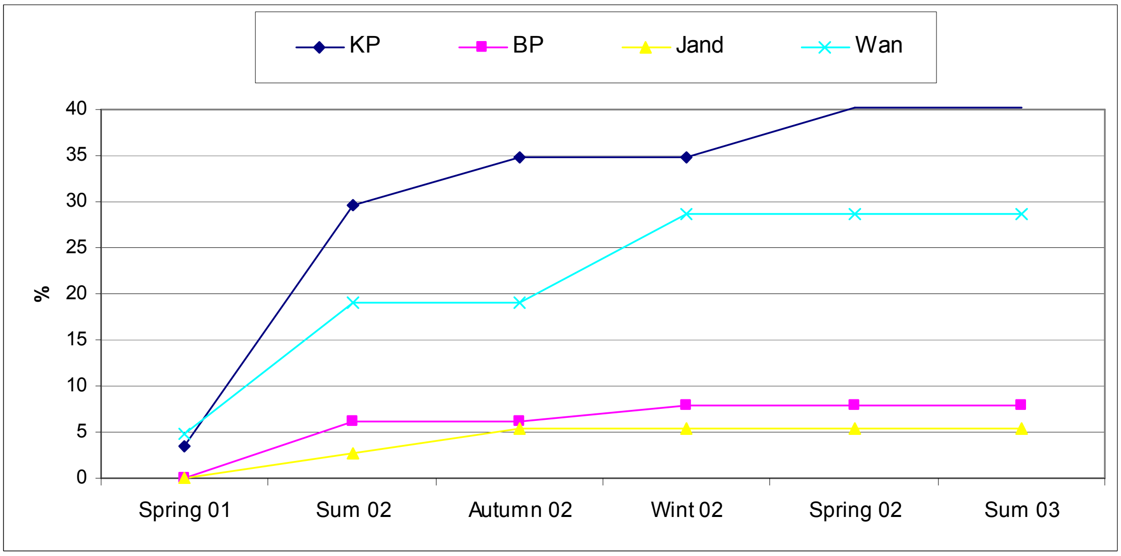

Fig. 3.11 *Banksia menziesii* developed fallen infructescences. Percentage for sites for each of the four locations.

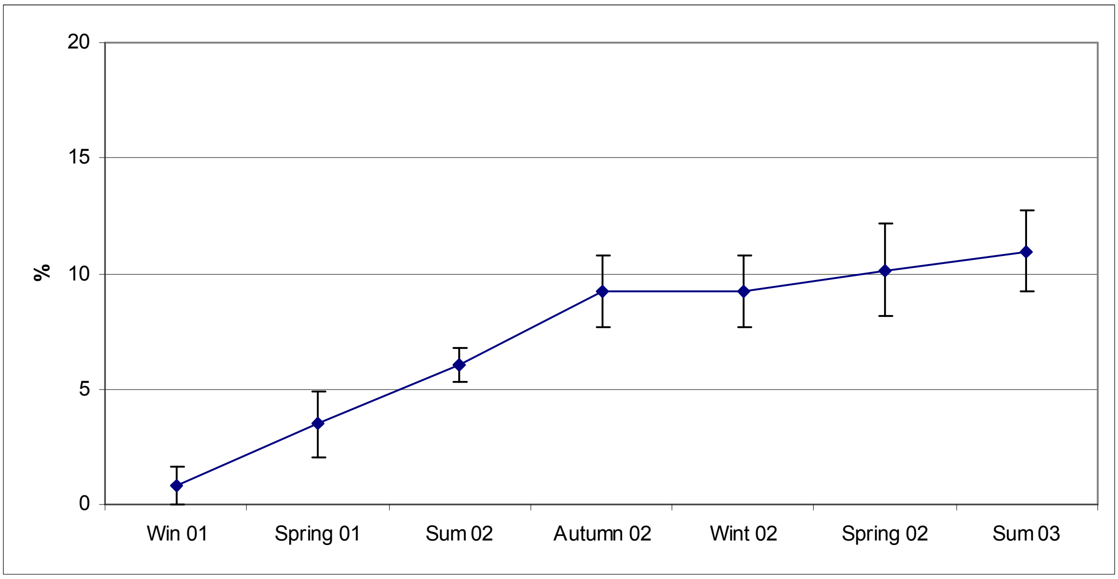

Fig. 3.12 *Banksia attenuata* undeveloped fallen infructescences. Mean percentage for sites in the four locations.

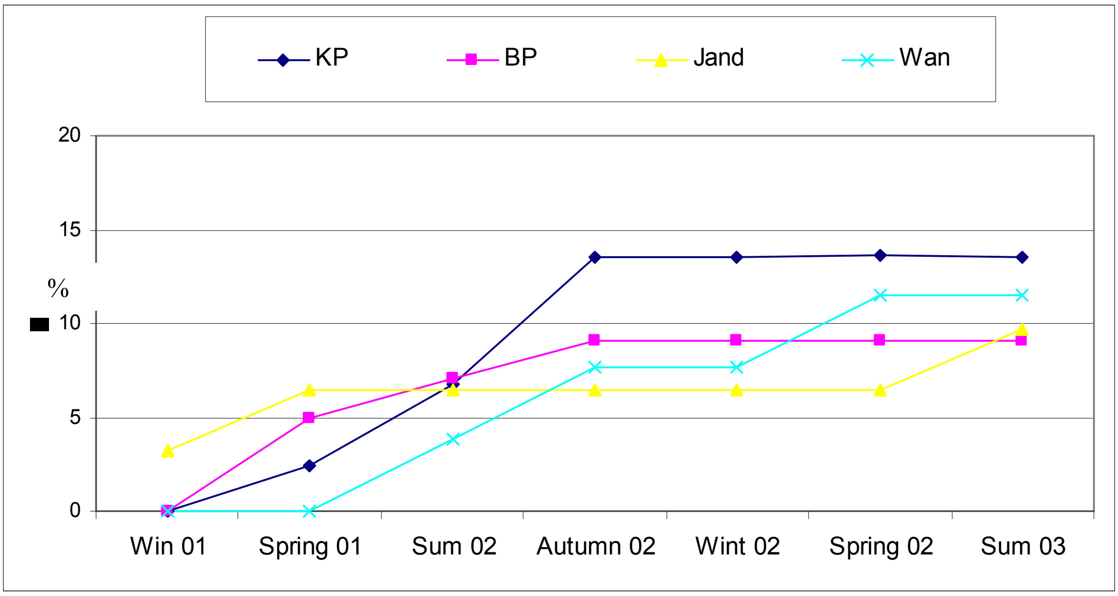

Fig. 3.13 *Banksia attenuata* undeveloped fallen infructescences. Percentage for sites for each of the four locations.

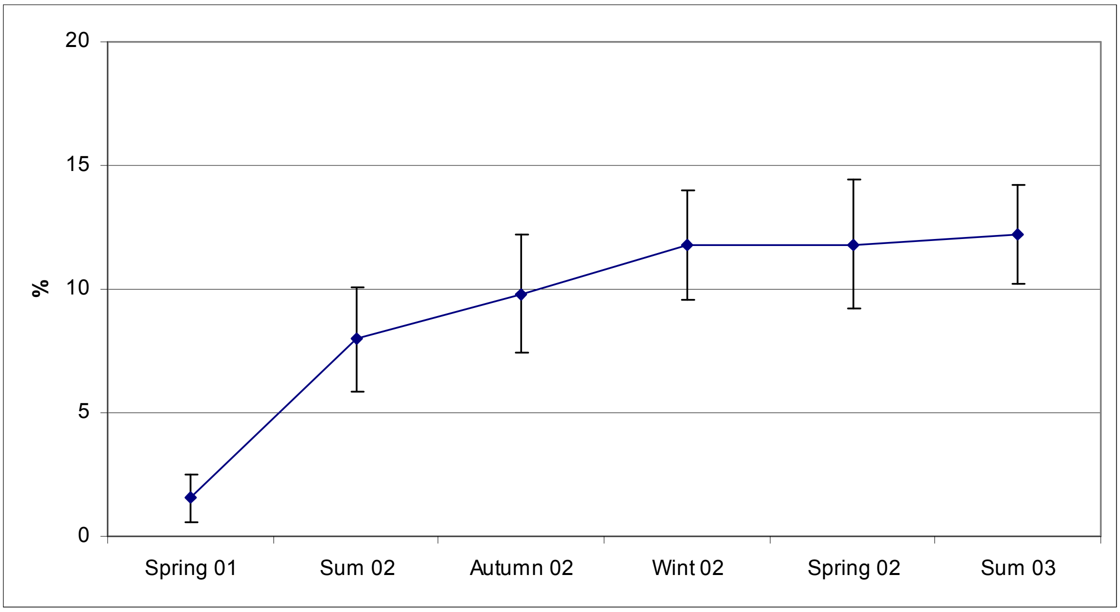

Fig. 3.14 *Banksia menziesii* undeveloped fallen infructescences. Mean percentage for sites in the four locations.

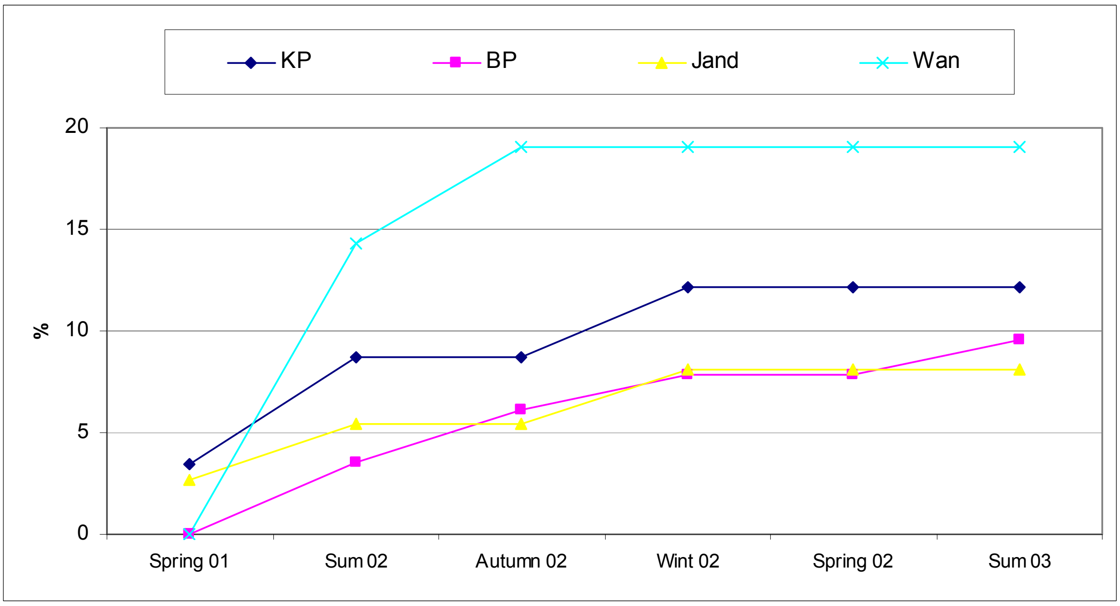

Fig. 3.15 *Banksia menziesii* undeveloped fallen infructescences. Percentage for sites for each of the four locations.

3.4.2 Seed traps

3.4.2.1 Seed traps in inter-fire period

The scoring of the six extras boxes (to which seeds had been added), positioned in two different locations, which tested the vertebrate exclusion device showed that seeds were not predated, and only one seed was missing from one site in Jandakot R.P. (< 2%), consequently the reliability of the method was confirmed.

Most of the *B. attenuata* (91.3%) and *B. menziesii* (85.4%) seeds trapped in the boxes were viable. *Banksia attenuata* released over twice as many viable seeds year^{-1} m^{-2} (18.5 ± 2.6) compared to *B. menziesii* (8.75 ± 1.4) (Fig. 3.17) and almost all of these fell under the parent tree. The number of seeds released from *B. attenuata* is significantly greater than the number of seeds of *B. menziesii* ($W=2730$; $P<0.05$, $P<0.001$ adjusted for ties).

Banksia attenuata viable seeds were present in the seed traps mainly at the Autumn and Winter scoring, while *B. menziesii* viable seeds were present in the boxes mainly at Summer and Autumn scoring (Fig. 3.18). This indicates that seeds begin to be released in Summer for *B. attenuata* and in late Spring for *B. menziesii*.

The amount of seeds collected in boxes under the tree canopies was much larger compared to the amount of seeds collected in boxes placed more than 3 metres from tree canopies. In these latter boxes only two *Banksia* seeds (*B. attenuata*) were trapped, one of which was not viable and of paper-like consistency. The variation in seed release between the four seasons showed that there is a statistical difference for *B. attenuata* ($DF=3$; $H=11.95$ $P<0.01$; $H=34.94$, $P<0.001$ adjusted for ties) while *B. menziesii* showed a smaller difference, however the statistical test would need more measurements as the results, with and without adjustment for ties, are either side of the probability value (P) of less than 0.05 ($DF=3$; $H=3.67$, $P=0.190$; $H=25.4$, $P<0.0001$ adjusted for ties). The number of seeds trapped in the boxes during the first year is not statistically different from the number of seeds trapped in the second year for both *B. attenuata* ($W=37830$; $P=0.104$, $P=0.0864$ adjusted for ties) and *B. menziesii* ($W=4166$, $P=0.852$). The number of separators trapped in the boxes is smaller than the number of trapped seeds (Fig. 3.18). In contrast to prediction, however, the number of trapped separators was well above the value of 50% of the trapped seeds (the expected frequency being one separator and two seeds within each follicle). This could be due to the fact that not always both seeds were mature in each follicle and poorly formed seeds are lighter and can fly further from the tree canopy.

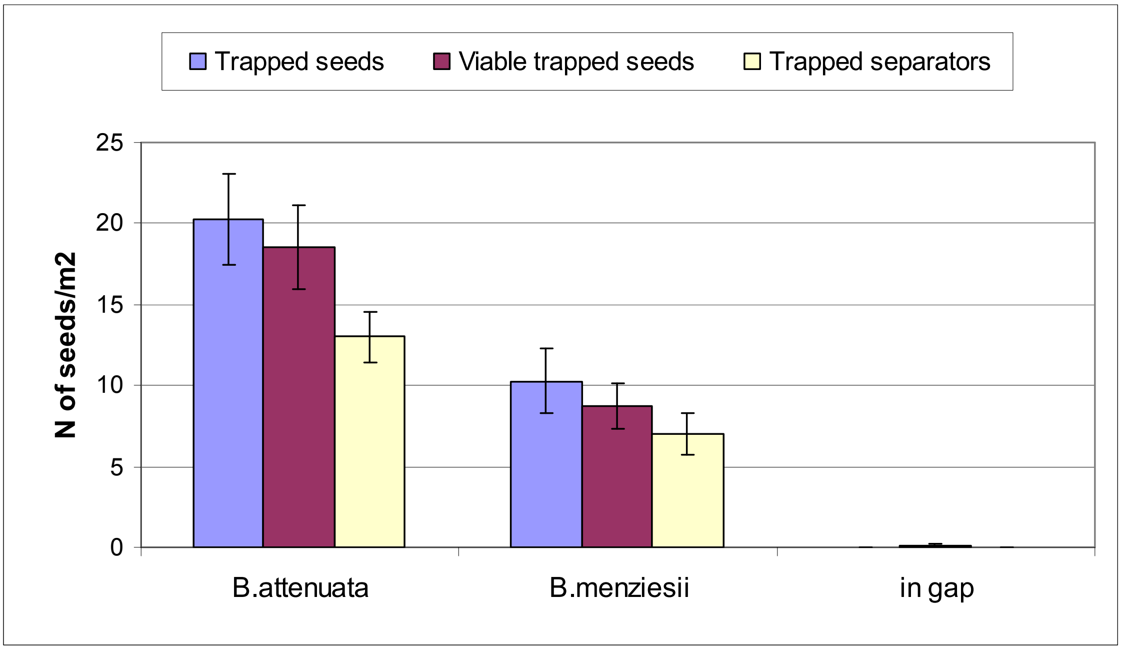

Fig. 3.16 *Banksia attenuata* and *B. menziesii* mean number of seeds m^{-2} y^{-1}. Difference between trapped and viable trapped seeds and separators in inter-fire period across all the survey period (24 months).

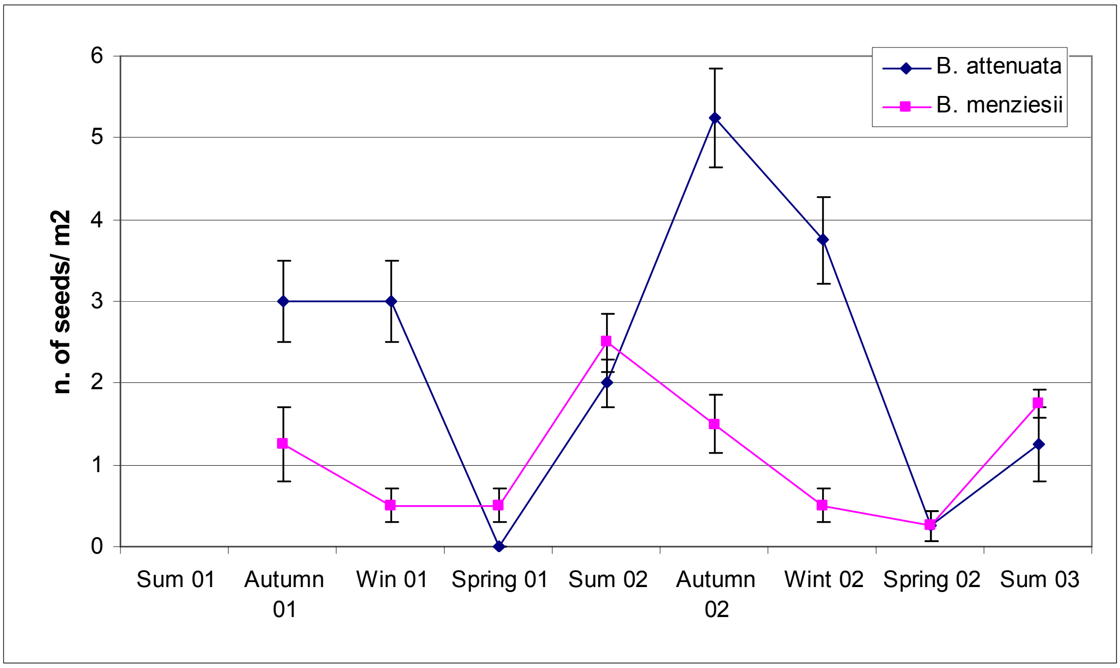

Fig. 3.17 *Banksia attenuata* and *B. menziesii* mean number of viable seeds and seasonal seed released in inter-fire period. Seasonal scoring.

3.4.2.2 Seed traps in post-fire period

Most of the seeds were trapped in the boxes, between the third and the twenty-first week. Most seeds of *B. attenuata* (64%) and of *B. menziesii* (75%) were viable. *B. attenuata* released 3 times more seeds compared to the congeneric banksia (Fig. 3.19). *Banksia attenuata* released seeds until between the 18th and the 21st week after respectively, the December and the February fire (Figs. 3.20, 3.21) while *B. menziesii* seed release timing was much more restricted with seeds falling until between the 6th and the 9th weeks after the first and second fire (Figs. 3.22, 3.23). Between the third and the ninth week there was no statistically significant difference between the number of seeds released between or within species (3.24A) and the post-fire seed release was similar within the two species for the two burn periods. The results of the scoring after the ninth week (3.24B & 3.24C) showed instead a significant difference between the two species, as *B. menziesii* did not release any more seeds. However, overall the entire length of the experiment, *Banksia attenuata* released more seeds and for longer than *Banksia menziesii*. The outcomes of the Kruskal-Wallis test, testing the medians for the four sites in Bold Park, for survey A (DF=3; H=1.09, P=0.780; H=6.91, P=0.095 adjusted for ties) and for survey C (DF=3; H= 0.36, P=0.948; H=1.09, P=0.778 adjusted for ties) showed that the P-value is greater than the critical 0.05 level. Consequently the null hypothesis, that the four sites have the same median, was accepted (Fig. 3.24C).

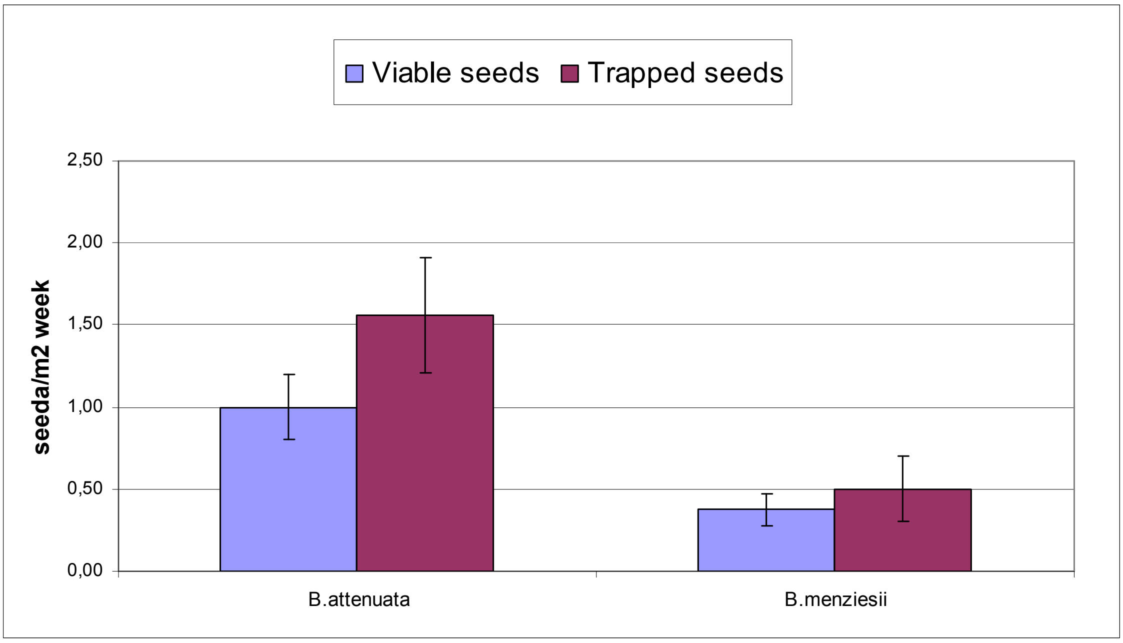

Fig. 3.18 *Banksia attenuata* and *B. menziesii* mean number of seeds m^{-2} week^{-1}. Difference between trapped seeds and viable seeds in the burned areas.

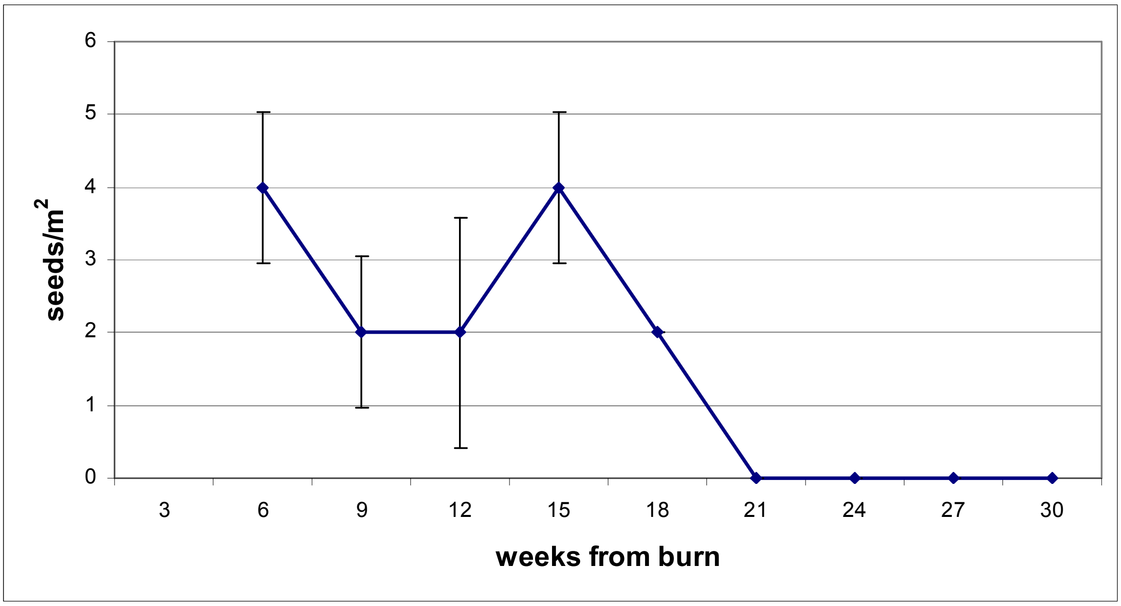

Fig. 3.19 *Banksia attenuata* mean number of viable seeds m^{-2} trapped in boxes placed beneath the tree canopy after the December 2000 fire.

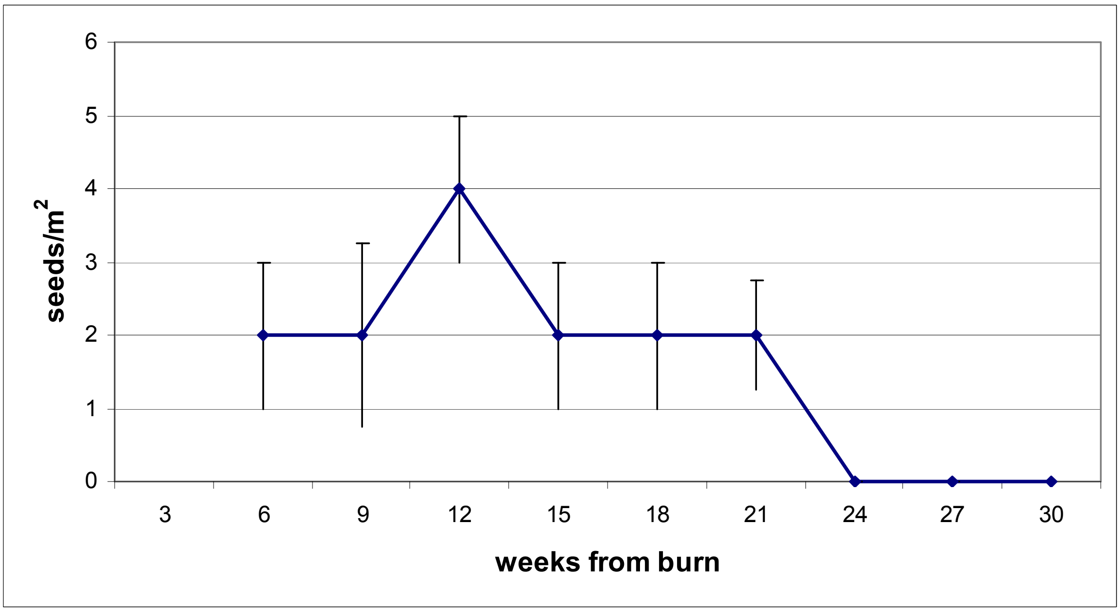

Fig. 3.20 *Banksia attenuata* mean number of viable seeds m^{-2} trapped in boxes placed beneath the tree canopy after the February 2001 fire.

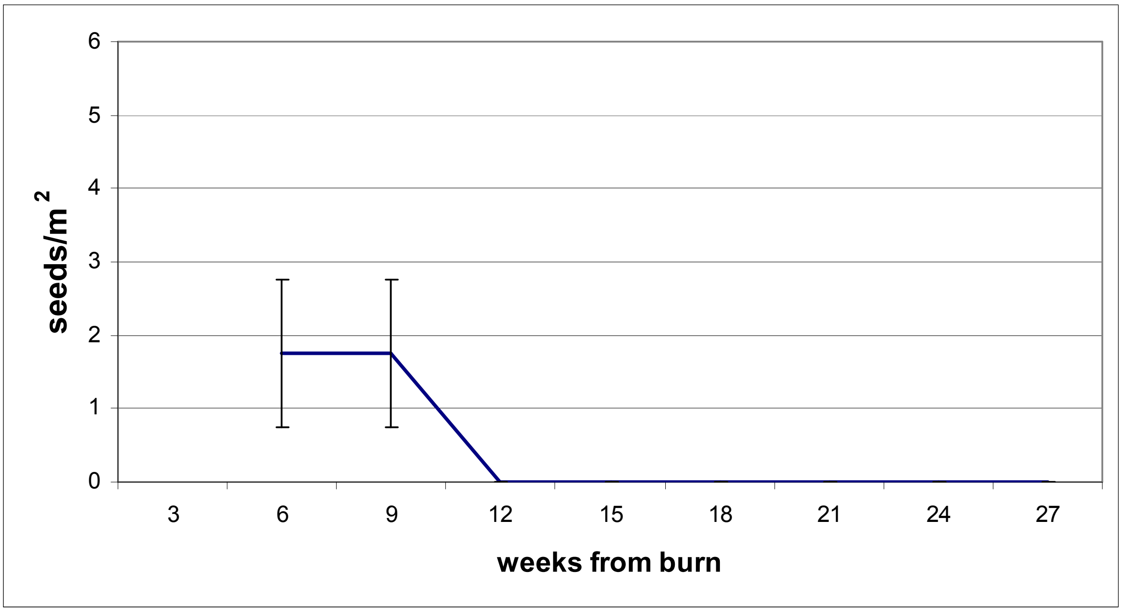

Fig. 3.21 *Banksia menziesii* mean number of viable seeds m^{-2} trapped in boxes placed beneath the tree canopy after the December 2000 fire.

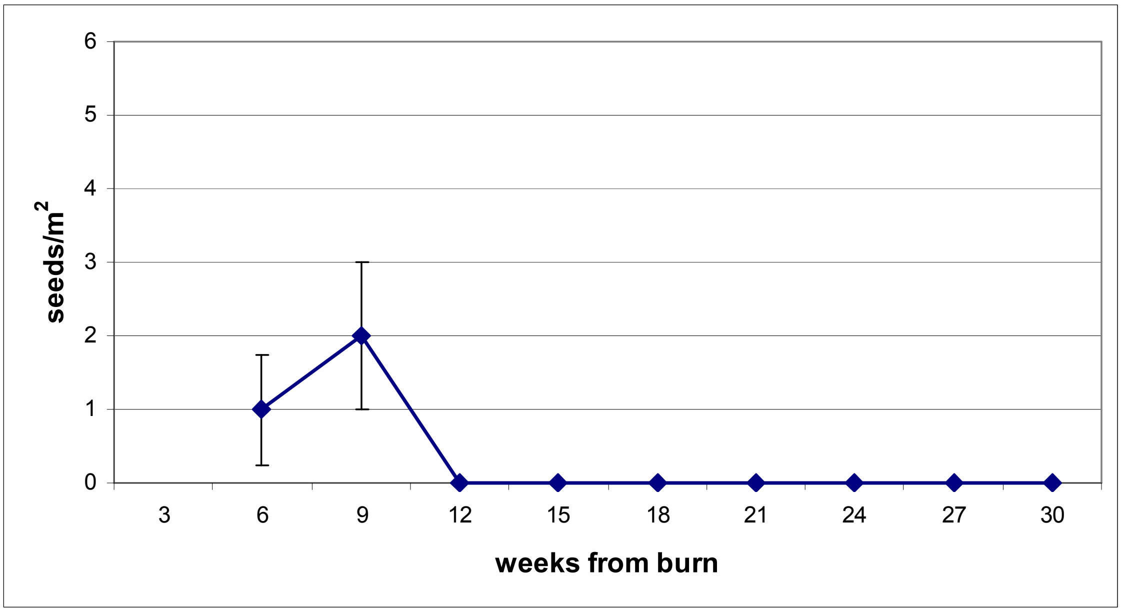

Fig. 3.22 *Banksia menziesii* mean number of viable seeds m^{-2} trapped in boxes placed beneath the tree canopy after the February 2001 fire.

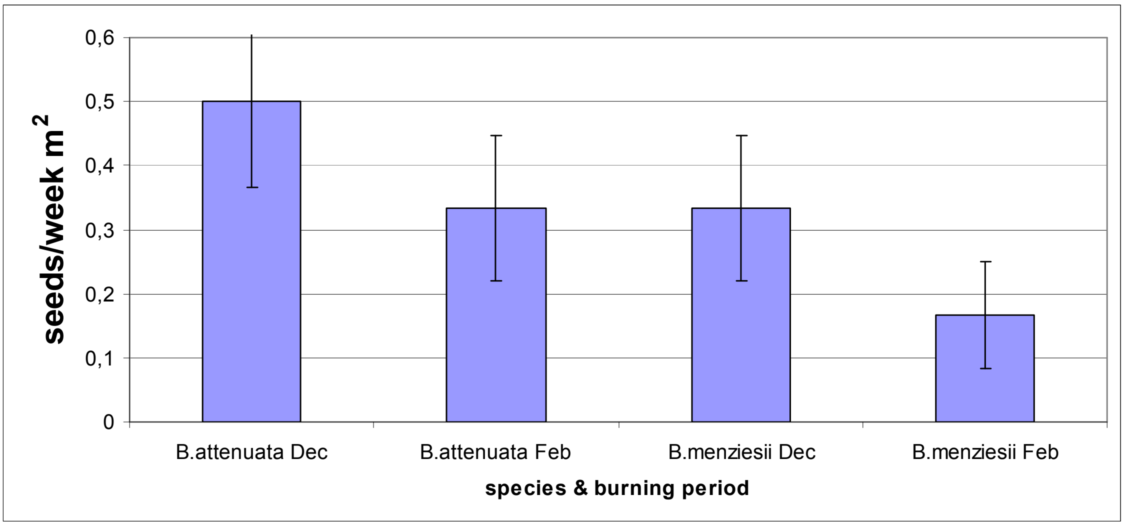

Fig. 3.23A Mean number of viable seeds m^{-2} week^{-1} trapped in boxes placed beneath the tree canopy of *B. attenuata* and *B. menziesii* between the third and ninth weeks after the December 2000 and February 2001 fire.

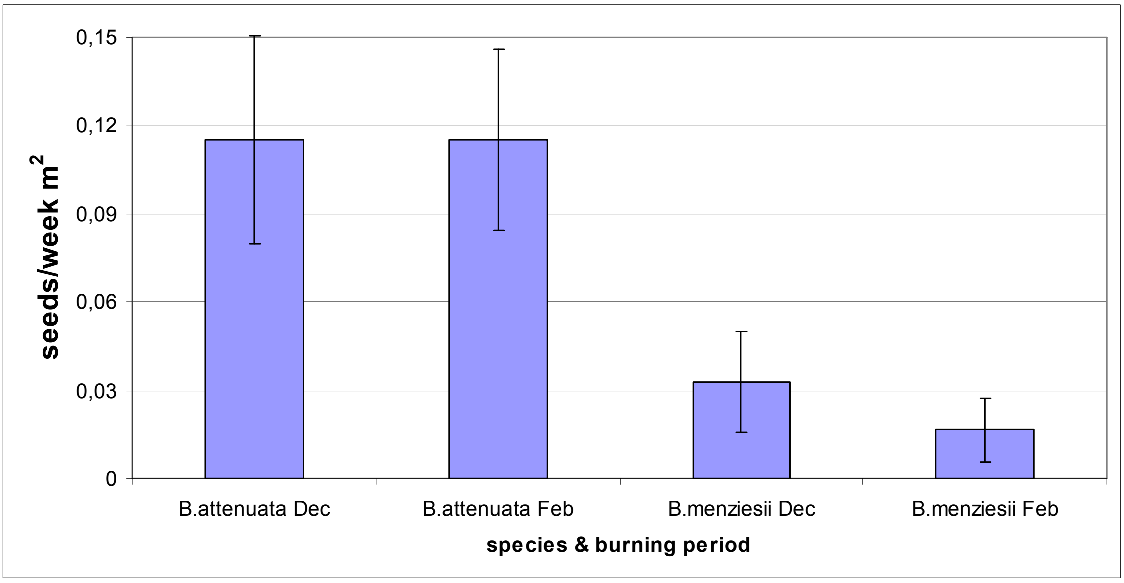

Fig. 3.23B Mean number of viable seeds m^{-2} week^{-1} trapped in boxes placed beneath the tree canopy of *B. attenuata* and *B. menziesii* between the third and twenty first weeks after the December 2000 and February 2001 fire.

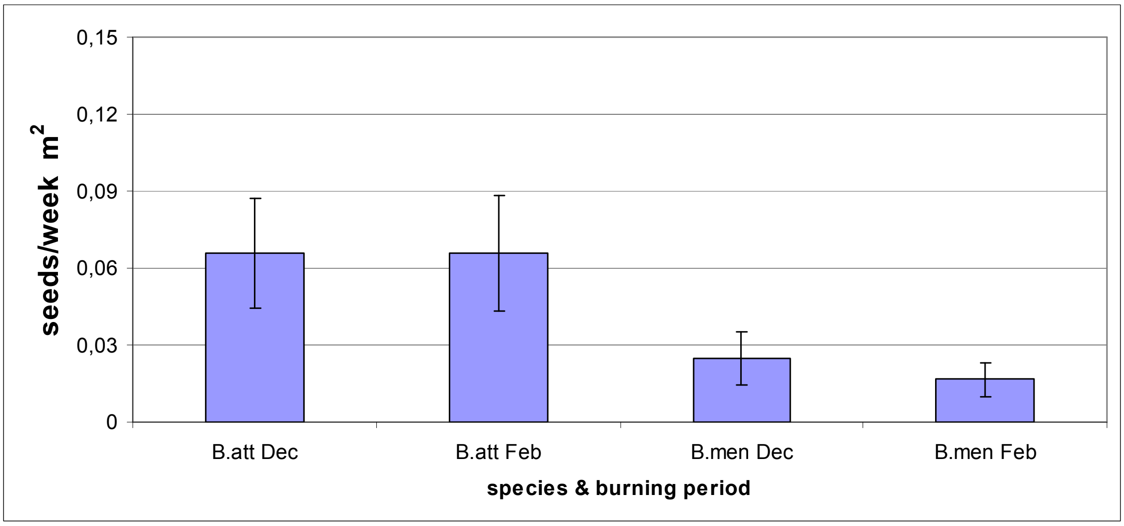

Fig. 3.23C Mean number of viable seeds m^{-2} week^{-1} trapped in boxes placed beneath the tree canopy of *B. attenuata* and *B. menziesii* between the third and thirtieth weeks after the December 2000 and February 2001 fire.

3.4.3 Quadrats used to estimate post-fire seed fall

Examination of quadrats for seeds and separators under and away from tree canopies (Fig. 3.25) showed that:

a) *B. attenuata* seeds and separators had a similar density of 2.5 m^{-2} under the canopy.

b) *B. menziesii* seed density was 0.9 m^{-2} while the separator density was 0.2 m^{-2} under the canopy.

c) Within 3 metres of the canopy of a *B. attenuata* the seed density was 0.36 m^{-2} while the separators' density was 0.2 m^{-2}.

d) Within 3 metres of the canopy of a *B. menziesii* no seeds were found in the 12 plots while the separator density was $0.2m^{-2}$.

e) At a distance greater than 3 metres from any banksia canopy, the seed density was $0.12m^2$.

The amount of seeds released under the tree canopy of *B. attenuata* (a) is significantly greater than the number of seed released under the canopy of *B. menziesii* (b) (W=2725; P<0.001; P<0.001 adjusted for ties).

For *B. attenuata* there was little difference between number of separators and seeds in the quadrats both underneath the canopy (a) (W=3937, P=0.34; P=0.32 adjusted for ties) or within three metres from the canopy (c) (W=1389; P=0.445, P=0.258 adjust for ties). Furthermore, the number of seeds collected underneath the trees' canopies (a) is significantly greater than those collected within three metres from the canopy (c) (W=3664; P<0.001, P<0.001 adjusted for ties) and greater than seeds collected more than three metres from any canopy (e) (W=341.5; P< 0.001, P<0.0001 adjusted for ties). There were no statistical differences between the number of seeds found within 3 m of a *B. attenuata* canopy(c) and those found further than 3 m from a canopy (e) (W=417.5; P=0.67, P=0.44 adjusted for ties).

For *B. menziesii* there is a significant difference between the number of separators and number of seeds scored both underneath the canopy (b) (W=258; P<0.01; P<0.01 adjusted for ties) or within 3 metres of the canopy (d) (W=267; P<0.01; P<0.01). Overall, under the tree canopy, *B. attenuata* release 10 times more seeds compared to *B. menziesii*. In contrast to the inter-fire period *B. attenuata* seed release is much larger than *B. menziesii* confirming the fact that the latter species naturally releases seeds at the beginning of summer. This is also confirmed by the number of trapped separators, which usually persist longer in the follicles after the release of the seed. The difference between the two species is similar for the inter-fire and post-fire period.

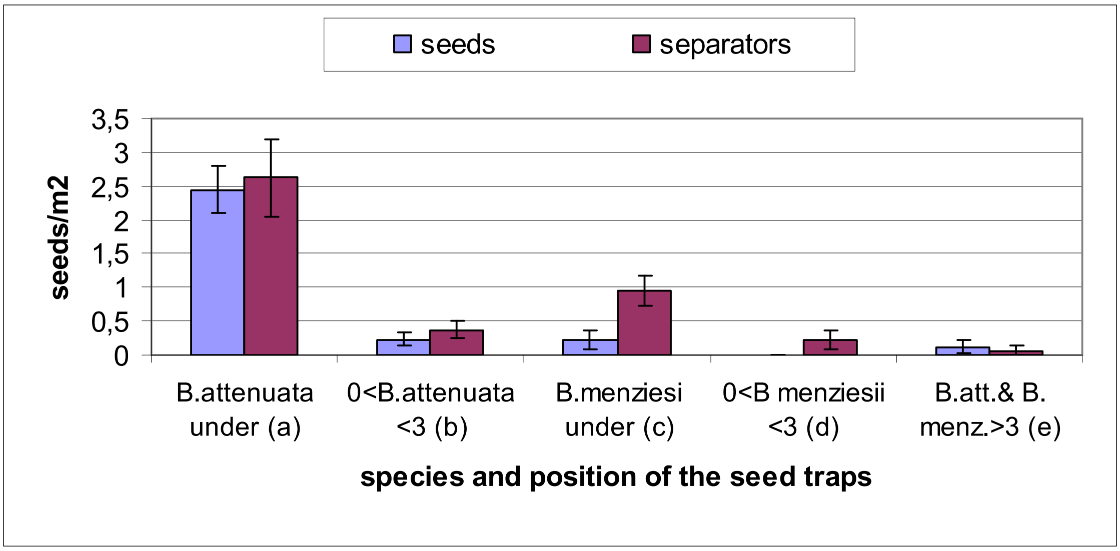

Fig. 3.24 Number of viable seeds and separators m^{-2} collected from the soil, between the 5th and the 6th week, after the December 2000 and February 2001 fires. Plots were located at different distance from the tree canopies.

3.5 Discussion

It has been proposed that fire dependent traits of *Banksia* such as serotiny originated at the first appearance of the taxon in the early Tertiary (He et al. 2011). In the paper by He et al. (2011) only eleven of the 85 *Banksia* taxa (*sensu stricto*) examined are classified as non serotinous. However on the Swan Coastal Plain, *B. attenuata* can be defined as weakly serotinous and *B. menziesii* not at all serotinous. In addition two other of the species examined in other parts of this study (*B. ilicifolia* and *B. grandis*) are also weakly to non serotinous. All are listed as serotinous by He et al. (2011). Cowling and Lamont (1985) showed variation in serotiny along a climatic gradient, with follicles being more serotinous in arid conditions. This is confirmed by the results of a study carried out on the south coast of Western Australia by Wooller *et al*. (2001) which showed that *B. attenuata* is more serotinous in the Fitzgerald River National Park than on the Swan Coastal Plain and follicle set was 38% higher. Hopetoun at the eastern end of Fitzgerald River National Park, in fact, has an annual rainfall of 492mm – less than half that of Perth (Bureau of Meteorology 2011). Furthermore in the population within the National Park only 2% of *B. attenuata* follicles were open on infructescences produced over the previous five years, this being in stark contrast to the results from the Swan Coastal Plain showing by the second year 80% of the follicles opened. However it may not be only aridity that regulates the degree of serotiny. According to Whelan *et al*. (1998) seed set in *Banksia* spp. varies among populations particularly in relation to fire regimes. Cowling and Lamont (1985) investigated the presence of viable seeds in follicles of harvested 'cones'. However in this study on the Swan Coastal Plain, the scoring of the open follicles started from labelling the inflorescences, which enabled a more precise assessment of the reproductive progression of the species. On the Swan Coastal Plain 59% of inflorescences of *B. attenuata* and 41% of *B. menziesii* developed fruit. This is much higher than the 1.5–4.6% of inflorescences producing fertile infructescences for *B. grandis* in jarrah forest south of Perth (Abbott 1985b). The present data also considered the number of inflorescence/infructescences that fell before follicle openings. Within the Fitzgerald River National Park 35% of marked *B. attenuata* inflorescences did not generate follicles, however there is no mention of the amount of fallen inflorescences/infructescences (Wooller *et al*. 2001). On the Swan Coastal Plain, by contrast, approximately 20% of inflorescences/infructescences (for both species) went missing (within 24 months) after being tagged and this is attributed mainly to cockatoo damage. Low numbers of voracious

vertebrate predators, such as cockatoos that feed almost entirely on seeds enclosed in woody fruits, in the Fitzgerald National Park may explain this difference in fruit maturation.
The degree of serotiny and pattern of seed dispersal in the different locations chosen for the study on the Swan Coastal Plain was similar and no specific gradient was found between them. Differences were, however, present in values of "fallen cones" which were higher in Kings Park and Ridges S.F.

The majority of the non serotinous species listed by He et al. (2011) occur at the wetter end of the climatic gradient occupied by banksias e.g. *B. seminuda, B. brownii, B. canei*. Most of these species are killed by fire (Geoge1984) so depend on seed regeneration for survival of the population after any stand destroying disturbance. The four main banksia species in this study all resprout to various degrees after fire. However they are not long-lived and may be killed by severe fires so some regeneration from seed is necessary. The interaction of fire frequency and severity is likely to be a critical component influencing the degree of serotiny in different species (Ne'eman et al. 2004). Interfire recruitment in the general area of Perth is important for *B. attenuata* (Hobbs and Atkins 1990) and *B. menziesii*. This will be dependent on two main things – the presence of sufficient microsites to enable recruitment into the habitat that is vegetated and sufficient fire free time for the saplings to develop a lignotuber so they can resprout after the inevitable fire (Whelan et al. 1998). In addition it has been proposed that a high risk of predispersal seed predation might also select for weak serotiny where seeds released between fires may have some chance of establishment rather than being eaten. However where interfire establishment is unlikely a greater degree of serotiny might be favoured in order to at least have some seeds survive the predispersal predation and may favour greater investment in follicle wall development (Whelan et al. 1998). Evidence from areas north of Perth show that cockatoos descend on banksia plants after fire to feed on seeds expose in cones prior to dispersal (Cowling and Lamont 1987). However this may be a stochastic effect related to whether the birds find the burnt trees and will also depend on the season, as black cockatoos (recorded as feeding on *B. attenuata* by Cowling and Lamont 1987 after a fire) migrate between site where they breed (often inland) to the coast during the non breeding season. Birds that breed over 100km north east of Yanchep spend the summer in the Yanchep area feeding in pine forests and native vegetation (Saunders 1980). Aspects of predator satiation may be relevant here as found for *Pinus halepensis* (Nathan and Ne'eman 2004) but definitive studies on this aspect have not been completed before this study on the Swan Coastal Plain.

Banksia attenuata starts flowering in November and peaks in December-January, while *B. menziesii* starts flowering in February and peaks June-July. These two species also released seeds at different times of the year; for *B. attenuata* (Summer and Autumn) and for *B. menziesii* (Spring and Summer). This has strong repercussions for the pattern of seed fate between the two species. Specifically for *B. menziesii*, there are advantages and disadvantages. Early seed release may avoid times when black cockatoos are feeding in the non breeding season. However lower seed production, longer exposure on the soil before rain comes leading to the likelihood of higher post dispersal seed predation and desiccation, and presence of seeds on the soil surface before the period when fires are more likely means potential recruitment will be lower compared to *B. attenuata*. Consequently, increased fire frequency at the beginning of Summer and presence of terrestrial "granivorous" vertebrates may favour *B. attenuata* recruitment against *B. menziesii*. Seeds are not dispersed far from parents as for other serotinous species (eg Nathan and Ne'eman 2004), even in post-fire conditions when wind could be presumed to influence the immediate dispersion of the seeds more than when the plant canopy is intact. In inter-fire periods, for both species, viability of the seeds trapped was high with more than 90% of seed viable; on the other hand in post-fire conditions only 60% of the *B. attenuata* trapped seeds were viable, while for B. menziesii the percentage of viable seeds was only slightly smaller than in the inter-fire period.

Due to the different flowering phenology and degrees of serotiny the time of a fire is likely to influence the success of establishment of the two species differently. Early to mid summer fires will tend to favour *B. menziesii* as *B. attenuata* will be in the middle of the flowering season and with immature fruits (as shown by the higher proportion of inviable seeds for *B. attenuata* after the summer fires, so relatively more *B. menziesii* seeds will be available than after later fires). However the greater degree of serotiny of *B. attenuata* fruits will still ensure some *B. attenuata* seed is available. In contrast fires will favour *B. attenuata* when seeds of *B. menziesii* on the ground will be destroyed and its weak serotiny will mean there is only a small amount of seed still in the canopy. In addition the shorter time before late autumn and winter rains will mean seeds are exposed on the soil for a much shorter time than from a summer fire and proportionally more *B. attenuata* should successfully establish.

In summary banksia recruitment to the adult population in the Perth area is related to a number of factors, particularly

1. predation of seeds

2. availability of suitable microsites for recruitment
3. survival of seedlings after establishment.

These aspects are examined in the following chapters.

4 CHAPTER 4: SEED PREDATION

4.1 Introduction

The study of the vegetation changes over time in Kings Park showed that vegetation structure, species abundance and distribution have changed considerably in the last 60 years. While the reasons for the changes have been shown to be complex, the survey undertaken in 1939 by Alison (M) Baird in Kings Park showed that *Banksia* spp. were once dominant in the bushland. At present, by contrast, it is dominated by *Allocasuarina fraseriana* and by shrubs such as *Acacia saligna* and *Dryandra sessilis*. Furthermore in the last 60 years (Baird 1977, Anonymous 2000) the presence of non-native species has dramatically increased.

Amongst other reasons, banksia seed predation has been considered a possible cause of decline of the *Banksia* species, or, in addition, if the changed environment could have created conditions in which the recruitment of *Banksia* spp. would be more difficult, so that the species could be locally extirpated.

This chapter investigates the different features of seed predation and how seed predation can influence recruitment in some of the Kings Park species, especially banksias.

Seed predation The plant life cycle is a succession of processes whereby seeds produced by an adult plant are dispersed, germinate to seedlings and recruit to the adult plant. For the recruitment process trees have to flower, set and disperse viable seeds and appropriate condition are needed to start the germination process (Harper 1977). Pollination requirements, allometric and genetic factors influence seed set, while predation and environmental factors such as fire affect seed availability. Once a seed is shed, various factors associated with the regeneration may determine the number of individuals that will recruit to the standing population. Periodic fires, predation, wind-throw, disease or old age affect plant mortality and subsequently determine the population structure.

Within this sequence of events the effect of seed predation on the survival and dynamics of plant populations is not well known and in Australia there is need of further study (Auld and Denham1999). The importance of predation in different communities may vary. In a boreal forest it has been suggested that seed predation is not influential in recruitment (William et al. 1992), while in a rain forest (Janzen 1971) and in forest plantation (Gashwiler 1970 in Nilson 2000) it is assumed to be an important factor in population growth. In the *Banksia* dominated woodlands of coastal Western Australia there is little information on this aspect of population ecology.

Predation is defined as the consumption of one organism, the prey, by another organism, the predator, in which the prey is alive at the moment of the attack (Begon et al. 1990). This definition does not always fit the interaction between seeds and animals, as ingested or removed seed are not always predated and sometime, the species may benefit from wide dispersal. Seeds with a fleshy covering such as *Macrozamia riedlei*, are eaten and later eliminated in faeces by emus (Ballardie and Whelan 1986); in this case the seed can be dispersed and the passage through the digestion system of the bird may favour germination. For mistletoes there is an obligate relation between the plant and its bird seed disperser (Zhaogui 1993). Many seeds, such as those of acacias occurring in the Kings Park bushland, have an external appendage called an elaiosome that attracts animals to the seeds. The animal is drawn more to this lipidic structure than to the seed itself. The seeds can consequently be dispersed but their fate once the elaiosome is removed varies in relation to the different removers and on the species. It is assumed (Auld 1995) that seeds taken by granivorous ants may escape mammal predation. In mediterranean-type woodland, predation is lower in the vicinity of ant nests (Albert et al. 2005); but in rain forests (Andresen and Levey 2004) and deserts (Brown et al. 1979) ants are the main predators.

Seed predation can be distinguished as pre-dispersal and post-dispersal (Janzen 1971), or pre-seedfall and post-seedfall (Kjellsson 1995 in Zhang et al. 1997). Pre and post-dispersal predation respectively influence the quality and quantity of seeds in the seed bank.

Pre-dispersal predators are often specialists and if predation is widespread it is often a major reason for poor seed production (Harper 1977; Louda 1982). A wide taxonomical range of insect, bird and mammal seed predators can attack seeds. Pre-dispersal predation by insects may cause up to 80% mortality of the seeds produced in many grassland and forest habitats (Andersen 1988; Janzen 1980, 1987). Seeds stored on the mother plant are usually protected by woody structures (serotinous species) or camouflaged to look like other plant parts (eg., the two-leaf hakea - see Groom et al. 1994). While seeds are generally clumped together, of predictable distribution and may provide a reliable food source, the predators need to be specialised to overcome their protection. In rare cases some animals that attack fruits can actually increase seed set by selectively destroying other more harsh pre-dispersal predators such as borers, as in the case of *Banksia tricuspis* and black cockatoos (Lamont and Groom 1988).

Post-dispersal predators are more generalists as the seeds are less predictably distributed and if present, they are readily available. Seeds liberated from the mother plant rely mainly on mimicking the surface onto which they are dispersed to avoid predation (Saracino et al. 1997). Post-dispersal predation can occur both on the soil surface or in the soil and may account for significant loss of propagules (Kjellsson 1995 in Zhang et al. 1997). Carabid beetles, ants and rodents are the most studied post-dispersal seed predators. Post-dispersal predation is considered a major determinant of seed survival, plant distribution patterns and community composition in some communities (Ashton 1979; Schupp 1988).

Predation behaviour differs between rodents and ants. In deserts of the northern hemisphere rodents are efficient in finding and harvesting seeds both on or below the soil surface; rodents are nocturnal while ants are mostly diurnal, large seeds are utilised by the former while the latter can also act as seed dispersers. The interaction between the two predators/removers is minimal (Abramski 1983). However competition may occur between ants and rodents in low density *Acacia* stands in Southern Africa (Holmes 1990). In Australia post-dispersal seed predation is largely confined to ants, with mammals being regarded as insignificant consumers of seed in arid and mediterranean regions (Milewski and Bond1982; Morton 1985 in Auld and Denham 1999).

Seeds contain the primary food resource for the plant embryo including storage reserves made up of carbohydrates, fats, oils and protein. These are resources that many wild animals, and also humans, rely on for their own diets. In the low nutrient environment of the south-west Australian mediterranean woodland, banksia seeds are rich in nitrogen, phosphorus and essential micro-nutrients (Pate et al. 1986). Seed availability differs according to the different reproductive strategy of the plants. Seeds that belong to the transient soil seed bank, such as those of *B. attenuata, B. menziesii*, *Allocasuarina fraseriana*, *Eucalyptus marginata* and *Dryandra sessilis* are available only in the period between seed dispersal and germination, which occurs between Autumn and early Winter. Seeds that belong to the long-lived seed bank, such as *Acacia saligna* and *A. pulchella*, can accumulate in the seed bank until germination. Not all seeds have features making them attractive to a predator. Seeds can carry compounds that make them unpalatable or indigestible. However none of the seeds used in this study has these characteristics.

Habitat characteristics are important in influencing the abundance of the predators. Seed abundance and a sheltered environment play significant roles in the choice of the habitat. High levels of seed predators can be expected where seeds are abundant (Angelstam et al. 1987;

Fortier and Tamarin 1998) and where shelter due to understorey vegetation, is abundant (Callaway 1992; Myster and Pickett 1993; Schreiner et al. 2000). A fragmented habitat can also influence the presence of seed predators (Andreassen et al. 1998) and can increase rodent population density in contrast to a more uniform habitat. All these features are present in Kings Park bushland and, in particular, the study on vegetation changes showed also a structural change from open woodland to a more closed formation with abundant understorey.

High seed abundance may affect predation by satiation; alternatively, reducing abundance could cause the predator to feed on an alternative more abundant food source, even if it is not the preferred one. If seed density is constant over a number of years the population levels of predators may be more stable but if there are seasons with much higher seed production, the predator population may be easily satiated during those years. Different predator types are likely to access seed resources differently where species with longer term life cycles have relatively stable populations that cannot track variable seed crops (Summers 2011). Seed production of banksias may differ over the years possibly due to climatic reasons. This cannot be considered mast seed production (when plants in a population all produce seeds at the same time) as occurs in some northern temperate tree species. Nevertheless when seeds are dispersed *en mass* after a fire, it could be considered a 'mast-year' from a post-dispersal point of view.

For some plant-animal seed systems not all seeds are eaten upon encounter, for example seeds may be stored for later consumption (Cromar et al. 1999; Murphy et al. 2005). In this case the seed can sometimes escape consumption by germinating or may enter the soil seed bank. In the banksia woodland this is unlikely to occur for the serotinous species and due to the fact that seeds of many species belong to the transient soil seed bank.

Seed size will influence predation in relation to the size and/or specialisation of the predator. Small predators can better handle small seeds while for larger predators the ratio of energy spent in collection versus energy gained will be too low for energetic efficiency (Murston *et al.* 1966). In contrast large seeds often are too large or have a testa too tough to be exploited by small predators. Thus small seeds in general can be better exploited by small predators, such as ants, while large seeds are attractive to large predators such as rodents. The seven species used for the experiment have various seed sizes. *Allocasuarina fraseriana*, *Eucalyptus marginata*, *Dryandra sessilis*, *Acacia pulchella* and *A. saligna* produce many more seeds of smaller size compared to *Banksia attenuata* and *B. menziesii*. Consequently *B. attenuata* and *B. menziesii* are likely to be predated by rodents while seeds of the other investigated species are not, but could be predated by invertebrates. All the species selected for the experiment produce seeds every year but, being perennial, do not rely solely on an annual seed set for regeneration.

The significant effects of seed predation on population maintenance are difficult to assess, even over several years of study. Although seed loss may be high on average it may also be highly variable and one periodically good seed survival year may be sufficient to maintain population numbers. In addition, for much of the time predation may be removing propagules which may not have found a suitable site for establishment or may have died due to competition with other seedlings (Andersen 1989).

Nevertheless it is likely that seed predation, like any other factor causing consistent loss of young individuals will influence population ecology. As a component of the regeneration niche it is important to understand the magnitude, spatial and temporal variability of seed removal in order to combine this information with other aspects of the species' auto-ecology such as recruitment, seedling and adult survival and the influence of disturbance on the population maintenance.

4.2 Aim

The aim of this chapter is to determine the quality and quantity of *pre* and *post* dispersal seed predation of the *Banksia* spp. occurring in the Kings Park *Banksia* woodland and to compare this to values from other locations on the Swan Coastal Plain with the same type of vegetation. Furthermore the study investigates the post-dispersal predation of the other dominant species (community level) occurring in the Park and in other banksia woodlands located on the Swan Coastal Plain.

Comparison between locations and species were made in order to assess whether values of seed predation could be more severe in Kings Park and affect species recruitment.

The species used in this study represent a range of plant families, seed traits, seed dispersal mechanisms and seed bank dynamism.

4.3 Pre-Dispersal Seed Predation

Pre-dispersal seed predation is widespread and often considerably reduces plant recruitment (Harper 1977). In Australia pre-dispersal seed predation by insects may be a great cause of reduction of viable seed and could limit plant population growth (Andersen 1988, 1989). Scott (1982), Cowling and Lamont (1987), Vaughton (1998), Auld and Denham (2001) and Figueroa *et al*. (2002) investigated seed predation, recording damaged or intact seeds by examining the contents of mature fruit collected from the plant. All these studies represented an underestimation of the real predation, as they did not take into account losses of complete infructescences or the early abortion of seeds due to predation; in addition, no experiment was set up to exclude seed predators. Vaughton (1990) found seed pre-dispersal predation by insects damaged follicles in *Banksia spinulosa* while no damage was observed on samples with invertebrate exclusion. According to Andersen (1988) estimating seed loss by inspecting mature seeds and fruit for sign of attack must be questioned as insect exclusion experiments showed there was a much higher loss of seeds than would be recorded by observation only.

In Australia cockatoos are the main granivorous species on taxa that possess woody fruit (Saunders 1980, Groom *et al.* 1997), they are particularly fond of seeds of *Eucalyptus, Acacia, Hakea, Banksia* and introduced *Pinus* trees (Forshaw 1969 in Saunders 1980). Furthermore, many flower heads may be destroyed by larvae-seeking cockatoos (Scott and Black 1981; Lamont and Van Leeuwen 1988). Attack from parrots on *Grevillea* spp. destroyed 40% of the initiated fruits and an exclusion experiment showed that fruits would have matured if they had not been damaged by the parrots (Vaughton 1998). The beak of Black-cockatoos is thought to be an adaptation for eating seeds contained in hard, woody nuts that must be removed via cutting instead of by compression (Homberger, 2003). The Psittaciformes, the order to which the cockatoos family belong, seems likely to be Gondwanan in origin (Franklin et. al 2000), it can, thus, be expected that the feeding apparatus has been affected by the changing selective regime arising from the gradual shift from the original Gondwanan subtropical rainforest to the sclerophyllous communities, often with serotinous species that developed across Australia in the course of its desiccation since the mid-Tertiary (White 1990).

On the Swan Coastal Plain, many of the native sclerophyllous plants that are exploited by cockatoos are serotinous (Lamont 1991; Lamont et al. 1991a; Groom et al. 1997).

In Kings Park both cockatoos and parrots were often recorded on tree canopies damaging inflorescences/infructescences.

The mechanical strength applied from the cockatoos on the cone could snap the head from the tree so that attacked cones fall under the canopy. Furthermore movements of jaw muscles result in transverse movement when the beak is closing which simulates a cutting motion that could cut the inflorescence/infructescence (Homberger, 2003).

On the Swan Coastal Plain, consequently, it is likely that pre-dispersal predation on *Banksia* is due to birds. Castro *et al.* (1999) monitored bird predation on pine cones by collecting the number of cones found under the canopy of the trees and quantifying the damage showing that birds consumed more than 80% of the seed before dispersal.

4.3.1 The Study on pre-dispersal seed-predation

The research described in this chapter was undertaken to assess the presence and magnitude of pre-dispersal seed predation for *Banksia attenuata* and *B. menziesii* in Kings Park and in three other locations on the Swan Coastal Plain. Observations were made with the purpose of assessing the following details for the two *Banksia* spp. under examination.

1. Occurrence of *Banksia* pre-dispersal predation;
2. Difference in seed predation within the *Banksia* spp. present in Kings Park;
3. Investigation of the main predator group (vertebrate or invertebrate) and
4. Investigation of the values of predation and comparison between the different locations (habitat).

According to the position of the seed (infructescence) at the time of the scoring, the surveys were differentiated into "*in situ*" and "*ex situ*".

In situ. With the inflorescence/infructescence present on the tree.

Ex situ. With the inflorescence/infructescence not present on the tree and collected from the ground below the tree canopy

4.3.2 Material and methods

The rate of seed predation was estimated with two different investigations that assessed the status of the follicles according to the position of the infructescence. The locations where the surveys were undertaken were: Kings Park, Bold Park, Jandakot Regional Park, Ridges State Forest.

A. Infructescences on trees (*in situ*). Assessing follicle damage on infructescence 'cones' positioned on the tree. *Banksia* inflorescence 'cones' were labelled and the infructescence development was followed over two years.. *Banksia* inflorescence and infructescence 'cones' were scored in each season. The plants selected for the labelling of the inflorescences were mature trees with more then 5 inflorescences. On each tree no more then 50% of the inflorescences were randomly labelled. The height of the labelled 'cones' was no more than four metres above the ground. The number of trees and labelled flowers varied between the four different populations (the four locations). In total, across all location, 372 inflorescences of *B. menziesii*, of which 208 developed into infructescences, and 382 of *B. attenuata*, of which 160 developed into infructescences, were labelled. The tagging of the inflorescence started in 1999 (January 2000) and the scoring of the follicles was recorded for two years until summer 2003. In Kings Park four different sites were chosen while in the other investigated locations only two sites were used.

B. Infructescences below tree (*ex situ*). Assessing follicle predation on infructescences and number of inflorescences/infructescences collected on the ground. Along transects with a predefined direction North-South or East-West all the yearly infructescences (both developed or undeveloped) found on the ground under the canopy of the first 10 mature trees of a species were collected and examined. In Kings Park four different sites were chosen while in the other investigated locations only two sites were used for the investigation. Infructescence scoring was undertaken in Winter 2002 and the trial was replicated three times for each site.

In both surveys, frequencies of open, closed, predated and damaged follicles were recorded. When there were clear and group-specific signs of predation the predator group (vertebrate or invertebrate) was also documented.

4.3.2.1 Description of surveys

Seed removal scoring

Labelled inflorescences were scored and when the infructescences were present the status of the follicles was assigned to one of the following, reciprocally exclusive, categories:

1. Open: the follicle was open, even partially, with no sign of any damage. When the follicles were only partially open, seeds were still subject to predation; though preliminary observation and the results of the study on the fruit phenology showed that when the follicle is partially open, the seed will be dispersed before the following season (chapter 3).
2. Closed: the follicle was closed, with no sign of damage.
3. Invertebrate: on the follicle there was a clear sign of invertebrate predation such as the presence of holes with a clear shape or tiny excoriations of the follicle.
4. Vertebrate: on the follicle there was a clear sign of vertebrate predation such as bites or beak marks.
5. Damaged: the follicle was damaged. However the damage could not be attributed to predation or to any specific group of predator and weathering and predation could be considered as the main reasons for the harm.

4.3.2.2 In situ scoring

Scoring was undertaken each season. The numbers for the different categories were taken from the final scoring of the infructescences. The final scoring could be either the assessment at the end of the complete monitoring period or the assessment at the stage where there were no closed follicles left or the assessment made before an accidental removal of the infructescence. If the cone was removed before the first two seasons from the initial labelling, the data were not taken into account as potential predation values could not be defined.

The aluminium tags, used for labelling, were carefully attached at the stem well below the inflorescence, so that, if the inflorescence/infructescence would snap from the stem, the tag could still be tracked and the fate of the 'cone' scored. In any case, the aluminium tags were positioned so that each tag could belong only to one specific inflorescence/infructescence.

In a small percentage of cases, neither the 'cone' nor the tag was found in one of the seasonal scoring; in this case, the infructescence was not considered for the study. The interaction between the shiny aluminium tags and the behaviour of the predators was not investigated.

4.3.2.3 Ex situ scoring

Scoring was undertaken once, in Winter 2002.

Some of the collected infructescences had immature follicles and a further category was introduced:

6. Not mature: at the scoring, the follicle had not properly developed the typical woody structure. As the 'cones' were collected on the ground, immature follicles had no chance to mature, while for the infructescence in the *in situ* study the category was not needed as the follicles had time to mature and were considered 'closed'.

4.3.2.4 Data analysis

The descriptive statistics of the collected data are summarized and displayed on bar charts with mean ± 1 S.E. bars.

Data are displayed as frequency or percentage of frequency.

For the *in situ* study both the initial number of inflorescences labelled and the number of mature infructescences were different in the different sites due to initial availability of the inflorescences and variable reproductive effort by different trees. In the graphs the data are shown for all the different categories at the different locations and are expressed as the average percentage number of follicles.

For the *ex situ* study, in the main graphs all the different categories for each location are expressed as the total number of infructescences and of follicles for each location, or as percentage of follicles. Follicles are divided into three different categories: predated, not matured, not predated.

The variation between different categories, the comparisons between locations and the consistency of seed predation between the years were examined using non-parametric tests as the original observations did not satisfy the parametric assumptions.

The Mann-Whitney U test was used to test differences of observations taken from two groups. When there were more than two groups the Kruskal-Wallis test was used, in the latter case the Mann-Whitney U test was used as the *post hoc* test. All the outputs account for tied data.

4.3.3 Results

4.3.3.1 In situ

For *B. attenuata*, at the end of the investigated period, most of the follicles were in the 'open' category, 63.4% across all locations while approximately 15% of the follicles were predated (Fig. 4.1).

Invertebrate predation was lower compared to vertebrate predation, across all location respectively 4.3% and 10.5%, and was not significantly different between the four locations (H=9.47; DF=3; P<0.1); vertebrate predation was statistically different between locations (H=167.5; DF=3; P<0.001) with greater seed loss in Kings Park and in the Ridges S. F. 18.6% and 22.1% respectively.

Banksia menziesii followed a similar trend. Across all locations 72.2% of follicles were in the 'open' category and 23.1 % in the predated category. Vertebrate predation was significantly different across locations, (H=12.34; DF=3; P<0.01) with high frequency only in Kings Park, 17.2% and in the Ridges S. F., 19.6%; invertebrate predation showed no statistical differences between the locations (H=4.85; DF=3; P<0.1) with an average across all location of 5.1% (Fig. 4.2).

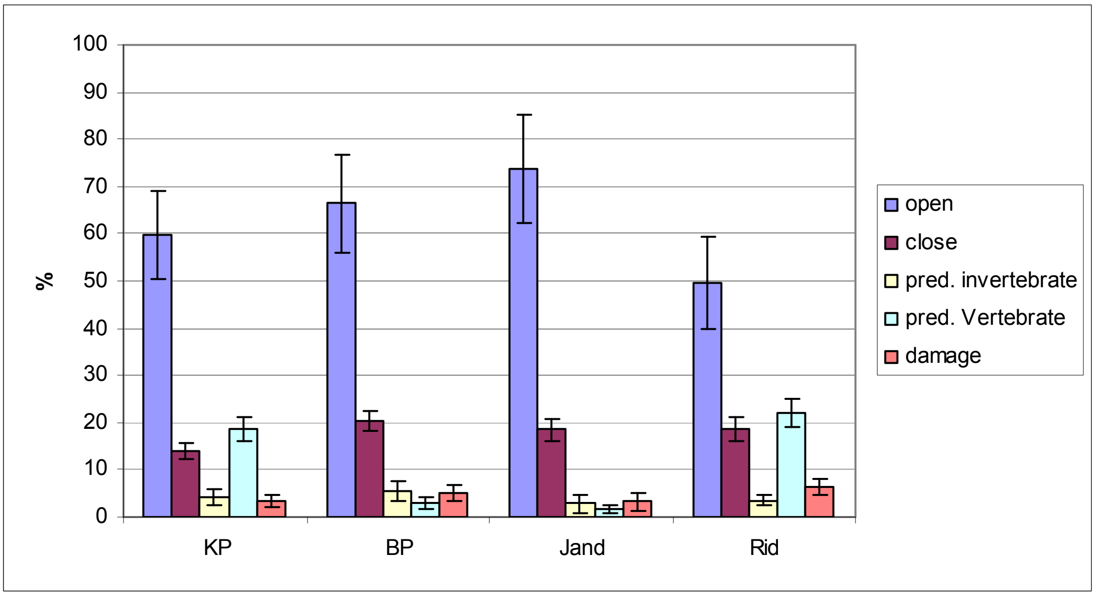

Fig. 4.1 Relative mean percentage of the different follicles states, recorded in five categories. *Banksia attenuata* infructescences positioned on the tree (*in situ*) in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F. (Rid).

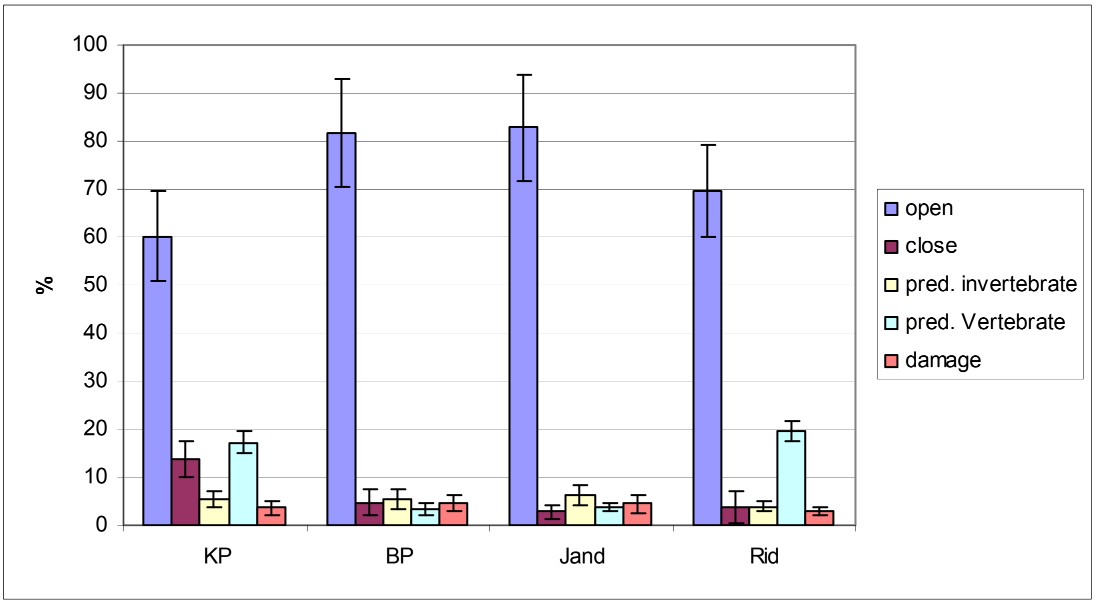

Fig. 4.2 Relative mean percentage of the different follicles state, recorded in five categories. *Banksia menziesii* infructescences positioned on the tree (*in situ*) in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F: (Rid).

4.3.3.2 Ex situ

For *B. attenuata* only Kings Park and the Ridges State Forest locations showed a large number of yearly 'cones' on the ground with an average of 2.5 'cones' under each tree canopy (Fig. 4.3). The *Kruskal-Wallis* test – one way analysis – showed a statistical difference between the four locations (H=37.64; DF=3; P<0.001), with Kings Park and Ridges S. F. having a greater number of infructescences on the ground and between the six categories (H=29.53; DF=5; P<0.001) with most of the follicles being within the open or predated by vertebrate category (Fig. 4.5).

Within Kings Park there is a statistical difference between the six categories (H=19.86; DF=5; P<0.001) as there is in Ridges S. F. (H=17.74; DF=5; P<0.01); both locations showed a higher number of follicles that were open or predated by vertebrates. The statistical difference between locations for vertebrate predation (H=11.92; DF=3; P<0.01) is clearly shown in Fig. 4.5 with Kings Park and Ridges S. F. having much higher frequency of follicles predated compared to the other two locations of Jandakot R.P. and Bold Park (Figs. 4.5; 4.7).

A similar trend was found for *B. menziesii,* with most of the fallen 'cones' occurring in the Ridges S. F. and Kings Park, with an average of 1.8 'cones' under each tree canopy (Fig. 4.4). Testing single variables, a statistical difference was found between the four locations (H=24.86;DF=3; P<0.001) and the six categories (H=26.94; DF=5; P<0.001) with most of the follicles being within the open or predated by vertebrate category (Fig 4.6) and with no interaction between the two variables (P=0.2), according to the *Scheirer-Ray-Hare* test. Between locations, the number of follicles predated by vertebrates was found to be statistically higher (H=10.87; DF=3; P<0.01) in Kings Park and in the Ridges S. F.

In the Ridges S. F. and Kings Park most of the infructescences collected on the ground had been attacked (Fig. 4.7, 4.8). Furthermore, both in Kings Park and Ridges S. F. the 'cones' that had fallen on the ground had a high average number of follicles per infructescence, compared to the infructescences found on the ground in the other locations (Figs. 4.5, 4.6). Most of the attacks on the follicles were due to vertebrates (92%).

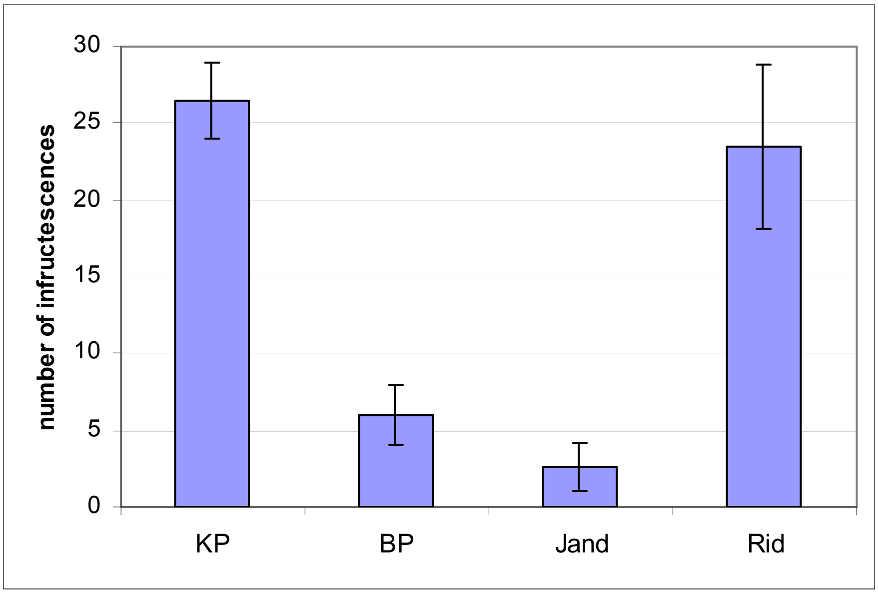

Fig. 4.3 Mean number of *Banksia attenuata* infructescences collected on the ground along the transect of 10 *B. attenuata* trees in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F. (Rid).

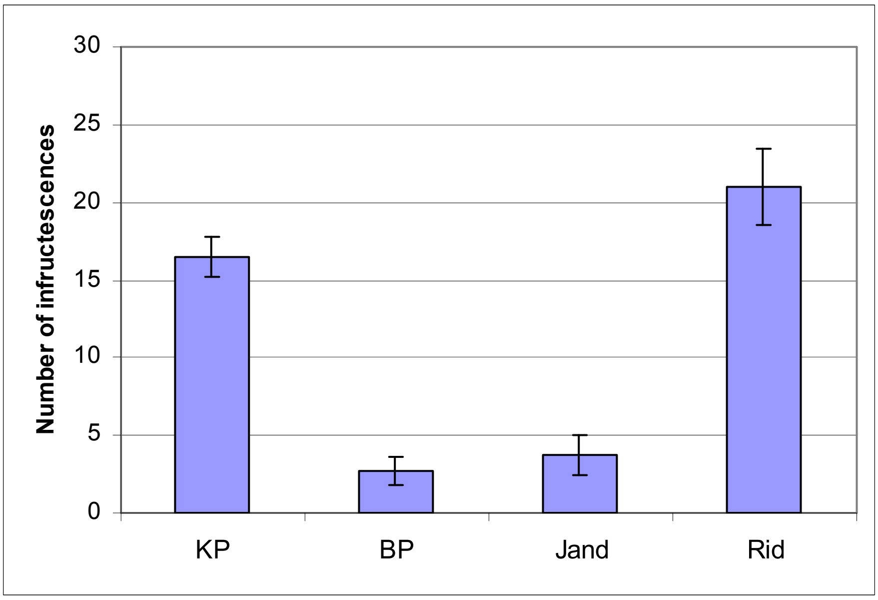

Fig. 4.4 Mean number of *B. menziesii* infructescences collected on the ground along the transect of 10 *B. menziesii* trees in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F. (Rid).

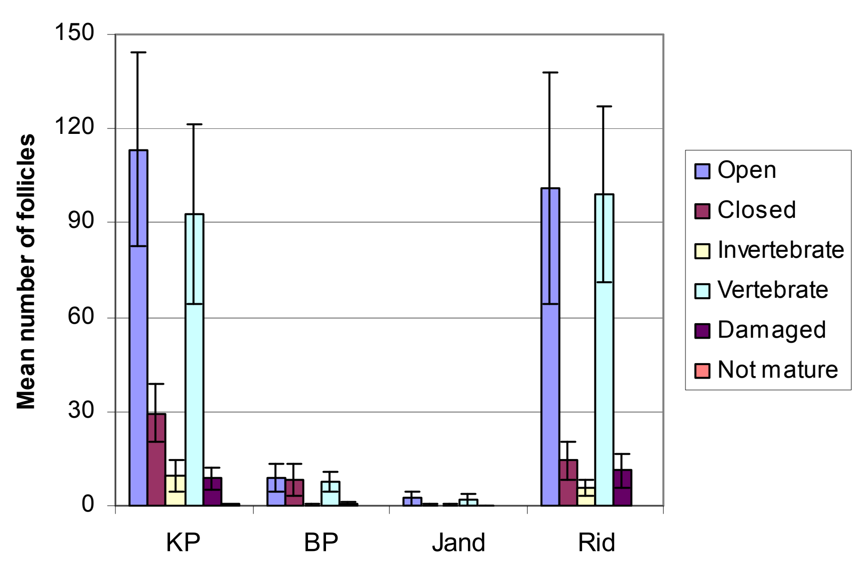

Fig. 4.5 Mean number of follicles, recorded in six categories. *Banksia attenuata* infructescences collected under 10 *B. attenuata* trees (*ex situ*) along transects in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F. (Rid).

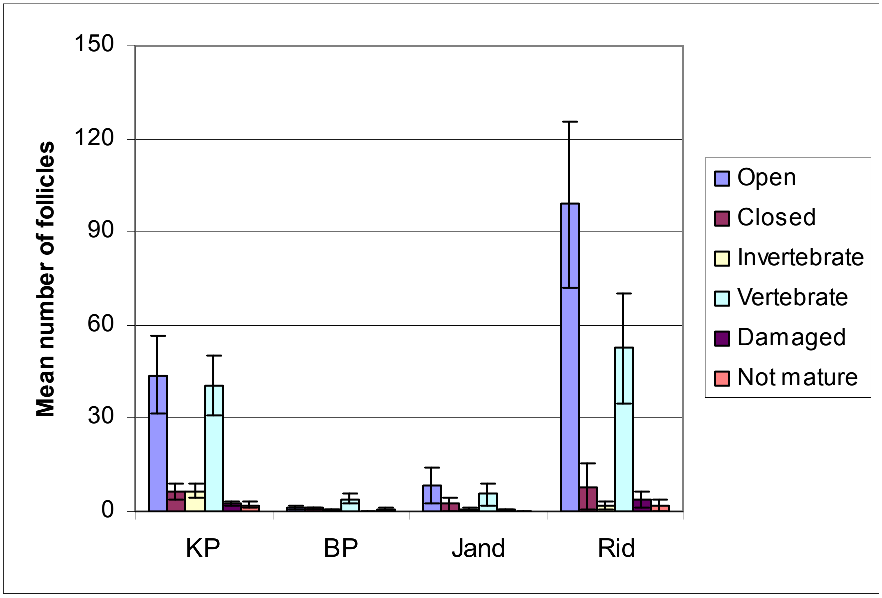

Fig. 4.6 Mean number of follicles, recorded in six categories. *Banksia menziesii* infructescences collected under 10 *B. menziesii* trees (*ex situ*) along transects in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F. (Rid).

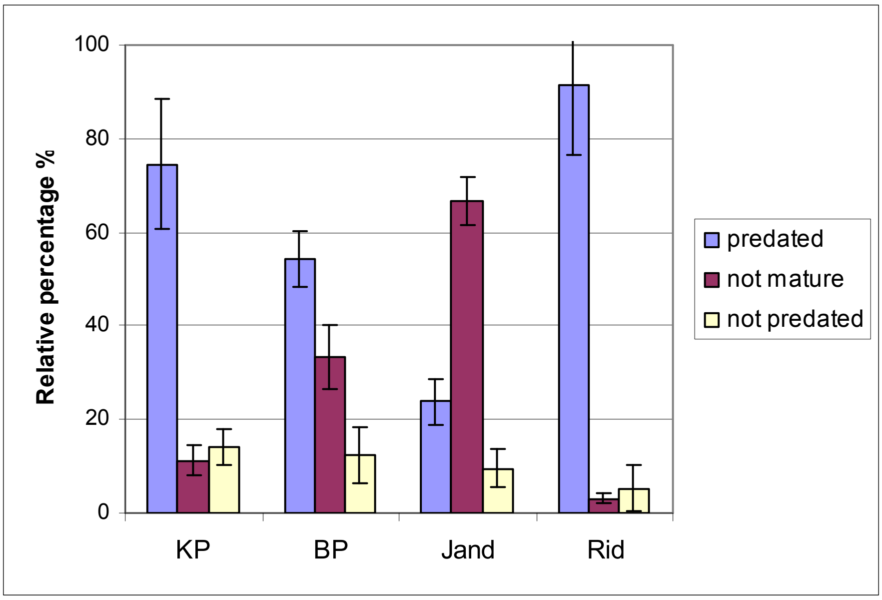

Fig. 4.7 Relative mean percentage of *B. attenuata* infructescences collected on the ground (*ex situ*) along a transect of 10 *B. attenuata* trees in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F. (Rid).

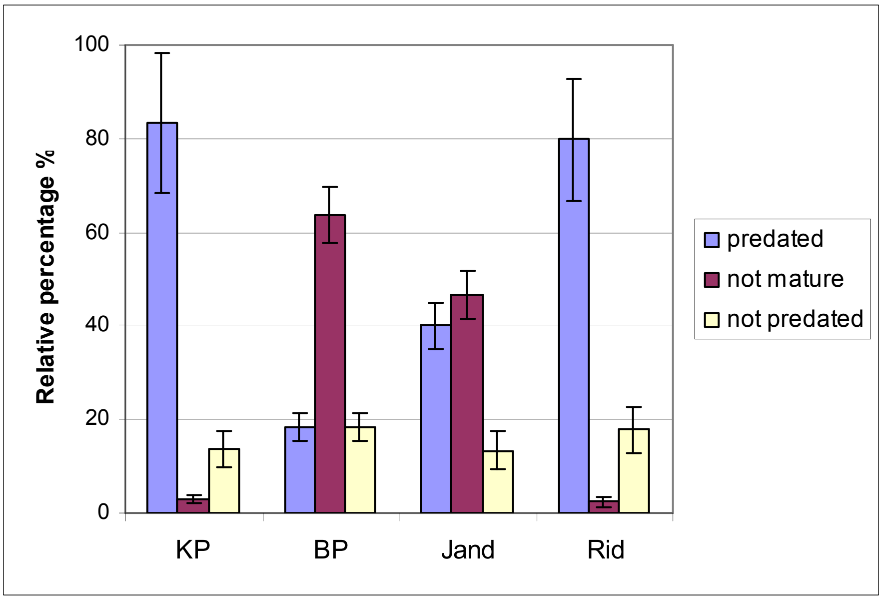

Fig. 4.8 Relative mean percentage of *B. menziesii* infructescences collected on the ground (*ex situ*) along a transect of 10 *B.menziesii* trees in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges S.F. (Rid).

4.4 Post-Dispersal Seed Predation

Inter-fire post-dispersal predation

Once the seed is dispersed from the mother plant, it can be destroyed by a variety of animals but particularly by mammals and insects (Zhang *et al.* 1997). Period, consequences, quality and quantity of predation could differ according to the type of predator. Predation studies, which fail to quantify separately the impact of the different types of predator, may fail to elucidate the patterns of seed removal (Hulme 1998b). According to Westoby *et al.* (1991), in Australia, ants are the most important seed dispersers and mammals are not important seed predators in arid or mediterranean vegetation. Nevertheless, in some particular local conditions rodents, native or otherwise, can influence the number of seeds available for germination or dispersal; this has been showed for species of the jarrah forest (Abbott and Heurck 1985), in *Macrozamia communis* (Ballardie and Whelan 1986) and for *Grevillea* spp. (Vaughton 1998; Auld and Denham 1999). However, in general, the importance of seed predation by mammals in Australia has been underestimated.

In Australia, the study by Abbott and Heurck (1985) was one of the first to investigate the simultaneous contribution to predation by both vertebrates and invertebrates. This study was undertaken in a jarrah forest just north of Perth. Of the six species involved three are also included in this study: *B. grandis, E. marginata* and *A. fraseriana*. Exclusion treatment showed that caging to exclude vertebrates had no effect on seed removal for *E. marginata* and *A. fraseriana* while invertebrate exclusion showed no effect on *B. grandis*. Removal started soon after the seeds were placed on the ground and predator preference was *B. grandis* >*E. marginata*>*A. fraseriana*. This study was undertaken from April to September so no seasonal differences were analysed. No specific vertebrate predator was identified but ‘house mice’ and ‘ship rats’ were considered potentially responsible. Interestingly Abbott and Heurck commented that *B. grandis* seeds were rarely removed before the introduction of rodents.

Auld and Denham (1999) examined the impact of ants and mammals on six *Grevillea* species of the Sydney region. While ants removed only seeds possessing an elaiosome, mammals, such as rodents and macropods, effectively predated all the *Grevillea* seeds. The amount of seed consumed by mammals was so high that predation was considered a major cause of reduction in the quantity of seed reaching the persistent seedbank. According to the authors, the rarity of some of the *Grevillea* species could be explained by the high seed predation due the presence of granivorous mammals. High levels of seed loss due to rodent predation was also found by Vaughton (1998) for the rare *Grevillea macleayana*.

The presence of undecomposed litter can influence seed predation (Abbott and Quink 1970; Price and Jenkins 1986; Kaufman and Kaufman 1990), furthermore Clarke *et al*. (1991) and Myster and Pickett (1993) found that seed predation was reduced if seeds were covered with litter suggesting that the increased seedling density they found could be due to leaf litter reducing predation. Maron and Simms (1997) suggested that on dunes where seeds are dispersed on bare sand, granivory was higher than in grassland where the presence of senesced grass stems could reduce seed predation. The presence of litter affects rodents' ability to detect seeds because they rely on olfaction to locate seeds and litter may affect odour diffusion (Price and Jenkins 1986).

Relationship between seed size and the size of the particles in which the seed is located may be of greater importance than seed size itself as it may increase the time and energy necessary in discerning the seeds from the particles. For example, Price and Jenkins (1986) showed that there was a relationship between seed size and soil particles size and the value of seeds acquired by rodents.

In the boreal forest, seed burial can reduce seed loss from vertebrates by 50% and small seeds can escape predation better then big seeds (Hulme and Borelli 1999, Maron and Simms 1997). According to the different foraging behaviour of the predators (Reichman and Oberstein 1977 in Myster and Pickett 1993) predation may be density dependent (as in Casper 1988) or density independent (as in Webb and Willson 1985).

Hulme (1997) and Hulme *et al*. (1999), found that for some species, rodents consumed a constant proportion of seeds irrespective of the number available while for other species no effect of initial seed density was found in the final proportion of removed seeds. Seed density significantly influenced loss of *Fraxinus americana* but not of *Acer rubra*, two dominant species in the old-growth forest predated by ‘gray squirrels’ and ‘white-footed mice’ (Myster and Pickett 1993). Satiation of seed predators is one of the explanations for the success of seedling establishment after “mast seed year” and post-fire dispersal.

Post-fire post-dispersal predation

Australian fire prone vegetation offers examples of self-organisation, with many taxa expressing many different regenerative strategies as a result of wildfire. When a catastrophic event occurs, the complexity and specialisations of the ecosystem are likely to be partially disrupted; these perturbations also include interactions with animals such as pollination, dispersal and predation.

After a wildfire, small mammals are greatly affected (Bamford 1985) and predation processes are likely to be disrupted (Quinn 1986; Reed et al. 2004). Urban remnants such as Kings Park or Bold Park bushland could be more sensitive to disturbance events due to the isolated nature of the bushland and lack of connectivity with other bushland sites. For example a large wildfire in 1989 over part of the Kings Park bushland led to a decline of the avifauna and slower recovery rates compared to similar bushland of substantial size (Recher 1997). In south-eastern Australia (Andersen 1988), following prescribed Spring burning an uncommon species of seed eating ant, *Rhydidoponera tasmaniensis,* became abundant immediately after the fire, but seed removal from artificial baits dropped, presumably due to post-fire massive release of *Eucalyptus obliqua* and *Casuarina pusilla* seeds, which caused predator satiation. Seven weeks after the fire the number of ants and rate of seed removal were both higher than any other level recorded. Results from a nearby previously burned area, showed that this trend can persist for at least two years. Ants can strongly influence the build up of the soil seed bank especially with seeds that display a food body rich in nutrients such as the elaiosome. These seeds, according to the size in relation to the ant, can be carried towards the nest or inside the nest (Hughes *et* al. 1988) and ants may be the first vector to carry seeds from the nearby unburned bushland to the burned area.

There is no unique pattern of post-fire post-dispersal predation by mammals, in fact while in eucalypt forests the presence of granivorous mammals such as *Rattus fuscipes*, and consequent seed predation, was reduced in the first five years after the fire, *Mus musculus* may be common in the first two years after fire (Fox and Mckay 1991). By contrast according to Auld (1995) and Auld and Denham (1999; 2001) seed predation by mammals is constant throughout post-fire fruiting. In South African fynbos mammal seed predation after fire is usually very severe (Bond 1984).

4.4.1 The study of post-dispersal predation

The study mainly focused on the post-dispersal seed predation of the *Banksia* spp. However, to gain a clearer understanding of the role of predation at the community level, the investigation of post-dispersal seed predation also included several other dominant species of the Kings Park bushland.

4.4.1.1 Inter-fire period

Experiments were set up and observations were taken with the objective of assessing the following details of seed predation/removal of the dominant species in the Kings Park bushland inter-fire environment:

- Occurrence of post-dispersal seed predation/removal;
- Dependency between predation and seed density;
- Presence of sites safe from predation/removal of seeds due to the soil surface attributes.
- Difference in seed predation/removal between the dominant tree and shrub species present in the park;
- Type of the main predator group (vertebrate or invertebrate);
- Coincidence of seed removal and consumption of the seed;

The first three points were also tested in the other locations such as: Bold Park, Jandakot R.P. and the Ridges S.F.. Each chosen location is referred to as a population.

4.4.1.2 Post-fire period

One of the four locations chosen to study *Banksia* spp. seed predation on the Swan Coastal Plain was Bold Park. In December 2000 a large area of the Park experienced a severe wildfire. Predation experiments were set up to investigate the magnitude of post-dispersal predation in a post- fire environment.

Originally, three sites, with increasing distance from the unburned area were chosen. In January 2001, however, a second fire altered one of the sites, the closest to the unburned area; subsequently only two of the sites were considered in this study.

In the burned area experiments were set up with the objective of assessing the following details of post-dispersal predation/removal for the seven tested species.

- Occurrence of post-dispersal seed predation/removal;
- Difference in seed predation/removal between burned and unburned areas;
- Effect of distance from the unburned area on predation/removal;
- Effect of time since fire on predation/removal.

4.4.2 Material and methods

4.4.2.1 Experimental unit (a-b-c)

The rates of seed removal were assessed by seed loss from an experimental unit (EU). The

EU consisted of a plastic tray (35x29x6cm) buried and levelled up to the soil surface. The tray was filled with locally collected loose sand or a sod of soil.

a) The standard EUa, consisted of ten seeds for each of the seven tested species (*Banksia attenuata, B. menziesii, Dryandra sessilis, Allocasuarina fraseriana, Eucalyptus marginata, Acacia saligna* and *A. pulchella*), which were placed in the tray filled with loose bushland sand.

Modifications of the standard experimental unit were:

b) EUb consisted of 20 seeds of each of the 7 species placed in the tray filled with sand;

c) EUc the tray was filled with a sod of soil with 10 seeds of each of the 7 species placed in the tray.

All the seeds were randomly placed simultaneously in the tray.

4.4.2.2 Treatments (1-2-3-4-5-6-7)

To determine the quantity of seed predation attributable to the different predator groups, and the reliability of the experiments, a series of treatments with and without exclosures was established in the study.

4.4.2.2.1 Exclusion treatments (1-4)

Experiments with an exclusion device were defined as exclusion treatments (1-4):

1) Ground dwelling (crawling) invertebrate exclusion: abundant sticky gel (Tanglefoot paste) was placed around the inside perimeter of the tray - EUa;

2) Vertebrate exclusion: a protection cage made of wire with a 1x1cm mesh was used; the cage was fixed to the ground with numerous metal pegs - EUa;

3) Complete exclusion treatment excluding predators using both the devices, cage and sticky gel – EUa;

4) Complete exclusion as in number 3 but with seed placed on a sod of soil - EUc.

4.4.2.2.2 Open treatment (5-7)

To assess the rate of seed predation, in different ground microhabitats and with different food availabilities, the fate of the seed was observed simulating normal conditions of predation. Experiments with no exclusion device and seeds available to any sort of removal, biotic or abiotic, were defined as open treatments (5-7).

5) Standard treatment: 10 seeds on loose sand. EUa;

6) Density treatment: 20 seeds on loose sand. EUb;

7) Safe site treatment: 10 seeds on a sod of soil. EUc.

4.4.2.2.3 Description of the treatments

Exclusion treatments

1) Invertebrate exclusion. A number of methods has been used in other studies to exclude invertebrates. Abbott and Heurck (1985) surrounded the sampling unit with insecticide. However more recent studies used sticky gel. Auld and Denham (1999) used the sticky gel between two petri dishes of different diameters placed one inside the other while Yates *et al*. (1994), placed the gel around petri dishes that were fixed onto plywood. The trap coating gel was used by Blaney and Kotanen 2001, covering the outer edge of the petri dish. McAlinden (1999) observed that the effectiveness of the gel, as a barrier against invertebrate entry, declined with time, due to the reduced stickiness and to the presence of lizard bodies and leaves acting as a bridge for invertebrates. To avoid these consequences, in this experiment copious sticky gel was placed around the inside perimeter of the tray and new gel was added after the first week so that the barrier of the gel lasted for the entire length of the experiment. In the experiment it was assumed that the sticky gel would not limit vertebrate access. In addition, with the sticky gel used on the inside periphery of the tray, there was a reduced risk of death to small crawling vertebrates passing by.

2) Vertebrate exclusion. Cages were specifically built to exclude vertebrate predators and placed on the EUs. The cages, with a 1cm^2 wire mesh, were buried deeper than 5 cm and many metal pegs were used to fix the cage to the ground. Furthermore, the distance between the mesh and the tray was 5 cm on the side and 10 cm from the top. All these precautions were necessary due to the extreme voracity of the predators in Kings Park. In fact, in the preliminary stages of a different experiment, set up to test germination but excluding seed predation, seeds were reached by the predator either through digging underneath the cage, by inserting body appendages through the mesh or by gnawing through the plastic trays or the metal fly screen. Similar exclusion precautions were also used at all the other locations where the experiment was undertaken even if such voracity had never been observed.

3) Complete exclusion treatment. This was used with the purpose of estimating the number of seeds lost in the absence of animals. Strong wind and raindrops were probably the main abiotic removal agents. Values of seed loss from this treatment if higher then 5% were subtracted from each of those other treatments with the EUs with sand. This treatment was undertaken in Bold Park in the burned area and in Kings Park. Values collected from the total exclusion treatment in the Bold Park burned area were subtracted from the EUs placed in this

area, while values collected in Kings Park were subtracted from the EUs placed in all other locations, as the vegetation structure present was similar in all other sites and locations.

4) The complete exclusion treatment with the seeds placed on a sod of soil. This was set up to estimate possible errors in seed scoring due to the presence of particles of litter, herbs and roots.

All the exclusion treatments were set up in Kings Park mainly in Winter for one year with the exception of some exclusion treatments set up in Bold Park in the burned area. Winter was chosen, as this was the season in which preliminary observations showed the highest levels of *Banksia* spp. seed predation.

Open treatments

5) This open treatment was the standard EU. Differences of seed loss between species and between the different locations were assessed using results from this treatment. Results were also used as a comparison with the other open treatments. Ten seeds were used for each species (as in Hulme 1998a and Hulme *et al.* 1999) in all the treatments, so that in each tray there was a total of 70 seeds. In other studies on post-dispersal seed predation, petri dishes were used as experimental units. The size of the petri dish was 9cm (Hulme 1998; Edwards and Crawley 1999) or 5 cm (Yates *et al.* 1994a; Auld and Denham 2001). This study did not use petri dishes in order to mimic, as closely as possible, the natural conditions of the ground surface. Seeds were displayed in a tray filled with local sand in order to simulate the environment on which the seeds would have fallen from the trees. In other studies that investigated more than one species at a time, only one species was usually placed in each experimental unit (Hulme 1998; Auld and Denham 2001; Figueroa *et al.* 2002); a minor number of studies displayed two or more seeds together (Hulme et al.et al.1999; Blaney et al.et al. 2001). In this study, with the seeds displayed all together, the predator, having encountered the EU, would have the opportunity to select the prey (seed) according to its foraging behaviour. Furthermore displaying all the species together reduced, by 1/7, the number of EUs spread in the field. The standard treatment was set up for two seasons and for two years.

To assess the values of predation/removal of all the four *Banksia* spp. present in Kings Park, in two different sites of the Park also the additional species *B. ilicifolia* and *B. grandis* were investigated using the EUa.

6) Density treatment 20 seeds. A double quantity of seeds for each species, was used in this treatment to be able to assess if the foraging behaviours of the predator could be related

to the density of the prey (seed). This treatment was set up for two seasons and one year.

7) Safe site treatment. A sod of soil was placed in the tray and the seeds were placed in it. Ten seeds were used for each species. The objective of this treatment was to assess if the presence of leaf litter and native ground vegetation could create sites where predation is reduced. A sod of soil, of an exact shape of the plastic tray, was excavated with a shovel and placed inside the tray, subsequently the tray was placed in the gap left from the excavating process. Sods, therefore excavated and placed in the trays were representative of the ground features present at each site. This treatment was set up for two seasons and one year.

4.4.2.2.4 Field arrangement and timing

Trials were set up in Winter and Summer in order to investigate any difference in the values of seed predation due to seasonal variations. The experiment was repeated for the standard treatment, for two years in order to determine the variation of seed predation between two different years. As in other similar experimental studies (Hulme 1998a; Hulme *et al.* 1999) treatments were replicated five times at each site. In order to avoid a dispenser, or contiguity, effect between trays the experimental units were placed at least 5 metres apart (Hulme 1998; Figueroa *et al.* 2002) and in random positions. Trays were not placed in the area of the seed shadow of investigated species; no care was taken to avoid contaminating the seed with ‘human odour’. However, olfactory traces, left after handling the seeds, would have been a potential deterrent rather than an encouragement to predation (Whelan *et al.* 1994). In all sites the experiment, using the standard treatment, started in Winter (July) 2000 and ended in Summer (January) 2002 with two recording periods (first week and third week) for each of the two seasons. The only exceptions were the new sites located in Bold Park where, due to the occurrence of a wildfire, three other sites were set up with increased distance from the unburned area. In these new sites, the experiment started in Summer 2001 and ended in Winter 2002.

The safe site treatment, had only one record (third week) for each of the two season (table 4.1).

The period of the post-dispersal experiments, locations and sites of the different treatments are shown in Table 4.1.

Table 4.1 Period of the experiments, locations and sites of the different treatments. s= number of sites.

Treatment/Location	Kings Park			Bold Park			Jandakot			Wanneroo		
	Winter	Summer	s	Winter	Summer	s	Winter	Summer	s	Winter	Summer	s
1 Invertebrate exclusion-sand	July 2000		3									
2 Vertebrate exclusion-sand	July 2000		3									
3 Total exclusion-sand	July 2000	January 2001	3									
3.1 Total exclusion-sand postfire				July 2001	December 2000	2						
4 Complete exclusion-sod	July 2000		3									
5 Open standard EU-sand interfire	July 2000&2001	January 2001&2002	5	July 2000&2001	January 2001&2002	2	July 2000&2001	January 2001&2002	2	July 2000&2001	January 2001&2002	2
5.1 Open standard EU-sand interfire with the 4 Banksia species	July 2000		2									
5.2 Open standard EU-sand postfire				July 2001&2002	December 2000&2001	2						
6 Open density-sand	July 2000	January 2001	5									
7 Open safe site-sod	July 2000	January 2001	5	July 2000	January 2001	2	July 2000	January 2001	2	July 2000	January 2001	2

Seed loss and removal In order to avoid an increase in invertebrate activity due to soil disturbance, the Greenslade (1973) protocol was used; seeds were placed in the EUs one week after the time of the tray installation and subsequent disturbance. Seed loss was scored twice during the length of the experiment. The first records were collected after the first week, at which point it was already clear that most of the predation occurs within this period (eg. Vaughton 1998). The second record was taken after twenty-one days as this is the length of time in which, under optimal conditions, *Banksia* seeds start to germinate. Other seed predation studies had a similar length of seed bait exposure (Marino *et al.* 1997; Wenny 2000).

Loss of seeds from the tray was scored. In the EUs with sand, the entire substratum was sieved to expose possible buried seed. Once the seeds were scored, after the first week, all the contents were replaced in the tray and then scored again at the third week. Seed scoring of the EUc with a sod had only one record at the end of the third week, as sieving would have destroyed the surface of the sod. Seeds with damaged embryos were classified as predated, but also included in the loss category. The number of predated seeds was obtained by reconstructing the seed from seed and seed-coat fragments. The reconstruction of seeds from the seed coat fragment is a certain indicator of the minimum number of seeds that were consumed at the site.

No attempt was made to investigate the specific identity of the predator but in the first week the sites in Kings Park were visited by the investigator twice a day, early morning and dusk, to determine whether most seed removal happened during the day or the night. Removal during the day is unlikely to be due to nocturnal predators such as rodents, while removal at night is unlikely to be attributed to diurnal predators such as birds.

Furthermore in Kings Park specific 'bait-devices' that would exclude birds were set up. Several banksias seeds were placed in a plastic pipe 30 cm long and of 8 cm diameter. Some pipes were laid horizontally on the ground while others were inserted vertically into the ground. It was assumed that only rodents could reach the seeds in these types of 'bait-devices'.

Comparisons between the values of the standard treatment and the other open treatments were only made between the sites that had all the different open treatments and only for that particular year. Comparisons within and between treatments were made both at a specific level, investigating the response of the species, and at a community level, investigating the response of all species together.

4.4.2.2.5 Post-fire post-dispersal predation

The experimental protocol was identical to the one used for the unburned sites. The standard experimental unit was used; EU field arrangement and timing were similar to experiments in the other locations and sites. A complete exclusion treatment was used to estimate seed loss in the absence of animals. The three post-fire sites were approximately positioned 0, 50 and 150 metres from the unburned bushland. Results were compared with the two sites located in two different unburned areas of Bold Park.

The experiment was set up in December 2000 (Summer) and repeated Winter 2001, Summer 2001 and Winter 2002. Data analysis was similar to that used for the unburned post-dispersal predation and comparisons were made between the results taken at the third week. The differences between the burned and unburned areas were seen both at community level: all the seven species together; and on a 'banksia level' with data of both the banksias together. In addition comparisons were made between data for years and seasons.

4.4.2.3 Data analysis

Collected data are summarized and displayed as bar charts with average and ± 1 S.E.

The form, distribution and homogeneity of the data did not allow for the use of parametric tests, so non-parametric statistical tests were used to assess differences between treatments and periods.

Paired comparisons: To test if observations were different, the Wilcoxon rank and the Sign tests were used; the null hypothesis of these tests is that difference of the medians is not significantly different from zero.

Unpaired comparison: The Mann-Whitney U test was used to test differences of observation taken from two groups. When there were more than two groups the Kruskal-Wallis test was used, in the later case the Mann-Whitney U test was used as the *post hoc* test. Both these non-parametric tests have a null hypothesis that the samples are taken from groups with the same median. All the outputs account for tied data.

4.4.3 Results

4.4.3.1 Exclusion treatments

1) **Invertebrate exclusion**. When access to seeds was designed to exclude only invertebrates, the *Banksia* spp. and *Dryandra sessilis* seeds were the only ones missing from

the trays. In Kings Park in Winter after the first week only the Proteaceae species were removed. At the third week the predation trend for the Proteaceae continued while approximately less than 7% of the seeds of the other species were absent. The difference between the first and the third week for small seeds could be due to the loss of part of the effectiveness of the gel barrier due to leaves, dead animals and sand that probably allowed some ground invertebrates to reach the seeds. Nevertheless the experiment showed clearly that if access to the seed source was limited to vertebrates only the Proteaceae seeds were removed (Fig. 4.9).

2) **Vertebrate exclusion**. With the access to the seeds designed to exclude only vertebrates, the *Banksia* seeds were the only ones that were not removed. All the other seeds were removed, including *Dryandra sessilis*. Seed removal started from the first week (Fig. 4.10)

3) **Total exclusion on sand**. The experiment in Kings Park showed that with the experimental unit designed to prevent access by any animal, none of the *Banksia* seed was removed and less then 4% of the other seeds were lost after three weeks (Fig. 4.11). The experiment in the burned area in Bold Park, in Summer, showed a greater loss of *A. fraseriana* (12%) than seeds of other species (Fig. 4.12).The high loss rate of *A. fraseriana* could be explained by the strength of the wind blowing in the burned area, as the morphology of the seed of *Allocasuarina,* with a relatively large wing, favours wind dispersal.

According to these results only the EUs located in the burned area in BP were adjusted for this abiotic loss.

4) **Total exclusion on sod sample**. At the third week, there was no seed removal of the *Banksia* and all others had a loss of less than 8%. Therefore data scored represent the real loss of seeds (Fig. 4.13).

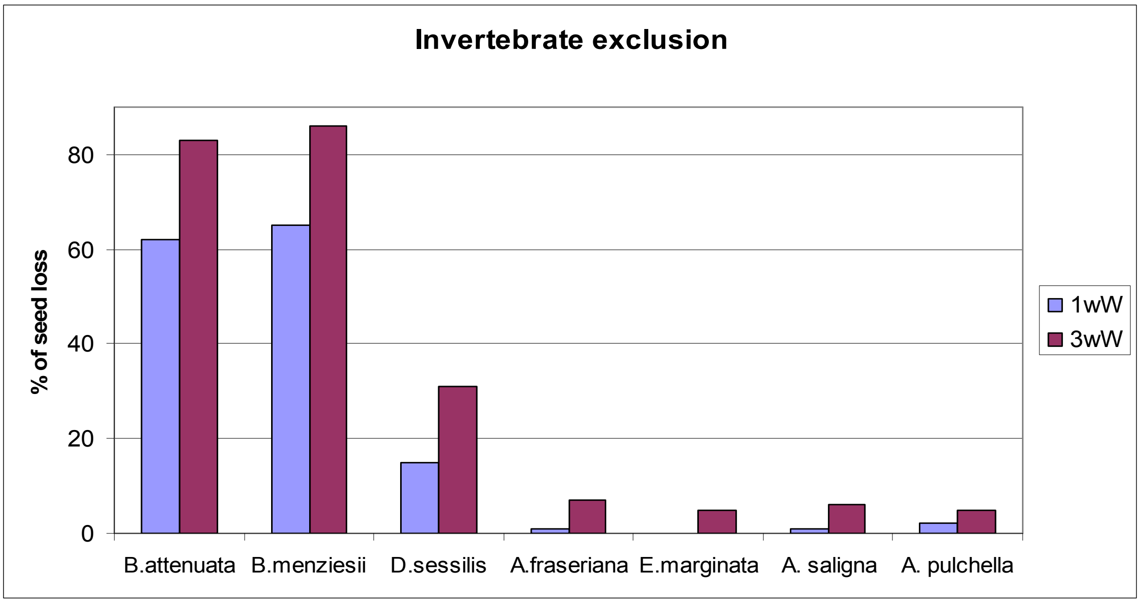

Fig. 4.9 Percentage of seed loss in invertebrate exclusion treatment for the seven investigated species. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter.

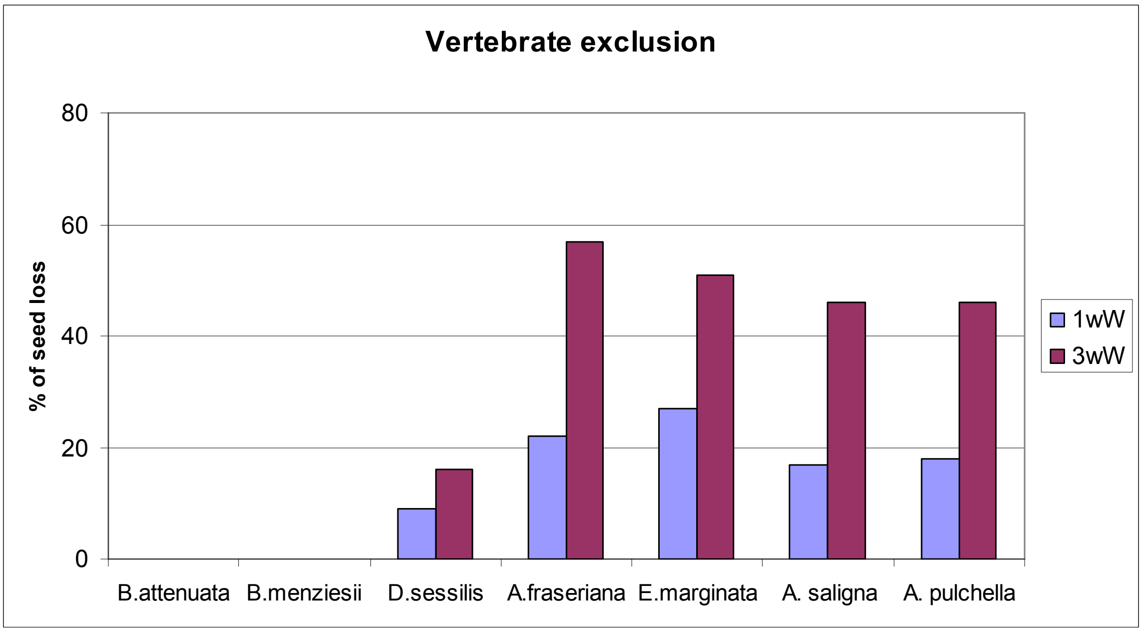

Fig. 4.10 Percentage of seed loss in vertebrate exclusion treatment for the seven investigated species. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter

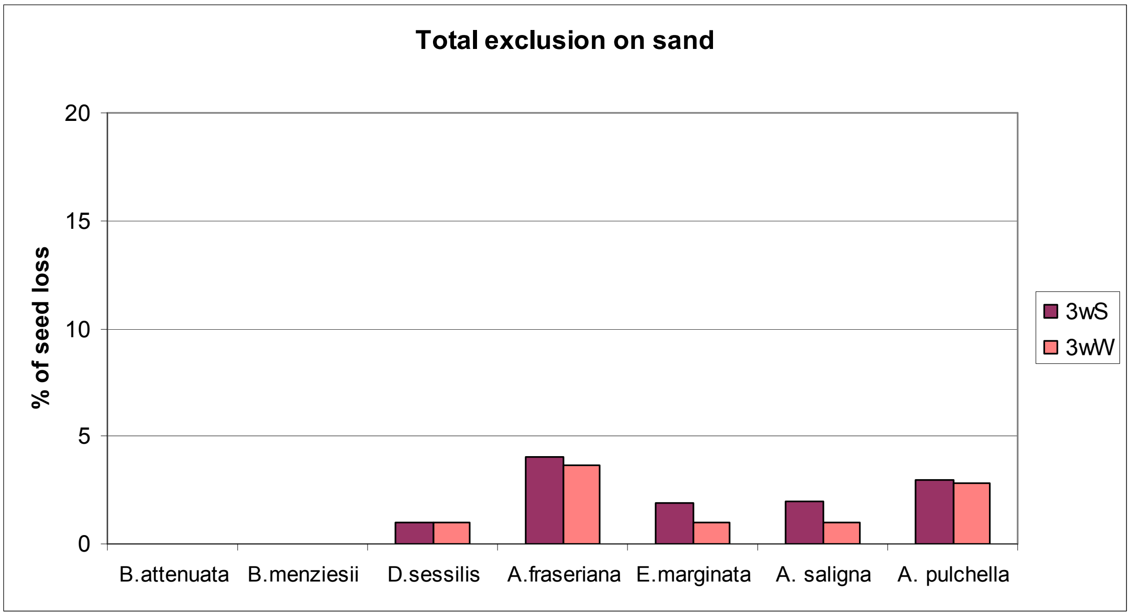

Fig. 4.11 Percentage of seed loss for total (invertebrate +vertebrate) exclusion treatment on sand-standard EUa- for the seven investigated species. 3w= Predation after the third week of exposure; W= in Winter; S= in Summer.

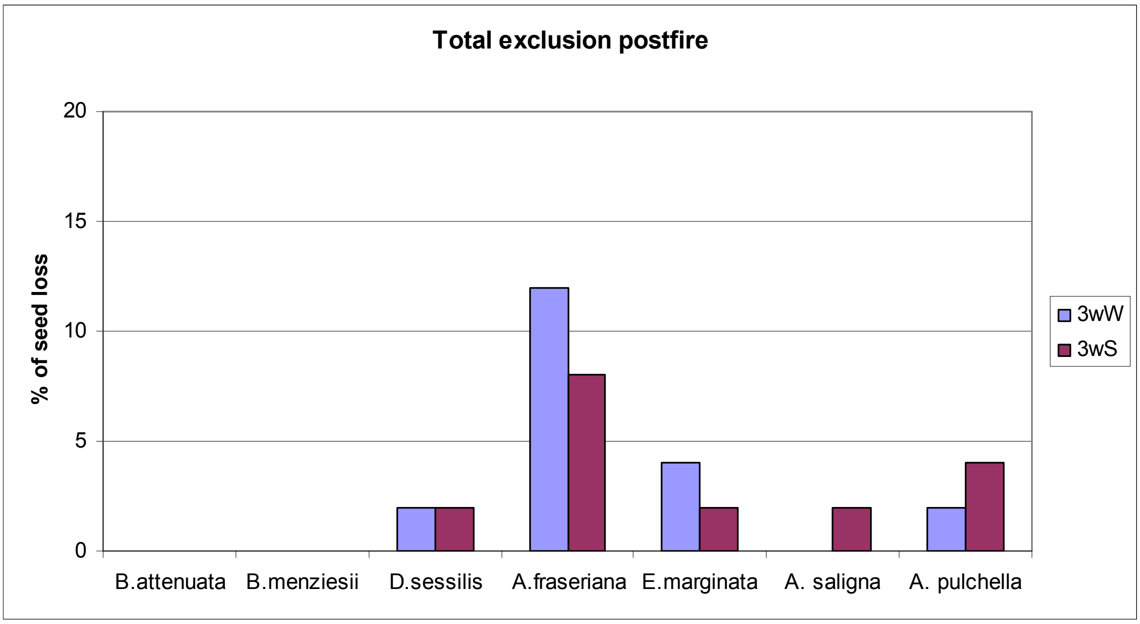

Fig. 4.12 Percentage of seed loss for total (invertebrate +vertebrate) exclusion treatment on sand in post-fire environment -standard EUa- for the seven investigated species. 3w= Predation after the third week of exposure; W= in Winter; S= in Summer.

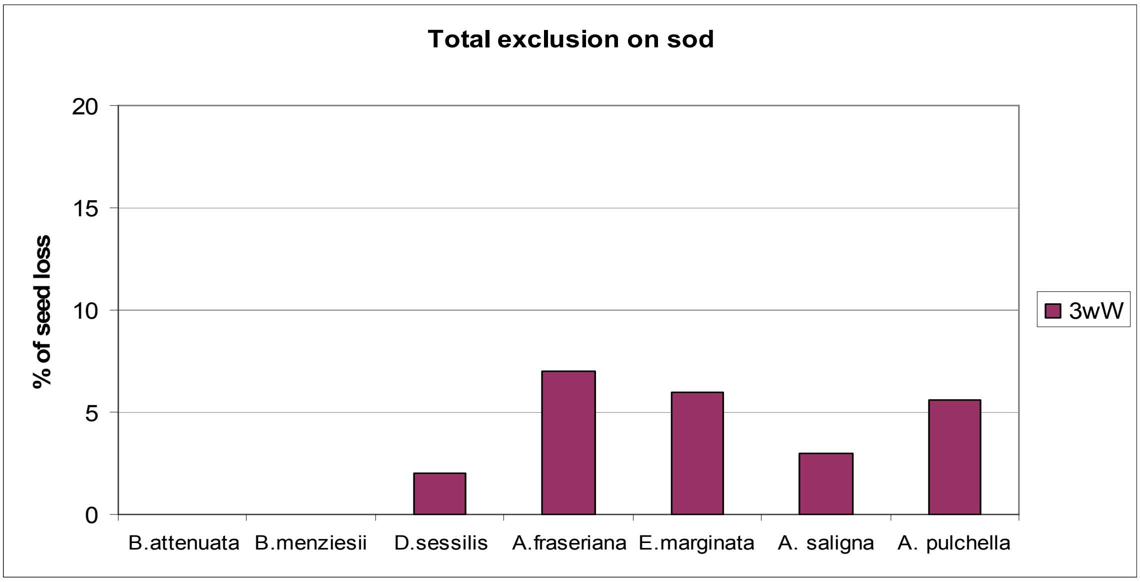

Fig. 4.13 Percentage of seed loss for total (invertebrate +vertebrate) exclusion treatment on sod-safe site EUc- for the seven investigated species. 3w= Predation after the third week of exposure; W= in Winter.

4.4.3.2 Inter-fire

4.5.3.2.1 Open treatments

Seed loss for *Banksia* spp. was significantly greater in winter than summer (P<0.001) (Figs. 4.14; 4.15). For this reason the analysis of results was broken down into Winter and Summer. Moreover, for some species such as *A. fraseriana*, *E. marginata*, *A. saligna* and *A. pulchella* for some recording period or season, in particular at the third week scoring in summer, the seed loss between the two years was statistically different (Fig. 4.16). However, at the community level (all the species together) there were no differences between years. Comparisons between the different species and the different locations (next in this chapter) were made combining values of the data collected over the two years keeping the two seasons separate.

Results of seed loss in Kings Park, after three weeks of exposure were:

5) **Standard treatment.** There was no statistical difference between the amount of seed lost for *B. attenuata and B. menziesii* in Winter or in Summer, both at the first and third week, between the two years (Fig. 4.16).

D. sessilis, A. saligna and *A. pulchella* had similar seed loss in Winter between the two years; seed loss in the second Winter was higher for *A. fraseriana* and lower for *E. marginata* compared to the first Winter. In Summer, by contrast, seed loss between years was similar only for *D. sessilis*; seed loss in the second Summer was lower for *A. fraseriana* and higher for *E. marginata* and the two *Acacia* species compared to the first Summer of scoring (Fig. 4.16).

Consistency of seed predation/removal between season:

Rates of loss between Summer and Winter were different between the *Banksia* spp. and the other investigated species (Figs. 4.16; 4.17). Removal of banksias seeds was higher in winter while for *A. fraseriana*, *E. marginata* and the two acacias species removal was higher in summer**.**

Values of seed predation/removal

Banksia spp.:

In Winter approximately 77% of the seeds of *Banksia* spp were removed from the tray compared to 20% in Summer (Fig. 4.17). Furthermore, when seeds from all the four species of *Banksia* were exposed to removal in two sites in Kings Park, loss of seeds was similar for all the species (Kruskal-Wallis test: H=0.64; DF=3, P=0.877) (Fig. 4.18) and in the two different sites of Kings Park (P= 0.675).

The additional record of the occurrence of seed husk and damaged seeds in the trays showed that in Winter, the season in which these records were taken, more than 75% of the *Banksia* spp. "lost" seeds were certainly predated (Fig. 4.19).

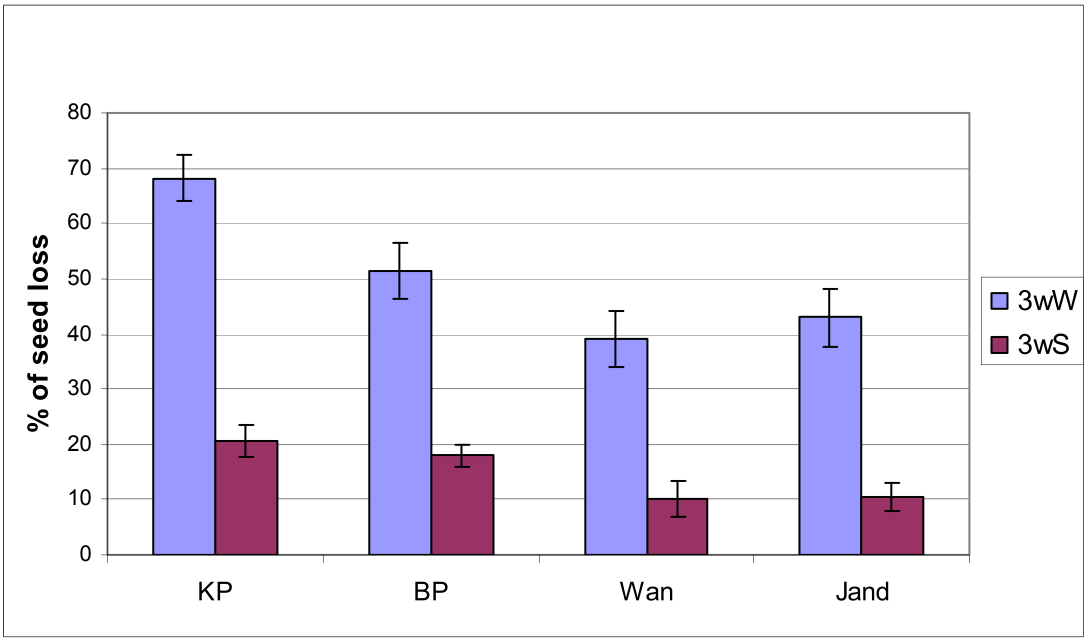

Fig. 4.14 Mean percentage of seed loss for *B. attenuata* in open treatment-standard Experimental Unit with 10 seeds in Kings Park.. 3w= Predation after the third week of exposure; W= in Winter; S= in Summer in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges Reserve (Rid).

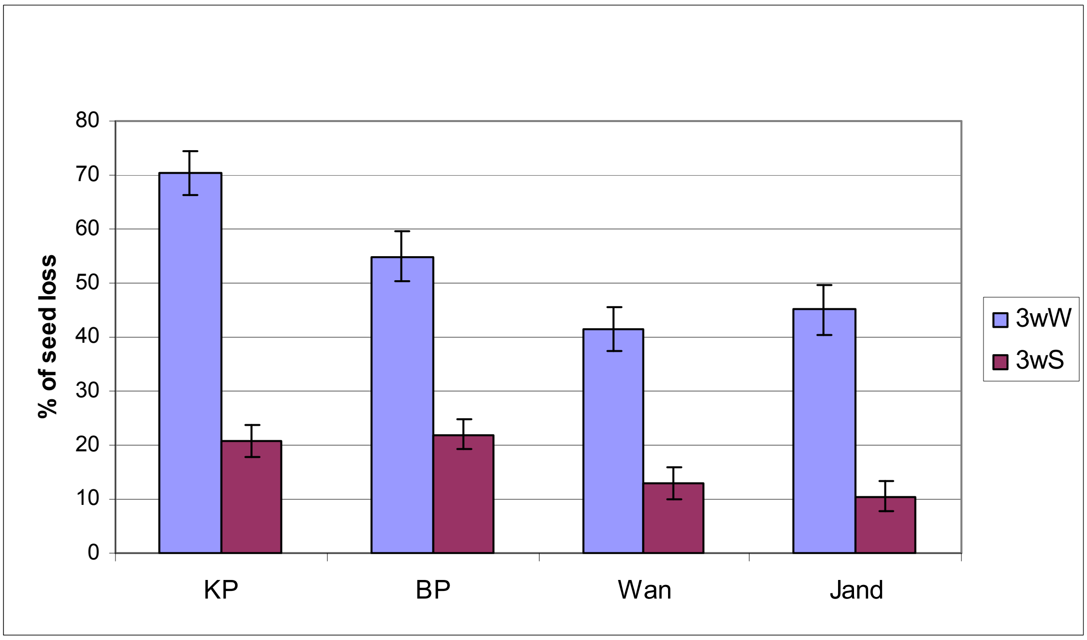

Fig. 4.15 Mean percentage of seed loss for *B. menziesii* in open treatment- standard Experimental Unit with 10 seeds in Kings Park.. 3w= Predation after the third week of exposure; W= in Winter; S= in Summer in Kings Park (KP), Bold Park (BP), Jandakot (Jand) and Ridges Reserve (Rid).

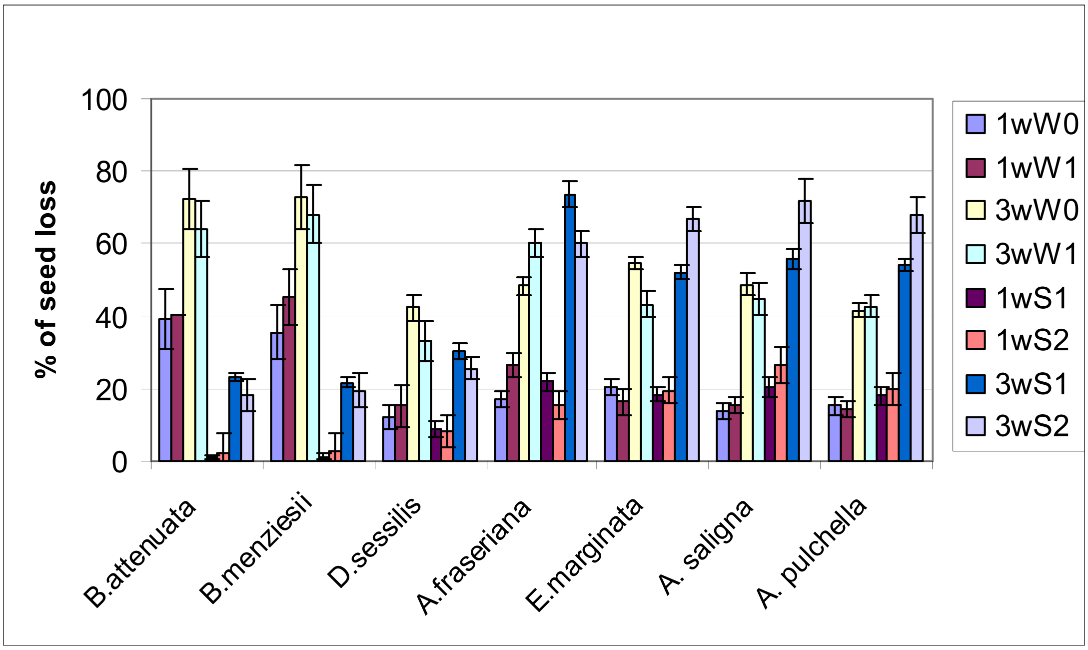

Fig. 4.16 Mean percentage of seed loss in open treatment on sand – standard Experimental Unit with 10 seeds in Kings Park. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer; 0= trial set up in 2000; 1= trial set up in 2001; 2= trial set up in 2002.

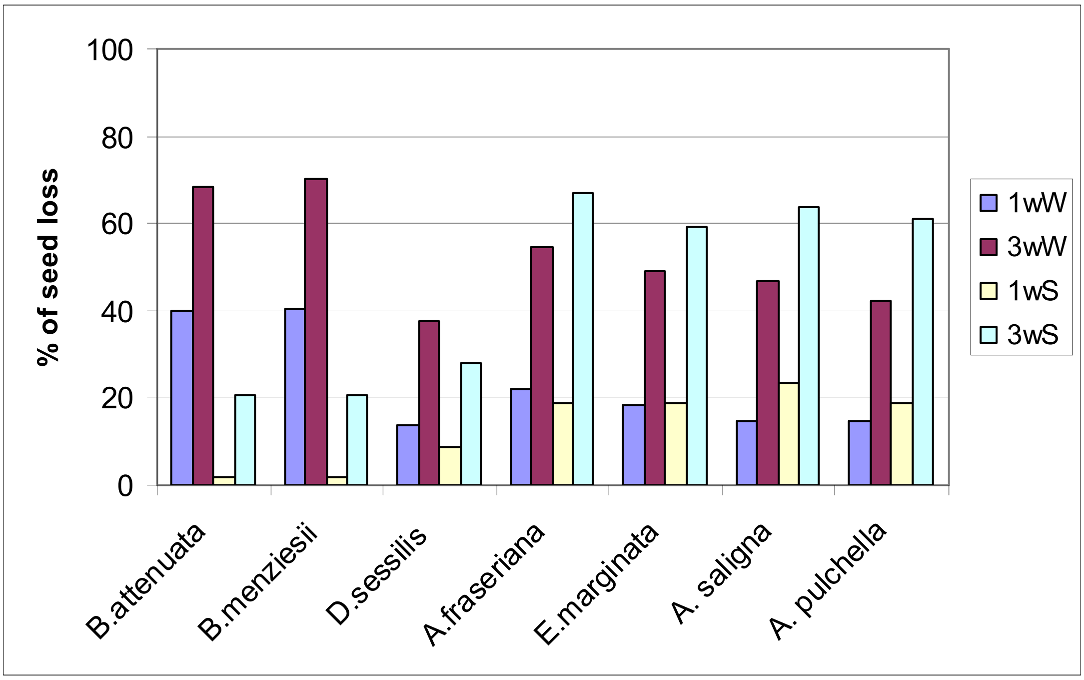

Fig. 4.17 Percentage of seed loss in open treatment on sand – standard Experimental Unit with 10 seeds in Kings Park. Results of the two year of survey combined together. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer.

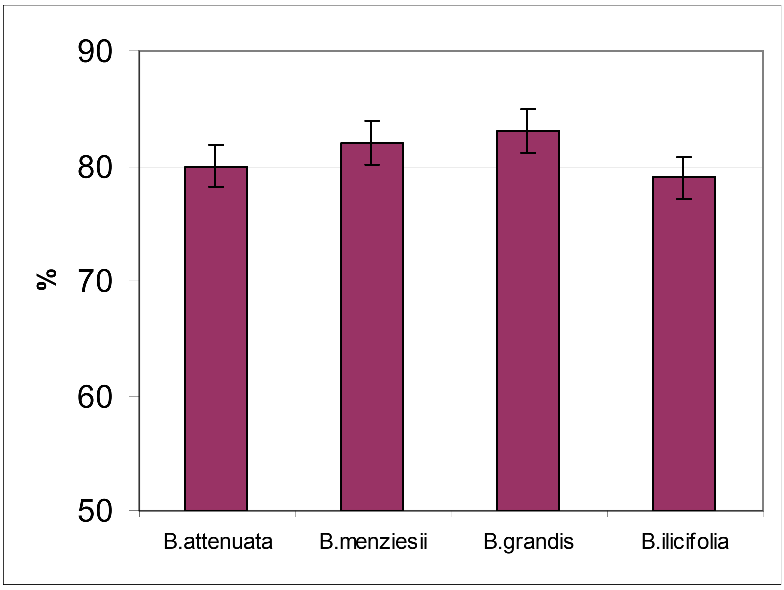

Fig. 4.18 Seed loss of the four *Banksia* spp. Records grouped together from two sites in Kings Park.

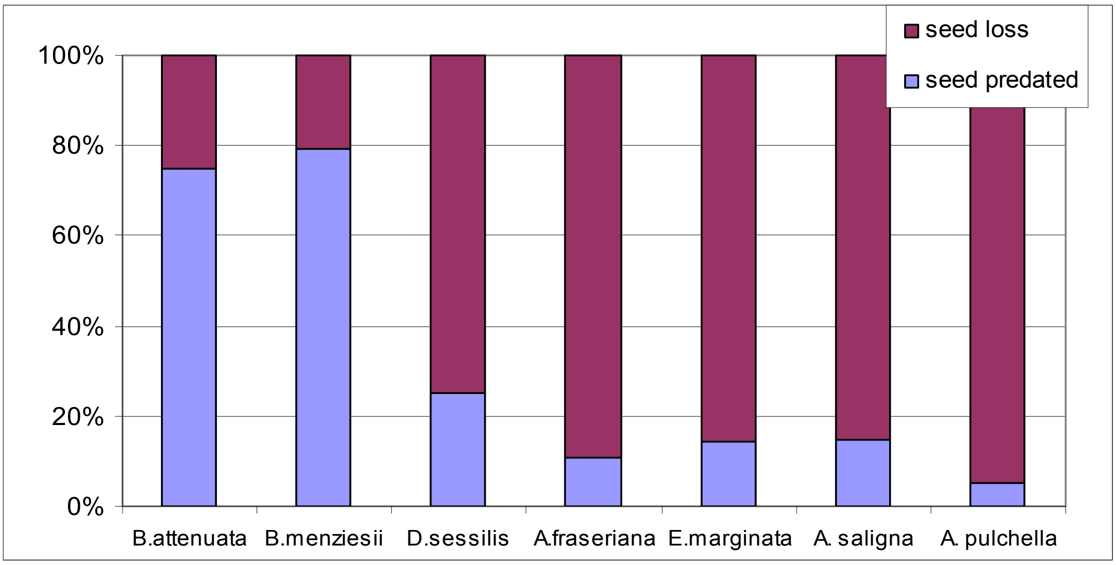

Fig. 4.19 Comparison between seed loss and seed predation for the seven investigated species during winter.

Community level Comparison between Summer and Winter for the other investigated species showed significantly higher predation in Summer ($P<0.001$), between the first and the third week ($P<0.0001$) but not between years ($P=0.941$). In particular in Winter removal at the third week showed no difference between years ($P=0.501$) but did show a difference between species ($P<0.001$); in Summer the pattern in removal was similar to Winter. In particular no differences between years ($P=0.41$) and significant differences between species ($P<0.0001$). *Dryandra sessilis* loss varied between approximately 33% in Winter and 43% in Summer, while seed loss for the other species varied between 41% and 60% in Winter and 52% and 73% in Summer. More than 20% of the *D. sessilis* seeds were predated (Figs. 4.16; 4.17). For the other species less than 15% of seeds showed evidence of seed coat fragments and consequently of effective consumption of the seed at the site (Fig. 4.19).

Most of the *Banksia* spp. seed removal and predation happened during the night (as it was recorded in the early morning scoring) and not during the day. Furthermore the seed were removed also from the specific 'bait-devices'. Consequently it was believed that rodents were the main animals responsible for the post-dispersal seed predation of *Banksia* seeds.

4.5.3.2.2 Comparison of seed predation between the different locations on the Swan Coastal Plain

In Winter in Kings Park the seed loss of the two *Banksia* spp. was significantly higher ($P<0.001$ for both the species) compared to the other locations (Figs. 4.17 , 4.21 , 4.23, 4.25). Though also in the Bold Park inter-fire sites there was also greater predation (approximately 50% of *Banksia* seed available in the EU) compared to the two semi-pristine sites of Jandakot R.P., and the Ridges S.F.. Statistically greater seed loss was also shown for *A. saligna* ($P<0.05$) and *A. pulchella* ($P<0.05$) from Bold Park (Figs. 4.20, 4.21) and Jandakot R.P. (Figs. 4.22; 4.23) than in Kings Park (Figs. 4.16, 4.17) or in the Ridges S.F. (Figs. 4.24, 4.25).

In Summer, differences were statistically significant for *A. saligna* ($P<0.01$) which showed (Figs. 4.22, 4.23) higher values of seed loss in Jandakot R.P. compared with all the other sites in the other locations (Figs. 4.16, 4.17, 4.20, 4.21, 4.24, 4.25). Across all locations there was a difference in community seed removal with higher values in Summer compared to Winter ($P<0.001$) (these values were driven by the small seeded species but there were no differences in community seed removal between the locations - $P=0.264$).

Considering data at a geographical level (all the locations together) there was a difference in removal between species (P<0.0001), with less removal of Proteaceae compared to the other taxa.

Heavy post-dispersal seed predation of *Banksia* spp. occurred in the Kings Park bushland, and to a lesser extent in Bold Park, in the Winter. All other dominant species tested in the experiment suffered greater seed removal in Summer. In all other selected locations post-dispersal seed predation for the *Banksia* spp. and seed removal of the other investigated species also occurred, however the level of *Banksi*a seed predation was much higher in Kings Park than in the other locations.

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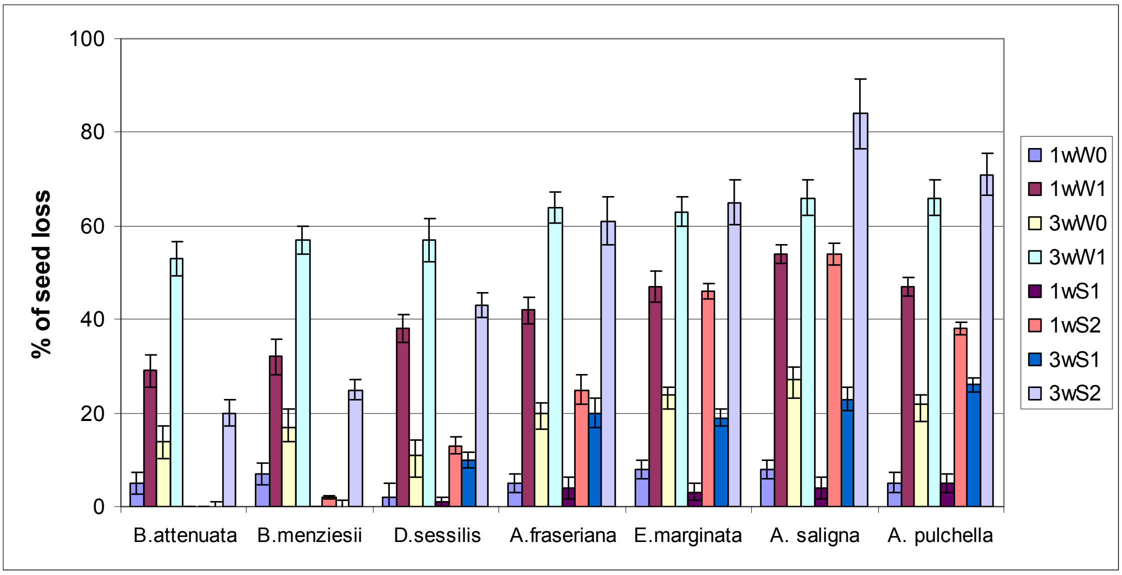


Fig. 4.20 Mean percentage of seed loss in open treatment on sand - standard Experimental Unit with 10 seeds for each species for the seven investigated species in Bold Park. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in Summer; 0= trial set up in 2000; 1= trial set up in 2001; 2= trial set up in 2002.

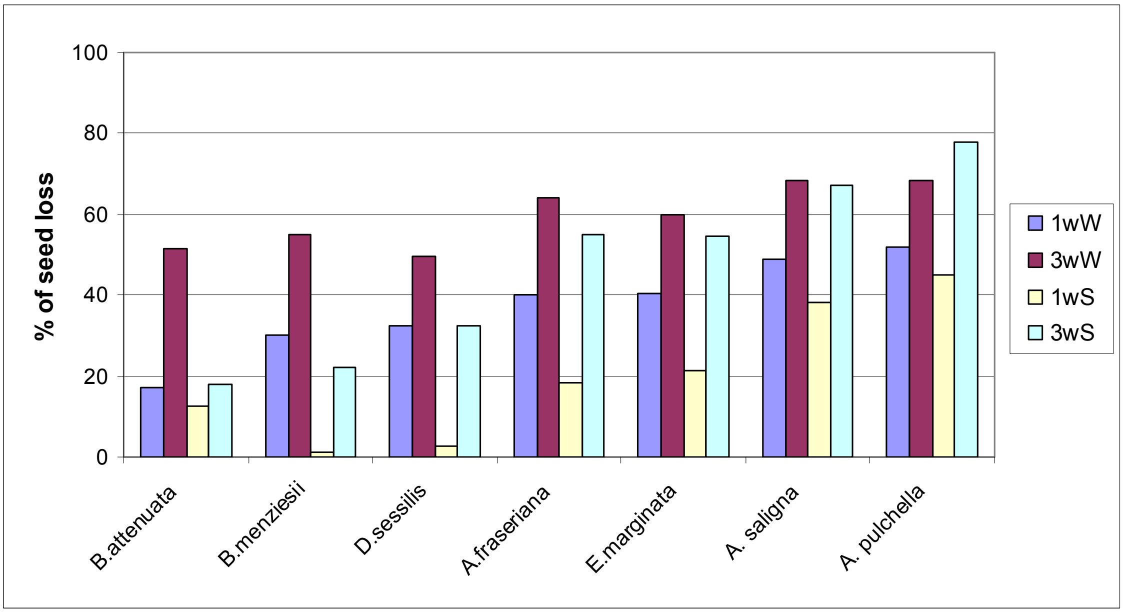


Fig. 4.21 Percentage of seed loss in open treatment on sand - standard Experimental Unit with 10 seeds for each species in Bold Park. Results of the two year of survey combined together. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in Summer.

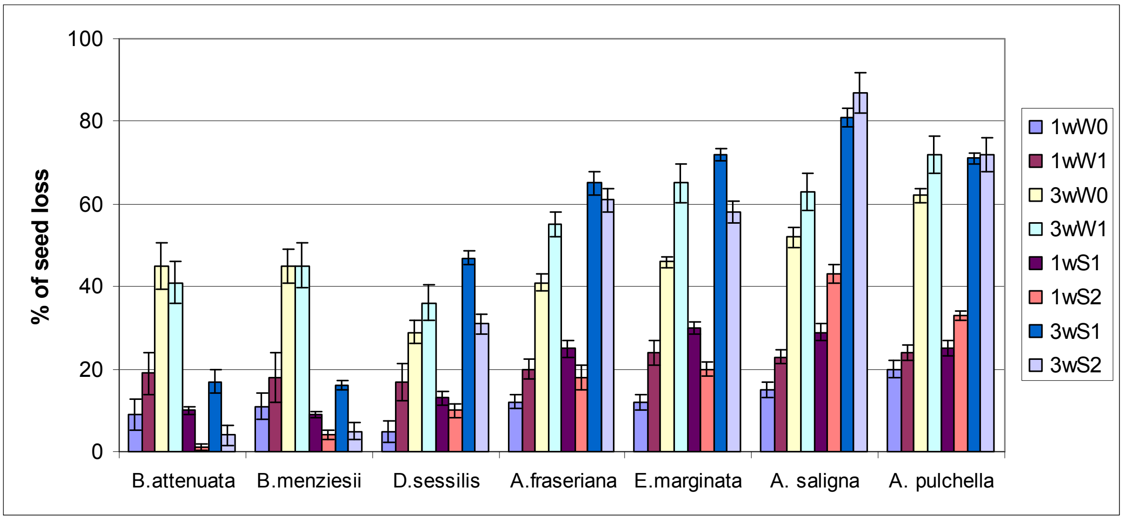


Fig. 4.22 Mean percentage of seed loss in open treatment on sand - standard Experimental Unit with 10 seeds for each species for the seven investigated species in Jandakot R.P.. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in Summer; 0= trial set up in 2000; 1= trial set up in 2001; 2= trial set up in 2002.

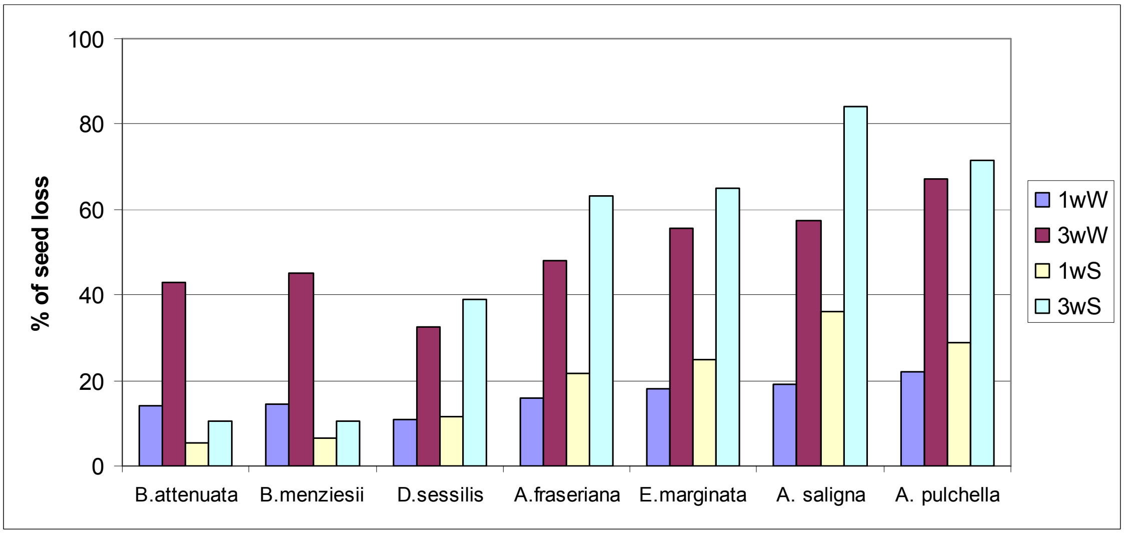


Fig. 4.23 Percentage of seed loss in open treatment on sand - standard Experimental Unit with 10 seeds for each species in Jandakot R.P.. Results of the two year of survey combined together. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer.

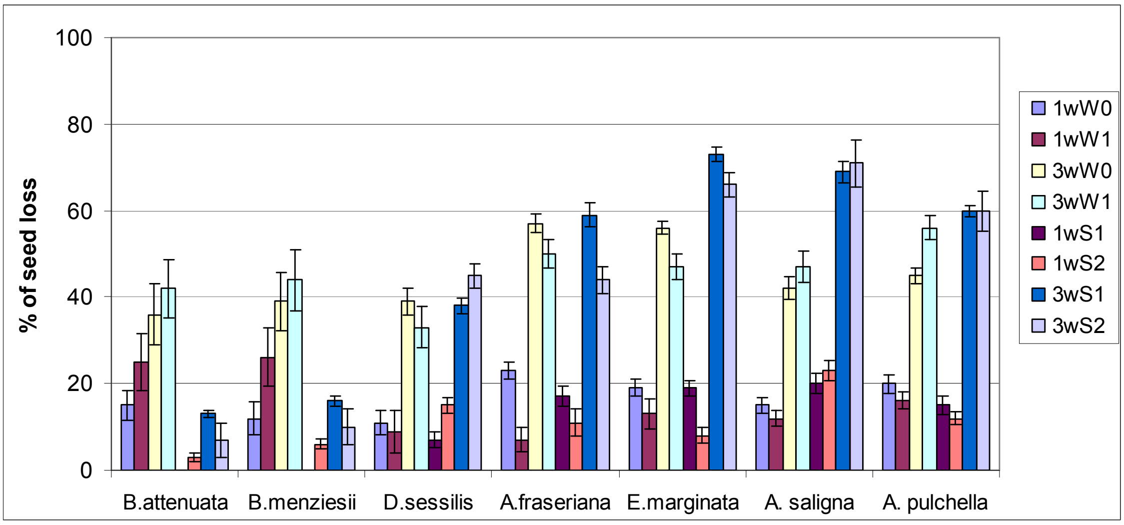


Fig. 4.24 Mean percentage of seed loss in open treatment on sand - standard Experimental Unit with 10 seeds for each species for the seven investigated species in the Ridges S.F.. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer; 0= trial set up in 2000; 1= trial set up in 2001; 2= trial set up in 2002.

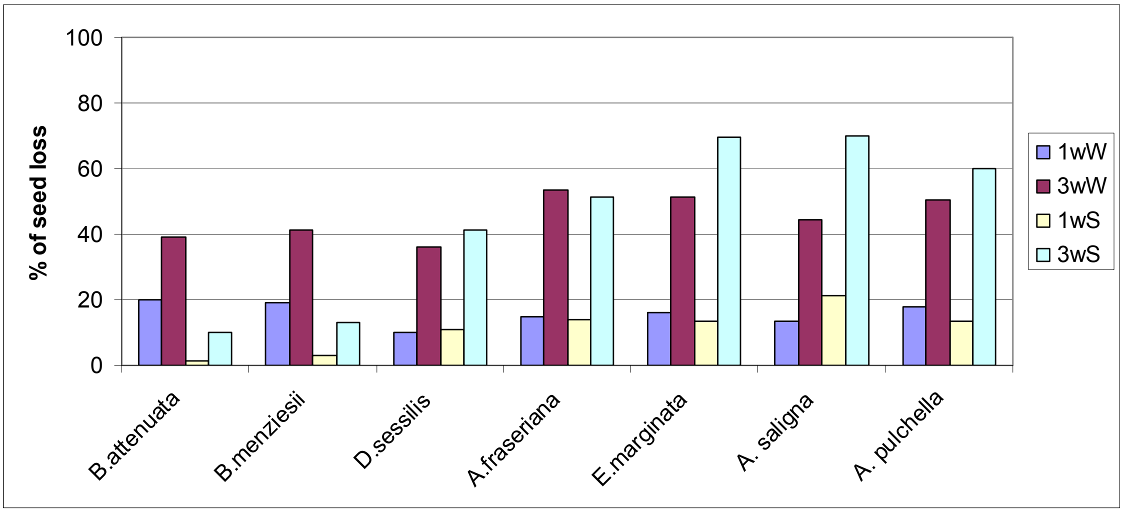


Fig. 4.25 Percentage of seed loss in open treatment on sand - standard Experimental Unit with 10 seeds for each species in the Ridges S.F.. Results of the two year of survey combined together. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer.

6) **Density treatment.** Comparing the proportion of seed loss between treatment 5, (EUa with 10 seeds for each species on sand substratum), and 6, (EUb with 20 seeds for each species on sand substratum), it was shown that there was no density dependence of seed loss for *B. attenuata* or *B. menziesii* in either seasons. In particular in Kings Park rodents predated all the *Banksia* seeds if the EU was found. The small seeded species, especially in Summer, showed a larger percentage of seed loss than in winter and there was a negative trend in the density treatment compared to the open treatment with 10 seeds (Fig. 4.26) where a smaller proportion of seeds was removed from EUs with more seeds.

On a community basis there was a highly significant difference (P<0.001) between the percentage of seed removed from trays with 10 seeds compared to trays with 20 seeds (Figs. 4.26, 4.27; 4.28; 4.29) across all locations

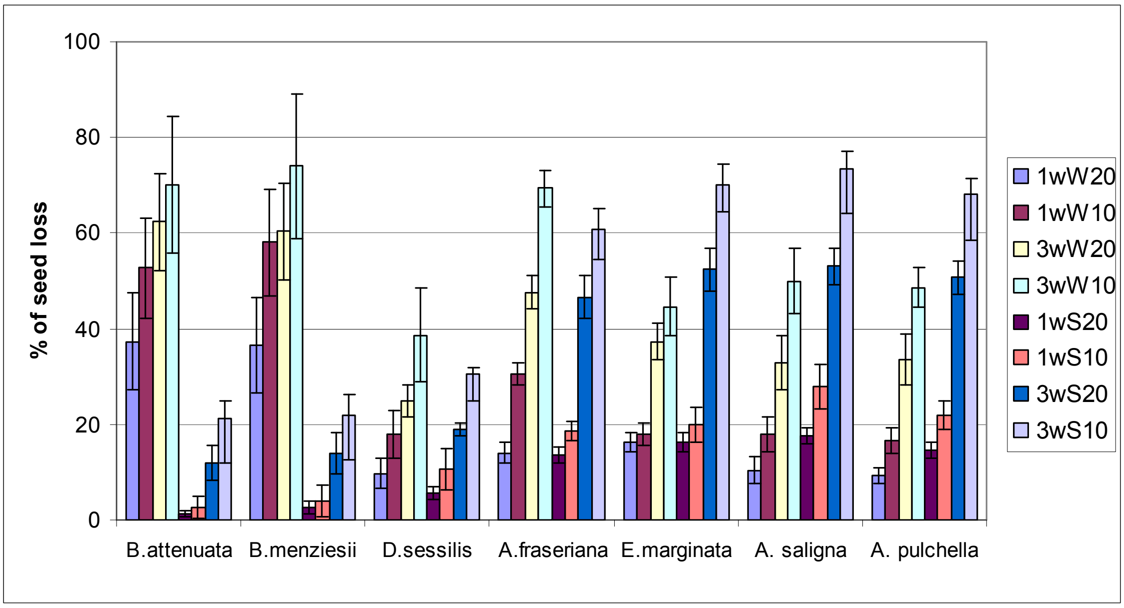


Fig. 4.26 Mean percentage of seed loss in the density treatment on sand - Experimental Unit with 20 seeds for each species in Kings Park, for the seven investigated species. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer; 10, 20 = number of seed used for each species;

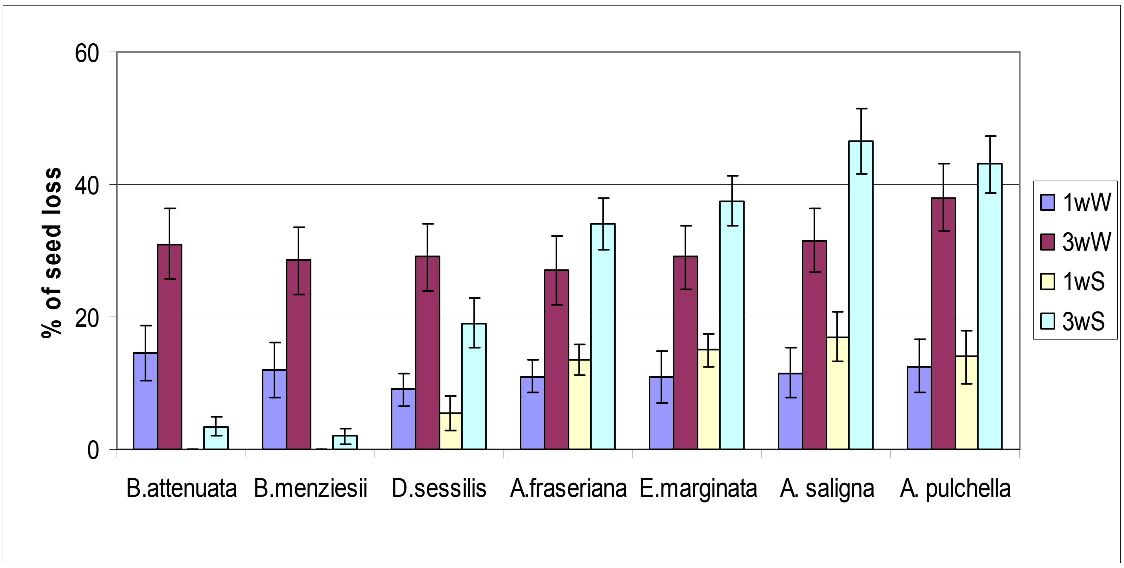


Fig. 4.27 Mean percentage of seed loss in the density treatment on sand - Experimental Unit with 20 seeds for each species for the seven investigated species in Bold Park. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer.

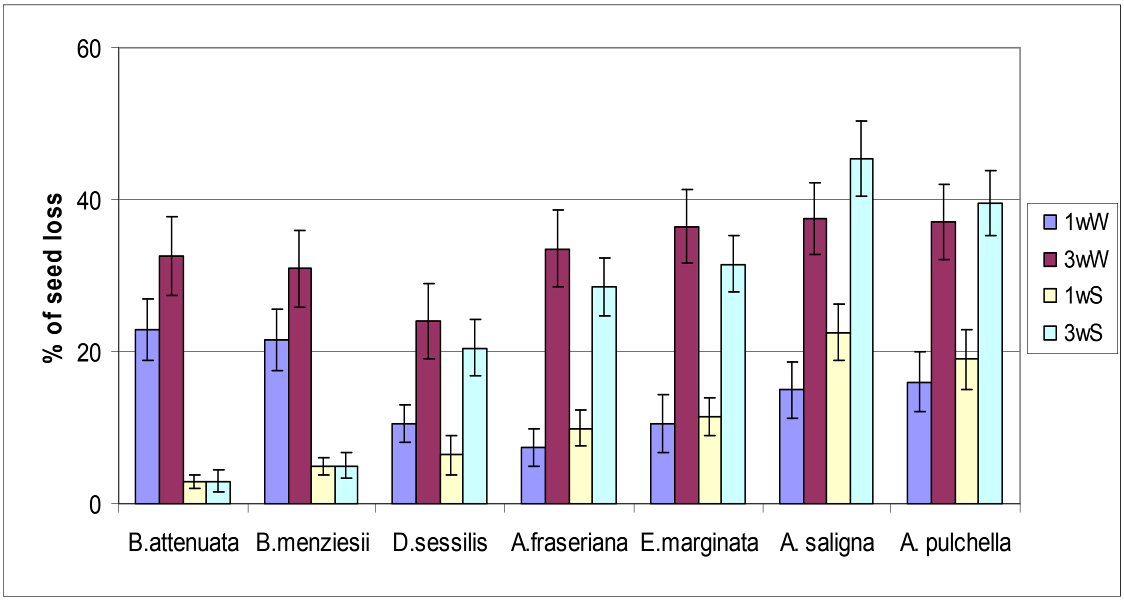


Fig. 4.28 Mean percentage of seed loss in the density treatment on sand - Experimental Unit with 20 seeds for each species for the seven investigated species in Jandakot R.P..1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer.

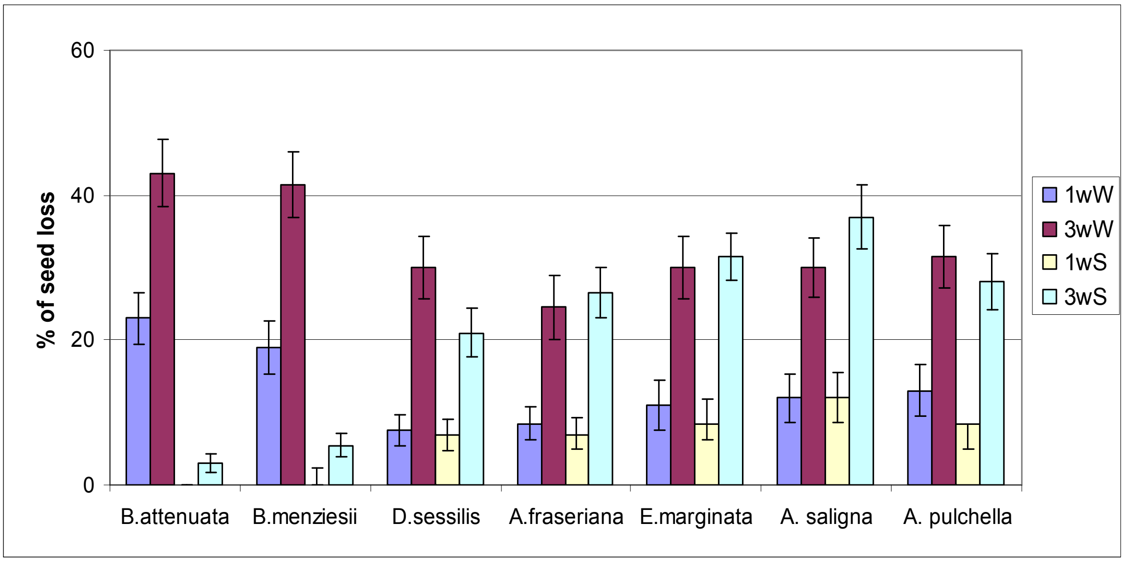


Fig. 4.29 Mean percentage of seed loss in the density treatment on sand - Experimental Unit with 20 seeds for each species for the seven investigated species in the Ridges S.F.. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in summer.

7) **Safe site treatment**. Comparing seed loss after three weeks between treatment 5, (EUa with 10 seeds of each species on a sand substratum), and 7, (EUc with 10 seeds of each species on a sod of soil substratum), it was shown that generally the presence of sod in the EU reduced the seed loss for all the species. For the Proteaceae, in Kings Park, predation was reduced to approximately half, while for the other species, it was reduced by approximately one-third. In particular in Winter, all the species showed a significant difference. In contrast, in Summer the *Banksia* spp. showed no significant difference while for all the other species there was a major difference between the two treatments. However, in Kings Park, the level of *Banksia* seed predation in Summer was low for both the treatments (Fig. 4.30).

At a community level, in Kings Park, presence of sod statistically reduced the amount of seed removal (P<0.001) in both the seasons (Fig. 4.30). At a geographical level (all the locations together) a similar trend was displayed (Figs. 4.30, 4.31; 4.32; 4.33).

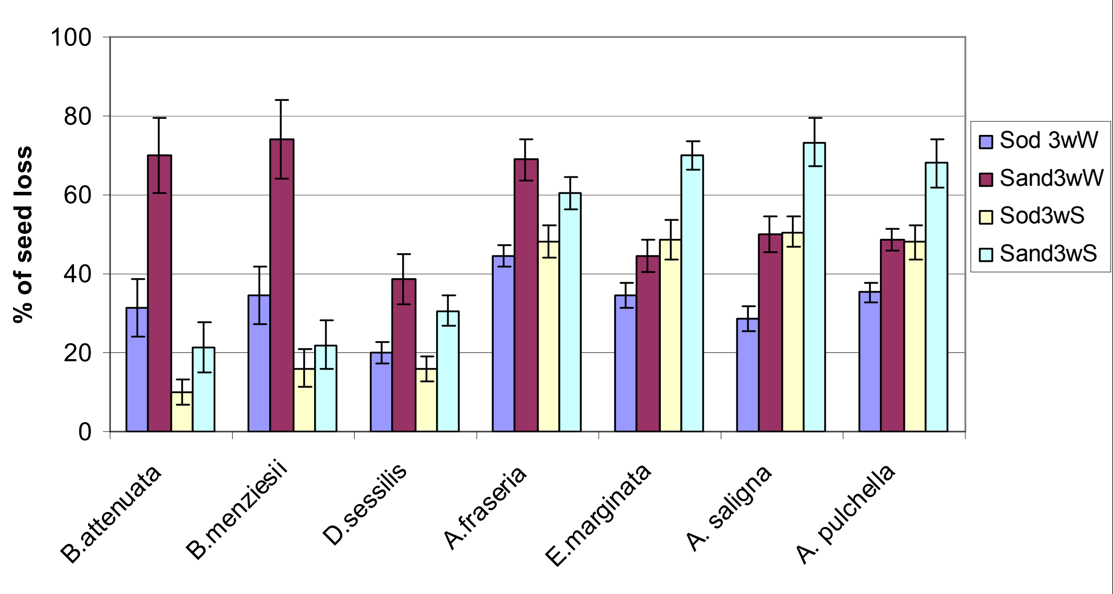


Fig. 4.30 Mean percentage of seed loss in the safe site treatment on sod - Experimental Unit with 10 seeds for each species and comparison with the open treatment on sand,- standard Experimental Unit with 10 seeds for each species- for the seven investigated species in Kings Park. 3w= Predation after the third week of exposure; W= in winter; S= in Summer; Sod= sod of soil used for the treatment; sand= sand used for the treatment.

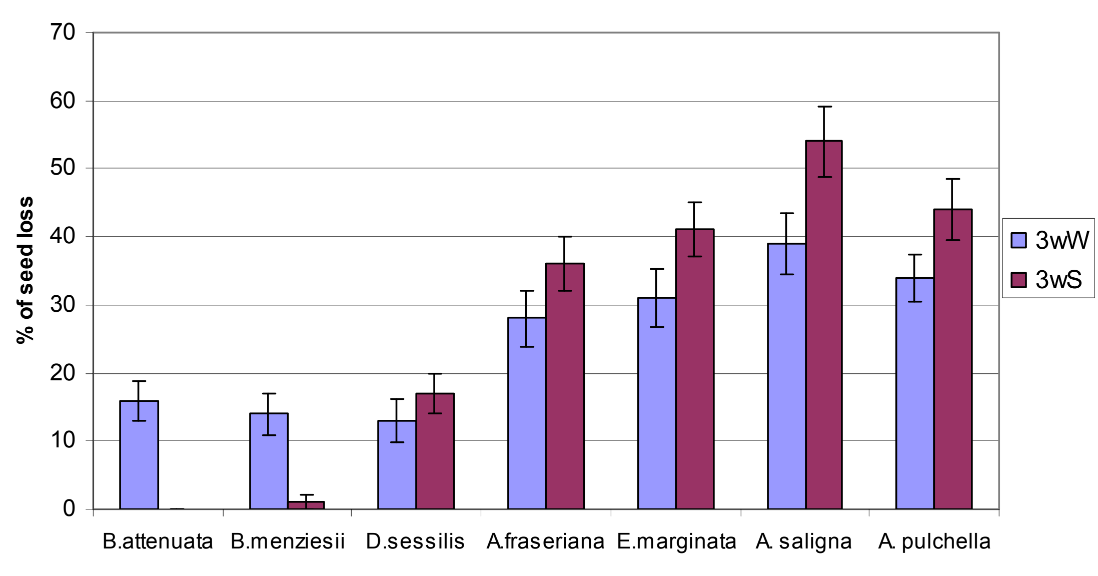


Fig. 4.31 Mean percentage of seed loss in the safe site treatment- Experimental Unit with 10 seeds for each species for the seven investigated species in Bold Park. 3w= Predation after the third week of exposure; W= in winter; S= in Summer.

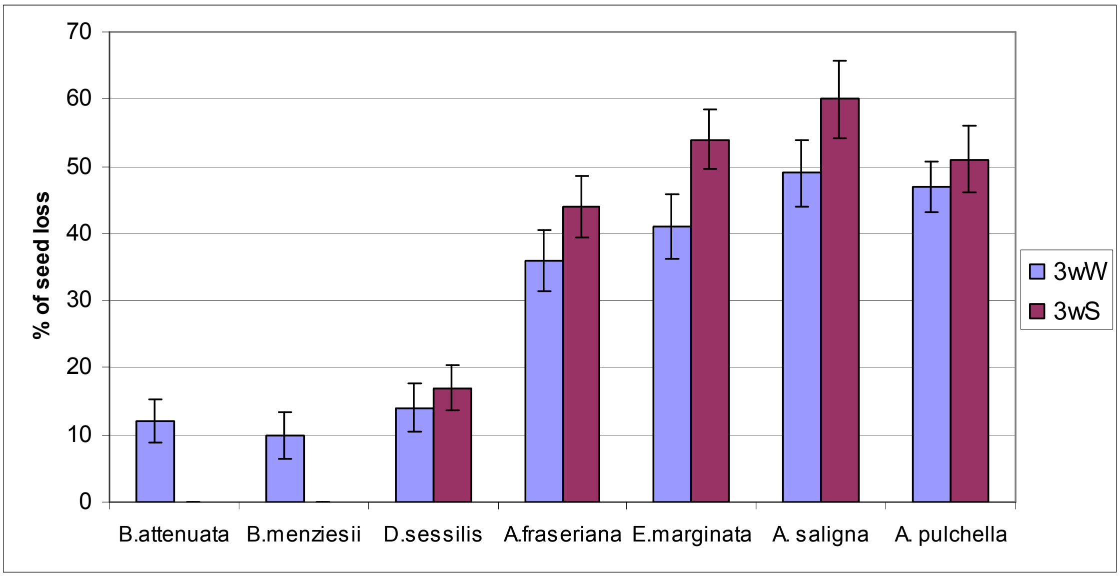


Fig. 4.32 Mean percentage of seed loss in the safe site treatment - Experimental Unit with 10 seeds for each species for the seven investigated species in Jandakot R.P. 3w= Predation after the third week of exposure; W= in winter; S= in Summer.

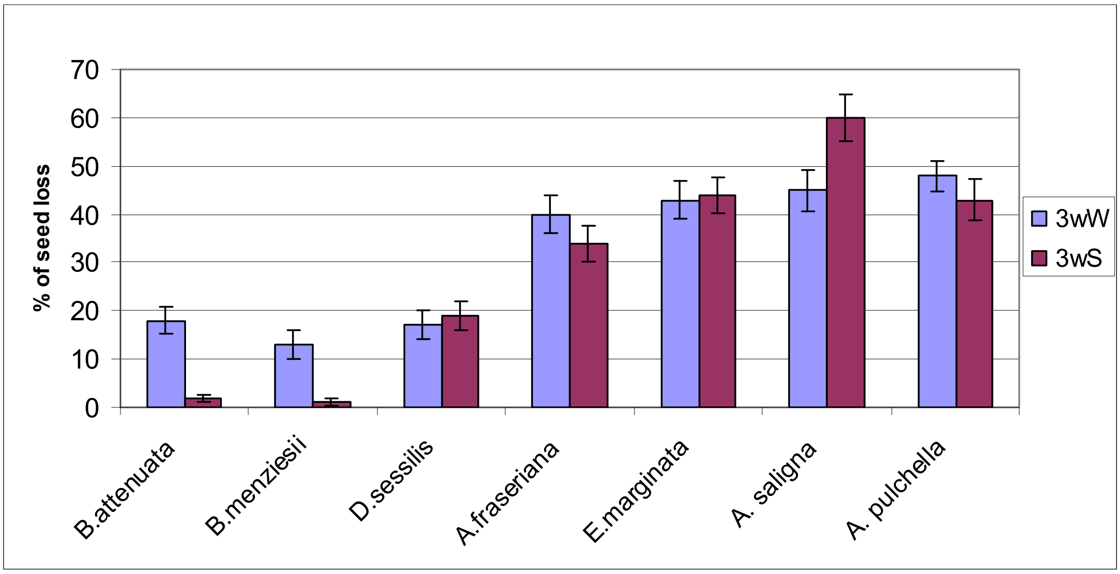


Fig. 4.33 Mean percentage of seed loss in the safe site treatment - Experimental Unit with 10 seeds for each species for the seven investigated species in the Ridges S.F.. 3w= Predation after the third week of exposure; W= in winter; S= in Summer.

4.4.3.3 Post-fire

As stated in the previous results, the total exclusion treatment on sand in post-fire conditions showed that after three weeks, in Winter, *A. fraseriana* had 12% of the seed missing from the trays, while in the same period of time all the other selected species had less than 4% of the seed missing (Fig. 4.12); data on *A. fraseriana* seed removal were consequently adjusted taking into account this seed loss.

In Bold Park seed predation/removal occurred at all the post-fire sites in the two years of the study (Figs. 4.34; 4.35). Predation was higher for all species in unburned sites than in burnt sites ($P<0.001$) and was greater for smaller seeded species than for banksias ($P<0.001$). However there was a difference in the values of removal at the burned sites. The five different sites in Bold Park used for the seed predation investigation (two in the unburned area and three in the burned area) showed, differences between the median values of total removal/predation of the *Banksia* seeds (Kruskal-Wallis test DF=4 $P<0.001$) with unburned sites being more predated (Figs. 4.36; 4.37).

Seed removal was greater in the second year after fire for all the species in the burnt sites (Fig. 4.34). Removal of *Banksia* seeds was greater in Winter than in Summer ($P<0.05$), while for the small seeded species removal was greater in Summer (Fig. 4.35) following the same trend detected in the interfire period. For the investigated *Banksia*, in winter, there was a significant difference ($P<0.01$), in seed loss, between sites in the first year after fire (between burned and unburned sites). In the second year after the fire, this difference was smaller but still significant ($P<0.05$).

Both in the first and second year, the site nearer the unburned area had greater predation. In particular predation decreased with the distance from the unburned area.

In the two years after the fire, seed predation/removal however was still lower compared to the sites in Bold Park not recently exposed to fire.

Percentage of seed loss in burned area in relation to the distance to the unberned areas (Figs 4.36; 4.37) showed interesting results, in particular for the *Banksia* specis (Fig. 4.36). Predation was higher in the second year, compared to the first year of the experiment and at the third week, compared to the first one. Predation was much higher in winter compared to summer.

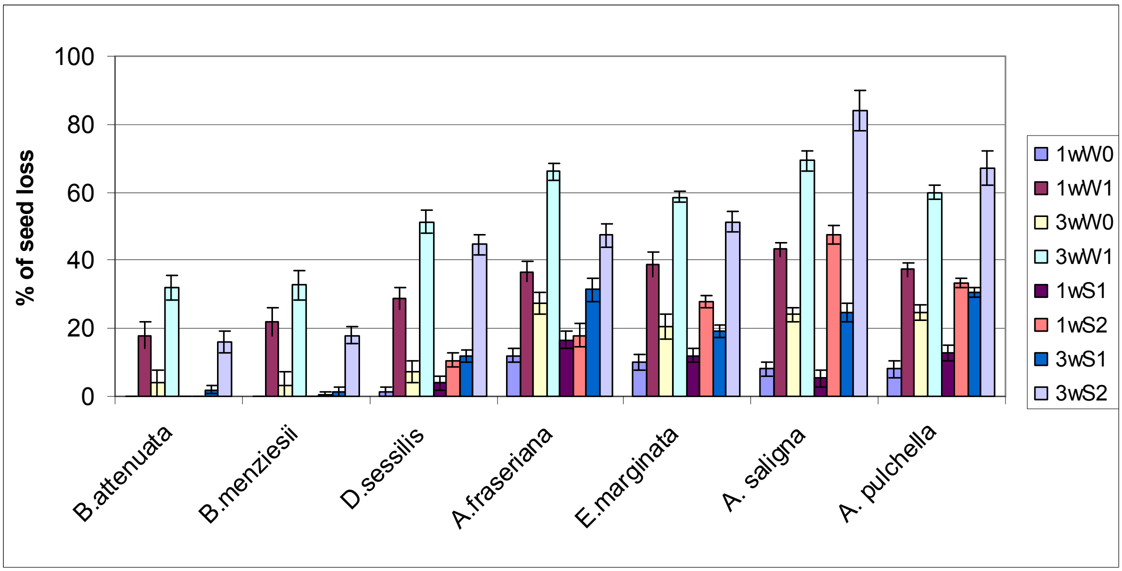


Fig. 4.34 Mean percentage of seed loss in open treatment on sand in post-fire conditions - standard Experimental Unit with 10 seeds for the seven investigated species in Bold Park. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in Summer; 0= trial set up in 2000; 1= trial set up in 2001; 2= trial set up in 2002.

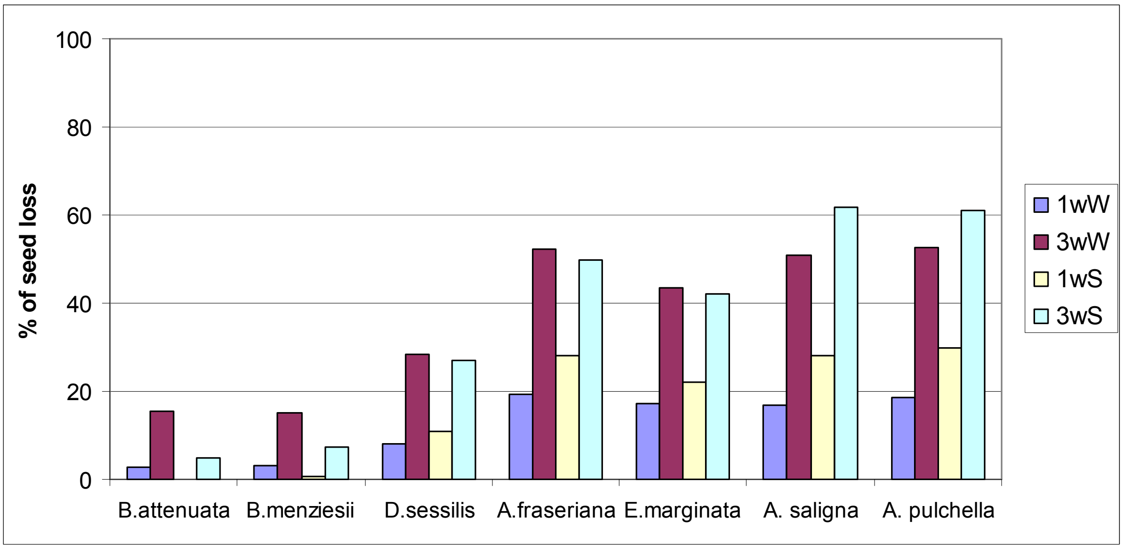


Fig. 4.35 Percentage of seed loss in open treatment on sand in post-fire conditions - standard Experimental Unit with 10 seeds in Bold Park. Results of the two year of survey combined together. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in Summer.

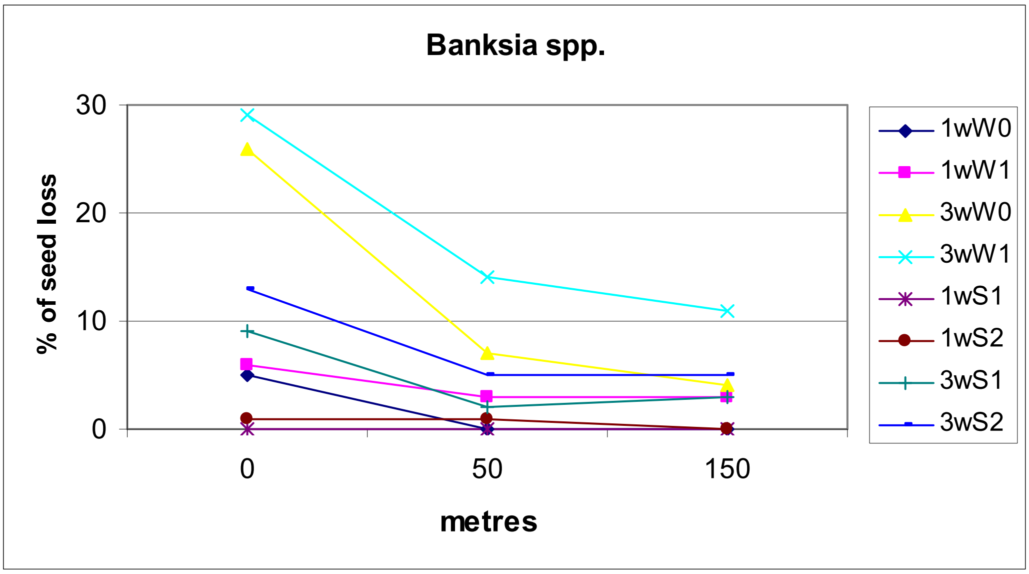
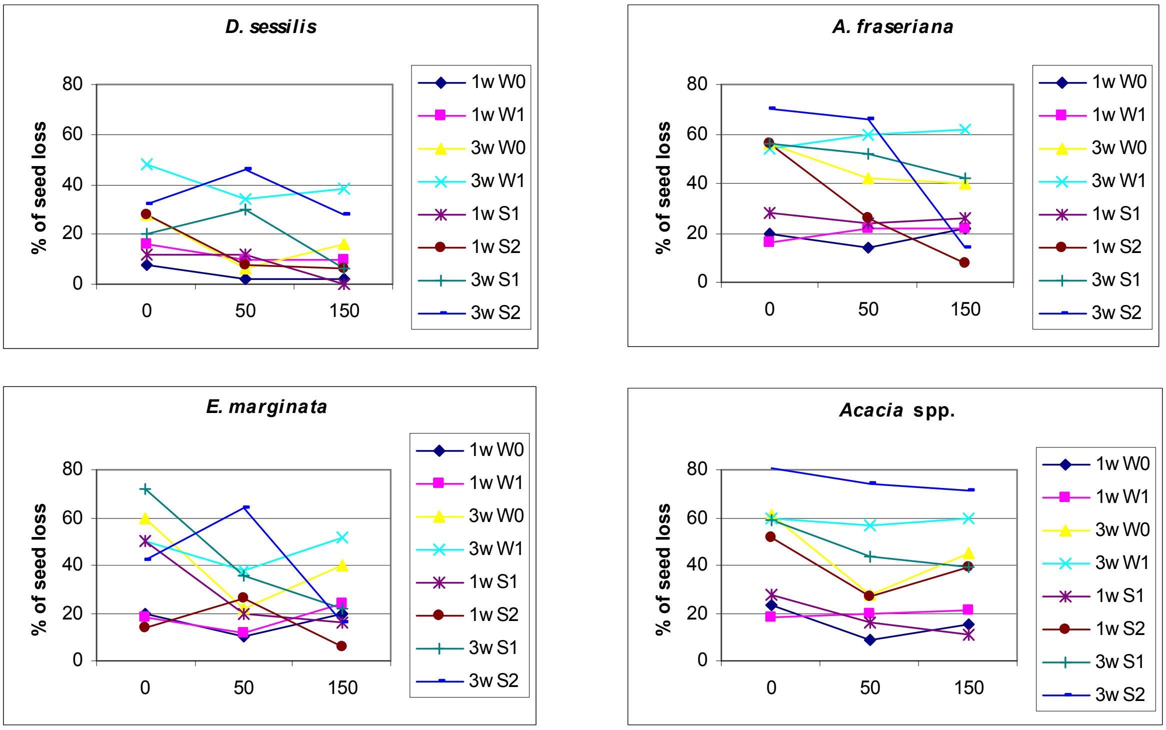


Fig. 4.36 Percentage of seed loss in post-fire conditions against distance from the unburned area for *Banksia* spp..1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in Summer; 0= trial set up in 2000; 1= trial set up in 2001; 2= trial set up in 2002. Trial set up in Bold Park.



Figs. 4.37 Percentage of seed loss in post-fire conditions against distance from the unburned area for the investigated species. 1w= Predation after the first week of exposure; 3w= Predation after the third week of exposure; W= in winter; S= in Summer; 0= trial set up in 2000; 1= trial set up in 2001; 2= trial set up in 2002. Trial set up in Bold Park.

4.5 GENERAL DISCUSSION

4.5.1 Pre-dispersal predation

Animal use of food resources can be divided into functional and numerical responses (Krebs 2008). Food specialists tend to have a numerical response, exploiting a resource intensively when it is abundant but possibly switching to other food resources when a particular type is less abundant, if they can switch resources. If they are unable to switch to another food (eg. insect seed predators obligate on a particular species) they will suffer population decline. This leads to heterogeneous seed loss in both time and space and it is a lack of knowledge about the life cycles and variability of predator behaviours that is the main difficulty in assessing the extent of seed loss between and within plant species (Van be Berg 1980; New 1983; Auld 1986).

In this thesis the results may represent an underestimation of the real impact of seed pre-dispersal predation as only the status of the follicles was recorded; no ovule abortion values due to predation were assessed. Furthermore no exclusion experiment was undertaken to properly estimate the role of predators. However the seasonal monitoring of the inflorescence/infructescences and the scoring of fruit removal helped to identify the origin of possible seed death and to indicate the magnitude of predation, as well as allowing comparisons between the different locations.

Predispersal seed predation is generally due to invertebrates that mostly develop inside the seeds/fruits (Moles et al. 2003). Invertebrate pre-dispersal predation (lepidopteran and curculionid larvae) in the Perth area has been reported as quite severe for *B. attenuata* with seeds consumed in 58% of first year follicles but less so for *B. menzeisii* where only 11% of follicles had seeds eaten (Scott 1982). This is the reverse of results from Mt Adams (330 km to the north of Perth) where Cowling and Lamont (1987) found 13% of *B. attenuata* and 54% of *B. menzeisii* follicles were attacked by insects but that attacks were not limited to only the first year infructescences. It is in a nearby location that *B. tricuspis* infructescences were attacked by cockatoos selectively seeking invertebrate larvae (Lamont *et al.* 1988). In another study, White-tailed black cockatoos devoured seed-eating weevils from *Banksia attenuata*. The birds tended to attack trees with larger numbers of infructescences. In addition, the proportion of infructescences containing weevils was greater in those that the cockatoos attacked than in those they did not. However if the weevils were absent the birds still destroyed follicles (Scott and Black 1981). In the seeder species *B. baxteri, B. speciosa* and *B. coccinea* in southern Western Australia insect larvae destroyed a mean of 18-40% of seeds per species (Witowski *et al*. 1991). In this present study pre-dispersal predation was patchy, being limited to only half of the selected locations of this study and unlike the previous studies birds are likely to be mainly responsible.

The relative importance of invertebrate versus vertebrate pre-dispersal predation is not entirely clear. However in Bold Park and Jandakot R.P. the results of both the *in situ* and *ex situ* studies clearly showed that pre-dispersal predation does not play a significant role in diminishing the amount of canopy-stored seed. Low levels of predation were recorded both from invertebrate and vertebrate predation. In the Jandakot region, Carnaby's Black-Cockatoo is known to be moderately common in pairs and small flocks, occasionally seen in larger flocks and very rarely seen in larger aggregations (Johnstone 2004), however they do not seem to attack banksia fruit in the area.

A number of conifer species have similar seeding behaviour to *B. attenuata* and *B. menzeisii* in the Perth area. Cross bills and squirrels remove *Pinus sylvestris* seeds before they are shed and cross bills, unlike squirrels, show a numerical response, particularly in relation to mast coning of the trees. Importantly squirrels seemed to be resident in the pine forest and would remove a high proportion of cones in non-mast years while cross bills seemed to focus on the pines in years of high cone abundance. The behaviour of the main pre-dispersal consumer of banksia seeds in this study – black cockatoos show similar behaviour to cross bills in that they can easily switch food sources. Cockatoos utlise a wide range of plants for seed (Saunders 1980; Johnstone and Kirkby 1999) and this is facilitated by the abundance of serotinous species in Australian forests – a contrast with the northern hemisphere. Pines are currently an important food source for black cockatoos but the birds continue to also utilse natural vegetation as well feeding on seeds of Proteaceae, *Eucalyptus calophylla* and *Pinus* spp. (Saunders 1980).

In Kings Park and Ridges S.F. high levels of pre-dispersal predation were observed. Short-Billed Black cockatoos (*Calyptorhynchus funereus latirostris*) have often been sighted in the Ridges S.F. and Kings Park feeding on *Banksia* infructescences. However feeding patterns have not been geographically studied yet. These White-tailed Black cockatoos occur in the in the Perth area, generally extending to the north. An influential factor related to the different predation levels in the four areas is the proximity of the sites to plantations of the introduced

Pinus pinaster. Saunders (1980) reported movement of black cockatoos from inland Western Australian locations to the Wanneroo area (where Ridges State Forest is located) in the non-breeding season from summer through to early winter where they fed in pine plantations and to a lesser extent in native bush. In fact, the Swan Coastal Plain is recognised as a particularly important non-breeding foraging
area for the cockatoos, where they often feed in *Banksia* woodlands and *Pinus* plantations (Saunders 1980, 1990) with large flocks (several hundreds) frequenting the Yanchep (neaby the Ridges State Forest) region (Saunders 1980). The pine plantations in the north of the Perth region (Gnangara, Pinjar and Yanchep plantations) have been recognised as an important food resource for Carnaby's Black-Cockatoo for over 70 years (Saunders 1974; Valentine and Stock 2008).

Near Kings Park there are small areas of pines in reserves but there are no pine plantations close to the study sites in Bold Park or Jandakot Regional Park. There is insufficient information to determine why cockatoos feed on different plant species but pine seed is certainly a favourite food. There may be aspects of numerical response where the birds move to native species if the pine resource is depleted but switching may also be related to the birds maintaining a varied diet, as birds in large plantations still foraged on native species (Saunders 1980) even when it is hard to see that the pine resource was exhausted. On the infertile soil of South Western Australia *Banksia* seeds possess high energy and mineral content. While this energy is obtained at the expenses of the time required to remove the seed from the follicle, *Banksia* seeds still provide a high food value per handling time for the white tailed black cockatoo (Cooper et al. 2000).

There were vertebrate attacks on many of the follicles on the attached infructescence and on most 'cones' on the ground. It is expected that trees with high levels of vertebrate attack on infructescences will also have high concentration of 'cones' fallen under the canopy as the two measures are likely associated. In Kings Park and in the Ridges S.F. the 'cones' attacked by birds showed a higher number of follicles compared to unmolested 'cones', this could be due to the choice of the bird to attack a more appetising 'cone' or to the higher likelihood that a heavy 'cone' will fall under attack. The difference in level of pre-dispersal predation cannot be explained by the varying levels of urbanization of the sites. Ridges S.F. and Jandakot R.P. are relatively pristine while Kings Park and Bold Park are urban remnants.

4.5.2 Post-dispersal predation

Post dispersal seed predation is considered to be influential in the regeneration and reproductive ecology of trees (Hulme and Hunt 1999). Seed size and predator size influence seed removal. Small seeds can be better handled by small predators such as ants, so a large seed has more chance to escape predation from invertebrates (Janzen 1969). Conversely small seeds can better escape predation from larger predators such as rodents.

The trend of the effect of predation on population density is difficult to measure in terms of magnitude due to variability across years. Although seed loss may be high on average, it is also highly variable and a proportion of seeds that were removed may not have been effective in recruiting seedlings to the community even if they survive predation. For example predation could reduce the density of seed that would not in any case have found a suitable site or would have died from competition with other seedlings (Andersen 1989).

Seed predation, however, like any other factor causing consistent loss of ‘young’ will normally influence population ecology, consistent loss could have an impact on plant abundance, distribution and competitive status (Fenner and Thompson 2005; Lopez and Terborgh2007).

This study clearly shows that post dispersal seed predation does occur on the Swan Coastal Plain (SCP) in banksia-dominated vegetation, that both vertebrates and invertebrates are involved but that there is variation in relation to predator type, seed species, time of the year, location and whether fire had influenced the vegetation recently. It has been proposed that in Australia mammals are not important seed predators in arid or mediterranean-type vegetation (Westoby 1991). However at the SCP sites in this study mammals were likely the only post dispersal predators of banksia seeds while *Dryandra sessilis* was removed by both vertebrates and invertebrates. This accords with other evidence from Western Australia from the jarrah forest (Abbott 1985a) and for eastern states *Grevillea* species (Vaughton 1998; Auld and Denham 1999).

In Kings Park the specific identity of the mammal predator(s) is lacking but the fact that most removal of *Banksia* seeds was overnight and seed testa material was left in the EUs does support the suggestion that rats or mice may have been the predators, as has been shown in other areas (Auld 1995; Auld and Denham 1999; Blaney 2001; Ruscoe et al. 2005). Both feral rats and mice have been recorded in Kings Park (How and Dell 2000). The fact that the seeds were dismembered on site also means that seeds were not being hoarded and so could not later become available for germination.

Removal of *Banksia* seeds was much higher in Winter than in Summer at all sites and was much higher in Kings Park than at other locations. This contrasted with the general results for the other species, which are mainly taken by invertebrates. Removal was mostly higher in Summer but with consistent values of predation also in Winter and there was little difference between sites. However there were some localised significantly higher removals in Summer (*A. saligna* – Jandakot; *D. sessilis* – Jandakot, Ridges S. F.) and Winter (*Acacia* spp. – Bold Park, Jandakot). Higher Summer predation corroborates previous studies in Kings Park where removal of *A. fraseriana*, *D. sessilis* and *E. marginata* was also higher in Summer and was attributed to invertebrates (McAlinden 1999, Ruthrof 2001).

It is not entirely clear why *Banksia* seed predation occurred most severely in winter. In late Spring and Summer most of the plant species in the Park release seeds so food is more available than later in the year, consequently the presence of seed bait would be less desirable for a granivorous predator. Furthermore rodents can smell food more easily when the level of moisture in the soil is higher (van der Wall 1998). However rodents may be also eat insects that are more abundant in summer than in winter. The native *Rattus fuscipes* in Victoria has been shown to change diet from insects in summer to mainly plant material and fungi in winter due to the decline in insect availability in the colder season (Robinson 1987).

In New Zealand house mouse populations in beech forest declined in spring and summer due to the decline in beech seed food at that time (Ruscoe et al. 2005). In the Perth area however mice usually breed in Spring and population density tends to reduce in Winter. If good weather conditions prevail (as in the relatively warm Perth winters) and if food resources are available the breeding season can be extended and the population may remain at a higher level longer over the year (Kemper 1980). As Kings Park bushland is completely surrounded by an urban environment, it is more likely to be exposed to introduced rodents that are linked to humans and populations numbers will be higher than in more pristine locations. Furthermore the increased plant density in the Park, especially the increased abundance of shrubs, would have created a more sheltered environment that usually increases their presence. Seed predation rises with increasing structural density and greater complexity of the vegetation (Thompson 1982; Casper 1987; Xiao et al. 2005). Invertebrates, by contrast, are more active in Summer and this could be the reason why seed loss of the small seeded species is higher in this season.

The seasonal features of *Banksia* seed predation needs further investigation as seeds that can escape predation in Summer are not capable of germination until the following Winter. Consequently even if seeds are not consumed in Summer they are still susceptible to predation until Autumn/Winter, when germination starts.

In part the predation trials, though field-based, were artificial as seeds were offered at times when they might not have been naturally available. The importance of predation for the population biology of the plants must be assessed in relation to time of predator activity and time of seed release. Invertebrate activity is greatest in the hotter Summer months and this was when the highest rates of removal of smaller seeds were recorded. This is ecologically realistic as this is also the main time of seed release for the smaller seeded species. However for the *Acacia* species, the removed seed may not have been destroyed but merely pass into the soil seed bank for later germination when appropriately stimulated. *Banksia* seed release is predominantly in the Summer to Autumn period but germination will not occur until the first substantial rains in the Autumn to Winter period. Thus the seed must lie on the ground for some time (as the 'flat' shape does not favours self burrowing in the sand) and will be available for consumption for some time. The low removal rate of *Banksia* seeds in the Summer indicates that the seed will initially not be under predation threat until 'rodent' activity increases, as has been indicated by the high removal rates in the EUs set up in Winter. Anecdotal evidence indicates higher movement and lower food availability for rodents in Autumn-Winter, but it is not clear when this begins or if it varies between years. However it is likely that the earlier the Autumn-Winter rains begin the more likely it is that *Banksia* seeds will germinate and hence escape predation.

Increased seed availability seems to have had a different effect depending on the species involved. For the banksias, removal was an all or nothing event. If a predator found the seeds all were consumed no matter how many were present. Finding the seed cache was a chance event and some seeds lots were never located. This imparted a high variance to the data but indicates that the rodent-banksia seed system is relatively stochastic and not density dependent. However as most banksia seeds fall under the tree canopy there will be a higher density of seeds present than outside the canopy and this may lead to higher seed predation and lower seedling establishment under parent trees as predicted by the Janzen (1970) hypothesis for scarcity of seedling establishment under parental canopies. In contrast, for the invertebrates, increasing the seed availability decreased the relative rate of seed removal. That is, proportionally fewer seeds were removed from the more concentrated caches than would have been expected from the results for the lower density seed lots and this was consistent across the small seeded species. This indicates that the invertebrate seed predators may become satiated at higher seed densities as is found after fire in eucalypt forests (eg. O'Dowd and Gill 1984). Alternatively this may be related to the relatively large size of the EUs in comparison to some invertebrate seed removal studies that use small petri dishes. The small sensing distance for invertebrates in contrast to vertebrates may mean that widely distributed seeds limit invertebrate predation more than vertebrate predation. However the search activity of invertebrates, particularly in warm to hot conditions is very intense so this may not be relevant.

The percentage of seed loss was not influenced by the number of seeds displayed in the EUs especially for *Banksia* spp and partially for *Dryandra sessilis*. *Banksia* seed predators seem not to be satiated by the number of seeds. This accords with the results of Hulme (1994) where some species of rodents consumed a constant proportion of seed irrespective of the density. In the current study *Banksia* seeds were consumed in a similar way and in Winter, consequently, there could be the potential to remove most of the seeds found on sand (where recruitment is more likely to occur) which means there is a potentially reduced possibility of recruitment from seed.

For all the other species the percentage of seed removal was negatively related to the density of the seeds in the tray. While in this study, the natural ground characteristic of the bushland were replicated in the trays, the natural density was difficult to simulate as both the low and high number of seeds used in the treatment showed a higher seed density compared to natural conditions; still, with the use of large trays as EUs, instead of petri dishes, the seed density was closer to a natural density then in a petri dish.

Banksia seeds are to some extent camouflaged by a dappled light and dark patterning. However the results of the predation experiment on open sand show predators can easily find them in interfire conditions. In the undisturbed vegetation simulated with the sod sample, there was far more cover (of leaf litter and plants) than on bare sand, producing sites safer from predation (Howe 1986). The removal rate for the banksia seeds was much reduced (30%) when seeds were located in leaf litter and plant parts than when they were on the bare sand as was also shown for a dune system (Maron and Simms 1997) and *Castanopsis* forest ((Xiao et al. 2005). The effect was also seen for the smaller seeds but to a lesser degree, presumably due to the more intensive searching by invertebrates, than vertebrates. This shows that litter cover increases the safe sites (*sensu* Harper 1977) for seed subject to both invertebrate and vertebrate predation but is more effective for the larger seeds.

While the *Banksia* species in Kings Park are not reliant on fire for reproduction it is still a very important environmental influence in the system. The influence of fire on seed predation was observed in Bold Park, which has different characteristics from Kings Park but occurs on the same landscape system so it is likely that any general principles from Bold Park can in part be transferred to Kings Park.

In Bold Park, where levels of *Banksia* seed predation, inter-fire, were lower than Kings Park, in post-fire conditions seed removal from the experimental unit was lower but from the second year increased. A similar trend was seen in other investigated species though the difference in removal between unburned and burned sites is less distinct. The site nearer to the unburned area showed higher levels of predation/removal.

Predation rates overall were lower in Bold Park than in Kings Park. However significantly the predation of banksia seeds, in particular, was much lower in the burnt than the unburnt areas at Bold Park. This contrasts with South African evidence showing that predation rates by rodents on proteaceous and Restionaceae species after fire in fynbos is a severe limitation on seed availability for regeneration (Bond 1984). Predation tended to increase over time as the burnt area regenerated indicating that the return towards more cover over time may have allowed more extended foraging by seed predators.

As the banksia species in the Perth area are not or weakly serotinous they have somewhat similarly reproductive characteristics to some northern hemisphere conifers (*Pinus sylvestris*, Summers 2011; *P. halepensis*, Ne'eman et al. 2004) or non-cone bearing species. In subtropical rainforest in south western China large seeds tend to be hoarded (Xiao et al. 2006) while smaller seeds are consumer in situ. In northern temperate Pinus sylvestris forests pine seeds may be hoarded by squirrels but consumed at the site of collection by birds. At the

Chinese study site there were 11 species of rodent (Xiao et al. 2006). This is far higher than in Western Australian forests where before European settlement only approximately seven rodent species may have been present. The paucity of large seeds and seeds borne in dry cone-like fruits correlates in Western Australia with a low number of rodent seed predators. In fact there may have been fewer than seven species present in the Perth area as current ranges of several Psuedomys species are only near Perth and have current ranges more towards arid areas. The main species that was probably in the Perth area is *Rattus fuscipes* that extends across all of southern Australia (van Dyck and Strachan 2008), Just as the introduction of species such as Pinus pinaster as a plantation species has likely changed the feeding biology of species such as cockatoos, so too has the introduction of northern hemisphere mice and rat species probably changed the seed predation environment in Western Australia in the last 200 years. Woylies (*Bettongia penicillata*) do consume and cache seeds of some species (*Santalum spicatum*) in wandoo forests (Murphy et al. 2005) and this animal would probably been present in Kings Park before European settlement. However it is not known if that species would forage for fallen banksia seeds. Native rodents are not particularly diverse and may not have been major seed consumers. In plant populations changes in structure and density are mostly the result of processes during early stages of recruitment (Nathan and Ne'eman 2004). In general, changes in the vegetation of Kings Park over time involved a decrease in the importance of banksias and an increase in the density of other species such as acacias and *D. sessilis*. The post dispersal predation of banksia seeds is certainly higher in Kings Park than in other similar environments, both disturbed and relatively undisturbed, on the coastal plain near Perth Within the ultimate aims of this study the seed predation patterns are one step towards understanding the decline of banksias and the proliferation of other species over the last 60 years. Predation levels (both pre- and post dispersal) in Kings Park compared with other similar bushland areas on the Swan Coastal Plain point towards a lack of seed to support recruitment. However there are population and environmental aspects, such as the period of time when these eager vertebrate predators started feeding in the Park, which must be considered in working towards a synthesis of the changes that have been observed. The post dispersal predation of seeds of other taxa such as dryandra, casuarina and acacias is also high, especially in summer, and due to different predators, thus it seems counterintuitive that many of these taxa have increased population density. However the much higher seed production per adult plant for these taxa (related in part to the smaller seed size) means that seed availability may not be a limitation for their population replacement, especially for taxa such as acacia which have a soil seed bank accumulated over the years between disturbances.

Other changes in the Kings Park environment are likely to have been instrumental in favouring the recruitment of these species while banksia recruitment declined.

To properly evaluate the significance of seed predation on the recruitment of *Banksia* spp. it is important to investigate the other limitations on seed germination and seedling establishment. The next chapter investigates germination in different microhabitats and in different field conditions.

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5 CHAPTER 5: SEED GERMINATION AND SEEDLING SURVIVAL

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5.1 Introduction

In chapter 2 of this thesis it was suggested that in the last 60 years, environmental disturbances such as weed invasion, seed predation and new fire regimes have likely contributed to changing the habitat and vegetation pattern in the Kings Park bushland. These changes influenced the structure of the vegetation, the relative abundance and the recruitment potential of different species. Recruitment is a vital component of vegetation recovery after disturbance and the changes in Kings Park have influenced the microhabitat conditions that strongly influence the success or not of the establishment of young plants.

The processes whereby seeds produced by an adult plant are dispersed, germinate to seedlings and recruit to the stage of adult plants can be thought of as a seed dispersal cycle (Wang and Smith 2002). All the different stages of the cycle are important, and need to be properly investigated. However for plants that do not live naturally for a long time (<70 years) such as *Banksia* spp., it is important to assess the early steps, or the early parts of the recruitment cycle for conservation, environment management, horticulture and ecosystem restoration.

In this chapter I investigate the effect of different types of micro-habitat on the recruitment of the four main *Banksia* spp. present in Kings Park bushland and in other locations on the Swan Coastal Plain in order to determine which most affects establishment of the offspring through their influence on germination and subsequent recruitment. I also investigate potential recruitment of several other major dominant and subdominant species of the Kings Park plant community to assess if alteration to the soil micro-habitat could have changed the recruitment pattern of the different species from that which operated in earlier times.

Seeds of some species, once they are shed from the mother plant, germinate as soon as there are appropriate germination conditions (Eriksson and Ehrlén 1992). Others, by contrast, may spend some time in the soil seed bank. For the latter, specific mechanisms can delay germination for some months or for years. If all the appropriate conditions for seed germination are present and the seed does not germinate, the seed is defined as dormant. Dormancy, in fact, is really the absence of germination of (viable) seed in conditions deemed favourable for germination (Nikolaeva 1969). Dormancy mechanisms have evolved in plants to maximise the success of seedling establishment and survival in the plant's local environment (Bewley & Black 1994).

Presence of soil moisture is the primary factor for germination because, before being released from the mother plant, seeds reduce their moisture content in order to slow all metabolic processes. These will resume when all conditions suitable for germination, starting from the soil moisture content, are present. In a dry environment or environments with a periodic dry season, as in the mediterranean-type climate of the south-west of Western Australia, soil moisture content is above all the main germination cue. In many species of the kwongan, appropriate moisture levels and fire are two of the most important germination cues, ensuring germination occurs under favourable environmental conditions (Bell, 1999).

Water, apart from starting the metabolic process, is a cue that indicates the arrival of a season with water availability. For some species, water is just one of the germination cues. In order to avoid germination in a highly competitive environment seeds may also need another cue: for example heat or smoke, which is an indication of the removal of much of the adult biomass that would compete with seedlings for limited resources.

In mediterranean-type ecosystems, harsh summer conditions, with high temperatures and a long period without rain, will lead to prolonged drought stress in plants (Testi *et al*., 2004), and especially in seedlings, that cannot access groundwater. Consequently seedling establishment and recruitment are limited more by dry summers than by the cool conditions of winters. Reproductive phenology features, such as season of seed dispersal and germination are thus important traits to take into consideration for species survival. Earlier germination has been observed to be beneficial as it tends to increase seedling vigour (Trabaud and Oustric 1989). Survival of seedlings over the hot dry summer may be linked to their capacity to reach soil moisture that in summer dries out from the surface down into the soil profile. In such conditions a small and undeveloped root architecture would make them more susceptible to water deficiency (Lamont *et al*., 1991b; Enright and Lamont 1992; Moreno *et al*., 1996). Autumn germination allows more time for the root system to develop in order to keep pace with the drying front in summer. All the species investigated germinate in this season.

Two different types of seed bank can be distinguished according to the time the seeds spend in the soil: 1) transient seed bank, in which all seeds germinate or die within a year of dispersal; 2) persistent seed banks in which a fraction of the dispersed seed survives for more than one year in a dormant condition in the soil (Hutchings 1986). Most of the species investigated in this chapter belong to the transient seed bank, although the two *Acacia* can persist in the soil for longer due to the impermeable hard seed coat that delays water entering the seed. This process is called physical dormancy.

In this chapter, a number of manipulative experiments and surveys was carried out on the four main *Banksia* species of Kings Park and in a few experiments also other dominant species of the plant community of this urban bushland. Surveys and experiments were undertaken both in the field and the greenhouse.

5.2 Aim

The aim of the study reported in this chapter was to investigate seed germination in different types of micro-habitat in the *Banksia* bushland and to investigate germination and recruitment potential of other dominant species. The study focused on several *Banksia* species, as they have shown a significant decline in abundance over the last 60 years.

5.3 General Materials and Methods

Species: *Banksia attenuata, B. menziesii, B. grandis* and *B. ilicifolia* were the four banksias investigated. The other species of the Kings Park plant community investigated in this chapter were *Dryandra sessilis, Eucalyptus marginata, Allocasuarina fraseriana, Acacia saligna* and *A. pulchella*.

Locations: The main four locations where surveys and experiments were performed were: Kings Park bushland, Bold Park bushland, The Ridges State Forest and Jandakot Regional Park For some experiments the Murdoch University Bushland was also used. *Ex situ* experiments were undertaken in the Kings Park nursery both in the glasshouse and the tunnel house.

5.3.1 Surveys and Experiments

A combination of field surveys and field and greenhouse experiments were conducted.

<u>*Surveys:*</u>

A) Transects to quantify natural germination of *Banksia* in the bushland in different types of micro-environment.

<u>*Manipulative experiment in the field:*</u>

B) Seed manipulation on different substrata in Kings Park bushland with the dominant species;

C) Seeds tested for germination in natural habitat conditions with *Banksia* spp. (seed placed in Autumn) in the soil seed bank;

D) Seeds tested for germination in natural habitat conditions with *Banksia* spp. (seed placed in early Summer) in the soil seed bank;

E) *Banksia* seeds sown in the bushland in different types of environment in 10 1x1 metre quadrat arrays.

Ex situ experiments:

F) Experiment in the glasshouse, investigating germination of *Banksia* spp, on different types of substrata;

G) Experiment in the tunnel house with all species on different substrata as in the B 'field' experiment.

5.3.2 Seeds

5.3.2.1 Seeds collection

The provenance and period of harvesting may cause variability in seed viability/germination within the same species (Suszka et al., 1996; Mugnaini et al., 2004). For example in South Western Australia the gradation of dormancy response for *Anigozanthos manglesii* indicated a correlation between the provenance and ecological requirements of the species for germination (Tieu et al. 2001a). Time elapsed between harvest and the 'lab' investigation may affect the results of the experiment. For *Eucalyptus pauciflora* fresh seed germinated in 45% of cases but after one year of dry storage none germinated, though seeds were still viable (Beardsell and Mullett 1984). According to Baskin and Baskin (1998), using seeds dry stored for long periods or for an unspecified period of time is of little ecological value. Consequently, for the following experiment, seeds were collected, in the season of the experiments and on the Swan Costal Plain. Seeds of most species were purchased from accredited commercial collectors who guaranteed fresh seed, while seeds of *Banksia ilicifolia*, which were expensive to purchase, were self harvested.

5.3.2.2 Seed viability

The presence of a white, healthy and intact embryo was determined through the cut-test method; viability was evaluated from four replicates of 25 seeds each. The cut-test method has been used in many studies (Paynten & Dixon 1990; Roche et al. 1997; Tieu et al. 2001b) and is an efficient method for testing seed viability. Germination results were not adjusted to account for non-viable seeds.

Cut test results showed that average percentage viability ± Standard Error for the seeds of the investigated species were:

B. attenuata	94% ± 2
B.menziesii	92% ± 1.8
B. grandis	95% ± 2.3
B. ilicifolia	85% ± 5
D. sessilis	81% ± 2.5
A. fraseriana	86% ± 3.9
E. marginata	72% ± 3.2
A. saligna	95% ± 1.9
A. pulchella	90% ± 2.6

5.3.2.3 Seed experiment protocols

Each time soil or sods were collected from the field, special care was taken to choose an area not below a tree crown, to avoid the possibility of seeds being already present in the soil. Furthermore, soil control trays (with no seed augmentation), with the same number of replicates, were set up in the same trial sites as the experiments and surveys. This was done so that values could be adjusted in line with the control germination results. Knowledge of the shapes of early emergent seedlings allowed their identification in the early stages, avoiding the possibility that early death of the seedling would lead to subsequent errors in the final results. However at early emergence, seedlings of *Acacia pulchella* and *A. saligna* look similar, so identification was only possible by carefully noting what was left of the seed coat.

Seeds were spread evenly on the substrata avoiding clumping of seeds which can affect final germination results (Waite & Hutchings 1978; Bergelson & Perry 1989); also, with the *Banksia* seeds, which have a flat shape, the placement of seeds followed as closely as possible the natural dispersion, as seed orientation can cause differences in germination (Bosy & Aarssen 1995).

The length of the different germination experiments lasted from 9 weeks to 27 weeks, while experiments on seedling survival (E) lasted 3 years.

5.3.3 Greenhouse

Ex situ experiments were performed both in the glasshouse and the tunnelhouse.

The glasshouse has permanent transparent walls and roof and permits a considerable flexibility in environmental control and may be considered a 'semi-controlled environment' where there is mild daily variation in temperature.

The tunnelhouse, has a metal bow arch structure and is a 'minimal-controlled environment' where there is higher variability, compared to the glasshouse, in daily temperature.

In Kings Park nursery the tunnel house was used for soil collected from the bushland for experiments, so as to avoid potentially spreading pathogens into the glasshouse. Soil pasteurisation, which may invalidate the results of the experiments was not used.

Repeating some field experiments in the greenhouse allowed a better understanding of the response to specific treatments under controlled conditions where demographic and environmental stochasticity is limited.

5.3.4 Types of substrata

Before starting the experiments, a survey of the different type of substrata occurring in the Kings Park bushland was undertaken. In the South-West corner of the Park, where the long-term study on vegetation was undertaken (chapter 2), fifty 10x10 metre quadrats were randomly selected. For each quadrat the types of substrata present were scored in 5 different classes according to the cover percentage:

1 = 0% - 20%
2 = 21% - 40%
3 = 41% - 60%
4 = 61% - 80%
5 = 81%- 100%

For each class the mean value (for example for the second class the value is 30%) was used and results of the mean values of the fifty quadrats showed that in the Kings Park bushland: 31% of the soil is covered by a layer of leaf litter, 28% by native vegetation, 24% by weeds, 11% of land by bare sandy soil, 3% by (exposed) proteoid roots and 2% of other different type of substrata on the soils.

In the greenhouse and in the 'field' the different surveys and experiments were performed on various types of substrata:

Bushland sandy bare soil, leaf litter, mulch, weeds, cleared from weeds, burnt/fire residuals, proteoid roots, native vegetation.

The selected substrata are present in the following types of environment:

Semi-pristine vegetation, post-fire, weed invaded areas.

5.3.5 Statistical analysis

In the experiments each treatment used four replicates of 25 seeds for each species.

Descriptive statistics are displayed as bar charts and line graphs and expressed as percentages from mean values of replicates with ± 1 Standard error of the mean (S.E.).

Analytical statistics:

The experimental design with 25 seeds for each replicate satisfied the assumption of continuous data.

Distinctions between different treatments were tested via analysis of variance (ANOVA). The null hypothesis was that the variation within groups was the same as variation between groups. The Fisher LSD (Least Significant Difference) test was carried out as a post hoc test to assess difference between groups; the individual error rate with critical value was set at $P<0.05$.

The data sets were tested for normal distribution using the Anderson-Darling normality test, while the Levene's test was used for variance homogeneity. If one of the two assumptions was not satisfied, data were transformed using logarithmic or square root transformation. If even transformation failed to improve normality or homogeneity, the non-parametric tests Kruskal-Wallis, for more than two groups, and Mann-Whitney, for two groups, were employed.

In general, non-parametric tests are less prone to type I error (the error of rejecting a hypothesis that should have been accepted) (Martin & Bateson 1993).

P-values, the probability of statistical significance are indicated as:

* = $P<0.5$; ** = $P<0.01$; *** = $P<0.001$.

5.4 Aim, Methods, Results, Discussion of Single Surveys and Experiments

5.4.1 A: Transects to quantify natural germination of Banksia in the bushland in different types of environment (including sandy tracks)

5.4.1.1 Introduction

In the previous chapter it was shown that seed predation could limit *Banksia* recruitment. Recruitment and establishment processes are generally crucial for the survival of a plant population (Overbeck et al. 2003). For establishment a viable seed must reach a site that has suitable conditions for germination. Among the many and various factors that influence seedling recruitment micro-habitat is one of the most important (Grubb 1977). However for many species seed limitation is also an obstacle for recruitment (Turnbull et al. 2000).

5.4.1.2 Aim

The aim of this experiment was to examine natural seed germination of *Banksia* spp. in different types of micro-habitat and substrata in *Banksia* woodlands on the Swan Coastal Plain, to be able to quantify germination values and also to compare these with greenhouse and manipulative experiments and survey.

5.4.1.3 Materials and Methods

27 transects 50 metres long were used to monitor the relationship between the type of substratum and germination and the relationship between tree canopy and seed fall to determine values of seed dispersal. Data were collected for *Banksia attenuata* and *B. menziesii* in autumn, which is the period when it is likely to find *Banksia* seedlings.

The transect locations were randomly chosen within different types of environment, i.e.:

1) *Post-fire* (12 transects: Bold Park)
All transects were undertaken in Bold Park at different sites, seven of these experienced an early summer fire in 2000, while the other five sites experienced a late summer fire in the same year.
2) *Weed* invaded (3 transects: 2 in Bold Park and 1 in Kings Park)

The transects were undertaken in Bold Park and in Kings Park in areas where the understorey is dominated by weeds, in particular Veldt grass (*Ehrharta calycina*).

3) *Semi-pristine bushland* (9 transects)

3.1) bushland (6 transects: 2 in Kings Park, 2 in Jandakot Regional Park, 2 in the Ridges State Forest);

The transects were undertaken in semi-pristine sites in *Banksia* woodland.

3.2) next to sandy tracks (3 transects: 1 in Bold Park, 1 in Kings Park, 1 in Jandakot R.P.);

The transects were undertaken in semi-pristine bushland parallel to those on the sandy tracks, described below. This allowed comparison between the germination on bare sand and in semi-pristine bushland, as the transects were close enough to ensure that the density of existing seed would be similar.

4) Sandy tracks (3 transects: 1 in Bold Park, 1 in Kings Park, 1 in Jandakot R.P.)

Sandy tracks cleared of vegetation, were examined to assess germination on bare and relatively non-compressed sand.

Transects consisted of contiguous 1m x 1m plots delimited by a metal frame (subdivided into 10cm x 10cm squares) which was considered the statistical unit.

For each 1m^2 the number of germinants of each species and type of substratum (micro-habitat) present was recorded.

The seven kinds of substrata recorded were:

1) Bare sand

Relatively non-compressed sand with no vegetation

2) Proteoids roots

Proteoids roots, or cluster roots, can form a dense layer below the trees. When there is no understorey (as in post-fire conditions) it is easier to detect this type of substratum. Cluster roots are typical for most members of the grevilleoid group of the Proteaceae family.

3) Weeds

4) Native vegetation

5) Fire residuals (in Post-fire conditions)

small parts of unburned plant material combined with ash and charcoal clumped together in small soil depression, by wind and rain. The residuals create a soft and moist micro environment where seeds carried by weathering agents (such as rain and wind) are concentrated. Presence of seeds and type of micro environment favour seed germination in the spot (safe site as in Enright and Lamont 1989).

6) Leaf litter

The main species that contribute to the formation of the layers are *Banksia* spp. (with broad leaves) and *A. fraseriana* (with needle-like branchlets).

7) Leaf litter matt

Uniform and thick (more than 2 cm) layer of undecomposed scleromorphic leaves.

For each transect there were seven categories corresponding to the different substrata.

Transects were considered representative of the environment but not of the location in which they occurred.

The number of germinants/seedlings present and the kind of substratum was recorded for each quadrat within the transect. Subsequently for each type of environment the mean number of germinants and seedlings per square metre for each kind of substratum was calculated.

The same calculation was used considering only the scoring of the quadrats located under tree canopies. Furthermore for each 1m^2 quadrat if the canopy of one of either *B. attenuata* or *B. menziesii* was above more than 50% of the quadrat this was scored. The percentages for each species of germinant found below the tree canopy was also calculated. This survey allowed better comparison of germination values between the two species ('species weighted').

Figures with bar charts were generated for groups of transects, the number of transects used is shown in brackets, as values for some transects have been used in more than one group:

Total (27): all the transects together;

Post-fire (12): all the post-fire transects subsequently divided into early summer and late summer burn;

Inter-fire (15): all transects except post-fire;

Sandy track (3);

Next to sandy tracks (3);

Weedy (3);

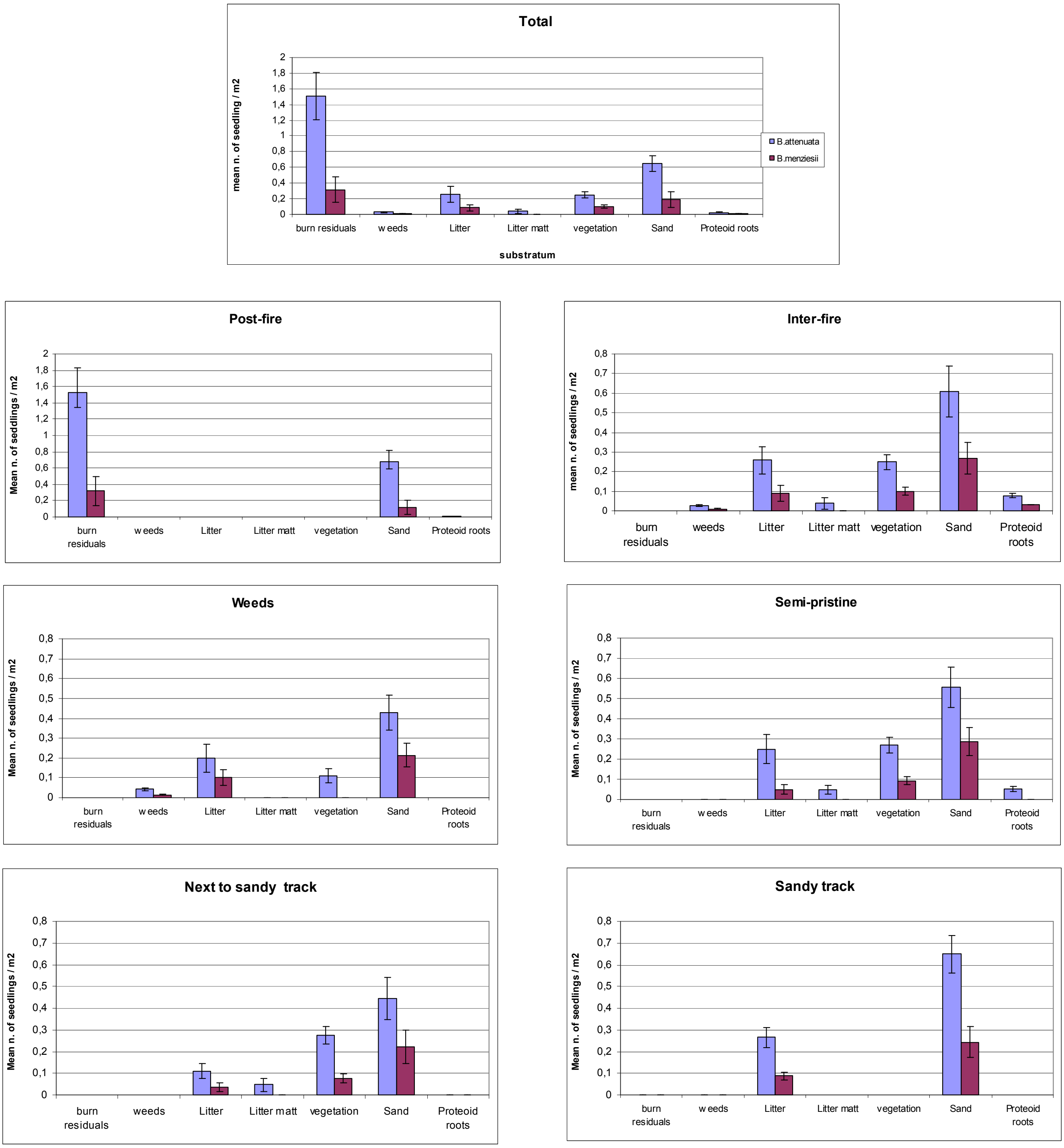
Semi-pristine (9): all except post-fire, sandy tracks and weeds.

Results are displayed as the number of germinants m^{-2} and as plant relative frequency (%).

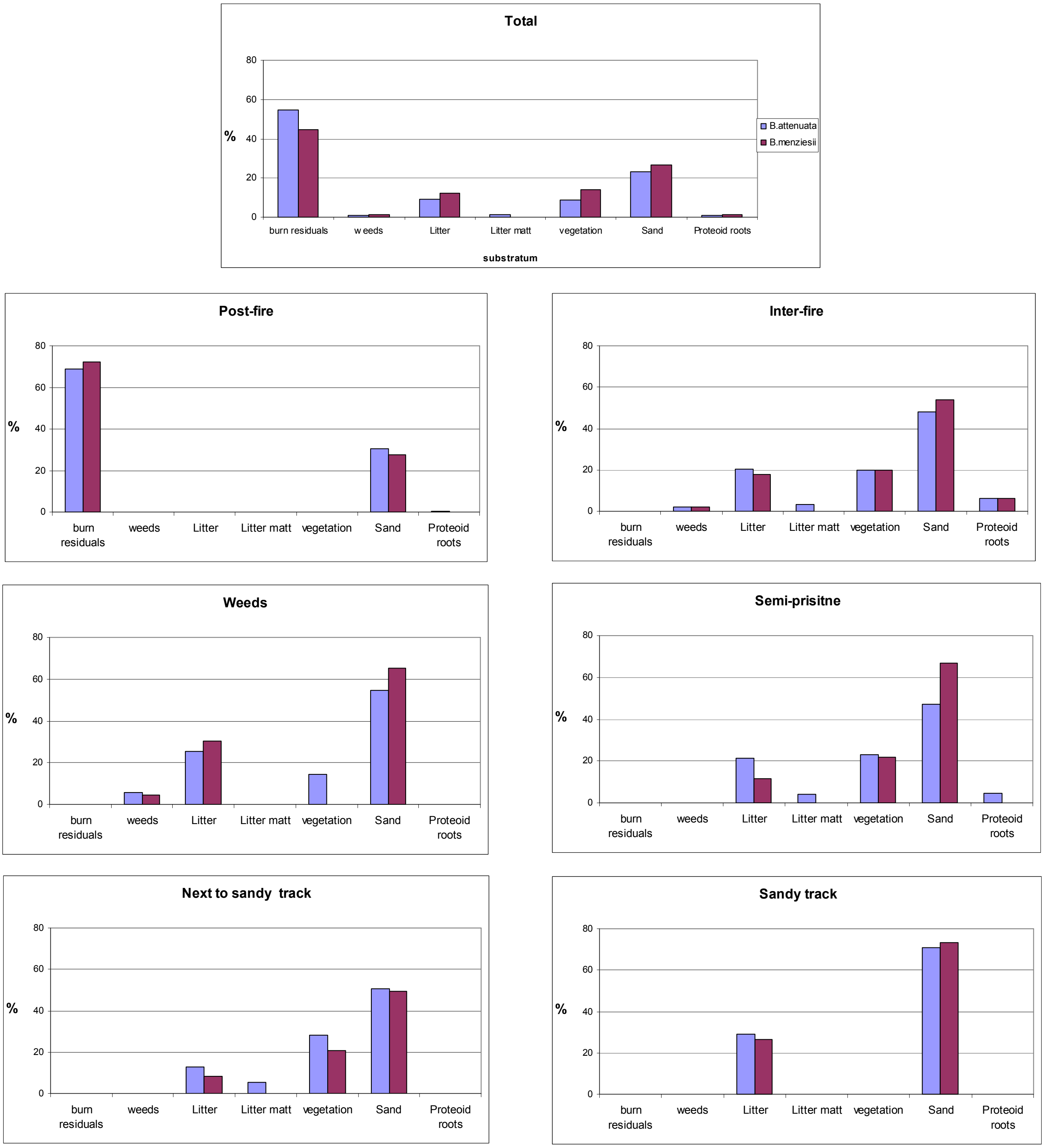
The chi-square goodness of fit test was used to determine if germination was related to a specific micro-habitat or was occurring equally on each substratum. The null hypothesis was that the observed and expected frequencies were not different from one another.

5.4.1.4 Results

For all 27 transects across all substrata, there was an average of 0.46 m^{-2} germinants for *B. attenuata* and 0.12 m^{-2} for *B. menziesii* (annex III).
Specifically for the substratum, a higher number of germinants (mean value across all substrata) was found in post-fire conditions on burn residuals with 1.51 m^{2} *B. attenuata* and $0.32 \cdot m^{-2}$ for *B. menziesii*. On sand substratum there was an average of 0.65 germinants for *B. attenuata* and 0.19 for *B. menziesii* (Figs 5.1 & 5.2; annex III).



Figs. 5.1 Mean number of germinants$\cdot$m^{-2} for the seven substrata (*x axis*), for different transects grouped together, for *B. attenuata* and *B. menziesii* (different scale on y axis of post fire).



Figs. 5.2 Percentage of relative frequency for the seven substrata (*x axis*), for different transects grouped together, for *B. attenuata* and *B. menziesii.*

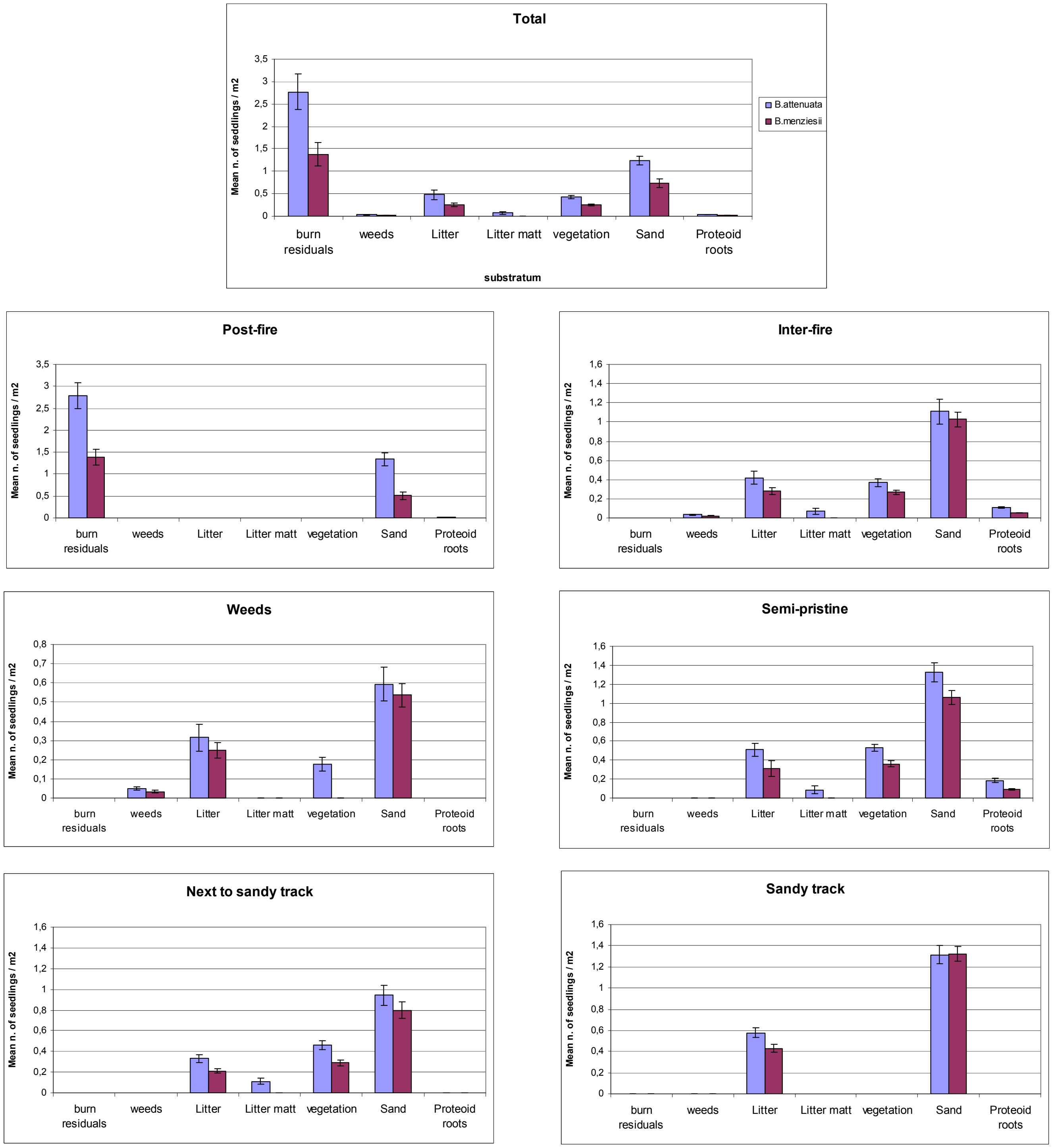
In the post-fire environment *B. attenuata* on sand had mean number of germinants per m^2 (0.66), however values do not differ significantly from the number of germinants on the "sandy track" environment (0.54). In the weedy environment there was a lower number of germinants (0.08 m^{-2} for *B. attenuata* and 0.03 m^{-2} for *B. menziesii*).

On sandy tracks there was more than double the germination compared to the transects parallel to it (in native vegetation) for both species (0.54 m^{-2} *vs* 0.22 m^{-2} for *B. attenuata*; 0.20 m^{-2} *vs* 0.09 m^{-2} for *B. menziesii*). The total number of germinants per m^2 in the semi-pristine environment was three times greater than in the weeds environment.

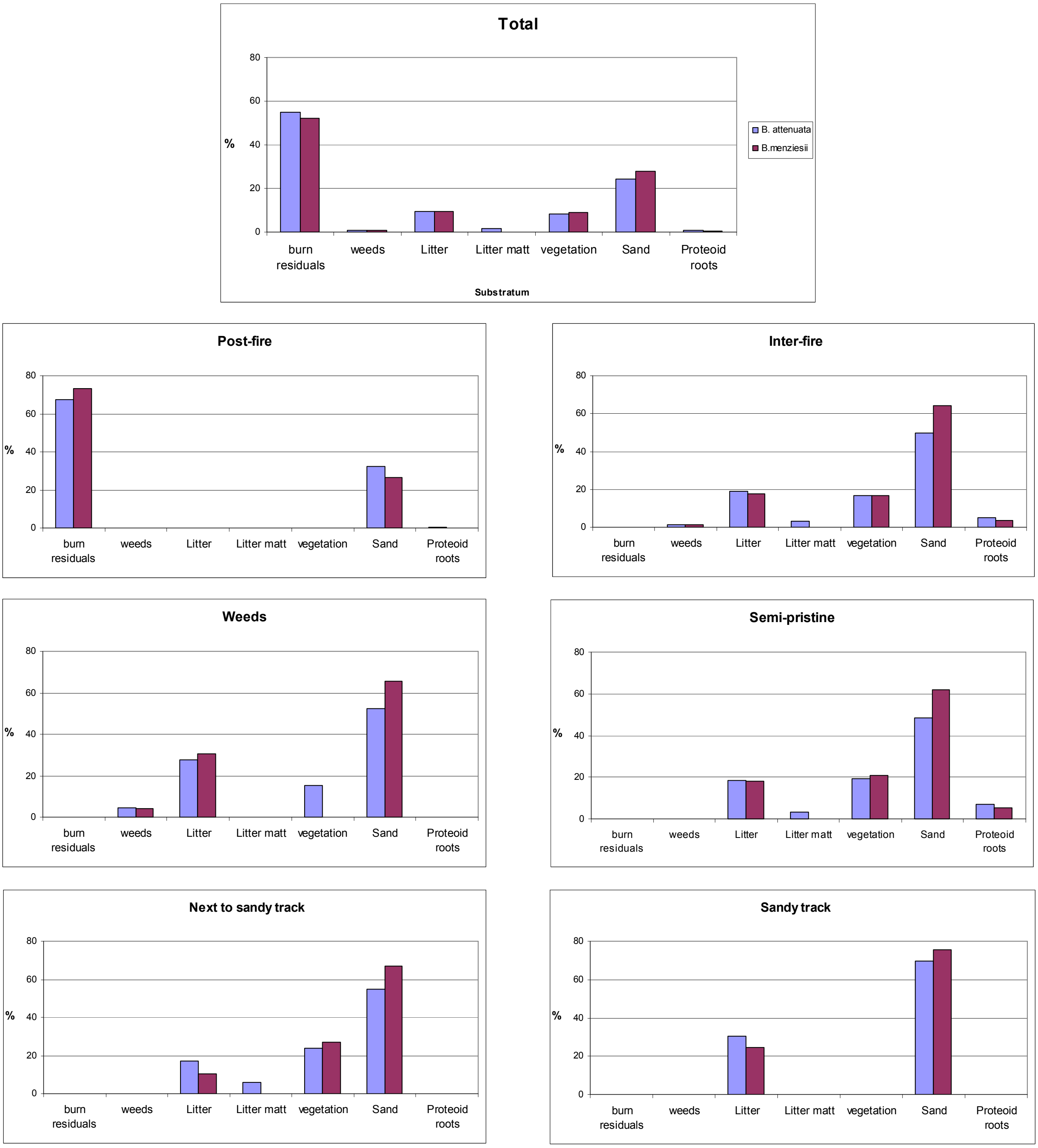
For *Banksia attenuata* the number of germinants in the post-fire environment was double the number in inter-fire conditions (0.66 m^{-2} *vs* 0.30 m^{-2}). For *B. menziesii,* by contrast, the values were similar (0.13 m^{-2} *vs* 0.11 m^{-2}).

Across all types of environment most germination occurred on the sandy substratum except in the post-fire environment, where higher values of germination occurred on burn residuals which, however, are likely to have bare sand below.

When the number of germinants was calculated only on quadrats located below a tree canopy (Figs 5.3 & 5.4), in order to be able to compare the environments and the substrata with the same abundance of trees for each species, in total there was an average of 0.85 m^{-2} for *B. attenuata* and 0.47 m^{-2} for *B. menziesii* (annex III). Specifically for the substratum, a higher number of germinants (mean value across all substrata) was found for *B. attenuata* on burn residuals (2.77 m^{-2}) and on sand (1.24 m^{-2}). *B. menziesii* followed the same trend but with lower values (1.38 m^{-2} and 0.74 m^{-2} respectively).



Figs. 5.3 Mean number of germinants m^{-2} for the seven substrata (*x axis*), for different transects grouped together, for *B. attenuata* and *B. menziesii*. Only quadrats under tree canopy were included in this scoring (different scales on y axes).



Figs. 5.4 Percentage of relative frequency for the seven substrata (*x axis*), for different transects grouped together, for *B. attenuata* and *B. menziesii*. Only quadrats under tree canopy were included in this scoring.

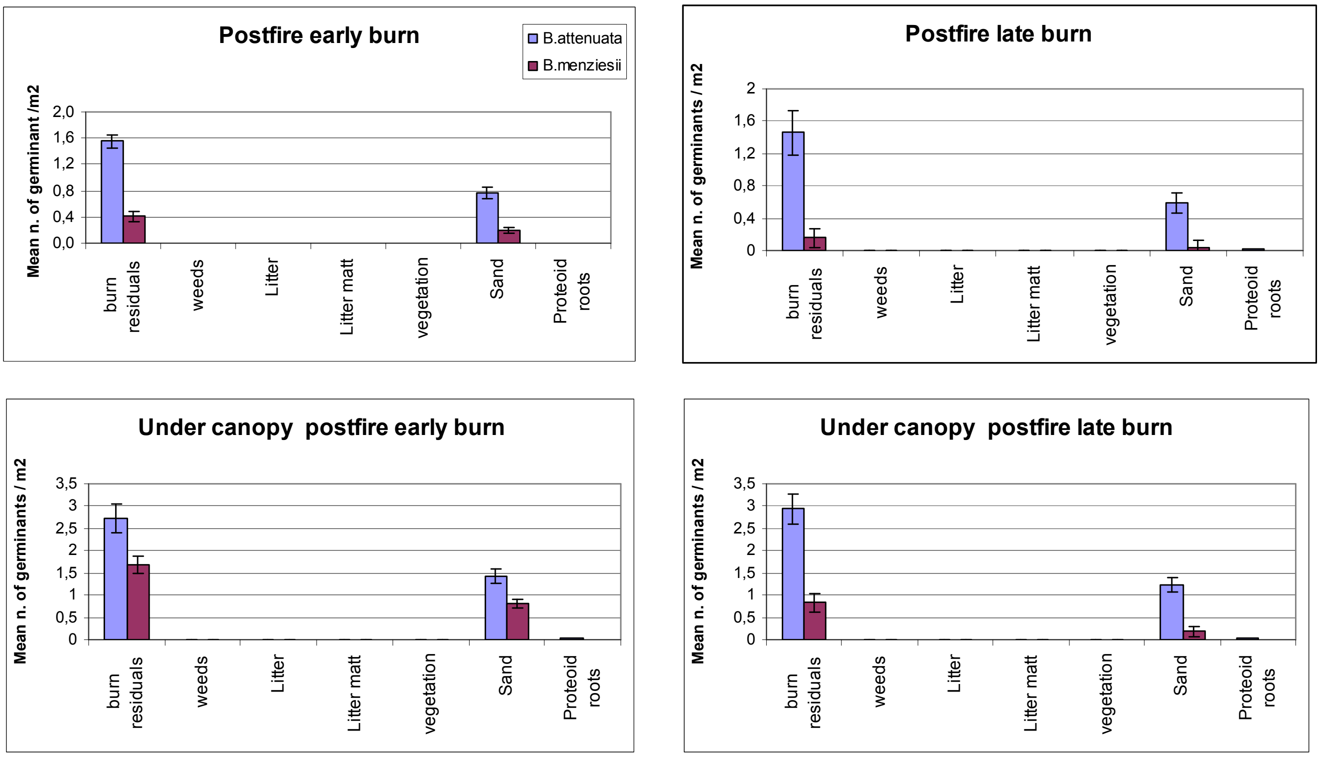
In general (see III) the environment with the highest difference in germination values between *B. attenuata* and *B. menziesii* is post fire. In this environment there was an average of $1.23m^{-2}$ for *B. attenuata* and $0.53m^{-2}$ for *B. menziesii* while in the "inter-fire environment" the values of germinants/seedlings were $0.53m^{-2}$ and $0.42m^{-2}$ respectively.

On sandy tracks there were 1.1 *B. attenuata* and 1.08 *B. menziesii* per m^2 i.e. approximately double the values on the parallel transects in the vegetation.

The number of germinants in the weedy environment was lower compared to the other environments.

In particular, in the post-fire environment the results of the "early fire" and the "late fire", for the trials undertaken in Bold Park, were similar for *B. attenuata* (1.56 m^2 and 1.46 m^2) but were different for *B. menziesii* (0.41 m^2 and 0.15 m^{-2}) (Fig. 5.5). The trend for germination values under the tree canopies was similar.

The Chi square test showed that the distribution of scored seeds was significantly different ($\chi 2 = 16.93$ $P<0.001$) under and outside the tree canopy compared to expectation of equal values. In all 27 transects and in all environmental conditions, except in post-fire, there was a strong relationship between tree canopy and the location of the germinants. In most cases, the greater proportion of germinants was found below a tree canopy (69.8%). In the post-fire environment by contrast there was a similar proportion of germinants below (58.4%) and outside (41.6%) the tree canopy.



Figs. 5.5 Number of germinants$\cdot$m^{-2} , in the post-fire sites in Bold Park, for the early summer fire and for the late summer fire. Along the entire transects and only for quadrats under the tree canopy.

5.4.1.5 Discussion

Along the investigated transect, successful germination of *B. attenuata* and *B. menziesii* seeds seems to be very dependent on the micro-habitat. Values of germination on the different substrata seem not to differ according to the environment. However, some substrata appear only in a particular environment such as 'burn residuals'.For *B. attenuata* higher germination occurs in the post-fire environment and on the bare sand (sandy tracks) substratum. This confirms the fact that the increased germination after burning is due mainly to production of new sites available for germination (Enright and Lamont 1989). However similar values for the sandy track showed that the higher number of seed set due to fire is just one of the factors responsible for increased germination. For *B. menziesii* on the sandy track environment there were higher numbers of germinants compared to the post-fire environment. The reason may be due to the seed set period for the species. Seeds in *B. menziesii* are released at the beginning of the summer and as the species is weakly serotinous in the Perth area, it does not need fire to release seeds. Consequently fire can kill seeds that are already on the soil and no longer stored in the canopy. The season of burning is important for this species' recruitment. After the late summer fires in Bold Park there was not a particularly high number of *B.menziesii* germinants due to a depleted canopy seed bank at the end of the summer .

In Kings Park *Banksia* woodland the presence of leaf litter reduced germination and in the presence of a thick layer of plant litter germination was nil. In the Mediterranean-type climate of the south west corner of Western Australia most of the species in a *Banksia* woodland are evergreen with sclerophyll leaves that have a slow rate of decomposition. So the accumulation of leaf litter tends to create a thick mat that reduces the chance of a suitable site and consequently germination. Germination rates were also low in the presence of cluster roots, despite the fact that this type of substratum was mostly below the trees and so in the area of higher seed fall. The low number of germinants on a weedy substratum confirmed the negative effects of invasive species on the recruitment of native species. In the inter-fire period, most of the germination occurs under the tree canopies, showing poor dispersal of seeds. By contrast, in the post-fire period, the absence of undergrowth allows greater seed dispersal due to wind and rain wash.

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5.4.2 B: Seed manipulation on different types of substrata (in Kings Park bushland with the dominant species)

5.4.2.1 Introduction

Soil substrata onto which seeds drop and germinate have a major role in determining the composition and the diversity of plant communities. Abiotic and biotic factors can have an important effect in the early stage of the recruitment process and consequently on the plant populations.

5.4.2.2 Aim

In this 'field manipulative experiment' the germination and seedling survival responses on different types of substrata of the selected dominant species of the Kings Park *Banksia* woodland were evaluated in order to estimate their effect on seed germination and seedling establishment.

5.4.2.3 Material and Methods

After a preliminary investigation (see introduction to this chapter) on the main types of soil substrata present in the Kings Park bushland different types of substrata were selected, including: soil predominantly covered with bare sand, leaf litter, native species and weeds. Furthermore a new substratum was created: soil with weeds physically removed. All these were the ‘in field’ treatments. A further substratum was the bare sand in the “Old Tip” area inside the Kings Park bushland, the Tip site was considered a “low competition” site as there were just few scattered plants, most of them seedlings. For each substratum a sod of soil of 30 x 45 cm (the size of a nursery tray) was selected and it was delimited on site with metal wire pickets. Areas not directly below tree canopies were chosen in order to avoid soil with seeds already present. The sod of soil represented different microcosms present in *Banksia* woodlands on the Swan Coastal Plain; each one was a sample unit and was replicated four times.

Consequently for this field experiment the different treatments were soil samples of bare soil, leaf litter, native species, weeds and weeds removed. At the Tip site the substratum was sand. All the treatments were also replicated protected from vertebrate removal with a metal cage. This experiment approximates the protocol in method II of Calvino-Cancela (2011). Twenty-five seeds of the following species: *Banksia attenuata, B. menziesii, B. ilicifolia, Dryandra sessilis*, *Eucalyptus marginata*, *Allocasuarina fraseriana*, *Acacia saligna* and *A. pulchella* were added to each sod sample. The experiment started in autumn and continued for 24 weeks. Results are displayed as line graphs with all the weekly scoring and as a bar chart with results of the 9th week (usually higher germination) compared with the 24th (the end of the experiment).

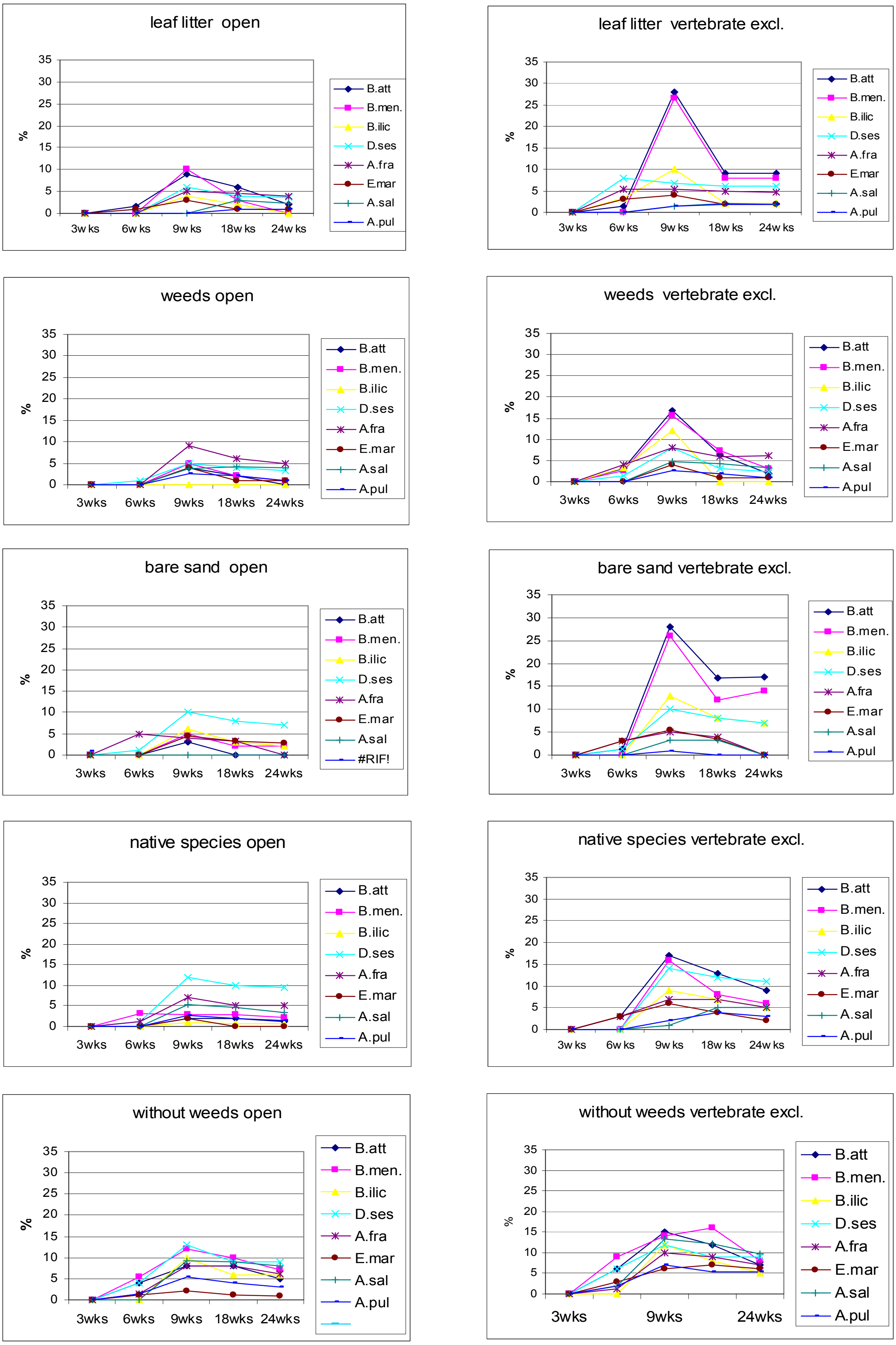
Comparisons were made between and within species at the 9th and 24th week. The mean number of germinants was compared using one-way ANOVA after data were examined for homogeneity of variances and normal distribution.

However due to the small number of germinants present in the sod samples that were not protected with a cage, parametric assumptions were not satisfied. In these cases, therefore, the Mann-Whitney test was used.

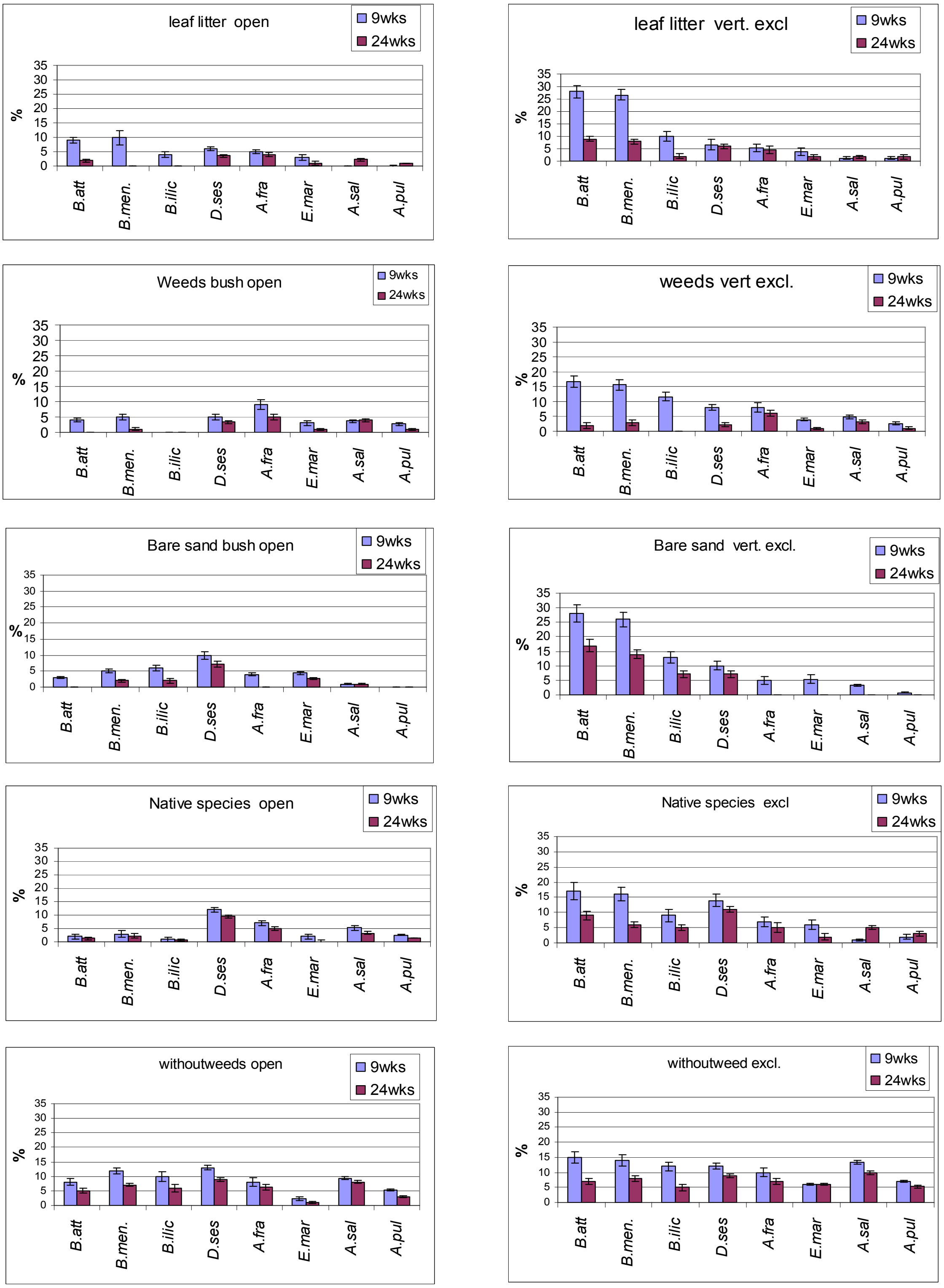
5.4.2.4 Results

Germination was higher on bare sand at the Tip site (Figs. 5.8) than on the sod samples in the other field sites(Figs. 5.6 & 5.7). Treatments 'in the field' with vertebrate exclusion had higher germination values compared to the same treatments without a wire cage (Figs 5.6; 5.7 B3; Table 5.1).

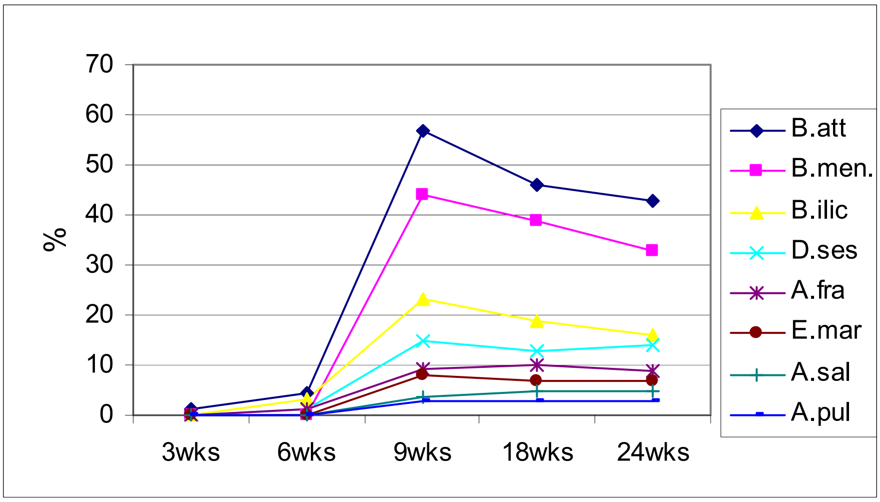
In uncaged sod samples *Banksia* germination was approximately 10% on leaf litter and on "weeds removed" and below 5% on native and bare soil. In uncaged sod samples *D. sessilis* and *A. fraseriana*, of the species selected in this experiment, were the species with highest germination and survival values. In caged sod samples *Banksia* spp. had higher germination with values near 30% for leaf litter and bare soil and around 15% for weeds, native and "weeds removed". The number of *Banksia* germinants at 9 weeks was significantly higher than the number of survivors at week 24 (Table B1). However in general, for *D. sessilis* and *A. fraseriana* there was no statistical difference between the mean number of seedlings at week 9 and survivors at week 24. Germination values of *Acacia* spp, were low due to the presence of the hard seed coat that imposed dormancy. At the Tip site almost 50% of *B. attenuata* and *B. menziesii* had germinated by week 9 while only 20% of *B. ilicifolia* and 15% of *D. sessilis* had germinated by that time. All the other species had germination values below 10%. Survival of *Banksia* germinants at week 24 was lower than at week 9, but seedlings of most other species that had germinated at week 9 survived until week 24 (Figs.5.8).

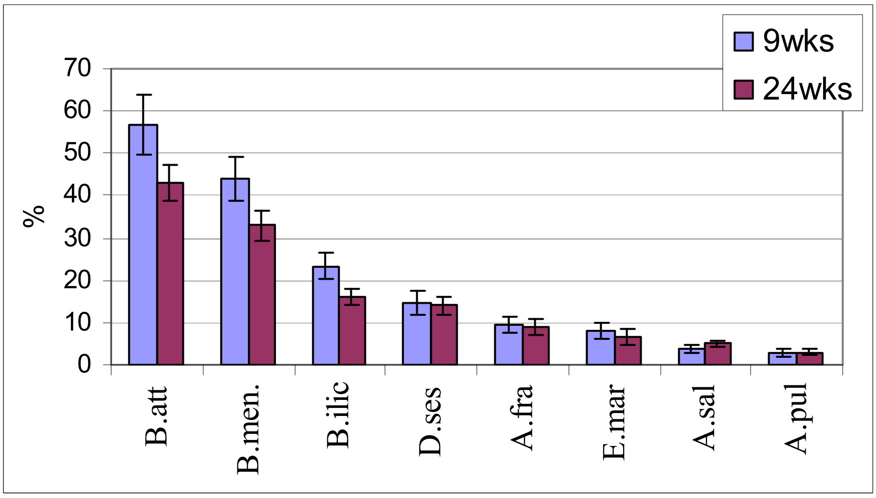


Figs. 5.6 Percentage survival of seedlings in the first 24 weeks from sowing for the investigated species. Five different treatments all with “open” and “vertebrate exclusion device”.



Figs. 5.7 Comparison of mean percentage survival of seedlings between weeks 9 and 24 for the investigated species. Five different treatments all with “open” and “vertebrate exclusion device”.





Figs. 5.8ab Percentage survival of seedlings in the first 24 weeks and mean percentage survival of seedlings between weeks 9 and 24 for the investigated species for the trial at the 'Tip site' in Kings Park. Abbreviations: B.att. = *Banksia attenuata;* B. menz = *B. menziesii*; B.gra = *B. grandis*; B.ilic = *B. ilicifolia*; D.sess. = *Dryandra sessilis* ; E.mar =*Eucalyptus marginata* =.; A. fras = *Allocasuarina fraseriana*; A.sal = *Acacia saligna*; A.pul = *A. pulchella*.

5.4.2.5 Discussion

This experiment highlighted the negative influence of weed and leaf litter on germination and survival of all the species in the bushland.

On all the different substrata *B. attenuata* and *B. menziesii* had higher germination values in comparison with the other investigated species. However mortality of *Banksia* seedlings after germination was high across all the substrata and in all the treatments. When seed predators were excluded from sod samples *Banksia* seeds had higher seedling survival compared to the "open" experiment. Smaller seeds might get under the leaves and benefit from a moister micro environment and this could be the reason why many of these germinants survived to 24 weeks.

In this study comparison between germination and survival started with the same number of seeds for each replicate (n=25). However, taking into consideration the different magnitude of seed production of each species, recruitment potential may have been different. Large-seeded species usually produce fewer seeds compared to small-seeded species (Henerey and Westoby 2001). If the results had been adjusted to the real community seed set, the species with smaller seeds such as *A. fraseriana*, *D. sessilis, E. marginata* and *A. saligna*, which produce many more seeds than banksias, would have shown a greater number of offspring compared to the banksias.

Table 5.1 Table showing statistical differences between number of seedlings at weeks 9 and 24. In treatments with and without vertebrate exclusion cages. * P<0.05; ** P<001; ! higher number of seedlings at the 24th week.

	Tip site	In field without vertebrate exclusion					In field 'vertebrate exclusion'				
		Leaf litter	Bare soil	Natives	Weeds	Withoutweeds	Leaf litter	Bare soil	Natives	Weeds	Withoutweeds
B. attenuata	*	**	**		**	*	**	**	**	**	**
B. menziesii		**	**		**	**	**	**	**	**	**
B.ilicifolia		**	**		na	*	**	*	*	**	**
D.sessilis		*		*		*				**	*
A.fraseriana			**		*			*			
E.marginata					*			*	*	*	
A.saligna		* !						*	* !		*
A. pulchella			na	*	*	*				*	

5.4.3 C & D: Seeds tested for germination in natural habitat conditions with *Banksia* spp. (seeds placed in autumn and in early summer in the soil seed bank)

5.4.3.1 Introduction

Serotiny is considered a specific characteristic of fire prone species and *Banksia*, for the Southern Hemisphere, and *Pinus* (Schwilk and Ackerly 2001), for the Northern Hemisphere, are often quoted as genera with a serotinous strategy that enables them to survive severe fires and promote seedling recruitment (Crosti et al. 2006).

However, while woody infructescences and cones open when exposed to heat, it is also true that for many species in these genera, seeds can be released due to dry conditions and ageing (Nathan et al. 1999; Tapias et al.et al. 2001). Cowling & Lamont (1985) suggested that higher seed release of *Banksia* species from southwestern Australia when burnt cones were subjected to wet-dry cycles, could be an environmental control ensuring minimal interval between seed drop and germination.

In addition, different species have different degrees of serotiny and even within the same species there may be differences in the degree of serotiny between different populations.

Banksia attenuata and *B. menziesii* are species considered to have a variable degree of serotiny, with plants in some populations retaining seeds for several years while those in other populations may release seeds soon after they mature (Cowling & Lamont 1985; 1987). On the Swan Coastal Plain south of Perth the investigated species can be considered weakly serotinous or not serotinous at all (Abbott 1985b and in chapter 3 of this thesis) in contrast to populations further north (Cowling and Lamont 1985). Most of the seeds of these two species are dispersed in the first summer after pollination, and after two years from seed maturation most of the viable seeds have been released.

After release *Banksia* seeds become part of the transient seed bank, meaning that the seed germinates as soon as there are proper germinating conditions, which usually occurs soon after the first rains in autumn. As for most of the main tree and shrub species of the *Banksia* woodland, soil moisture is the main germination cue.

The time elapsed between seed release and germination may be crucial for recruitment. If seeds are exposed for too long in the soil seed bank this will increase the risk of predation and/or other causes of death. Consequently, as *Banksia* germination occurs in autumn, the timing of seed release could be important for recruitment.

5.4.3.2 Aim

This experiment examined the germination process in relation to different periods of dispersal simulating two different scenarios of seeds released in different periods of the year, with a consequent different length of time spent in the transient soil seed bank before germination. Furthermore the experiment also examined differences in germination in relation to the position of the seed in the soil seed bank: displayed on the soil surface or buried under 1 cm of soil, as in Williams *et al*. (1996). Soil burial, in fact, can affect seed germination in different ways, from accelerating scarification, preventing seed predation (Hulme 1994, 1998) or increasing seed mortality due to internal decay, buried germination and fungal attack (Thompson 2000).

5.4.3.3 Material and Methods

For this experiment, seeds were protected with an appropriate metal cage (see chapter 4 of this thesis), which was placed on top to protect seeds from predation.

Seed germination was tested mimicking, as closely as possible, natural conditions. Seeds were placed in fine mesh bags (sachets). The weave of the nylon fabric used had openings of <0.4 cm which was fine enough to prevent the escape of the *Banksia* seeds but provided the possibility for the seed to be exposed to natural soil moisture, temperature conditions and soil microbes. The mesh bags were sealed and positioned in two ways: either placed on the soil or buried 1 cm underneath the soil. In the sachets, seeds were mixed with inert gravel (approximately 1/6 of the dimensions of the seed) so that seeds could be separated easily once removed from the soil and taken back to the laboratory to examine the fate of the seeds.

Sachets were placed in/on the soil in two different periods:
C) In Autumn (May) when moisture was present in the soil. This trial is the ‘short term experiment’;
D) In Summer (December) when the soil was dry.
This trial is the “long term experiment”.
Sachets with the seeds were exhumed every three weeks.
The species used in the experiment were *Banksia attenuata*, *B. menziesii*, *B. ilicifolia*, and *B. grandis*.
For each species each treatment had three replicates of 50 seeds. For each site in total there were, for each species, 9 sachets for the ‘short term’ and 27 for the ‘long term experiment’.

For the latter just 15 sachets were taken into account in the analysis as the seed testing started from the 15th week; in the first period, in fact, seeds were nearly 100% dormant.

The locations chosen for the experiment were Kings Park, Bold Park, Ridges State Forest, and Jandakot Regional Park. All the sites, except the one in Bold Park, were placed in areas of semi-pristine bushland. In Bold Park sachets were placed in disturbed sites. In the "short term experiment" sachets were positioned in a weed-dominated area, while for the 'long term experiment' two sites in areas exposed to burning at two different times in the previous summer were added. One set of sachets was placed in an area burned at the beginning of the Summer and another in an area burned at the end of the Summer.

The sachets were opened and the seeds were examined to assess germination (emergence of the radicle and/or presence of bright green cotyledons), death (dark yellow, brownish – "smelly" cotyledon) or dormancy (undamaged seed with presence of healthy and intact cotyledon); in the latter case the definition of dormancy is used even if this could not be appropriate as in the second experiment in particular (the long term experiment) summer dry soil conditions generate unfavourable environmental conditions for germination. Often in long term studies on buried seeds the first two categories cannot be easily discerned. However, in this study, as the seed had not been in the soil for long, it was possible to distinguish germinated seeds from entirely decomposed seeds.

Figures are expressed as percentage from mean values of the three replicates with ± 1 Standard Error.

Data were tested for parametric assumptions and output showed that there was little or no violation of data distribution, so a one-way analysis of variance (ANOVA) was chosen as the statistical test.

Analysis was undertaken for the "long term experiment" to test differences within locations, seed position in the soil, species, and length of the time spent in the soil seed bank. Differences were tested only on data from the 5th scoring (15th week) as for the previous period seeds were nearly 100% dormant.

For the "short term experiment" analysis was undertaken but only tested differences between locations. For the rest, descriptive statistics were considered sufficient to illustrate the results.

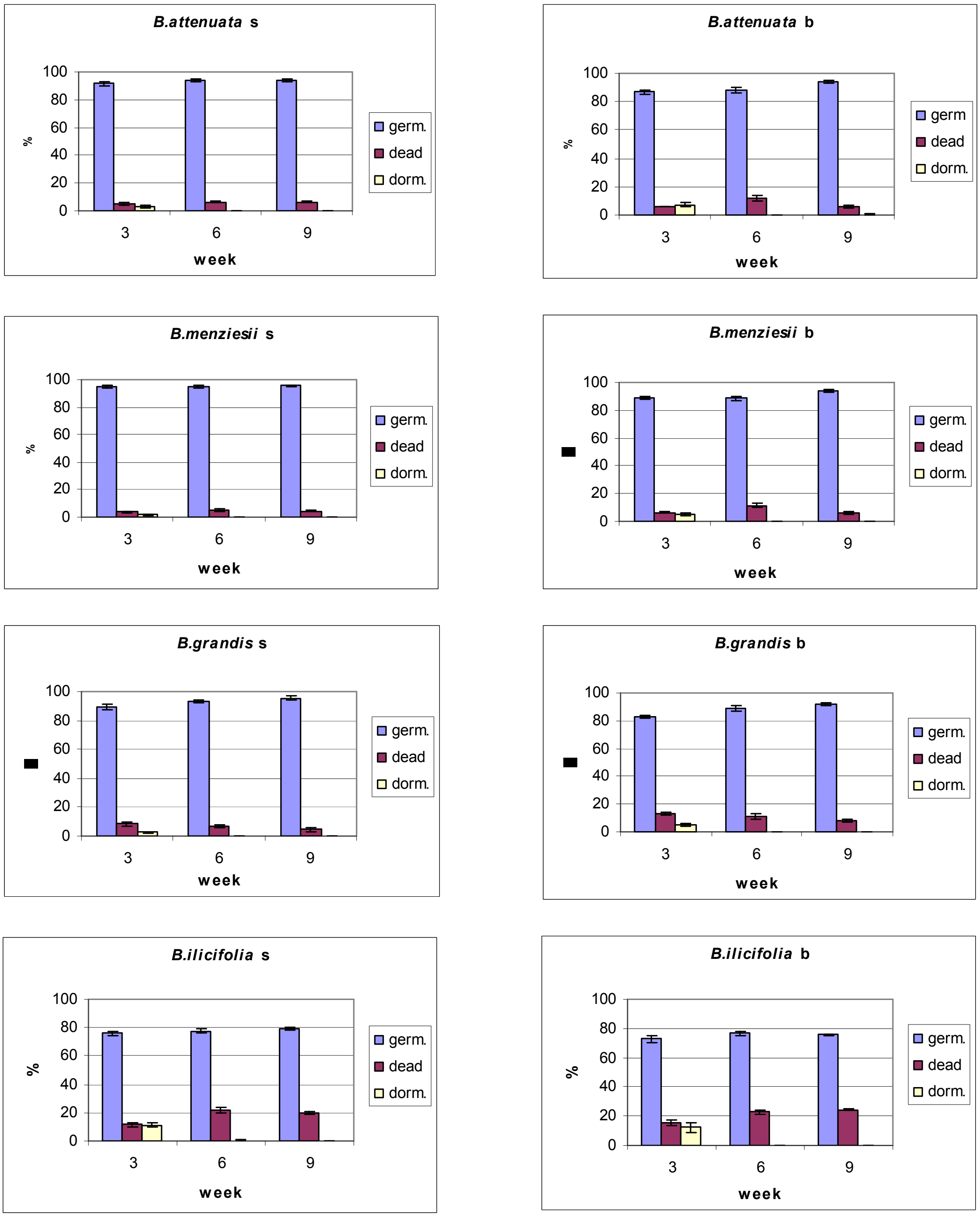
5.4.3.4 Results

C) "<u>Short term" experiment</u>. Most of the seeds that were placed in the soil in May germinated three weeks after the beginning of the experiment. Across all locations the germination (at three, six and nine weeks) was between 80% and 95% for *Banksia attenuata*, *B. menziesii* and

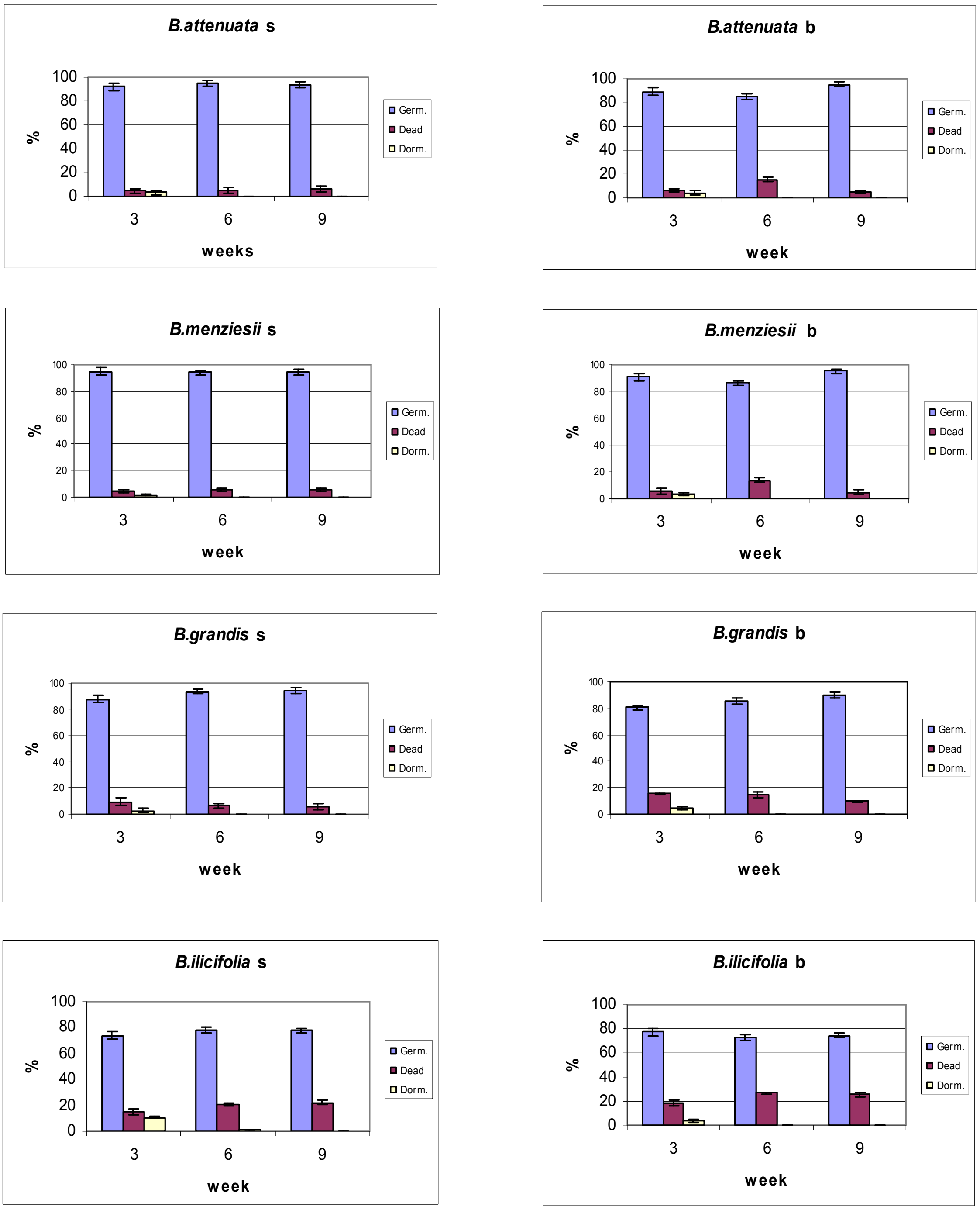
B. grandis. For *B. ilicifolia* germination values were significantly lower, between 70% and 80% (P<0.05), than for the other banksias. In addition, there were no differences in germination across the sites (Figs. 5.9, 5.10, 5.11, 5.12, 5.13 and Table 5.2).

Dormant seeds were present only at the three week scoring, while the percentage of dead seeds was similar across the length of the experiment.

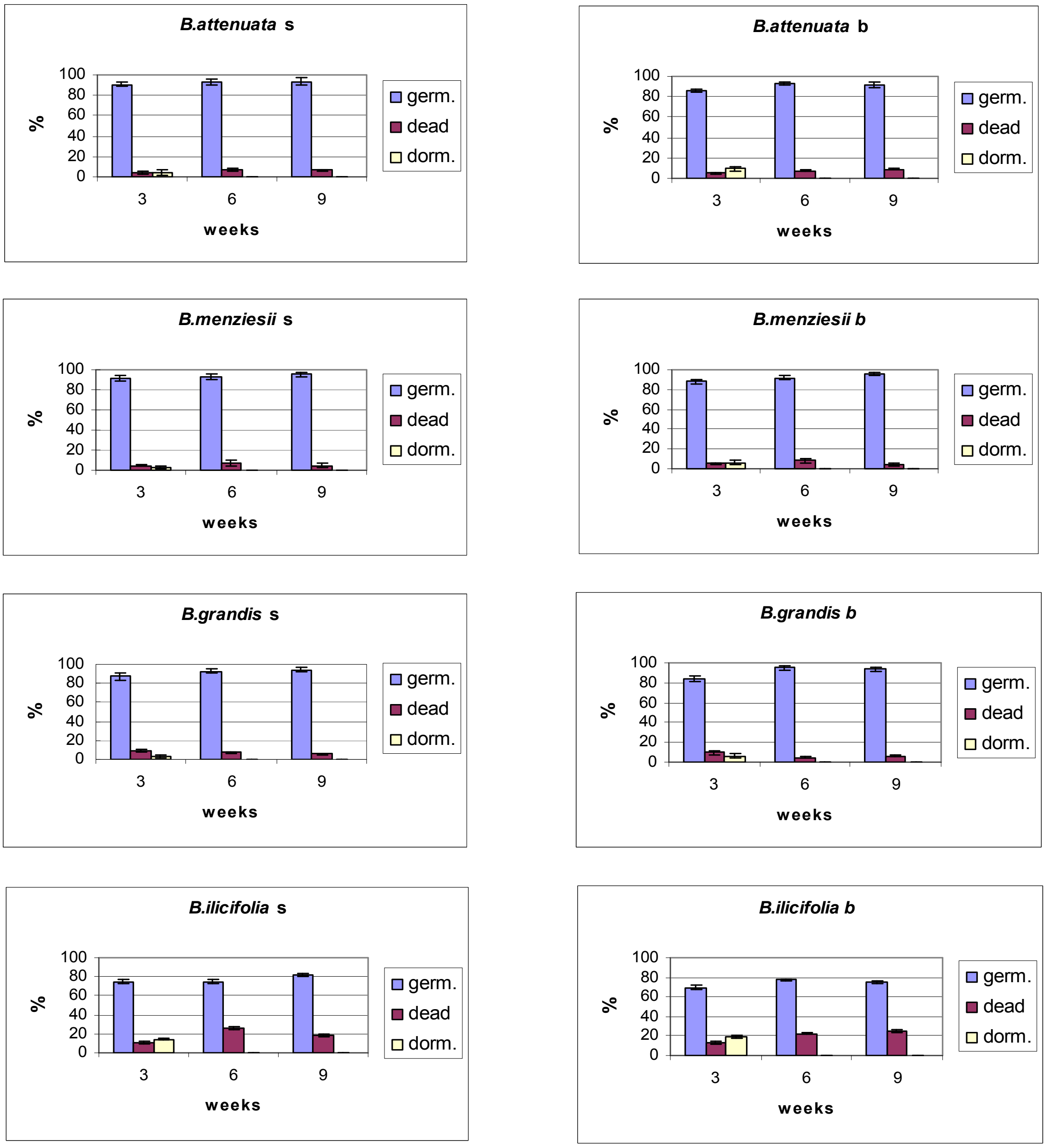
The mean number of germinants was significantly higher (P<0.01) for buried seeds (45.8 ± 0.3) compared to sachets placed on top of the soil (43.1 ± 0.39). The number of germinants at 3 weeks (43.2 ± 0.44) was significantly lower (P<0.01) than the number after nine weeks (45.7 ± 0.39). The number of dormant seeds was significantly higher for *B. ilicifolia* at three weeks compared to the other species. No difference was found between the locations (P=0.9) or the substrata (P=0.8). The number of dead seeds in sachets in the buried treatment was significantly higher (P<0.001) compared to that of seeds placed on the top of the soil. *B. ilicifolia* had higher numbers of dead seeds compared to the other species (Table 5.2).



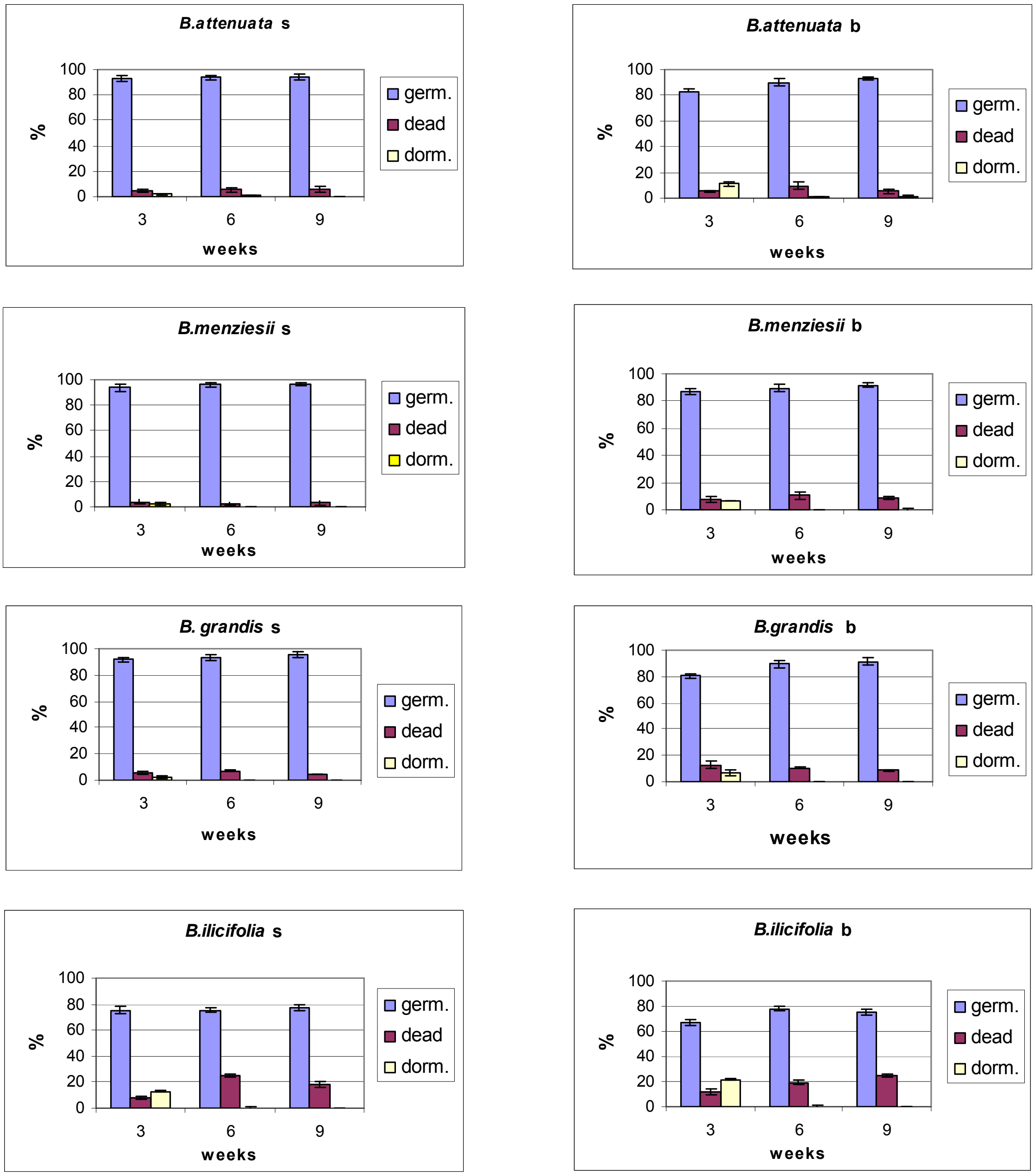
Figs. 5.9 Short term experiment, results across all the different sites. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 9 weeks.



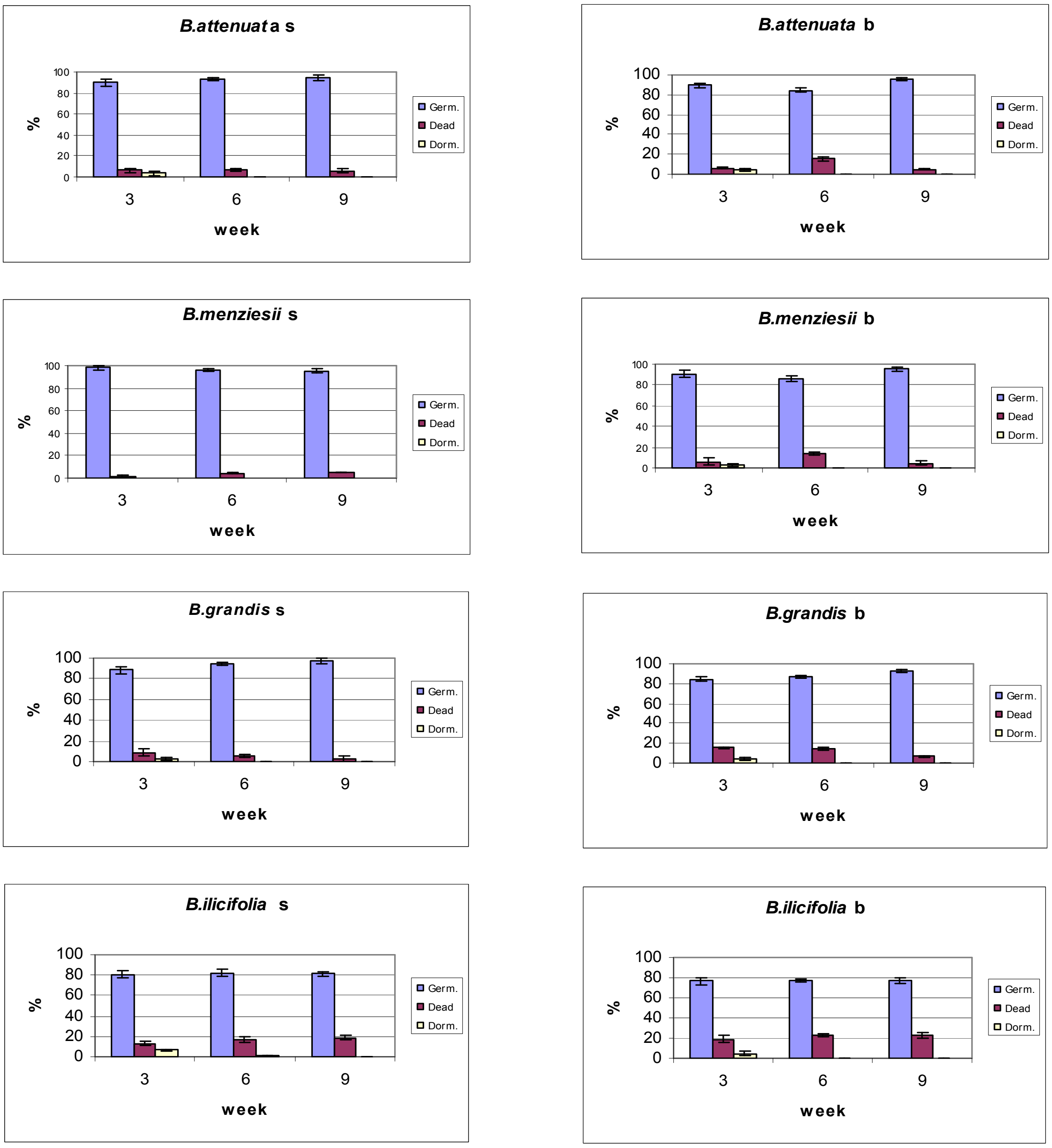
Figs. 5.10 Short term experiment, results in the Kings Park site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 9 weeks.



Figs. 5.11 Short term experiment, results in the Jandakot R.P. site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 9 weeks.



Figs. 5.12 Short term experiment, results in the Ridges State Forest site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 9 weeks.



Figs. 5.13 Short term experiment, results in the Bold Park site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 9 weeks.

Table 5.2 Short term Experiment. 50 seeds for each replicate, 1 way ANOVA, testing differences within groups of species, sites, weeks, seed display on the soil: germinant, dormant and dead seeds. * = P< 0.05; ** = P<0.01.

		Species				**Sites**				**Weeks**			**Position**	
		B.attenuata	*B.menziesii*	*B.grandis*	*B.ilicifolia*	Jand (5 & 6)	KP (2 & 3)	KP (5 & 6)	Rid (5 & 6)	3	6	9	buried	surface
n. of replicats tested		*72*	*72*	*72*	*72*	*72*	*72*	*72*	*72*	96	96	96	144	144
						GERMINATION								
Mean number of seeds		45,97	46,75	45,48	40,12	44,02	44,78	44,50	45,02	43,38	44,7	45,7	43,3	45,8
Species														
B.attenuata					**									
B.menziesii	**				**									
B.grandis					*									
B.ilicifolia		**	**	*										
Sites														
Jand (5 & 6)														
KP (2 & 3)														
KP (5 & 6)														
Rid (5 & 6)														
Weeks														
3												**		
6	**									*		*		
9										**	*			
Display														
buried	**													
surface														
						DORMANCY								
Mean number of seeds		0,68	0,48	0,56	1,74	1,29	0,58	0,56	1,02	2,58	0,02	0,00	1,07	0,66
Species														
B.attenuata					*									
B.menziesii	**				*									
B.grandis					*									
B.ilicifolia		*	*	*										
Sites														
Jand (5 & 6)							*	*						
KP (2 & 3)						*								
KP (5 & 6)						*								
Rid (5 & 6)														
Weeks														
3											*	*		
6	**									*				
9										*				
Display														
buried														
surface														
						DEAD								
Mean number of seeds		3,34	2,76	3,94	8,13	4,68	4,63	4,93	3,94	4,03	5,28	4,33	5,55	3,54
Species														
B.attenuata					*									
B.menziesii	**			*	*									
B.grandis					*									
B.ilicifolia		*	*	*										
Sites														
Jand (5 & 6)							*							
KP (2 & 3)						*								
KP (5 & 6)														
Rid (5 & 6)														
Weeks														
3											*			
6	*									*				
9														
Display														
buried	**													
surface														

D) "Long term" experiment. Seeds germinated in May at the beginning of autumn, in coincidence with the autumn rains, 16 weeks after they were placed in the soil. Seeds were "dormant" for the first three months from the start of the experiment. Across all locations the maximum germination percentage was between 70% and 80% for *Banksia attenuata*, *B. menziesii* and *B. grandis,* with *B. ilicifolia* significantly lower, between 50% and 65%, with significant difference (P<0.05). The number of germinated seeds per sachet was statistically lower for *B. ilicifolia* (25.6±0.4) compared to the other species (32.3±0.5). There was no apparent difference between germination values in unburned sites (30.0±0.4) and burned sites (31.1±0.6) or position (Figs 5.14, 5.15, 5.16, 5.17 and Table 5.3).

The percentage of dead seed was significantly (P<0.01) higher (11,2%) compared with the seeds of the "short-term experiment" (4,5%).

At Bold Park, the number of germinants at the unburnt site was significantly lower compared to the other locations (P<0.01). However within Bold Park germination at burned sites was significantly higher than at the unburned site (P<0,05). The germination of seeds in the two burned sites (burned at different times in summer) was no different from that of the other (unburnt) locations away from Bold Park chosen for this experiment. Germination at the Bold Park highly disturbed site (presence of weeds), was much lower (26.2±1.0) than all the other sites (32.3±0.4) (P<0.01) (Figs 5.18,; 5.19 & Table 5.3).

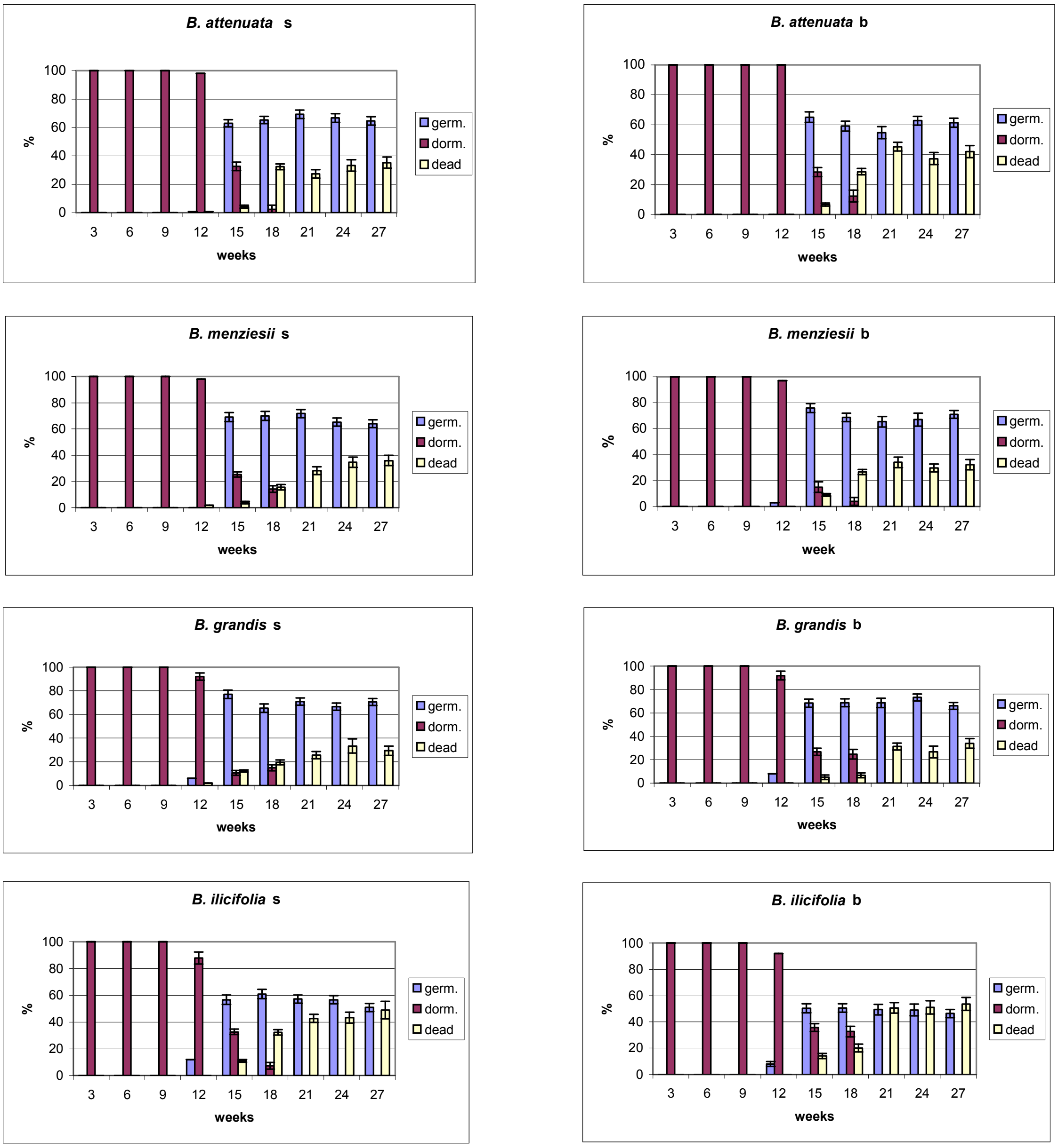
There was no significant difference in the number of dormant seeds between species. However mean values were higher for *B. ilicifolia* (8.3±0,6) and lower for *B. menziesii* (6.7±0,5). The number of dormant seeds in the sample placed on the surface of the soil was higher (8.0±0.7) than for buried seeds (6.6±0.6).

Dormancy was higher at burned sites compared to unburned (P<0.01) and in Bold Park compared to the other locations. Between the Bold Park sites no difference emerged between burned and unburned sites (P=0.4) or between the two burned sites (early and late Summer fires).

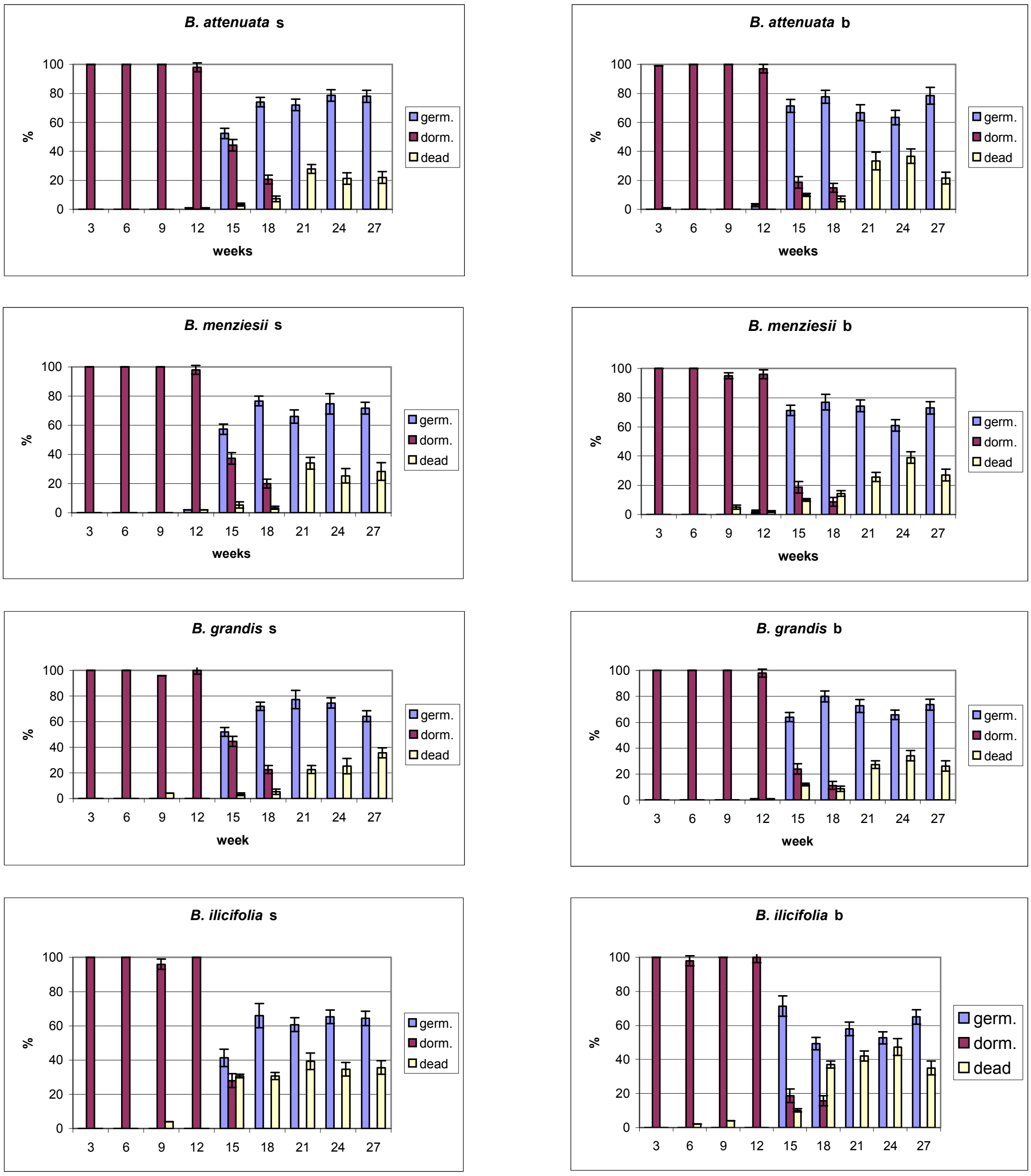
B. ilicifolia had a higher number of dead seeds (16.2±0,7) per sachet compared to the other (10.5±0,4) tested species, with difference also assessed between locations (P<0.01). In burned sites 19% of seeds were dead while in unburned sites 25% were dead (P<0.01).

Table 5.3 Long term Experiment. 50 seeds for each replicate, 1 way Anova, testing differences within groups of species, sites, weeks, seed display on the soil, fire and Bold Park burned for: germinated, dormant and dead seeds. * = P< 0.05; ** = P<0.01.

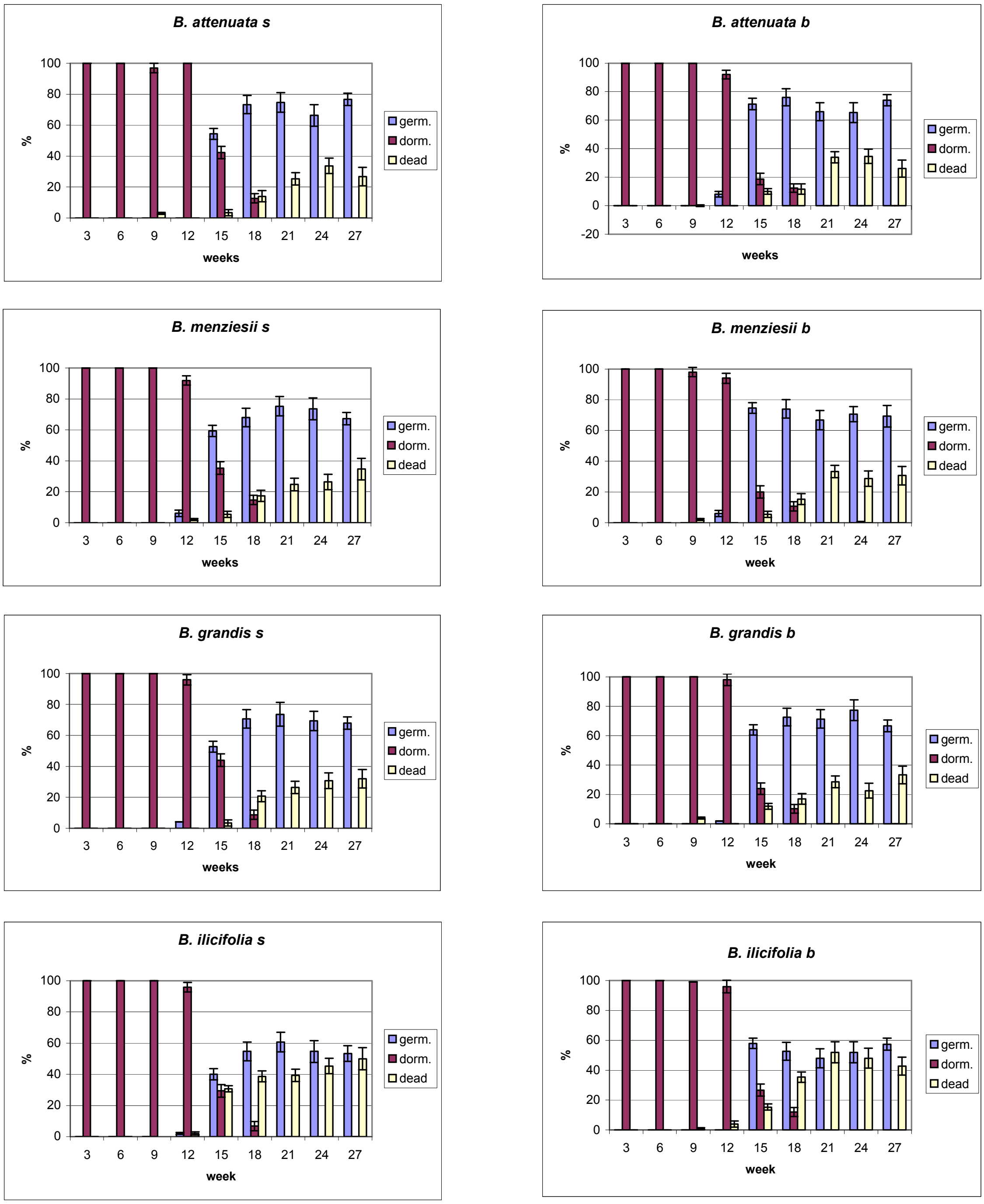
	Species				**Sites**					**Week**					**Position**		**Fire**		**BP burned**	
GERMINATION	*B.attenuata*	*B.menziesii*	*B.grandis*	*B.ilicifolia*	Jand (5 & 6)	KP (2 & 3)	BP (4 & 8)	BP (1 & 2)	Rid (5 & 6)	15	18	21	24	27	bur.	surf.	burned	unburned	BP old burn	BP new burn
		**					**					**								
n. of replicats tested	180	180	180	180	120	120	240	120	120	144	144	144	144	144	360	360	240	480	120	120
Mean number of seeds	32,08	32,6	32,83	25,68	32,68	31,79	30,12	26,17	33,93	20,0	33,2	33,5	33,5	33,8	31,21	30,39	30,12	31,14	29,89	30,31
Species																				
B.attenuata				*																
B.menziesii				*																
B.grandis				*																
B.ilicifolia	*	*	*																	
sites																				
Jand (5 & 6)						*		*												
KP (2 & 3)					*			*												
BP (4 & 8)								*												
BP (1 & 2)					*	*	*		*											
Rid (5 & 6)								*												
week																				
15																				
18										*										
21										*										
24										*										
27										*										
DORMANCY	*B.attenuata*	*B.menziesii*	*B.grandis*	*B.ilicifolia*	*Anka*	*KP*	*BPf*	*BPw*	*Wan*	15	18	21	24	27	*bur.*	*surf.*	burned	unburned	BP old burn	BP new burn
							**					**						**		
Mean number of seeds	7,36	6,65	6,93	8,27	4,11	4,00	10,01	11,24	4,47	26,6	8,19	1,38	0,19	0,01	6,57	8,04	10,01	5,95	9,81	10,17
Species																				
B.attenuata				*																
B.menziesii				*																
B.grandis				*																
B.ilicifolia	*	*	*																	
sites																				
Jand (5 & 6)							*	*												
KP (2 & 3)							*	*												
BP (4 & 8)					*	*		*	*											
BP (1 & 2)					*	*	*		*											
Rid (5 & 6)							*	*												
week																				
15											*									
18										*										
21										*	*									
24										*	*									
27										*	*									
DEAD	*B.attenuata*	*B.menziesii*	*B.grandis*	*B.ilicifolia*	*Anka*	*KP*	*BPf*	*BPw*	*Wan*	15	18	21	24	27	*bur.*	*surf.*	burned	unburned	BP old burn	BP new burn
		**					**											**		
Mean number of seeds	10,57	10,81	10,28	16,15	13,31	14,18	9,97	12,67	11,60	3,25	8,72	15,1	16,3	16,4	12,29	11,61	9,97	12,94	10,38	9,53
Species																				
B.attenuata				*																
B.menziesii				*																
B.grandis				*																
B.ilicifolia	*	*	*																	
sites																				
Jand (5 & 6)							*													
KP (2 & 3)							*	*	*											
BP (4 & 8)					*	*		*	*											
BP (1 & 2)					*	*	*													
Rid (5 & 6)						*	*													
week																				
15											*									
18										*										
21										*	*									
24										*	*									
27										*	*									



Figs. 5.14 Long term experiment, results in the Kings Park site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 27 weeks.



Figs. 5.15. Long term experiment, results in the Ridges State Forest site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 27 weeks.



B. attenuata s

B. attenuata b

B. menziesii s

B. menziesii b

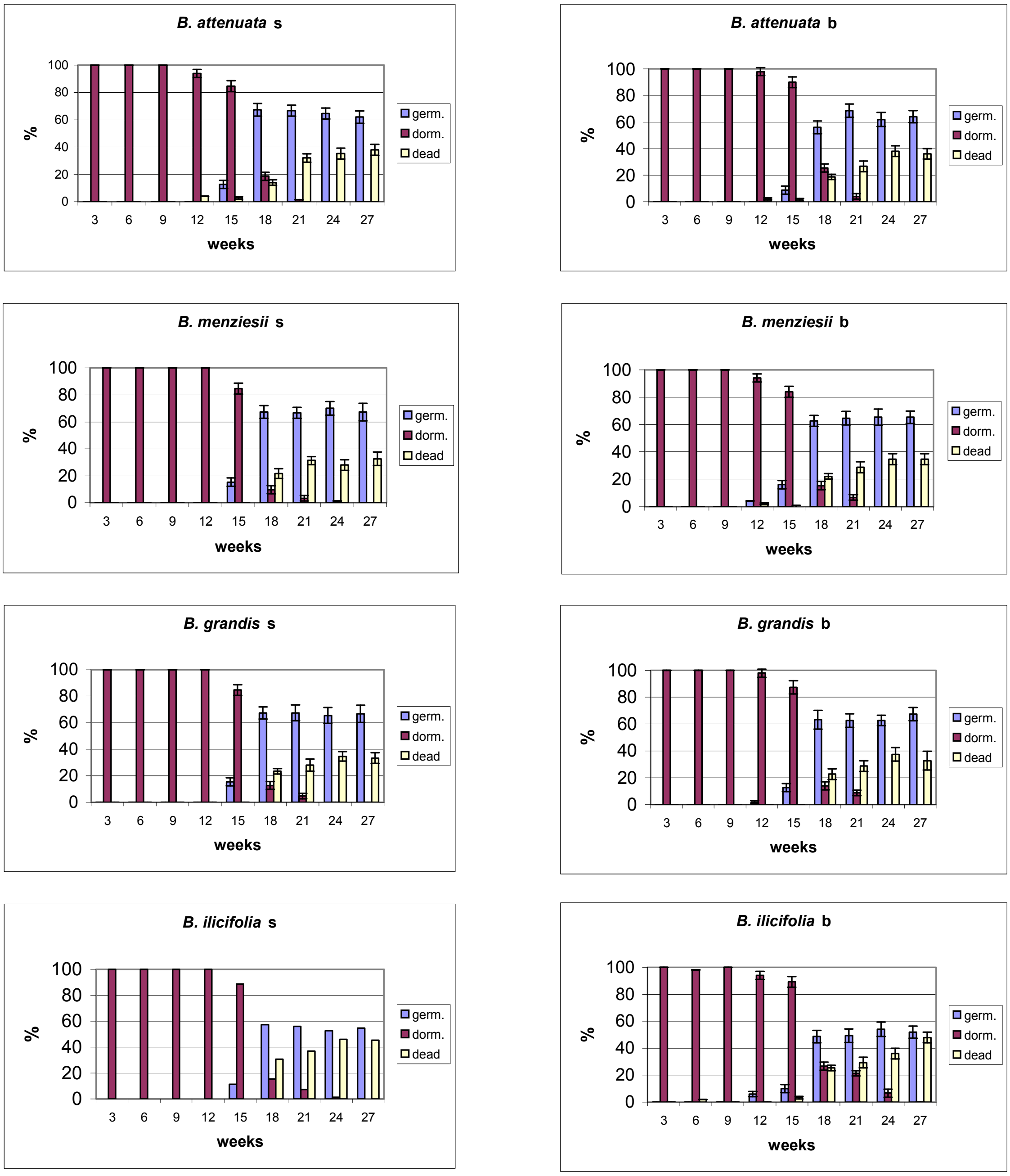
B. grandis s

B. grandis b

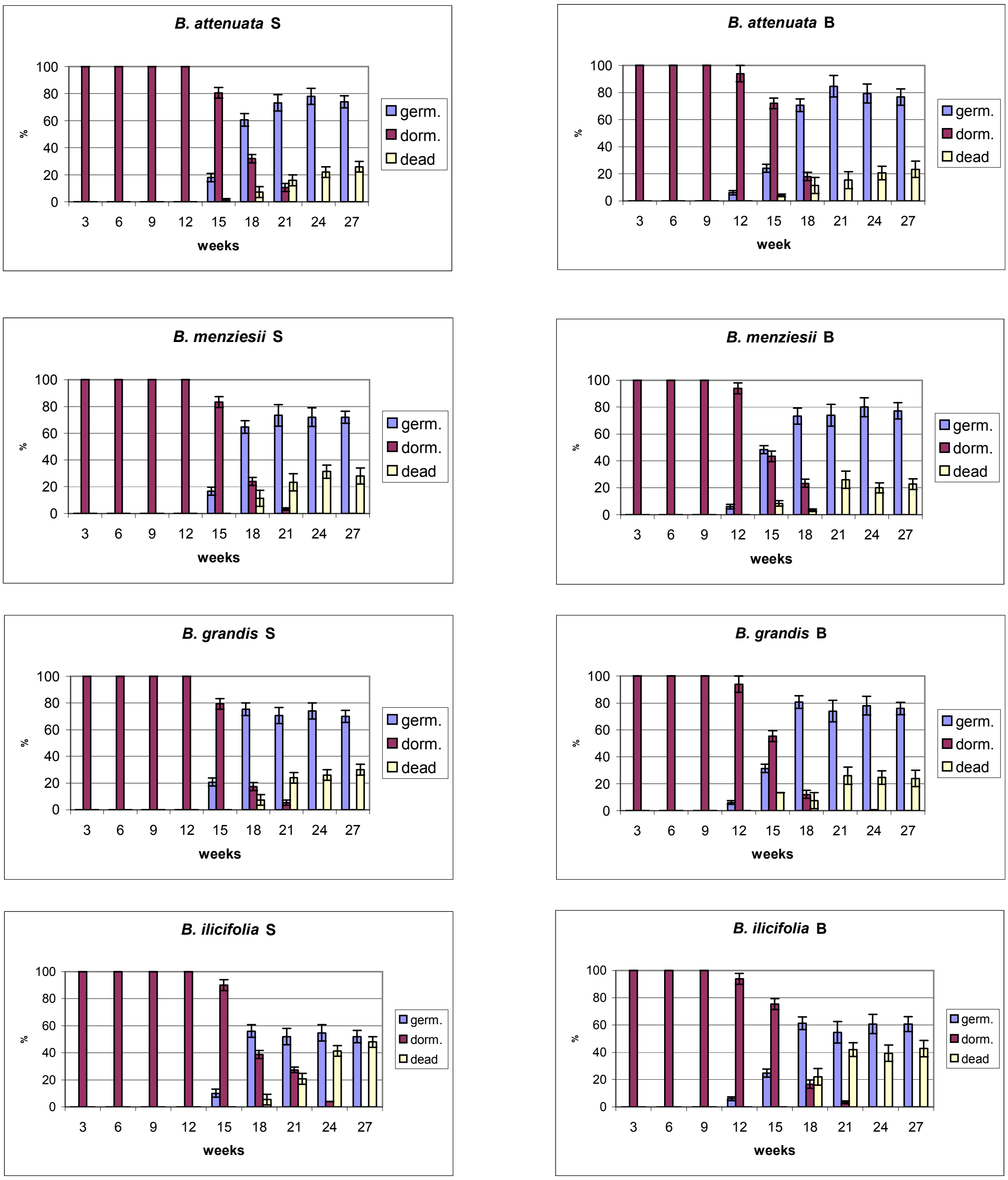
B. ilicifolia s

B. ilicifolia b

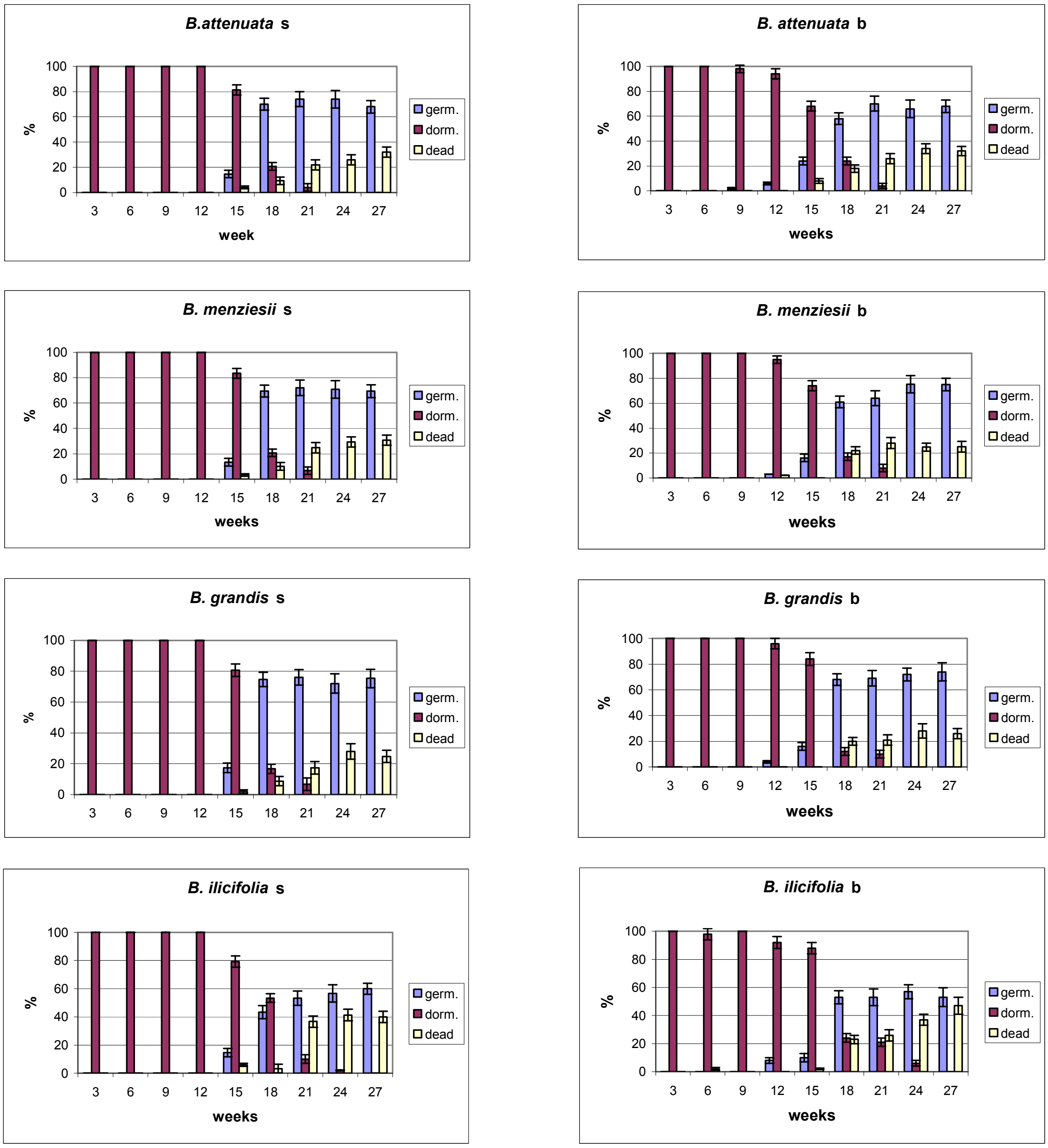
Figs. 5.16 Long term experiment, results in the Jandakot R.P. site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 27 weeks.



Figs. 5.17 Long term experiment, results in the Bold Park site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 27 weeks.



Figs. 5.18 Long term experiment, results in the Bold Park early summer burn site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 27 weeks.



Figs. 5.19 Long term experiment, results in the Bold Park late summer burn site. Mean percentage of germinated, dead and dormant seeds from mean values of the 3 replicates ± Standard Error. Seeds displayed on the surface (s) of the soil or buried (b) 1 cm underneath the soil. Scoring was undertaken each 3 weeks for a total of 27 weeks.

5.4.3.5 Discussion

The experiment confirmed, as in Cowling *et al.* (1987), that *Banksia* seeds, once released from the infructescence, become part of the transient soil seed bank of the banksia woodland. Seeds germinate as soon as the first abundant rains occur in Autumn. In natural habitats with appropriate soil moisture and temperature conditions seeds germinate within 3-4 weeks. This fact was also confirmed by the experiments in the greenhouse. When seeds are released in a period when conditions are unfavourable for germination the time they spend in the soil seed bank is longer and final germination values are lower, even in the absence of predation. All banksias had similar germination values except for *B. ilicifolia* which was lower. However, estimates of seed viability had already shown that this species had a lower proportion of viable seed in the seed sample used.

The only difference between locations/sites was for poorer germination at the unburned (weed invaded) site in Bold Park in the ‘long term experiment’. In the ‘short term experiment’ there were no differences across locations. The different response could be due to the fact that, for seeds placed in Autumn, favourable germination conditions occurred sooner and allowed the seed to germinate more quickly without a long period exposed to unfavourable environmental conditions aggravated by the dominance of weeds.

In the ‘short term’ experiment, buried seeds displayed better germination compared to the seeds placed on the surface. Higher and more consistent soil moisture at depth is probably the reason for better seed germination. However, for seeds placed in Summer there was no difference between buried seed and seed placed on the top of the soil presumably due to the extended time of dry conditions.

In the Bold Park unburned site, germination was also delayed compared to the other sites that were positioned in semi-pristine vegetation. This could be explained by the severe depletion of surface soil moisture by the abundant weeds preventing seeds from imbibing sufficient water for germination.

In general, the number of germinants was higher in the “short term” compared to the “long term” experiment as fewer seeds died in the soil due to shorter exposure time.

Seeds that are released starting from the end of Summer beginning of Autumn, as for *B. attenuata*, are favoured compared to seeds released at the beginning of summer. Being on the surface longer after dispersal reduces seed germination and consequent recruitment. In addition the seed “resting” for a long time in the soil seed bank is exposed to predation for a longer period so it is important for a species to reduce the time between seed release and favourable germination conditions.

5.4.4 E: Banksia seeds sown in the bushland in different types of environment in a 1x1 metre quadrat scheme

5.4.4.1 Introduction

Many factors can affect the recruitment capacity of reproductive individuals. Recruitment however for taxa such as some Swan Coastal Plain Banksia spp., which produce a transient soil seed bank, depends mainly on abundance of viable seeds, emergence and survival of seedlings.

As shown in the previous part of this thesis, the density of viable seeds of Banksia species in the soil can vary according to the season, the presence of predators and time after fire (post-fire or inter-fire). The relationship between number of seeds in the soil seed bank and number of emerging seedlings is difficult to evaluate; it is even more difficult to estimate the survival of seedlings (Nathan et al. 2000; Wang and Smith 2002). Being able to determine the minimum number of banksia seeds in the transient soil seed bank which would be adequate to ensure recruitment is crucial for the management and conservation of the banksia woodlands.

5.4.4.2 Aim

The aim of this manipulative experiment is to evaluate the recruitment capacity of the four Banksia species in different types of environment, starting from a known number of seeds sown in the soil.

5.4.4.3 Materials and Methods

In different sites of the 5 locations used in this thesis for experiments and surveys, a trial on seed germination and seedling survival started in autumn 1999, with the sowing of seeds, and was followed until Summer 2002, with the scoring of germinants and seedlings every 3 months. For the first month the trials were watered in order to avoid death of germinants due to early drought, being aware, however, that soil aridity is one of the stochastic natural disturbances which interfere with natural recruitment of the species.

In this experiment ten seeds of each of the four *Banksia* species: *B. attenuata, B. menziesii, B. grandis, B. ilicifolia* were sown in a 1x1 metre grid (subdivided into 100: 10x10 cm quadrats). Each 1x1 m quadrat was considered a sampling unit. Each seed was sown in a randomly determined 10 x 10 cm subdivision of the 100 available. Being able to relocate exactly where the seed was sown allowed separation of the scoring of sown germinants from naturally recruited seedlings. Furthermore, quadrats were not located directly underneath the canopy of *Banksia* species. Before sowing the seeds, the small quadrat was cleared of vegetation and the soil was cultivated.

Each location had the following number of sites:

• Kings Park	n=4
• Bold Park	n=1
• Murdoch University	n=1.
• Ridges State Forest	n=3
• Jandakot Regional Park	n=1

In each site there were 10 sampling units (1m x1m quadrat) with a total of 100 sampling units across all sites. The types of environments characterized by the sites were (for correspondence between number-#- of the site and names see annex I):

- Post fire (2): in Ridges State Forest (site # 3 & 4);
- Weeds (2): in Bold Park (# 1) and in Kings Park (# 8);
- Semi-pristine vegetation (4): 1 in Kings Park (# 2), 1 in Jandakot R.P (# 3).; 1 in Murdoch University (# 1); 1 in Ridges State Forest (# 1);
- Bare sand “low competition”(1): in Kings Park (# 1)
- Thick shrub-land “high competition” (1): in Kings Park (# 9).

The scoring of germinant and seedling survival was undertaken each season. At the first scoring after seed sowing only the number of germinants was recorded; after that, the number of seedlings in each quadrat together with the height of each individual at the highest leaf was recorded.

To compare sites and environments also a ‘biomass index’ (BI) was determined by adding up the heights (in cm) of the seedlings present in each quadrat. For each site the average of the 10 quadrats was calculated to provide the mean for each site for each species. For the first scoring the height of each emergent was approximated to 0.5 cm.

The Tip site could be considered a “low competition” site as there were simply a few scattered plants, most of them seedlings.

The dryandra site could be considered a “high competition” site as the area is characterized by the presence of a thick vegetation of native scrub dominated by *Dryandra sessilis*.

Results are displayed for site and type of environment for each seasonal scoring.

5.4.4.4 Results

Across all sites, the germination values of *B. attenuata*, *B. menziesii* and *B. grandis* were similar while germination values of *B. ilicifolia* were approximately three times less (Figs 5.20).

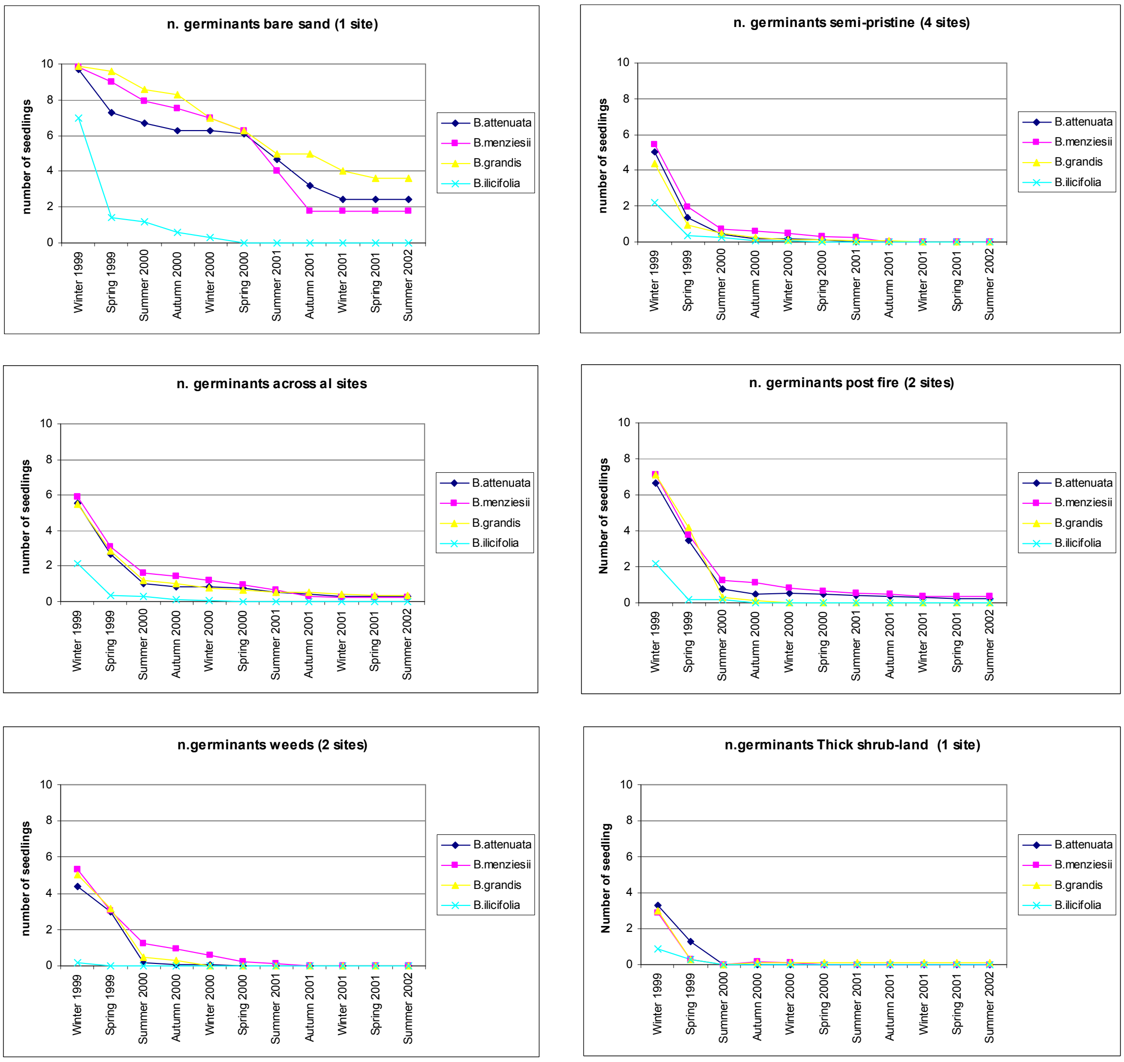
The “Tip site” on bare sand described as a “low competition site” showed higher values of germination up to 90% for the first three banksias. Lower germination occurred in the Thick shrub-land (“high competition”) site, with approximately 30% germination occurring for the 3 more prolific banksias. All the other sites displayed intermediate values. Germination was higher in post-fire sites compared to semi-pristine ones.

Except in the Tip site many of the seedlings did not survive to the first autumn scoring and most survivors had perished by the second summer scoring.

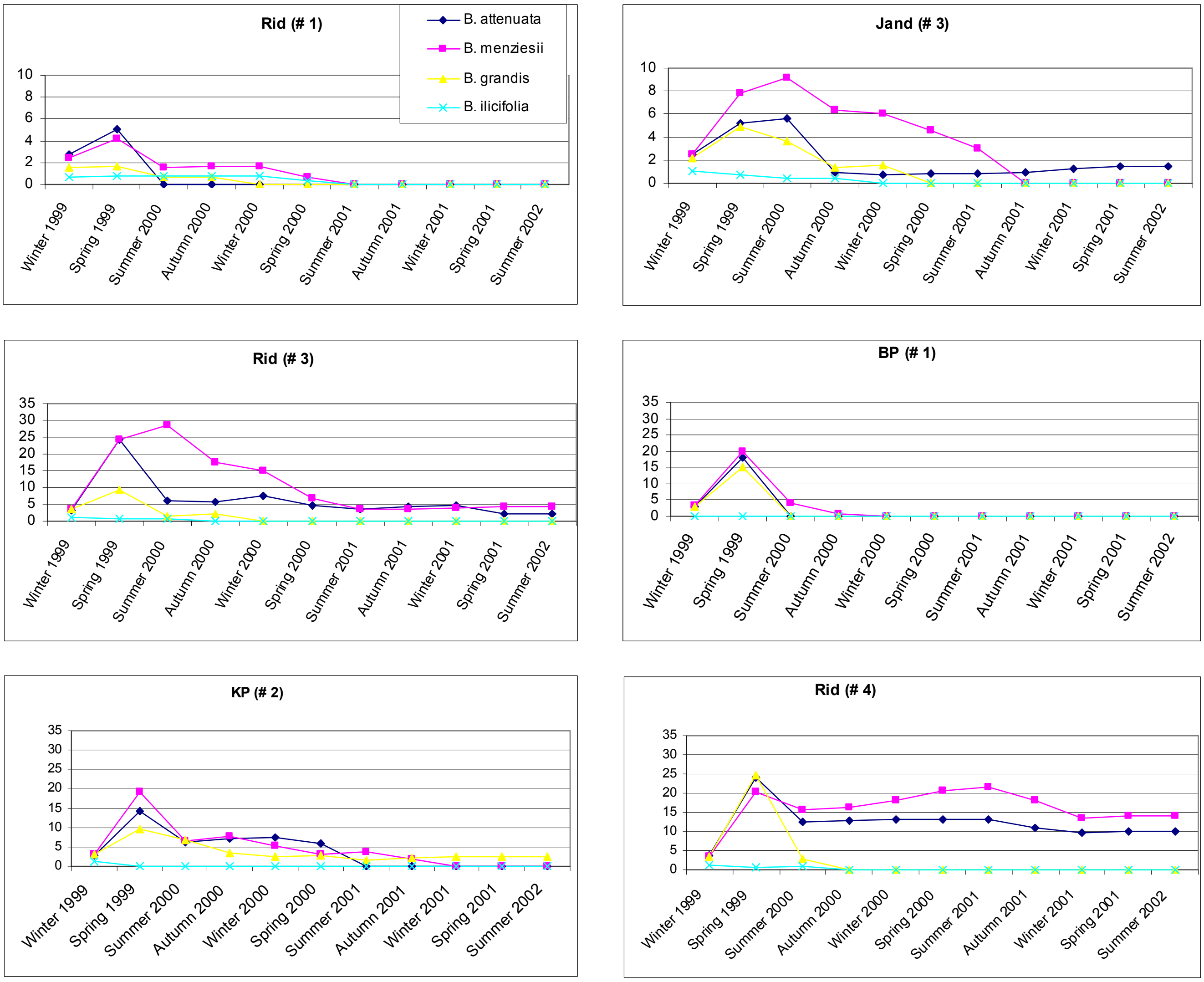
The “biomass index” (BI) showed, in all but the tip site, higher values only at the first spring (when many seedlings were still present). In some sites there were also high values of “BI” at the 2nd summer, however, these values were due to the presence of just a few taller seedlings (Figs. 5.21).

The most successful sites for recruitment were the Tip site in Kings Park (the Low competition site), followed by the two post-fire sites in the Ridges State Forest. However, the average size of seedlings in the Tip site was lower compared to the post-fire sites. Between the species, apart from *B. ilicifolia* that did not recruit in any site, there was no specific trend.

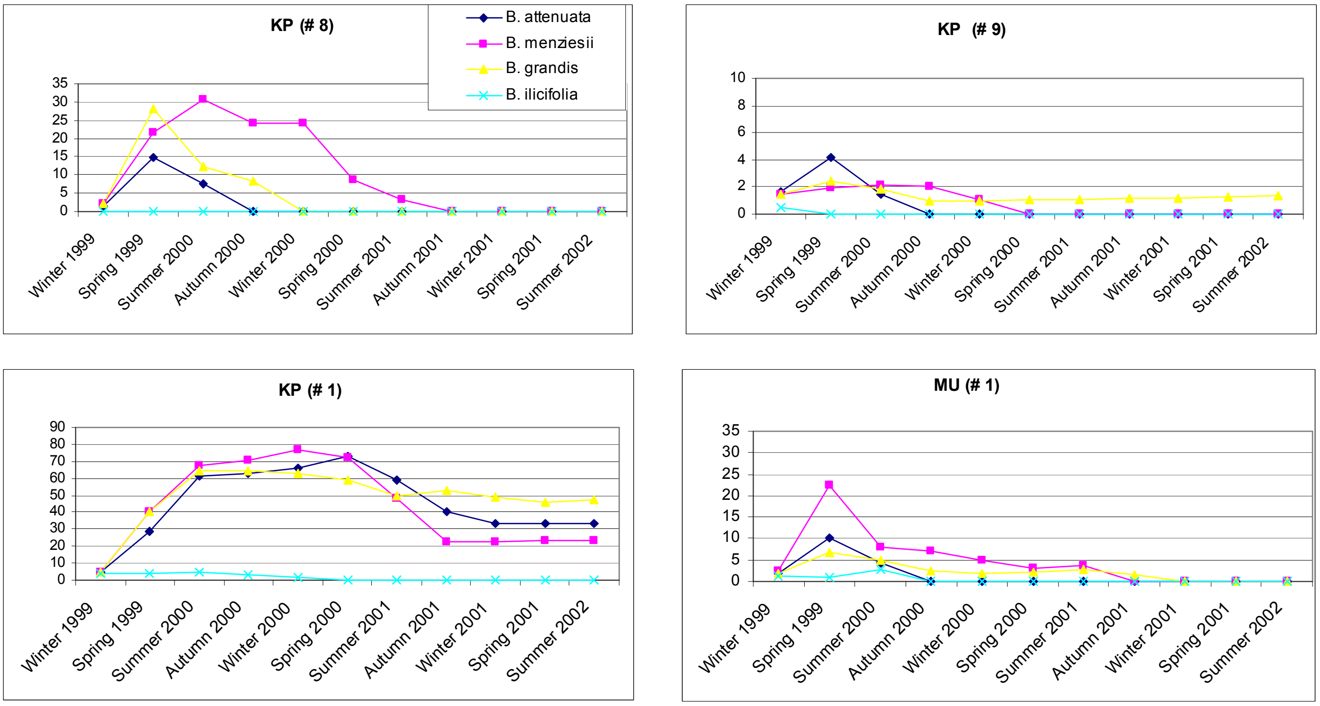
After nearly 3 years of monitoring, out of 4,000 buried seeds and 1,880 germinants only 91 seedlings survived, 97% of which were in the 3 “low competition” sites with sandy substrata (the Tip site and the post-fire sites). 83% of surviving seedlings were all concentrated in one site (the Tip site), and 11% in the two post-fire sites The type of environment was more important for seedling survival than for seed germination. Of the three sites where 97% of the total number of seedlings survived, only 48% of the sown seeds germinated (Figs 5.20 & 5.21).



Figs. 5.20 Number of seedlings, grouped for the different types of environments, for experimental unit (1mX 1m quadrat). Scoring was undertaken each season.



Figs. 5.21. Biomass Index, the sum of the heights of the seedlings for experimental unit (1mX 1m quadrat) for each site. Scoring was undertaken each season. See annex I for correspondence between # and site name.



Figs. 5.21. Biomass Index, the sum of the heights of the seedlings for experimental unit (1m X 1m quadrat) for each site. Scoring was undertaken each season. See annex I for correspondence between # and site name.

5.4.4.5 Discussion

For this manipulative experiment, seeds were placed in conditions conducive to germination with soil cultivated, seeds sown and soil watered for the first month. Nearly 50% of the seeds germinated which was higher than recorded for *B. integrifolia* seeds planted in cleared and uncleared microsites in mature banksia woodland in Victoria (Price and Morgan 2003). However, after 3 years only 2% of the planted seeds had recruited. Most of the seedlings were missing at the first scoring after summer endorsing the fact that in mediterranean-type vegetation the difficult period for seedling survival is the dry summer.

Absence of competitors and consequent increase in abundance of elements such as light, water and nutrients seems to be the best recruitment strategy for *Banksia* spp. In fact after three years of monitoring only 2,3% of 4.000 sown seeds survived as seedlings. However, in this present study it is likely that clearance of adult canopies from a site, rather than fire itself, favours recruitment. For seeds stored in post-fire soil, fire with its by-products, such as heat, chemical stimulants and changes in the microsites (Baskin and Baskin 1998) is a signal for seeds that a new environment with low competitors is present. *Banksia* seeds, however, have no such types of germination cue. Increased recruitment in post-fire conditions is dependent mainly on the number of seeds released by the follicles opening in the woody infructescence and for the microsite changes that increase the abundance of environmental factors such as light, water and nutrients at the soil level. In this experiment, the germination values of seeds sown in the post-fire habitat were higher than germination values of the seeds sown in the semi-pristine environment. In a weed-dominated environment germination is not much lower than in a semi-pristine environment, though seedling survival is much reduced. This is confirmed in this experiment, where no seedling survived in the two weedy sites. Similar results were shown in the KP dryandra site, the “high Competition” where the abundant presence of *Dryandra sessilis*, a native shrub with a weedy behaviour, reduced *Banksia* germination and recruitment.

5.4.5 F: Experiment in the glasshouse, investigating germination of Banksia spp, on different types of substrata

5.4.5.1 Introduction

Soil substrata have a major role in determining the composition and the diversity of plant communities. Leaf litter accumulation on the soil and weed proliferation are components that, if present, can influence early growth stages of perennial plant species as it is shown also in the tunnel house experiment later in this chapter. Recruitment of propagules is affected primarily by abundance of viable seeds, subsequently by seedling emergence and survival.

Leaf litter, especially of sclerophyllous leaves, can influence all recruitment stages by changing the physical, chemical and biological micro-habitat of sites suitable for seed germination and seedling survival (Rebollo et al. 2001).

Weed invasion progressively changes the flora composition either competing with the native plants or as a consequence in increasing the grass/fire cycle (Hopkins and Griffin 1989, D'Antonio et al 1992, Milberg and Lamont 1995). Furthermore the thickness and spread of underground root systems typical of the invasive species present in the ground layer of the banksia woodlands can reduce favourable germination sites.

5.4.5.2 Aim

The aim of this experiment in the glasshouse was to assess the response of *Banksia* germination and survival of germinants on different types of substrata under controlled conditions. The different substrata represented 5 different conditions on which *Banksia* seeds could be naturally or artificially dispersed.

5.4.5.3 Materials and Methods

A manipulative experiment was undertaken under a semi controlled environment in order to investigate the germination values and subsequent survival rates of three *Banksia* species of the Kings Park bushland in five different conditions. The investigated species were *B. attenuata*, *B. menziesii* and *B. grandis* (*B. ilicifolia* was omitted due to lack of seed).
Nursery trays (30cm x 45cm x 6cm) were filled with bushland sandy soil.
The experiment was undertaken with the following treatments:

1. Seeds were displayed on the surface of bare soil;
2. Seeds were buried under the bare soil;

3. Seeds were placed on the surface after dried leaves had been burned in the tray;
4. Seeds were placed on the surface after abundant leaf litter of native vegetation was laid on the tray;
5. Seeds were placed on the surface after mulch from native vegetation was laid on the tray. Mulch is compose by parts of plant material such as leaves in pieces and wood chips. The main functions of mulch is the conservation of soil moisture, the moderation of soil temperature and prevention from soil erosion. It is often used in restoration and gardening.

The five treatments attempted to create different scenarios on which *Banksia* seeds could be naturally dispersed (1-4) or disseminated in a restoration process (5).

Sandy soil was collected in the Kings Park bushland. For the burned treatment, the plastic parts of the trays were protected with aluminium foil and an oven-like cover consisting of a 35 cm perforated metal band within the sides of the tray. The "furnace" was filled with the dry parts of plants, collected in the bushland, in a quantity comparable to the natural accumulation of phytomass. Furthermore, to increase combustion, air was forced through with two small electric fans from two different points into the 'combustion chamber'; fire temperature, however, was not estimated.

In the leaf litter treatment, leaves collected in the bushland were placed on top of the soil in the tray, in a quantity similar to the leaf litter present in bushland areas not recently burned.

The experiment with mulch was undertaken to simulate manipulative dispersal and germination in a restoration process where mulch of native vegetation is usually used to retain soil moisture, reduce soil erosion and control weeds.

For each species there were four replicates with 25 seeds each. Trays were watered each two days to avoid water stress, germinants were monitored and survival recorded each week for 24 weeks.

Figures are expressed as mean percentage of germinants ± Standard Error.

Data from the experiment were tested for parametric assumptions with the Anderson-Darling Normality test and Levene's test for variance homogeneity; output showed that there was no or just mild violation of data distribution. Consequently a One Way ANOVA with Fisher LSD *post-hoc* test was carried out to examine differences between proportions of germinants.

For each treatment of the three species, the differences between values at the 9th and 24th (Fig. 5.22) weeks and within treatments comparing germination values at the 9th and 22^{4th} weeks were tested (Table 5.4).

5.4.5.4 Results

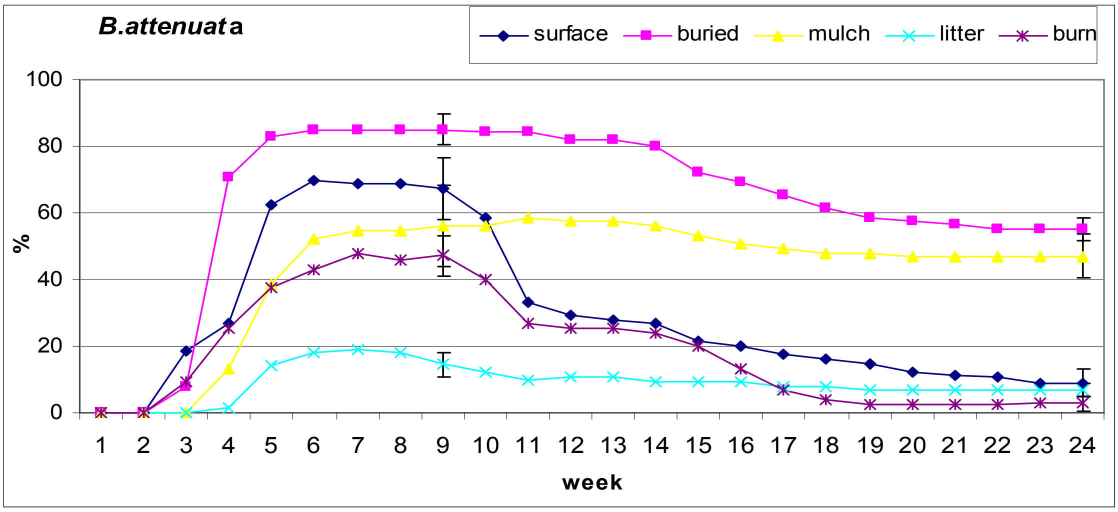
All the three *Banksia* species showed a similar trend. The number of germinants was higher for buried seeds followed by the treatments with seeds displayed on top of sand and on top of mulch. Lower numbers of germinants occurred in the leaf litter treatment. Germination started in all the treatments after the 3rd week and there were higher number of germinants in between the 6th and the 9th weeks.

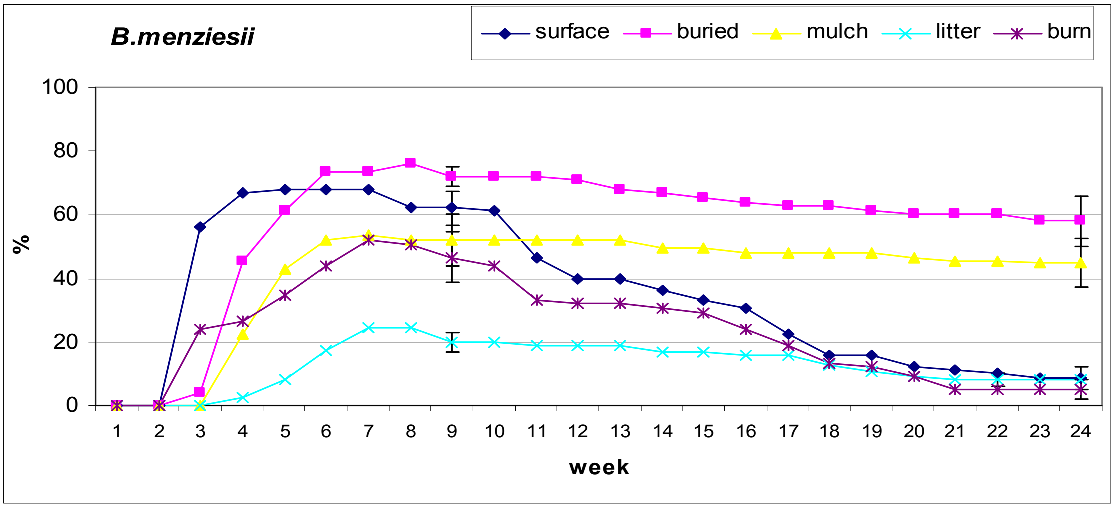
At the end of the experiment, most of the germinants in the treatments with seed placed on top of sand and on burned soil had died while, almost 50% of germinants in the buried and mulch treatment survived.

B. attenuata had respectively 85%, 70% and 58% germination for the buried, the surface and the mulch treatments, while only 48% and 20% germinated for the burn and the litter treatments. Statistical difference ($P<0.01$) in numbers of germinants, between the 9th and 24th week, was shown between the surface, the buried and the burn treatment (Figs. 5.22; Table 5.4), with lower survival values at the end of the experiment.

B. menziesii had slightly lower numbers of germinants, compared to *B. attenuata*, for the buried treatment at 73%, while other treatments showed similar values. Survival of germinants for the surface and the burn treatment at the 24th week was significantly lower (Fig. 5.22; Table 5.4; $P<0.01$) than at the 9th week

B. grandis germinant values for the surface, the burn and the mulch treatment were between 77% and 90%. Leaf litter treatment was just over 30%. Survival of germinants, at the end of the experiment, for the surface, the buried and the burn treatment was statistically lower ($P<0.01$) compared to the number of germinants at the 9th week (Figs. 5.22; Table 5.4).





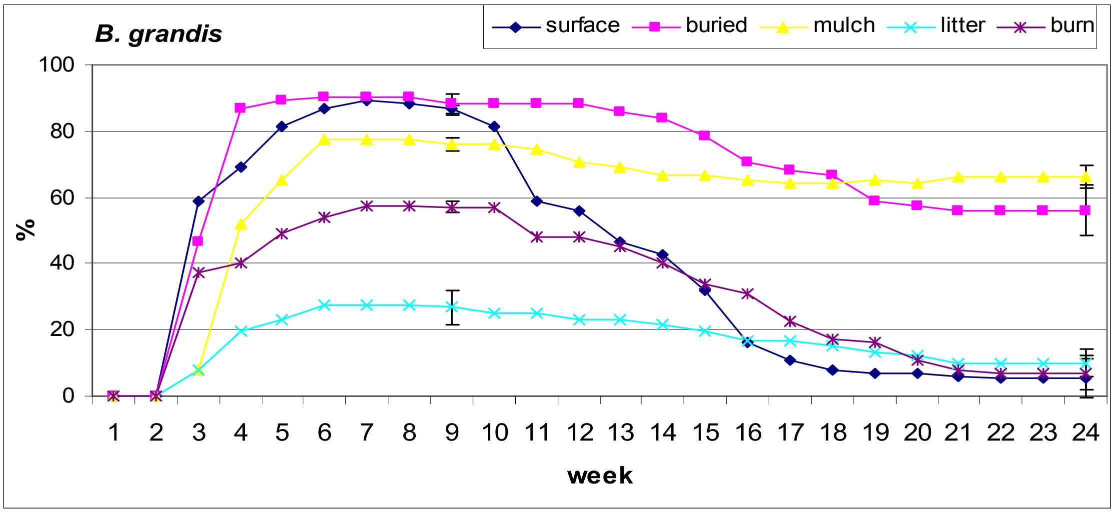


Figure 5.22. Weekly germination values of the 5 treatments. Values are mean of 4 replicates each with 25 seeds. SE bar present just for values at the 9th and 24th week only

Table 5.4. One way ANOVA testing differences between the 5 different treatments at the 9th and at the 24th week and within treatments comparing germination values at the 9th and 24th week for the *Banksia* species. * = P< 0.05; ** = P<0.01.; ***P<0.001

Banksia attenuata

week		treatment		Surface		Buried		Mulch		Leaf litter		Burned	
9	24			9	24	9	24	9	24	9	24	9	24
		Surface	9		**	*				**		**	
			24	**									
		Buried	9	*			**	**		**		**	
			24		**	**					**		**
***	***	Mulch	9			**				**		*	
			24		**						**		**
		Leaf litter	9	**		**		**			*	**	
			24				**		**	*			
		Burned	9	**									
			24				**		**			**	

Banksia menziesii

week		treatment		Surface		Buried		Mulch		Leaf litter		Burned	
9	24			9	24	9	24	9	24	9	24	9	24
		Surface	9		**			*		**		**	
			24	**			**		**				
		Buried	9				*	**		**		**	
			24		**	*			**		**		**
***	***	Mulch	9	*		**				**		**	
			24		**		**				**		**
		Leaf litter	9	**		**		**			*	**	
			24				**		**	*			
		Burned	9	**		**				**			**
			24									**	

Banksia grandis

week		treatment		Surface		Buried		Mulch		Leaf litter		Burned	
9	24			9	24	9	24	9	24	9	24	9	24
		Surface	9		**			**		**		**	
			24	**			**		**				
		Buried	9				**	**		**		**	
			24		**	**					**		**
***	***	Mulch	9	**		**			*	**			
			24		**			*			**		**
		Leaf litter	9	**		**		**			*	**	
			24				**		**	*			
		Burned	9	**		**				**			**
			24				**		**			**	

5.4.5.5 Discussion

The three *Banksia* spp. showed similar recruitment behaviour, across sites and treatments, both on germination and survival of germinants. Seeds perform better when buried or in the mulch treatment. Leaf litter, as found in other parts of this thesis and in other studies (Facelli & Pickett 1991; Hastwell and Facelli 2000) had a negative effect on germination although not on the survival of the germinants.

Survival of germinants was low for seeds displayed on the surface of the sandy soils such as the bare sand and the burned treatment. The reason is probably due to the difficulty for the roots to penetrate into the soil. Due to their flat shape the seeds tend to disperse with the embryo parallel to the surface and roots do not directly penetrate the soil. In addition the roughness of the soil, especially the burned surface could be a further obstacle for the appropriate development of the root, as in Harper and Benton (1966). The presence of plant material influences germination differently. While leaf litter reduced germination, mulch increased germination. The difference is probably due to the different type of barrier they make. The thick substratum of leaf litter, mainly formed by *Banksia* spp. and *Allocasuarina fraseriana* foliage, may act as a barrier for soil moisture preventing optimal germination conditions found in other treatments. However, most of the germinants reached the soil and survived by the 24th week. The equi-dimensional shape of mulch probably allows optimal moisture conditions for germination and most of the roots may have reached the soil. When seeds were buried in sand or displayed on mulch, where seeds can bury themselves more easily, germinants survived much better than the seeds displayed on sand or burned sand.

Between the five different treatments, the most appropriate to favour seed germination and propagules survival are those buried in the soil and displayed on mulch; consequently, in any restoration project for the conservation of *Banksia* species, seeds should be treated in a similar way when disseminated in the field.

5.4.6 G: Experiment in the tunnel house with all species on different substrata as in the B field experiment

5.4.6.1 Aim

The aim of this small-scale greenhouse experiment was to evaluate the effect of different types of substrata on seedling emergence (seed germination) and seedling establishment (survival of saplings) of the selected species in relatively controlled conditions.

5.4.6.2 Materials and Methods

In the Kings Park bushland, areas with different soil substrata such as: bushland sandy soil, weeds, leaf litter were selected. For each substratum randomly selected sods of soil were carefully excavated with a shovel and placed in nursery trays (30 X 45 X 6 cm). In order to avoid the presence of seeds in the soil, sods were excavated in areas distant from tree canopies. Sods of soil represented common microcosms of the "above ground" part of *Banksia* woodlands on the Swan Coastal Plain.

Each sod sample was a statistical unit and each treatment was replicated four times. To each sod sample 25 seeds for each of the 8 species were added for the 4 treatments. Consequently for the trial there were a total of 96 trays (8 species x 3 treatments x 4 replicates).

The sod samples in the trays were arranged randomly in an uncontrolled temperate greenhouse (tunnel house) and watered regularly so that water stress was minimal; substrata in the tunnel house were: leaf litter on bushland soil, bare sandy bushland soil and weeds. The species used in this experiment were: *Banksia attenuata, B. menziesii, B. ilicifolia, Dryandra sessilis*, *Eucalyptus marginata*, *Allocasuarina fraseriana*, *Acacia saligna* and *A. pulchella*.

Compared to the 'field' treatments described in the B section of this chapter, the treatments in the tunnel house were lacking the substrata with native species and the "TIP soil" as these were considered only for the "field" experiment.

The experiment started in autumn and was monitored for 24 weeks. The results as a mean percentage of germination of the four treatments are displayed as line graphs with all the periodic scoring and as a bar chart only with results of the 9th week (usually higher germination) compared with the 24th (the end of the experiment). The standard error bar represents ± 1 Standard Error.

For each species (population level) differences between number of germinants at the 9th and at the 24th week was statistically tested together with the differences between the 8 species (community level) at the 9th and then at the 24th week.

Seedling establishment was assessed through difference in seedling numbers between the 9th and the 24th weeks.

Prior to analysis all data were examined for homogeneity of variances and normal distribution) and when necessary transformed in order to use parametric statistical tests such as ANOVA. The null hypotheses were:

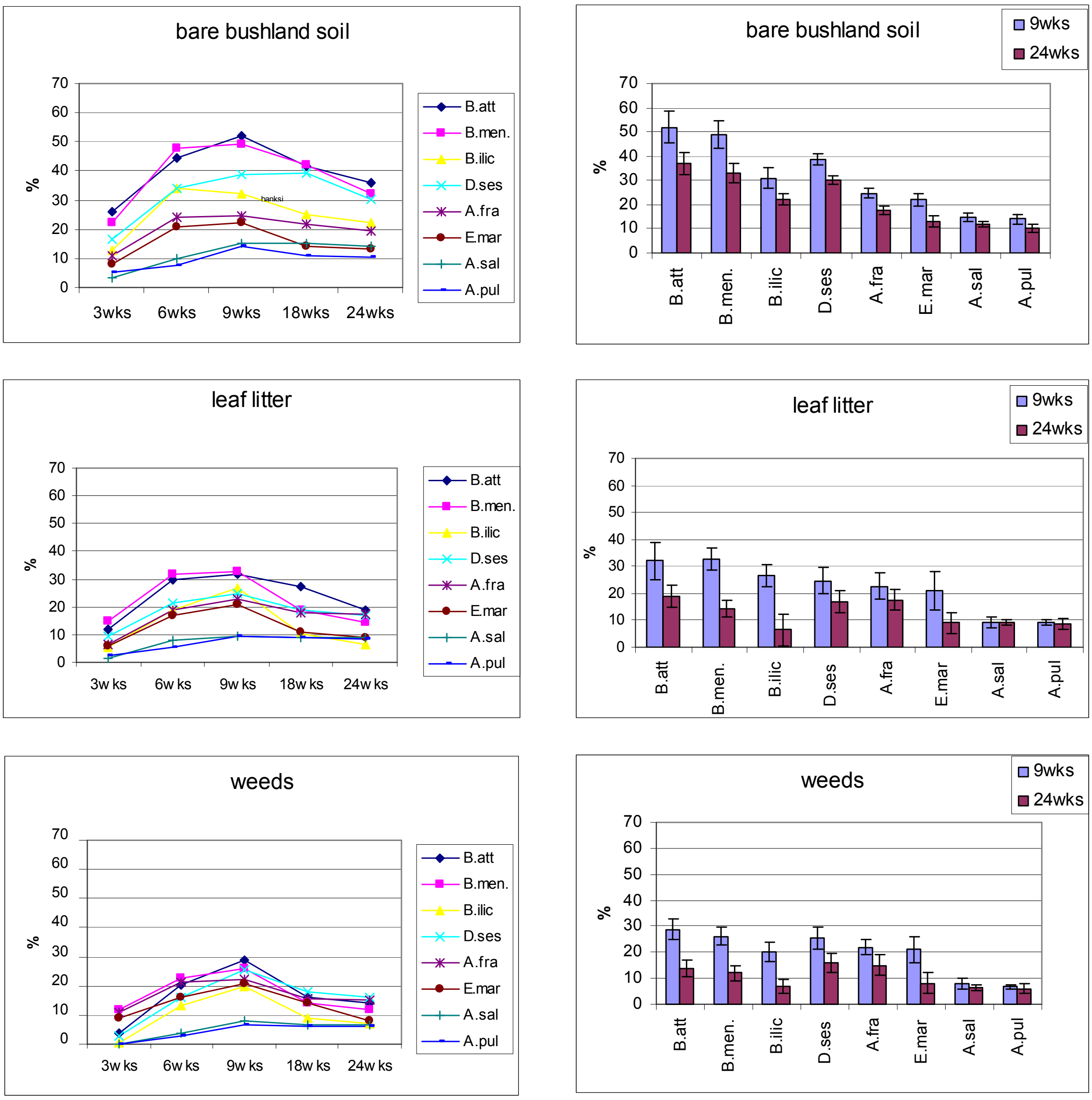
all the investigated species (community level) have the same mean for number of germinants, hypothesis tested at the 9th and at the 24th week; the single species (population level) have the same mean number of germinants at the 9th and the 24th week (table 5.5).

5.4.6.3 Results

In the glasshouse all the Proteaceae had higher germination values in contrast to the other four species; in particular *Banksia attenuata* and *B. menziesii* had higher values compared to *Dryandra sessilis* and *B. ilicifolia* while legumes had lower germination values. On sandy bushland soil germination was higher than on leaf litter and on weeds. For the *Banksia* species germination values were approximately 50% and were reached after 9th week. On the weeds substratum germination was, instead, reduced for all species to below 30% (Figs. 5.23).

Statistical difference, between the 9th and the 24th week ($P<0.01$) was assessed mainly for the *Banksia* across all treatments (Table 5.5). The results for the treatment on leaf litter and weeds were similar.

The two acacias had similar low germination values across all treatments and difference between the 9th and 24th weeks in number of germinants was low.



Figs. 5.23. Results for the three different treatments: bare bushland soil, leaf litter, weeds. Results displayed as: line graph with the percentage of the 4 replicates at different period of time: 3, 6, 9, 18, 24 weeks; mean percentage as bar chart with results of the 9th week and the 24th, ± 1 Standard Error.

Tables 5.5 Results for the three different treatments: leaf litter, weeds and bare bushland soil. *= P<0.5; ** = P<0.01; *** = P<0.001.
Abbreviations: B.att.= *Banksia attenuata*; B. menz= *B. menziesii*; B.gra= *B. grandis*; B.ilic= *B. ilicifolia*; D.sess= *Dryandra sessilis* ; E.mar= *Eucalyptus marginata*; A. fras= *Allocasuarina fraseriana*; A.sal= *Acacia saligna*; A.pul= *A. pulchella*.

Leaf litter

week		species		B.att		B.men.		B.ilic		D.ses		A.fra		E.mar		A.sal		A.pul	
9	24			9	24	9	24	9	24	9	24	9	24	9	24	9	24	9	24
		B.attenuata	9		**			*		*		*		*		**		**	
			24	**															
		B.menziesii	9				**			*		*		*		**		**	
			24			**													
		B.ilicifolia	9	*					**							*		*	
			24					**											
		D.sessilis	9	*		*					*					*		*	
			24							*									
**		*A.fraseriana*	9	*		*				*						*		*	
			24						*										
		E.marginata	9	*		*		*							*	*		*	
			24											*					
		A.saligna	9	**		**		*		*		*		*					
			24																
		A.pulchella	9	**		**		*		*		*		*					
			24																

Weeds

week		species		B.att		B.men.		B.ilic		D.ses		A.fra		E.mar		A.sal		A.pul	
9	24			9	24	9	24	9	24	9	24	9	24	9	24	9	24	9	24
		B.attenuata	9		**											**		**	
			24	**															
		B.menziesii	9				**									**		**	
			24			**													
		B.ilicifolia	9						**							**		**	
			24					**											
		D.sessilis	9													**		**	
			24																
*		*A.fraseriana*	9													**		**	
			24																
		E.marginata	9												*	*		*	
			24											*					
		A.saligna	9	**		**		**		**		**		*					
			24																
		A.pulchella	9	**		**		**		**		**		*					
			24																

Bare bushland soil

week		species		B.att		B.men.		B.ilic		D.ses		A.fra		E.mar		A.sal		A.pul	
9	24			9	24	9	24	9	24	9	24	9	24	9	24	9	24	9	24
		B.attenuata	9	▨	*		▨	**	▨	*	▨	**	▨	**	▨	***	▨	***	▨
			24	*	▨	▨		▨	*	▨		▨	**	▨	**	▨	**	▨	**
		B.menziesii	9		▨	▨	*	**	▨		▨	*	▨	**	▨	***	▨	***	▨
			24	▨		*	▨	▨	*	▨		▨	**	▨	**	▨	**	▨	**
		B.ilicifolia	9	**	▨	**	▨	▨	*	*	▨	*	▨	*	▨	**	▨	**	▨
			24	▨	*	▨	*	*	▨	▨	*	▨		▨	*	▨	*	▨	*
		D.sessilis	9	*	▨	*	▨	*	▨	▨	*	*	▨	*	▨	**	▨	**	▨
***	**		24	▨		▨		▨	*	*	▨	▨	*	▨	*	▨	*	▨	**
		A.fraseriana	9	**	▨	**	▨	*	▨	*	▨	▨			▨	*	▨	*	▨
			24	▨	**	▨	**	▨		▨	*		▨	▨		▨		▨	*
		E.marginata	9	**	▨	**	▨	*	▨	*	▨		▨	▨	*	*	▨	*	▨
			24	▨	**	▨	**	▨	*	▨	**	▨	*	*	▨	▨		▨	*
		A.saligna	9	***	▨	***	▨	**	▨	**	▨	*	▨	*	▨	▨			▨
			24	▨	**	▨	**	▨	*	▨	*	▨	*	▨			▨	▨	
		A.pulchella	9	***	▨	***	▨	**	▨	**	▨	*	▨	*	▨		▨	▨	
			24	▨	**	▨	**	▨	*	▨	*	▨	*	▨		▨			▨

5.4.6.4 Discussion

Banksia attenuata and *B. menziesii* in all the substrata and in all the different treatments in the greenhouse in accordance with their larger size had higher germination values than the other species. The mortality of *Banksia* seedlings that did emerge was relatively high in all the substrata and in all the treatments. However leaf litter and weed treatments showed greater decreases between germinants at the 9th week compared to the 24th week than did the bare soil treatment. *Banksia ilicifolia* seemed particularly disadvantaged in the germination and seedling survival stakes having a much smaller seed but a similar level of mortality rate to the the other two banksia species with larger seeds.

There was a negative influence of weeds and leaf litter substrata on germination of all the species. Weeds and leaf litter may intercept many seeds preventing them from reaching a suitable micro-habitat for survival leading ultimately to death. It was observed that the newly emerged roots of the investigated species often did not reach the soil and this was a particular problem for the larger banksia seeds. Furthermore a stratum of leaf litter can host seed predators and pathogens which can damage the delicate newly produced radicle and plumule.

While *E. marginata* and *A. fraseriana* compared to *Banksia*, showed reduced germination, the relative severity of reduction in germination and survival of seedlings was less for these species in the weeds and litter treatments than for the banksias. In particular *A. fraseriana* and the two investigated acacias across all treatments had low germination values but high survival rates.

Acacia spp. had smaller germination values across all the treatments than other species. The seeds accumulate as part of the persistent soil seed bank of the *Banksia* woodland and the presence of a hard seed coat allows the seed to resist mechanical damage and protects it from pathogens. However, this characteristic of the testa waterproofs the seed coat preventing the seed inside from absorbing water. Consequently the seed needs "ageing" or heating to allow water to enter the coat and start germination, so lower values would be expected in comparison to the non hardseeded species

The tunnel house results for the banksia species reinforce the findings from the more controlled glasshouse trial (section E of this chapter). Leaf litter is inimical to germination and establishment of banksia seeds and aspects of the adverse effects of weed coverage are likely to also be related to the same sort of effect on the physical microenvironment experienced by the seed. Also other studies found out that woody seedlings were more common with a lower litter cover, both in xeric (Hastwell and Facelli 2000) and fire-dominated (Matlack and Good 1989) plant communities.

In comparison with the experiment reported in section B the same pattern is evident in the field but with lower germination and survival in the less well controlled field conditions. This emphasises that water availability is one of the most critical factors in seed germination and establishment if predators are absent. The fact that burning the soil surface was disadvantageous to germination and seedling survival shows that fire itself is not useful to these banksia species except in that it removes competitors and leaf litter, which is beneficial. However, for the acacia species fire would have improved germination, as they are hardseeded but this was not tested here. For the other species fire would remove competition but the removal of litter is not relatively as advantageous to them as it is to the banksias.

The two glasshouse experiments also highlighted the role of empirical research in controlled conditions to analyse limited factors isolated from the complex interaction in the field.

5.5 General discussion

This section of the study of vegetation change in Kings Park concentrated on the germination and establishment of seeds and seedlings to unravel the details of behaviour of the species in relation to disturbance and stasis. Many studies of regeneration in Mediterranean-type vegetation focus on the influence of fire, as it is such a ubiquitous factor in community change and because there are such obvious changes over a short time (Bond and van Wilgen 1996; Ladd et al.et al. 2005) as plants re-grow and re-establish. Relatively little attention is given to vegetation processes between disturbance events.

Despite the high proportion of serotinous species in Australian fire prone communities many species with cone-like infructescences either are not serotinous (eg., Ladd 1989) or vary in the degree of serotiny in relation to location within their range (Enright and Lamont 1992; Enright *et al.* 1998; Tieu *et al.* 2001a). This variation means that precise conditions that enable the most effective establishment are closely related to the local habitat and cannot be predicted from studies in other areas, even if studies have been on the same species.

In the investigation on the germination of seeds and establishment of seedlings of *Banksia* spp. undertaken, through surveys (survey described in A) and manipulative experiment in the bushland (experiments described from B to E), in this study clearly the microsite most suitable for germination and establishment is bare sand. This confirms the fact that the increased germination after burning is mainly due to production of new sites available for germination (Enright and Lamont 1989). The poor survival of seedlings on burnt substrate in the tunnelhouse also emphasises that burnt soil itself is not particularly beneficial to the seeds for germination. This is similar to results for *B. serrata* from NSW where there was no greater establishment of seedlings early after fire than on sites burnt several years before (Denham et al. 2011). Absence of vegetation, both native and exotic, increases germination values and final recruitment. Lack of competitors, and the consequent larger availability of the main resources such as light, nutrients and water, is the primary environmental condition to favour recruitment, especially in a Mediterranean-type climate on low nutrients soils.

Higher values of natural germination can be found on sandy substrata while presence of weeds, thick layer of leaf litter, proteoid roots and native vegetation reduces germination and establishment. This trend was confirmed in both post-fire and inter-fire conditions, *Banksia* species are particularly affected as the magnitude of seed set is smaller compared to the other competitor tree species and the presence of sandy soils, free of other species and of organic matter, is the only substratum where the first stages of recruitment are more effective. In the partially controlled environmental conditions of the tunnel house the larger seeded species had higher germination than the smaller seeded species. The legumes had the lowest germination as would be expected, as the seeds were not treated to disrupt the seed coat. Many acacias have seed populations with variable hardseededness so some seeds will germinate without heat or abrasion of the seed coat. After fire, germination of banksias is often aggregated in clumps where seeds are likely converged by wind and "running" water together with leaves and, in post-fire conditions, burn residuals. Unlike bare burnt soil there is some advantage for germination as this "clumpy medium" helps the retention of humidity (as for mulch in the glasshouse experiment) and provides protection from predation (previous chapter). In unburnt bushland of Kings Park relatively bare sandy soils comprise only about 10% of the area so suitable microsites are sparse. In pre-European time medium sized mammals such as the woylie and quenda (*Isoodon obesulus*) would most likely have been present in the Kings Park area. These animals can create quite dense shallow diggings in their search for food and this would have increased the proportion of bare sandy substrate in the past. In semi-pristine conditions germinant establishment was less than 1%, confirming the delicate recruitment process of *Banksia* spp. In both the field and glasshouse survival of seedlings decreased over time. Moisture is clearly the main requirement to begin germination for the species studied here. However, in some cases continual high humidity could be detrimental due to the enhancement of conditions conducive to fungal attack that may have been the cause of some early seedling deaths in litter treatments.

In this study *B. attenuata* and *B. menziesii* have been an important focus of attention as they are the characteristic banksia species of the Kings Park vegetation. While *B. grandis* and *B. ilicifolia* are present in Kings Park the location is not part of their core range – *B. grandis* being much more prevalent on lateritic soils of the Darling Range and further south of Perth, and *B. ilicifolia* commonly associated with the margins of wetlands or sites where the water table is close to the soil surface. Both species are found more frequently in more humid locations and are less well adapted to the Kings Park environment, especially as the climate in the south west of Western Australia has progressively dried over the last several decades (CSIRO 2007).

Banksia seeds are initially retained within the woody infructescence before being released from the mother plant. However, in the presence of an unpredictable fire regime and predation a minimal time interval between seed release and favourable germination conditions will aid the likelihood of establishment. Furthermore seed desiccation due to long exposition of seed in dry and hot condition can reduce seed viability. The four *Banksia* species release most of their seeds in the first summer/autumn after flowering (they are weakly to nonserotinous). *Banksia menziesii* and *B. ilicifolia* are likely to shed seeds in summer/early autumn while in *B. attenuata* and *B. grandis* seed fall is later in Autumn (Abbott 1985b, for *B. grandis*). According to the period of the year of seed drop seed quantity in the soil bank and seed viability can vary. When the manipulative experiment in the field (described in C & D), simulated seeds released in different periods of the year, early autumn and early summer, consequently with different time spent in the soil seed bank, the long exposure reduced final seed germination showing that seeds that spent more time on the soil are more likely to have a lower germination success.

Fruit maturity and seed fall also interacts with fire, as the season of a fire will influence the individual species differently. A fire in mid summer would destroy inflorescences on *B. attenuata* and *B. grandis* leading to few seeds shed after the fire while the seedbank of *B. menziesii* would be almost intact to be shed onto the burnt soil. Alternatively a late autumn fire would burn any *B. menziesii* seeds already on the ground but would release *B. attenuata* and *B. grandis* seeds *en mass* to lie for a short period on the ground before the winter rains arrived to stimulate germination. In most years however, fire does not occur but all species will still release seeds. For instance *B. grandis* recruits every year in the forest at Ashenden south of Perth (Abbott 1985a). Little is know about recruitment in *B. ilicifolia* but it may require a consistently moist substrate as the seed is the smallest in the four species and the plants normally grow in areas with shallow water tables. Fires have occurred at different times of the year in Kings Park but unfortunately there has been little detailed follow up research to quantify seedling establishment after each fire. Baird (1979) reported general observations of regeneration after fires in different seasons and concluded that spring burns favoured shrubs and autumn burns herbaceous plants, but detailed assessment of seedling recruitment for the trees (except *A. fraseriana*) was not reported. After a fire in March 1952 abundant seedling regeneration of *A. fraseriana* was observed under female adult trees but most were destroyed in a subsequent fire in Spring 1954 (Baird 1979). Unfortunately seedling regeneration after this fire did not seem to be assessed.

Predation, both before and after seed dispersal, was quite aggressive in Kings Park decreasing possible seedling recruitment, with other locations not suffering from the same degree of seed removal (Chapter 4). Predation of seeds has been identified as limiting recruitment in *Grevillea* spp. Vaughton 1998; Regan et al. 2003) and *Telopea* (Denham 2008), and it is recognised that masting seed release from serotinous eucalypt capsules is one way of overcoming this (Wellington and Noble 1985b; O'Dowd et al. 1984). Herbivory has also been recognised as a problem for regeneration once seeds have germinated (Price and Heinz 1984; Abbott 1985b; Price and Morgan 2003; Yates et al. 2003) but this is not important in Kings Park where grazing animals have long been absent.

The experiment in the greenhouse (described in F & G) confirmed the results of the different surveys and of the manipulative experiment undertaken directly in the bushland. The poor germination of seeds on weedy substrates indicates the adverse influence of a dense understorey. When different types of habitat (different substrata taken directly for the bushland) were replicated in the glasshouse most of the germination and of the germinant survival occurred on bare sandy soils while on substrata with weed or leaf litter germination was reduced. This contrasts with evidence from *B. integrifolia* forest in Victoria where ground layer vegetation facilitated early seedling survival (Price and Morgan 2003).

In particular no advantages occurred for *Banksia* seeds when left to germinate and establish on burned soil, especially compared to seed buried under sandy soil or displayed on mulch. This confirms that it is the greater available space and more light, nutrients and water that favours the recruitment process rather than the burning itself. The inability of seedlings to root properly, possible allelopathy, diseases due to pathogens, competition with weedy species for space, light, nutrients and water are likely the main obstacles for *Banksia* recruitment on litter or in weedy locations.

The facility to successfully recruit between fires is somewhat similar to the situation in chaparral (Lloret and Zedler 1991) and the Mediterranean basin (Ladd et al.et al. 2005) where sprouter species are most often recruited inter-fire rather than immediately after fire. *Telopea speciosissima* recruits most successfully several years after fire in NSW where its rapid germination after water is provided is considered to be an adaptation to avoiding seed predators (Denham et al 2011). The thick follicle walls of the banksia species' fruits provide heat protection so all species can also derive benefit from a fire at the correct season for their seed release. This is mainly an advantage of synchronising and maximising seed release when there is abundant open ground. The fact that all the species are fire resistant to some extent means that many adults also survive a fire as large individuals that will quickly resume seed production, so recruitment failure due to inclement weather or grazing pressure is buffered by the trees' vegetative recovery.

In the field study, comparison between germination and survival started with the same number of seeds for each replicate (n=25). However, taking into consideration the different magnitude of seed production of each species, recruitment potential may have been different. Large-seeded species usually produce fewer seeds compared to small-seeded species (Henerey & Westoby 2001). If the results had been adjusted to the real community seed set, the species with smaller seeds such as *A. fraseriana*, *D. sessilis, E. marginata* and *A. saligna*, which produce many more seeds than banksias, would have shown a greater number of offspring compared to the banksias. However, seed size (mass) also relates to drought survival over summer. Summer drought survival increased with seed mass of taxa over several families (including banksias) in a field trial in the Gnangara area lass than 50 km north of Kings Park (Hallett et al. 2011) so the lower number of banksia seeds produced compared with other smaller seeded species is to some extent counteracted by the large seed size making banksias more likely to survive dry conditions than smaller seeded species. The timing of seed release (or germination cue) and its relationship to the site condition and soil moisture levels in the period following germination will all influence the success or otherwise of plant establishment.

The detailed information gained from this section of the study helps in visualising how regeneration of several key species in Kings Park occurs. This then needs to be put together with the information on predation, fire histories and the biology of some of the other species in the Park to provide a synthesis of the vegetation and plant community changes in Kings Park over the last 100 – 200 years. This is covered in the final chapter of the thesis.

6 CHAPTER 6: CONCLUSION

In some cities there are tracts of wild land that have been reserved as public open space. While they also provide a location for recreation their main purpose is to conserve remnants of the native vegetation and/or to generally intersperse urban development with what are considered "natural" areas. In Perth, the Kings Park bushland was set aside as a reserve in 1871 (Main and Serventy 1957) and nowadays the Park and the botanic gardens are visited by over five million people each year. Consequently it is the most popular visitor destination in Western Australia. The total area of the park and gardens is 400.6 hectares and it is located adjacent to the Swan River, approximately 1.5 km from the Central Business District of Perth. In the Kings Park bushland (approximately 260 hectares) 324 species of local native plants occur, which represents about 15% of the native flora of the Perth Region.

The initial reservation of the eastern part of Kings Park (referred to as The Park or Mt Eliza, 166 ha) was made very soon after the establishment of the Swan River colony. In 1831 John Septimus Roe (the surveyor general) refused an application to cut timber in the area as it was "to be reserved for public purposes" (Erikson 2009). Nonetheless, the reserved land was used and modified in various ways in the 1800s. In the western part timber was harvested by convicts between 1850 and 1868 and sawn in pits (Erikson 2009). Further land to the west was added in 1890 to bring the Reserve to approximately its current size. Over the years since 1900 there have been many attempts to excise parts of the Park for public buildings such as hospitals; however, local conservation groups have been steadfast in their support for a "native park" (Main and Serventy 1957).

Because of the urban context, biological isolation and high perimeter to area ratio, managing the Park is a considerable challenge that depends on several sources of information, including knowledge of past land-use, characteristics of the original vegetation, recruitment processes, frequency and the extent of significant disturbances. As the Park contains in part "natural" or semi-natural bushland knowledge of the vegetation dynamics and the impact of past and current management is essential for successful conservation. However, this knowledge is often difficult to obtain because changes in vegetation – in response to management – are most likely to occur over many decades, beyond the average time of research careers and most research projects. There is therefore a dearth of historical quantitative monitoring of vegetation through direct observation. In 1999, however, a chance find in the Kings Park and

Botanic Gardens archives of a 1939 map (by Alison Baird) with positions, along transects, of individual plants of 13 dominant native tree and shrubs species, occurring in a portion of the Kings Park *Banksia* bushland, allowed vegetational changes to be quantified over time. The same transect was resurveyed with the aim of determining whether the composition and structure of the vegetation had changed in 60 years.

The present structure of the vegetation and composition of the plant communities is a culmination of the response of the species to environmental influences including fires, climatic variation over time and human exploitation/interference in the area. It is apparent that the vegetation and community composition is not uniform over the reserve. In the 1950s Tuart woodland vegetation seemed to have been characteristic of the western and south western parts while banksia, casuarina and jarrah were more prominent in the eastern and northern parts, and this may be related to edaphic factors (Baird 1977).

While public interest in the Park has been high throughout its existence it was not until the mid 20th century that scientific study by botanists and ecologists began to try to understand the dynamics of the system. Papers on Kings Park vegetation were published at a decadal scale during this time and two of the early scientists – Beard (1967) and Baird (1977) commented on the "degeneration" of the vegetation and attributed this to several causes, notably the cutting of trees for lumber and damage from fires.

Main and Serventy (1957) considered that the Kings Park vegetation, dominated by *E gomphocephala* and *E. marginata*, was the "climax state" of a succession. However, due to the disturbance present in the Park (timber-getting, grazing, burning, weeds) the climax state had regressed to a previous successional stage. It was noted that the ground had sparse plant cover due to fallen branchlets and dense shade of *A. fraseriana*. This dense litter accumulation was also apparent in the present study and was associated with poor establishment of banksia seedlings. Beard (1967) also recognized tuart as formerly being one of the main dominant trees in the Park, in part because it is the species with the highest potential for height growth at this location. Early settlers (1831, 1836) further south in the State commented on the "fine park-like" appearance of tuart vegetation and the grassy understorey throughout that area (Haswell and Walker 2003). Throughout Kings Park the density of tuart trees varies from none to 47.5 ha^{-1} (Crosti et al. 2007), 5 – 23 ha^{-1} (Ruthrof et al. 2003) and 14 ha^{-1} (Beard 1967). In contrast to the early 1800s descriptions of "fine trees" on the southern coastal plain, the larger trees in Kings Park in the 1960's were recorded as being mostly unhealthy (Beard 1967) and this was representative of the Perth area generally at that time (Fox and Curry 1979). The large, often stage-headed tuarts, were indicative of a woodland structure but were surrounded by lower stature species. According to Beard the bushland was undergoing a process of replacement, where the tall open woodland dominated by eucalypts was being replaced by lower, denser bushland species such as *Banksia* spp. and *A. fraseriana*.

Ten years later, Alison. M Baird (1977) suggested that the historical disturbance regime of Kings Park and particularly the high fire frequency, not only adversely affected the dominant species such as *E. gomphocephala* and *E. marginata,* but concurrently facilitated weed invasion. The 1939 survey map made by Baird (chapter 2), that was the impetus for this project, had no accompanying notes and it was not possible to determine tree condition from the map. So it is not possible to speculate on the health of trees at the time of that survey, although Baird's (1977) paper implied that tree health of the eucalypts was not particularly good. Fires in Kings Park at that time mainly fell into two groups: devastating wildfires in mid-summer (January to February) and mild burns over smaller areas that occurred in spring and autumn (Baird 1977). The high frequency of intense fires, as well as competition from the understorey and its weed species, caused more damage to the fire-sensitive species and reduced seedling recruitment. Indeed, Baird noted that preventing fire over a 15 year period resulted in a gradual decrease in the number of *Ehrharta calycina* tussocks, the main weedy perennial grass in the Park.

In the last 20 years or so there has been considerable concern and debate about eucalypt dieback/decline in southern Australia. The causes of this tree decline encompass a range of factors from invertebrate and vertebrate herbivores, soil salinity, fire regime changes, to parasite infestation (Jurskis and Turner 2002). In most cases, the affected vegetation has been of isolated trees on farms or forest patches in the lower parts of the landscape. Inter-related combinations of environmental and biological factors have been held responsible for the decline in tree health. Forest patch changes in forest understories have been observed to accompany decline in eucalypt health. The decline in health of tuart trees in Kings Park show many similar characteristics to forest decline in other parts of Australia.

Jurskis (2005) advanced a simple model to explain forest decline throughout temperate Australia. Protection of forests from frequent fire has led to changes in the soil nutrient environment (increasing nitrogen and decreasing phosphorus) and to the development of more “mesic” understories that encourage the development of root disease particularly in the “*Monocalyptus”* group of the eucalypts. However, most researchers who have commented over the last 70 years on the vegetation of Kings Park and neighbouring Bold Park (Fisher et al. 2009) have blamed frequent fires for the decline in tree health. Main and Serventy (1957) decried the damage caused by severe summer fires but argued that early summer cool burns were an advantage if they prevented more severe fires.

The species in Kings Park, like those throughout the south west of Western Australia, have evolved in a fire prone environment. Fire was present in the Western Australian landscape well before humans arrived (Hassell and Dodson 2003) and once Aborigines arrived in Australia, fire regimes undoubtedly changed due to human utilization of fire for hunting and landscape management. Unfortunately it is not possible to completely understand the pre-Eurpoean fire regimes but fires were certainly recorded as frequent occurrences in the landscape in the early 1800s (Abbott 2003). It is also clear that fires occurred in Kings Park in the 1800s but there are no specific records of these. A graph of fire number per year from 1944 – 2005 indicates that fires have been less frequent since the 1980’s than they were from 1944 – 1980 (Erikson 2009). It is inevitable that the fire regime, in terms of frequency and intensity, has varied over the 200 years since European settlement and that it differs from the practices by the Aborigines prior to 1800. The fire history of sites surveyed in this present study varied from none to two over the 60 years.

In the late 1960’s Beard (1967) surveyed a central part of the park (more to the east of Baird’s survey area) and noted the poor condition of the tuart trees and the proliferation of banksia and casuarina. He attributed this to lessening of the competitive advantage of the large trees over the smaller understorey trees and shrubs, because of the tree canopy being opened up by logging in the past. This put more pressure on soil moisture resources for the tuart tree layer that in turn became more moribund as the smaller trees became more abundant. A further examination of this same area in 2007 (Ladd et al. 2007) confirmed that some large moribund tuarts had died but other tuart saplings had recruited and casuarinas had certainly become more abundant, but that in contrast to Beard’s prediction, banksias were much less common. This finding correlated to the situation in Baird’s mapped area.

Beard’s contention that the lower stature trees put pressure on soil moisture resources for large tuarts is similar to more recent investigation into tuarts about 130 km south of Perth.

Tuart overstorey trees in long unburnt sites (last burnt 1972) had poorer health and denser understorey vegetation than in more frequently burnt areas (every 5 – 15 years, Close et al. 2011). Close et al. argued that the thickening of the understorey and higher nitrate levels in the soil induce changes in the ecological processes of the vegetation. In addition, trees in the long unburnt sites had carbon isotope ratios in the leaves indicative of water stress and they attributed this to competition between the overstorey and understorey plants for water. This drives premature decline in the tuart canopy. However, the idea that lack of fire leads to understorey thickening is at odds with Beard's (1967) conclusions that it is frequent fires that have driven the decline of tuart (and jarrah) while the understorey has become denser. Close et al's (2011) views coincide with those of Jurskis (2005) about lack of frequent low intensity fire leading to eucalypt decline in southern forests. While Jurskis (2005) contends that simple explanations for eucalypt decline are superior to more complex explanations, the situation of the fire history in Kings Park (and the Perth area in general) is far from simple. In the southwest of Western Australia the plant features that enable them to persist and thrive in the Mediterranean climate will have variable expression in species and populations under different fire regimes (Burrows and Wardell-Johnson 2003).

Before European arrival the west coast of the south of western Australia was relatively densely populated in Aboriginal terms, and anthropogenic fires on the coastal plain may have been at about 2 – 3 year intervals (Hassell and Dodson 2003). It is likely that this sort of fire regime produced the woodland structure of tuart vegetation reported by the early European settlers and is evidenced by the sparse (mostly moribund or dead) large tuarts in Kings Park. Regeneration of tuart in Kings Park has received more attention more recently. Seeds sown in unburnt areas germinated but none of the seedlings survived to become a sapling (Ruthrof et al. 2003). The best recruitment for tuart is after a very hot fire that produces an ash-bed (Fox and Curry 1970). While tuarts are relatively fire resistant as large trees, moderate intensity fires will kill tuart stems less than 20 cm DBH, although the plant may subsequently sprout from a lignotuber (Burrows and Wardell-Johnson 2003). The past, somewhat sparse tuart overstorey with trees that have short boles and spreading crowns (as illustrated in Beard 1967) could be the result of infrequent hot fires (to enable tuart establishment) and subsequent frequent cool burns such as would be produced by patchy Aboriginal low intensity fires every several years. In the Vasse estuary area (south of Perth) at the time of European contact it was considered that tuart dominated vegetation was park-like, with tuarts dominating (approximately 20 - 25/hectare) over peppermints (*Agonis flexuosa*) and *B. grandis*. In contrast, to the north, *B attenuata* tended to replace *B. grandis* and shrubs became more common (Haswell and Walker 2003) and this is likely to have been the case around Perth.

Study of *Xanthorrhoea preissii* stem bands in plants from the jarrah forest suggest a marked decline in fire frequency over the last 250 years (Lamont et al.et al. 2003). There has been some criticism of the technique and results from *Xanthorrhoea* stem bands (Enright et al.et al. 2005) and the evidence from Lamont et al. (2003) is from the jarrah forest not the vegetation type at Kings Park. However, there is support for a change in fire regime since the 18th century. Cool fires would periodically burn back many lignotuberous small tree and shrub species preventing them from achieving full stature. Once such a fire regime was interrupted by European settlement, understorey species could be released from suppressed forms (gullivers *sensu* Bond and van Wilgen 1996) and the understorey would become more dense and hence more flammable. The inevitable fires that followed would be more intense than previously. These fires would damage the large tuarts and, although producing an ash bed for regeneration as found by Ruthrof et al. (2003), the subsequent lack of short period cool burns would allow other sprouter species to compete with the tuart regeneration. Similar features are apparent in other systems such as red wood forests in northwestern USA where frequent fires promote a low density stand structure (Brown and Butler 2003). To some extent the change in forest structure/species prevalence could be considered a change to an alternative stable state for the vegetation (Hobbs 2003). Once the understorey thickened, fuel loads would have increased and if fire frequency decreased, fuel loads would also be higher than during times when fires were more frequent. Thus fires, when they did, occur would be hotter and consequently more damaging to large trees.

Jarrah regeneration is generally similar to tuart but the development from seedling to a tree is very different. Jarrah plant development is much slower and lignotuber development is larger than in tuart. In jarrah forest on laterite soil it takes from 15 – 20 years before a seedling has a lignotuber of sufficient size to support growth of a leader stem (Abbott and Loneragon 1984). Jarrah tends to create a reserve population of juveniles in the understorey and conversion to a sapling occurs only after the demise of large trees nearby. While the jarrah lignotuberous coppice is very fire resistant, frequent fires are likely to prevent saplings surviving the transition to a tree. Thus recruitment of jarrah to the canopy would require a considerable fire free period. In all except one of the Baird sites jarrah density increased from 1939 to 1999 and this could be as a result of more time between fires that allowed plants to escape from the lignotuberous phase.

In contrast, very little work has been done on *Corymbia calophylla* but its regeneration and growth progression seems similar to that of jarrah and density of this species in all the Baird sites has also increased from 1939 to 1999. All the species studied here have a risk spreading reproductive strategy to a varying degree. For the eucalypts post-fire recruitment is more successful than inter-fire recruitment but for the banksias interfire recruitment may be equally important.

The degree of serotiny in banksia is an important factor in the Kings Park story. It is claimed that "banksias are born to burn" (He et al. 2011) and most are quite strongly serotinous. However, a number are either weakly or not serotinous (Whelan et al. 1998; Price and Morgan 2003; this study) and the suite of species that occur in Kings Park are included in the group with variable serotiny depending on their location within their range. Similarities in other groups are apparent with populations of *Pinus halepensis* varying in degree of retention of seed (Ne'eman et al. 2004) and *P. banksiana* showing a relationship between serotiny and intensity of fire (Gaulthier et al. 1996). In Kings Park *B. attenuata* and *B. grandis* are weakly serotinous and *B. menziesii* and *B. ilicifolia* are not serotinous at all. Modelling of canopy seed storage in *B. attenuata* showed that under fire intervals of less than 20 years strong serotiny was the optimal strategy. However, if fire was less frequent and interfire recruitment was just as likely as post fire recruitment, then the optimal strategy was for no serotiny (Enright et al. 1998).

The field trials described in chapter 5 showed that banksia seedlings can establish without fire if there is open sand substratum (as in Dixon and Barrett 2003). This is of fundamental importance both for wildlife ecologists and managers. Assertions about the dependence of vegetation in mediterranean regions on fire, are in fact influencing ongoing management practices (Bradshaw et al. 2011). Findings from this study suggest that it is the disturbance regime that is critical, and disturbance may come in many guises (including fire of course). In 1967 Beard mentioned "banksia and casuarina can be seen regenerating in open spaces". In fact burnt soil may be somewhat inimical to establishment if it hardens the soil surface (Chapter 5). That banksia recruitment is still occurring in the park was shown by the presence of sapling banksias in 2007 in the plots surveyed by Beard (1977) despite there being no fire in that area between 1977 and 2007 (Ladd et al. 2007). However, such establishment may be sparse as in the field trials of this present study no *B. ilicifolia* survived the first summer and only two out 2,800 planted seeds of *B. attenuata* and *B. menziesii* survived to 2002. Another species that seems to have increased in the understorey of Kings Park is *Dryandra* (now *Banksia*) *sessilis*. Like the coextensive tree banksias it is weakly serotinous but due to its flowering phenology can have a concentrated seed crop at the end of summer. As with other banksias it will establish after a fire at the optimal time (when the seed crop is ripe but the follicles still closed) but can also establish interfire. In the reassessed Baird plots *D. sessilis* density is highest in the two plots that had not been burnt and these plots also had the highest density of tuart.

Serotiny (bradyspory) however, does not protect *Banksia* spp. from both pre-and post dispersal predation. In the 1950s banksia and casuarina were prominent in Kings Park. Main and Serventy (1957) particularly mention patches of *B. Ilicifolia,* although this species is now virtually extinct in the Park. Beard (1967) considered that banksia and casuarina had formed a low canopy replacement of the taller sparse eucalypts. However, death of banksias was apparent in 1967. “Banksias...are relatively short-lived so that the bush is full of dead individuals which have succumbed naturally, especially in summer (Beard 1967), and “Banksia trees did not recover, but it is uncertain how many were dead or dying as a result of a long drought increasing the usual summer deaths” - Baird’s (1977) words after a fire in Kings Park. One impetus of this present project was the perception that banksias in the Park were following the eucalypts into decline. The banksia “autumn death syndrome” was considered to be severely depleting banksia stocks and replacement by saplings was not occurring. This decline of banksia and increased density of casuarinas was confirmed in Ladd et al’s (2007) reassessment of Beard’s (1967) plots.

The apparent decline of banksia may be related to recruitment failure due to fires at inappropriate times or seed predation. In Kings Park the level of *Banksia* seed predation is higher than in vegetation that is in somewhat less developed areas. In addition predation of seeds of other co-occurring species was relatively lower.

Increased density, increased intraspecific aggression, and a reduced fear of humans have been suggested as the more observable and frequently described characteristics of wildlife animal species in urban and suburban parks (Parker and Nilon 2008). Published literature examining the effect of wildlife populations on plant recruitment are, however, limited. In North America squirrel densities in urban areas in some cases exceed 33 individual per hectare. At these high densities, intensive predation by squirrels can eliminate opportunities for

regeneration. In fact the poor recruitment of oak in urban woodland in New York city have been attributed to high squirrel densities (Douglas et al 2011). Similarly in the mediterranean oak forest within the managed Protected Area of the Riserva di Castel Porziano (Rome) plant recruitment is strongly limited both by herbivory due to deers grazing and rooting casued by wild boars (Focardi et al. 2000; Smit et al. 2006).
Weed invasion may also be involved in reducing opportunities for recruitment. For banksias best germination occurred on clear sandy soil. Control burning was instituted in the 1940 – 1950s and Main and Serventy (1957) considered it was “over zealous” and the fire breaks accelerated the spread of Veldt grass (*Ehrharta calycina*). This interaction of fire and Veldt grass was also emphasised by Baird (1977). Grass proliferation is likely to have encouraged a grass fire cycle that detrimentally affected banksias but favoured casuarinas. The combination of frequent low intensity, occasional high intensity fires due to arson, plus rapid litter build up is likely to disadvantage banksia regeneration. Litter was shown to be more inimical to the establishment of banksia and eucalypt than to casuarina seedlings. *Allocasuarina fraseriana* seedlings have developed a lignotuber after three years (Baird 1977) but *B. grandis* needs at least five years (Abbott 1985a) and it is likely that the other banksias will be similar to *B. grandis*. Thus casuarina is likely to be fire resistant earlier than banksias. In addition, the elongated growth form of the casuarina shoots, in contrast to the broader spreading leaves of the banksia seedlings, are better able to extend above a competing weedy grassy sward.

Control burns were completely discontinued in Kings Park in 1984 (Dixon et al 1995c). However wild fires continue to damage the vegetation, particularly in summer, and the latest wildfire to burn the area of Baird’s plots was in 2008. The views of Jurskis (2005) and Close et al. (2011) and those of the earlier workers (Baird and Beard) and Fisher et al. (2009) about tree decline seem to be completely at odds. However, the rationalisation of this controversy may lie in considering the severity and frequency of fires. Jurskis’ low intensity fires every several years will not have the same effect on the vegetation as more severe fires at longer, or even shorter intervals if fuel loads allow. Baird (1967) advocated mild control burns every four to five years. Fire management at a local scale is recommended for biodiversity conservation (Hopper 2003) and for management purposes in other reserves such as the control of *Allocasuarina huegelinana* proliferation in wheatbelt reserves in drier areas to the east of Perth (Maher et al. 2010). In addition, banksia seeds suffer higher predation levels from cockatoos and rodents in Kings Park relative to other Perth reserves. Despite weeds and sclerophyll litter helping hide banksia seeds from predators, this also increases the relative establishment performance of *A. fraseriana, D. sessilis* and *A. saligna* in relation to banksia, as the smaller seeds can reach the mineral soil more reliably than the larger banksia seeds. Low intensity fires could be used to diminish litter loads and increase open soil patches if weeds can be controlled. Overall, more detailed information is needed on the precise role of fire in regeneration of the different dominant species, its effect on litter accumulation and interaction with weed proliferation. The role of wildfires, and weeds, in the dynamic of bushland is difficult to assess in the absence of a large scale, quantitative monitoring of the vegetation over time.

Weed dynamics in the Mediterranean urban ecosystem, seen both in an ecological and biological perspective, affects the survival and recruitment strategies of the various native phytocoenoses. Not only are weeds considered unsightly, but they may also give rise to ‘functional’ obstacles to wildlife regeneration (Benvenuti 2004).

6.1 Implications for conservation and management

As noted at the start of this discussion management of urban reserves benefits from a knowledge of past land use, characteristics of the original vegetation, recruitment processes and the frequency and extent of disturbances. Conservation of banksia woodlands especially in urban and suburban remnants is an important task both for environment managers and conservationists. These areas make an important contribution to biodiversity conservation, consequently preservation and enhancement of biodiversity in urban and suburban remnants is important, especially considering that many of these areas are impacted by various types of non-natural disturbances and are isolated islands of vegetation. The extent of *Banksia* woodlands on the Swan Coastal Plain is decreasing due to suburban development, environmental changes, extreme climatic events and diseases. This present research, thanks to the re-surveying of vegetation transects assessed 60 years ago, was able to confirm and quantify the decrease of banksia species (which until now was only assumed) in Kings Park and is likely to be representative of other reserves on the Swan Coastal Plain. In addition it has investigated whether the decrease was due to the recruitment cycle of the species or whether new types of microhabitat present in the bushland could influence recruitment, hastening the vegetation changes. Previous researchers have referred to declines in the vegetation and in some cases commented on possible ways to reverse the decline. However, decline is a value judgement and it is difficult to judge to what state the vegetation should be returned. Beard (1977) advocated rehabilitation of Kings Park bushland but noted it would be difficult to return it to a tuart woodland type of vegetation. It is perhaps better to consider the concept of "intervention ecology" rather than restoration (Hobbs et al. 2011). Kings Park has aspects of both natural vegetation and manicured gardens in different parts of the Park. Stewart et al. (2004) saw advantage in a sustainable mixed origin urban forest of indigenous and exotic species in Christchurch, New Zealand, and Kings Park has aspects of this. However, the strategic plan for Kings Park contains eight "functions" and four of these are to do with conservation of biodiversity and the natural environment (Botanic Gardens and Parks Authority 2009). Thus maintenance of the "natural" part of the Park seems a preferred option. Hobbs et al. (2011) advocate considering interventions as "reactive, active and proactive". Reactive intervention in Kings Park would attempt to maintain the current condition and halt loss of species. For instance, of the banksias *B. ilicifolia* is the species that shows the poorest recruitment. For this reason in any conservation program the species needs ongoing care. In particular, considering that the species is at significant risk of extinction in the Park (paying its extinction debt – Tilman et al. 1994), programs need to take into consideration the re-enforcement of the taxon using "indigenous" germplasm. Active intervention would attempt to change ecosystem properties in a particular direction, for instance improve banksia recruitment. Seed predation greatly affects banksia seed availability in Kings Park. Also the presence of sites unfavourable for germination are a great obstacle to establishment. By contrast, the recruitment potential of other dominant species, like *A. fraseriana*, *A. saligna* and *D. sessilis,* does not seem to be affected; predation (or removal) is not conspicuous and the prevalent substrata do not reduce the ratio between the number of germinants and seedlings. In addition, these small seeded species annually produce many more seeds than the *Banksia* spp. Various management actions could be taken to improve banksia recruitment. Within the four investigated banksias, one of the main obstacles to recruitment was the absence of sites suitable for germination and establishment, such as bare sandy soils because these are replaced by substrata with weeds and the presence of a thick layer of leaf litter. The presence of weeds is commonly associated with altered fire regimes (Baird 1977, Bridgewater and Backshall 1981). A lack of low intensity ground fires may be responsible for the presence of thick layers of sclerophyllous leaves (mainly from *Banksia* spp. and *A. fraseriana*). In this mediterranean-type habitat, decomposition of dead hard leaves takes a long time and fire will accelerate this process.

Alternatively, in addition to weed control programs mechanical comminution of litter, followed by redistribution of the ground material back to the soil, should be undertaken. This would provide a patchy pattern of “mulch” and bare areas and suitable sites for seedling establishment as was demonstrated in the various trials in this thesis.

The seed predation aspect of the banksia recruitment cycle is more complicated as the cockatoos that seem mostly responsible for predispersal predation of seeds are endangered (Australian Government undated) and providing food for the birds is considered a positive feature. However the post dispersal predators are likely to be introduced rodents so their removal through baiting programs would increase seed availability for interfire recruitment. The depredations by cockatoos could be counteracted by augmenting the banksia seed rain with seeds (of suitable local provenance) as long as post-dispersal predators have been removed or seeds can be protected from predation.

Proactive intervention limits “the human drivers of processes that assault ecosystems” (Hobbs et al. 2011) and is much more difficult to achieve in Kings Park. For example preventing arson occurrences can really only be addressed by education programs highlighting the value of Kings Park and its fragility to wildfires, and possibly vigilant action of park staff on high fire danger days in summer.

Research projects and management measures focusing on weed control, seed predation and litter transformation should be continuously monitored and outcomes evaluated within the general strategic management action plan of the Park.

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APPENDICES

Appendix 1: Sites and locations

		Locations →							Kings Park									Bold Park				
		Sites →	Greenhouse	Tip site	Banksia site	Banksia site 1	sandy track	Banksia (traps) site	Banksia (traps) site 1	Tobruk memorial	E site	Dryandra site	Driandra site	South West of the bushland	weed 1	weed next burn	Judy's site	early burn	low valley	sandy track	high valley	late burn
chapter ↓		Trials, surveys, experiments ↓																				
Vegetation changes over time		Vegetation surveys-transects												x								
seed production and dispersal		1 Tagged inflorescences			x	x		x	x						x	x			x		x	
		2 box Seed traps interfire			x	x		x					x		x	x						
		3 box Seed trap post fire																x				x
		4 Quadrates post-fire seed fall																x				x
seed germination		a) 50 metres transect			x		2x	x				x			x	x		7x		2x		5x
		b) seed manipulation		x	x			x				x										
		c & d) seed in soil			x			x				x			x	x		x				x
		e) seed sown 10X10																				
		f) germination and survival on different substrata	x																			
		g) germination and survival, seed manipulation	x	x	x						x	x			x							
seed predation	pre-dispersal	A pre-dispersal *in situ*			x	x		x	x										x		x	
		B pre-dispersal *ex situ*			x	x		x	x						x					x		
	post-dispersal	1 post-dispersal invertebrate exclusion			x					x		x										
		2 post-dispersal vertebrate exclusion			x					x		x										
		3 post dispersal total exclusion			x					x		x										
		3.1 post-dispersal total excluion post-fire																x				x
		4 post-dispersal complete exclusion on sod			x					x												
		5 post-dispersal open standard			x	x		x		x		x			x		x					
		5.1 post-dispersal open standard Banksia spp.			x			x														
		5.2 post-fire open standard post-fire																x				x
		6 post-fire open density sand			x	x		x		x		x										
		7 post-fire open density sod			x	x		x		x		x			x		x					

			Murdoch Uni	Ridges State Forest				Jandakot Regional Park				
			Bushland	4 banksia	caffeteria	burn plan	burn hill	sandy track	banksia plan (10X10)	Plan next 10X10	Alex jeorgia site	alex georgia 1
seed production and dispersal		1 Tagged inflorescences		x	x					x	x	
		2 box Seed traps interfire		x	x				x		x	
		3 box Seed trap post fire										
		4 Quadrates post-fire seed fall										
seed germination		a) 50 metres transect		x	x			2x	x		x	
		b) seed manipulation										
		c & d) seed in soil		x	x					x	x	
		e) seed sown 10X10										
		f) germination and survival on different substrata										
		g) germination and survival, seed manipulation	x	x		x	x		x			
seed predation	pre-dispersal	A pre-dispersal *in situ*			x	x				x	x	
		B pre-dispersal *ex situ*			x	x				x	x	
	post-dispersal	1 post-dispersal invertebrate exclusion										
		2 post-dispersal vertebrate exclusion										
		3 post dispersal total exclusion										
		3.1 post-dispersal total excluion post-fire										
		4 post-dispersal complete exclusion on sod										
		5 post-dispersal open standard			x	x					x	x
		5.1 post-dispersal open standard Banksia spp.										
		5.2 post-fire open standard post-fire										
		6 post-fire open density sand										
		7 post-fire open density sod			x	x					x	x

Appendix 2: **the species**

Data derived from '*Flora of Australia', 'Florabase' and 'The bushland plants of Kings Park'*

Banksia attenuata **R.Br**.

Shrub to 2 m or tree to 10 m tall, with lignotuber or fire-tolerant trunk. Bark thick, verrucose, friable, pale grey-orange. Stems pubescent. Leaves narrowed to petiole up to 1 cm long; lamina linear, 4–27 cm long, 5–16 mm wide, truncate; margins slightly recurved, obtusely and shortly serrate; upper surface hirsute, glabrescent; lower surface tomentose. Inflorescence terminal, 5–26 cm long; involucral bracts hirsute, viscid, persistent. Flowers bright yellow including styles. Perianth 15–22 mm long including limb of 3–4.5 mm, glabrous. Pistil gently curved, 15–22 mm long, glabrous; pollen presenter narrow, 1 mm long, smooth. Old flowers persistent, with styles curled against axis. Follicles broadly elliptic, 20–35 mm long, 10–15 mm high, 14–20 mm wide, smooth, densely hirsute, often darkly mottled. Seed obovate, 22–26 mm long; seed body cuneate, 12–14 mm long, 13–14 mm wide, smooth inside, rugose outside.
Widespread in south-western W.A. from Kalbarri to Cape Leeuwin and east to the Fitzgerald R., extending inland to Wongan Hills and Lake Grace. Grows in deep sand, sometimes over limestone or laterite, in kwongan, shrubland and woodland. Flowers mainly Oct.–Feb.

Banksia menziesii **R.Br**

Tree to 10 m with fire tolerant stems, or shrub to 3 m with lignotuber. Bark thick, verrucose, friable, greyish pink or pale brown. Stems pubescent, glabrescent. Leaves: petiole 8–17 mm long; lamina oblong, 8–25 cm long, 1–4 cm wide, truncate; margins recurved, shallowly dentate; both surfaces tomentose, glabrescent except pits in lower surface. Inflorescence terminal, 4–12 cm long; involucral bracts tomentose, falling early. Flowers pale to deep pink or red with silvery indumentum, sometimes cream or brown; style similar to perianth but pale in lower half. Perianth 29–38 mm long including limb of 5–6 mm, silky pubescent outside, glabrous inside. Pistil curved, 37–41 mm long, glabrous but minutely papillose in upper half; pollen presenter narrowly fusiform, 2–2.5 mm long, 8-ribbed. Old flowers usually soon falling. Follicles up to 25, prominent, narrowly obovate, 25–35 mm long, 10–15 mm high, 10–15 mm wide, beaked, smooth, closely pubescent, mottled. Seed obovate, 23–30 mm long; seed body obovate, 10–11 mm long, 11–14 mm wide, pitted near margin outside, muricate inside.
Occurs in W.A. near the west coast from the Murchison R. to Pinjarra, mostly on the coastal plain but with a few outliers farther inland, e.g. near Brookton. Grows in deep sand in low woodland and tall shrubland. Flowers Feb.–Aug.

Banksia grandis **Willd**

Tree to 10 m, in coastal areas sometimes a shrub, fire tolerant. Bark thick, rugose. Stems stout, tomentose, glabrescent. Leaves: petiole 10–35 mm long; lamina pinnatisect with 8–12 large, triangular lobes each side, obovate-cuneate, 10–45 cm long, 3–11 cm wide, truncate; margins recurved; upper surface tomentose, glabrescent; lower surface tomentose, glabrescent except fine wool in pits. Inflorescence 10–40 cm long, 7–9 cm wide at flowering; involucral bracts to 25 mm long, tomentose, falling after flowering. Flowers pale yellow; upper flowers often with turquoise or grey tinge; styles cream. Perianth 26–35 mm long including limb of 4–5 mm, hirsute both sides with glabrous limb. Pistil 35–40 mm long, glabrous; pollen presenter slightly thickened, 1–1.5 mm long. Old flowers soon falling. Follicles many in a massive cone, elliptic, 17–25 mm long, 3–10 mm high, 6–12 mm wide; valves smooth but groove wrinkled, tomentose. Seed obovate-cuneate, 32–38 mm long; seed body obovate, 12–16 mm long, 7–9 mm wide, smooth inside, somewhat rugose outside.

Widespread in W.A. from Mt Lesueur to Cape Leeuwin, east to Cape Riche and inland to Woodanilling. Grows in sand on the coastal plain, in woodland and kwongan; common in laterite in the Jarrah forest of the Darling Plateau. Flowers Oct.–Jan.

Tree to 10 m tall, fire tolerant. Bark thick, fibrous, fissured or tessellated, grey. Stems hirsute and tomentose, glabrescent. Leaves: petiole 3–10 mm long; lamina obovate-elliptic, undulate, truncate or obtuse, 3–10 cm long, mucronate; margins not recurved, serrate or sometimes entire; both surfaces hirsute-tomentose, glabrescent, shining except pits in lower surface. Inflorescence 7–9 cm wide, with 60–100 flowers; involucral bracts short, tomentose, persistent. Flowers cream and pink becoming dull red; style cream with green pollen presenter. Perianth 32–40 mm long including limb of 2.5–4 mm, shortly pubescent outside, glabrous inside; limb glabrous. Pistil straight, 27–35 mm long, glabrous except a few hairs above ovary; pollen presenter scarcely thickened, 1–1.5 mm long. Old flowers soon falling. Follicles 1–3, ovate, curved, 14–20 mm long, 13–24 mm high, 10–16 mm wide, smooth, tomentose. Seed transversely elliptic, oblique; seed body elliptic, often irregular, 5–7 mm high, 9–12 mm wide, rugose inside, smooth outside.

Occurs within 70 km of the coast of W.A. from Mt Lesueur to Cape Leeuwin and east to Albany and the Stirling Ra. In deep white or grey sand on consolidated dunes and low-lying flats, in woodland; near the south coast sometimes in tall shrubland. Flowers mainly from late winter to early summer, but along the south coast in most months.

Allocasuarina fraseriana (Miq.)

Tree 5–15 m high. Branchlets ascending, to 30 cm long; articles 7–15 mm long, 0.8–1.3 mm diam., occasionally strongly waxy; phyllichnia rounded, verruculose or smooth; teeth 6–8, somewhat spreading, 0.7–1.2 mm long. Male spikes 3–8 cm long, 5 or 6 whorls per cm; anther 0.7–1.2 mm long. Cones coarse, usually shortly cylindrical, warty, pubescent at least when young, sessile or on peduncle to 32 mm long; cone body 15–40 mm long, 15–22 mm diam.; bracteoles broadly acute to obtuse, protuberance slightly shorter than bracteole body and divided into 4–8 bodies, pungent or obtuse. Samara 9–10 mm long. $2n = 26$, B.A.Barlow, *Austral. J. Bot.* 7: 232 (1959).

Occurs from Perth to Albany, W.A., with an isolated population between Moora and Jurien Bay, W.A. On the Darling Ra. grows in lateritic soil in Jarrah (*Eucalyptus marginata*) forest; near the coast grows in sand in woodland and open forest.

Acacia saligna (Labill.)

Bushy shrub or tree mostly 2–6 m high. Bark grey. Branchlets often pendulous, normally slightly flexuose, often pruinose (especially when young), glabrous. Phyllodes often pendulous, variable in shape and size, linear to lanceolate, straight to falcate, 7–25 cm long, (2–) 4–20 mm wide, often larger towards base of plant, green to glaucous, glabrous, with prominent midrib, finely penninerved (absent on very narrow phyllodes); gland ±disciform, 1–2 mm wide, 0–3 mm above pulvinus; pulvinus mostly 1–2 mm long, coarsely wrinkled. Inflorescences mostly 2–10-headed racemes, enclosed when young by imbricate bracts, with

bract scars evident at anthesis; raceme axes mostly 3–30 mm long, glabrous; peduncles 5–15 mm long, glabrous; heads globular, mostly 7–10 mm diam. at anthesis and 25–55-flowered, golden. Flowers 5-merous; sepals c. 4/5-united. Pods linear, flat, shallowly constricted between seeds, 8–12 cm long, 4–6 mm wide, thinly coriaceous, glabrous. Seeds longitudinal, oblong to slightly elliptic, 5–6 mm long, shiny, dark brown to black; aril clavate.
Widespread, often common in south-western W.A., extending from Wilgiamia Pool (c. 30 km due NE of Kalbarri) SE to Ponier Rock (c. 65 km due S of Balladonia), but also occurring c. 230 km ENE of Kalbarri on Meka, Murgoo and Jingemarra Stns. Naturalised in S.A., Qld, N.S.W., Vic. and Tas. In W.A., grows in a variety of habitats, including poor sandy soils of the Swan Coastal Plain, clayey soil around Geraldton, the sandplains N of Gingin, the Darling Range and the Great Southern region (where it is ±restricted to creeks and rivers), deep sands associated with watercourses (e.g. south coast of W.A.), the base of granite boulders in the wheatbelt, and in coastal dune systems (often forming dense thickets in the hollows between sand hills).

Acacia pulchella R.Br.

Shrub mostly 0.5–1.5 m high. Branchlets hairy or glabrous. Axillary spines 1 or 2 per node, sometimes few or absent, mostly 2–20 mm long. Stipules scarious. Leaves bipinnate; pinnae 1 pair, 1–15 mm long; petiole < 0.5–6 mm long; pinnules 2–11 pairs, oblong to obovate or oblanceolate, 1–6 mm long, 0.5–2 mm wide, flat, green to glaucous, glabrous to puberulous; gland within axil of pinnae, stipitate, to 3 mm long. Inflorescences rudimentary 1–3-headed racemes with axes to c. 3 mm long; peduncles 1–15 (–20) mm long, glabrous or hairy; heads globular, 10–40-flowered, infrequently to 60-flowered, golden; bracteoles apiculate to long-acuminate. Flowers 5-merous; sepals 1/2–2/3-united. Pods narrowly oblong, flat or slightly undulate, 1.5–5 cm long, mostly 3–5 mm wide, crustaceous, glabrous or pubescent; margins thick. Seeds longitudinal, mostly oblong, 2.5–4.5 mm long, brown, arillate.
Widespread in south-western W.A. from Port Gregory to Cape Arid.

Dryandra sessilis (Knight) now known as *Banksia sessilis* (Knight) A.R.Mast & K.R.Thiele

Shrub or tree to 6 m, without lignotuber. Leaves sessile or on petiole to 5 mm long; lamina cuneate to flabelliform, sometimes almost oblong, 2–6 cm long, 8–40 mm wide, obtuse to acute, mucronate, sparsely hairy on upper surface and nerves but soon glabrous except pits in lower surface; margins ±flat, serrate with up to 9 teeth each side. Inflorescence terminal; involucral bracts ovate passing to linear; outer bracts ±glabrous except densely ciliate margins; inner bracts hirsute, to 10–11 mm long, pale; flowers 55–125 per head. Perianth straight, 20–32 mm long, pale yellow; claw pubescent; limb 3–4 mm long, glabrous. Pistil straight, 19–30 mm long, cream, glabrous; pollen presenter cylindrical to ellipsoidal, 1–1.5 mm long, smooth. Follicles 1–4 per head, ovoid, 10–15 mm long, appressed-pubescent, glabrescent, opening when mature.
Occurs widely in south-western W.A. from Kalbarri to Cape Leeuwin and east to Bremer Bay, inland to Wongan Hills and Kulin.

Conospermum triplinervium R.Br.

Small tree to 4 m tall; trunk grey with paler patches. Leaves oblanceolate to elliptic-oblong, 3–14 cm long, 3–13 mm wide, glabrous; apex acuminate; midvein, marginal and cross veins prominent. Inflorescence an elongated, spicate panicle, several from upper axils; peduncle

18–39 cm long, puberulous; bracteoles ovate, 2–2.6 mm long, 2–3 mm wide, velutinous, tomentose at base and sides, with an acuminate apex. Perianth greyish white, woolly, becoming pink in fruit; tube 2.5–4.2 mm long; upper lip ovate, acute, 1.8–2.2 mm long, 1–1.8 mm wide, puberulous at apex, woolly at base; lower lip united for 1–1.5 mm; lobes narrowly oblong, 0.7–1 mm long, 0.2–0.4 mm wide, obtuse. Nut 2.3–2.7 mm long, c. 2.5 mm wide, tan, cream- or orange-tomentose; circumference hairs 1.8–2.2 mm long, orange; central tuft of hairs to 2.5 mm long.
Previously occurred throughout the south-west from Albany to Yanchep, W.A., with an isolated collection known from Cunderdin; now common around Perth, but not in the far south-west. Flowers Mar., Sept.–Nov.

Eucalyptus marginata **Sm.**

Tree, to 40 m high, bark rough fibrous greysh-brown. Leaves up to 13 cm long, glossy green above and paler beneath. There are up to 8 flowers in a head. Fl. white, cream, pink . The operculum is green or red, the fruits are up to 1,5 cm across. Jun–Jan. Grey sand, clay or sandy loam, laterite.

Eucalyptus gomphocephala DC.

Tree, 10–40 m high, with pale grey fibrous bark and leaves 20 cm long. bark rough, box-type. Fl. white, Jan–Apr. Sand over limestone. Coastal plains There are up to 7 creamy-white flowers in a head. The buds have an operculum which is much broader then the floral tube. The fruit are up to 2 cm long and the bud shape characterises this species.

Corymbia calophylla **(Lindl.) K.D.Hill & L.A.S.Johnson**

Spreading tree to 40m high with rough, grey bark and leaves up to 18 cm Tree (mallee, rarely), to 40(–60) m high, bark rough, tessellated. Flower creamy-white, pink, Dec–May. The large fruit, commonly called “Honkey nuts”, are up to 3cm long and typically “urn” shaped. The species produces many seeds.
Red-brown clay loam, orange-brown sandy clay, gravel, grey sand over limestone, granite, laterite. Flats, hills, slopes, breakaways, wetlands, fringing salt marches, beside drainage lines.

Jacksonia furcellata **(Bonpl.) DC**

Prostrate to decumbent or weeping erect shrub, 0.4–4(–6) m high. Hairy, angular, stems and undivided branches. The leaves are reduced to scalesand the much divided branchlets are often mistaken for leaves. The flowers are up to 9mm long. The hairy calyx has 5, equal sized, spreading lobes which are often reflexed along the flower stalk. The stalked pod is up to 1cm long and 5mm wide. August to march. Fl. yellow, orange, red, Oct–Mar. Sandy soils. Sandplains, rises, swampy depressions, river banks.

Jacksonia sternbergiana Huegel

Leafless shrub up to 4 m high with pendulous branches. The hairless stems and branches are slightly flattened with the final branches pungent. The calix is 10-ribbed with the equal sized lobes reflexed back along the flower stalk. The flowers are nearly 1cm long. The stalked, hairy fruits are up to 1.5cm long. Flowers recorded most months of the year.

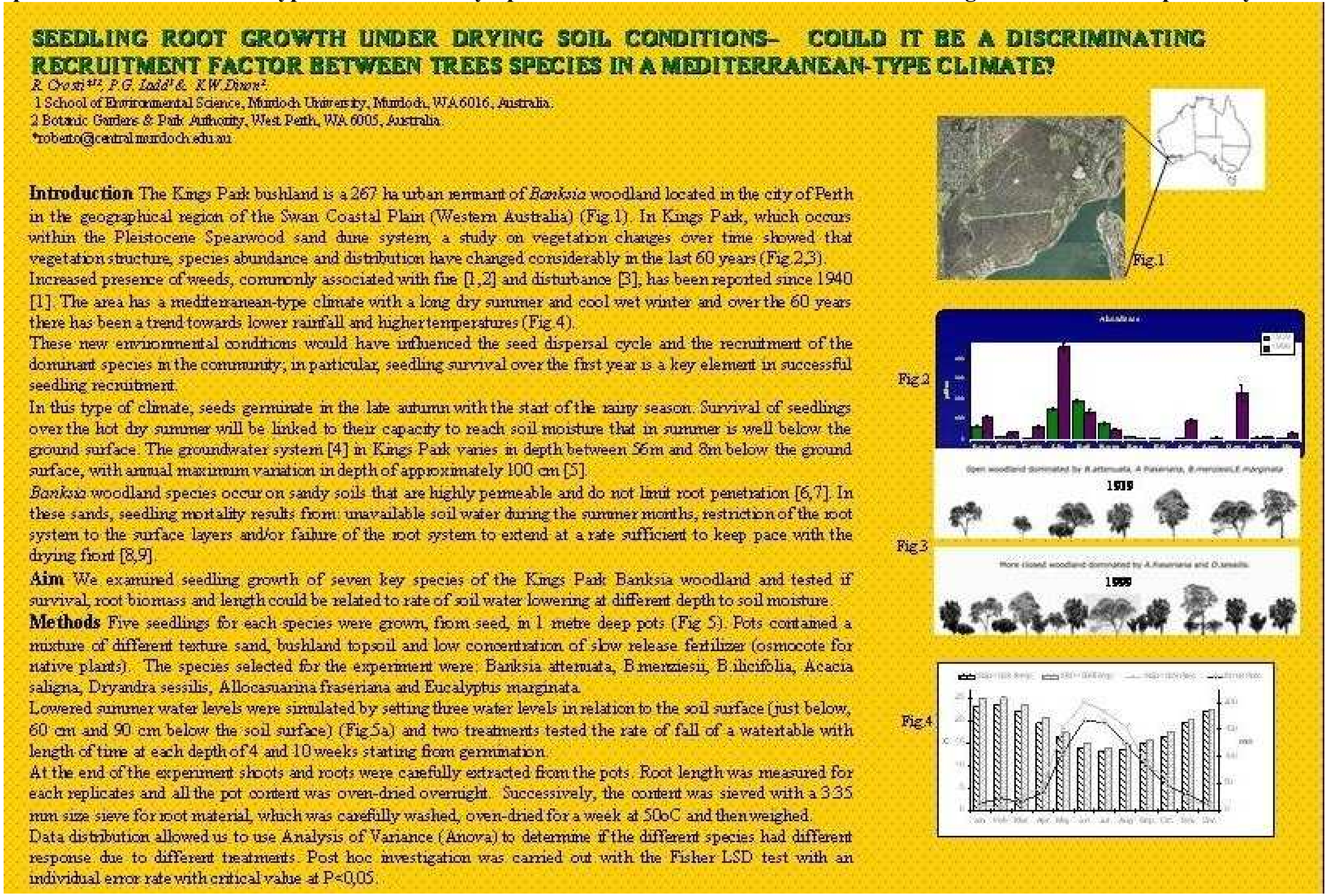
Erect, weeping shrub or tree, 1.5–5 m high. Fl. yellow, orange, Jan–Dec. Sandy soils. Along rivers & creeks, near swamps, flats, dunes.

Appendix III:

Number of germinants m^{-2} for each of the seven substrata for different transects grouped together, for *B. attenuata* and *B. Menziesii*

			substratum							
		species and position	burn residuals	Weeds	Litter	Thick litter matt	vegetation	Bare sand	Proteoid roots	Mean total
Transect grouped together according to thre type of environment	Total (27)	*B.attenuata*	1,51	0,03	0,25	0,04	0,25	0,65	0,03	0,46
		B.menziesii	0,32	0,01	0,09	0,00	0,10	0,19	0,01	0,12
		B.attenuata under canopy	2,77	0,03	0,47	0,07	0,42	1,24	0,05	0,85
		B.menziesii under canopy	1,38	0,02	0,25	0,00	0,24	0,74	0,01	0,47
	post-fire (12)	*B.attenuata*	1,52	n/a	0,00	n/a	n/a	0,68	0,01	0,66
		B.menziesii	0,32	n/a	0,00	n/a	n/a	0,12	0,00	0,13
		B.attenuata under canopy	2,79	n/a	0,00	n/a	n/a	1,34	0,03	1,23
		B.menziesii under canopy	1,39	n/a	0,00	n/a	n/a	0,51	0,00	0,53
	inter-fire (15)	*B.attenuata*	n/a	0,03	0,26	0,04	0,25	0,61	0,08	0,30
		B.menziesii	n/a	0,01	0,09	0,00	0,10	0,27	0,03	0,11
		B.attenuata under canopy	n/a	0,03	0,42	0,07	0,37	1,11	0,11	0,53
		B.menziesii under canopy	n/a	0,02	0,28	0,00	0,27	1,03	0,05	0,42
	semi-pristine (9)	*B.attenuata*	n/a	0,00	0,25	0,05	0,27	0,56	0,05	0,25
		B.menziesii	n/a	0,00	0,05	0,00	0,09	0,29	0,00	0,09
		B.attenuata under canopy	n/a	0,00	0,51	0,08	0,53	1,33	0,19	0,56
		B.menziesii under canopy	n/a	0,00	0,31	0,00	0,36	1,06	0,09	0,36
	weedy (3)	*B.attenuata*	n/a	0,04	0,20	0,00	0,11	0,43	0,00	0,08
		B.menziesii	n/a	0,01	0,10	0,00	0,00	0,21	0,00	0,03
		B.attenuata under canopy	n/a	0,05	0,32	0,00	0,18	0,59	0,00	0,11
		B.menziesii under canopy	n/a	0,03	0,25	0,00	0,00	0,54	0,00	0,07
	sandy track (3)	*B.attenuata*	n/a	0,00	0,26	0,00	0,00	0,65	n/a	0,54
		B.menziesii	n/a	0,00	0,09	0,00	0,00	0,24	n/a	0,20
		B.attenuata under canopy	n/a	0,00	0,58	0,00	0,00	1,32	n/a	1,10
		B.menziesii under canopy	n/a	0,00	0,43	0,00	0,00	1,32	n/a	1,08
	next to sandy track (3)	*B.attenuata*	n/a	0,00	0,11	0,05	0,27	0,44	0,00	0,22
		B.menziesii	n/a	0,00	0,04	0,00	0,08	0,22	0,00	0,09
		B.attenuata under canopy	n/a	0,00	0,33	0,11	0,46	0,94	0,00	0,42
		B.menziesii under canopy	n/a	0,00	0,21	0,00	0,29	0,80	0,00	0,26
	post fire early burn (7)	*B.attenuata*	1,56	n/a	0,00	n/a	n/a	0,76	0,01	0,70
		B.menziesii	0,41	n/a	0,00	n/a	n/a	0,19	0,00	0,18
		B.attenuata under canopy	2,71	n/a	0,00	n/a	n/a	1,43	0,02	1,26
		B.menziesii under canopy	1,69	n/a	0,00	n/a	n/a	0,80	0,00	0,74
	post fire late burn (5)	*B.attenuata*	1,46	n/a	n/a	n/a	n/a	0,58	0,01	0,57
		B.menziesii	0,15	n/a	n/a	n/a	n/a	0,04	0,00	0,05
		B.attenuata under canopy	2,94	n/a	n/a	n/a	n/a	1,23	0,04	1,18
		B.menziesii under canopy	0,83	n/a	n/a	n/a	n/a	0,18	0,00	0,24

Appendix IV: **Poster Crosti Roberto Seedling root growth under drying soil conditions –could it be a discriminating recruitment factor between trees species in a mediterranan-type climate? 46th Symposium of the International Association of Vegetation Science Naples Italy**



SEEDLING ROOT GROWTH UNDER DRYING SOIL CONDITIONS– COULD IT BE A DISCRIMINATING RECRUITMENT FACTOR BETWEEN TREES SPECIES IN A MEDITERRANEAN-TYPE CLIMATE?

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Introduction The Kings Park bushland is a 267 ha urban remnant of *Banksia* woodland located in the city of Perth in the geographical region of the Swan Coastal Plain (Western Australia) (Fig.1). In Kings Park, which occurs within the Pleistocene Spearwood sand dune system, a study on vegetation changes over time showed that vegetation structure, species abundance and distribution have changed considerably in the last 60 years (Fig.2,3).
Increased presence of weeds, commonly associated with fire [1,2] and disturbance [3], has been reported since 1940 [1]. The area has a mediterranean-type climate with a long dry summer and cool wet winter and over the 60 years there has been a trend towards lower rainfall and higher temperatures (Fig.4).

These new environmental conditions would have influenced the seed dispersal cycle and the recruitment of the dominant species in the community; in particular, seedling survival over the first year is a key element in successful seedling recruitment.

In this type of climate, seeds germinate in the late autumn with the start of the rainy season. Survival of seedlings over the hot dry summer will be linked to their capacity to reach soil moisture that in summer is well below the ground surface. The groundwater system [4] in Kings Park varies in depth between 56m and 8m below the ground surface, with annual maximum variation in depth of approximately 100 cm [5].

Banksia woodland species occur on sandy soils that are highly permeable and do not limit root penetration [6,7]. In these sands, seedling mortality results from: unavailable soil water during the summer months, restriction of the root system to the surface layers and/or failure of the root system to extend at a rate sufficient to keep pace with the drying front [8,9].

Aim We examined seedling growth of seven key species of the Kings Park Banksia woodland and tested if survival, root biomass and length could be related to rate of soil water lowering at different depth to soil moisture.

Methods Five seedlings for each species were grown, from seed, in 1 metre deep pots (Fig 5). Pots contained a mixture of different texture sand, bushland topsoil and low concentration of slow release fertilizer (osmocote for native plants). The species selected for the experiment were: Banksia attenuata, B.menziesii, B.ilicifolia, Acacia saligna, Dryandra sessilis, Allocasuarina fraseriana and Eucalyptus marginata.

Lowered summer water levels were simulated by setting three water levels in relation to the soil surface (just below, 60 cm and 90 cm below the soil surface) (Fig.5a) and two treatments tested the rate of fall of a watertable with length of time at each depth of 4 and 10 weeks stating from germination.

At the end of the experiment shoots and roots were carefully extracted from the pots. Root length was measured for each replicates and all the pot content was oven-dried overnight. Successively, the content was sieved with a 3.35 mm size sieve for root material, which was carefilly washed, oven-dried for a week at 50oC and then weighed.

Data distribution allowed us to use Analysis of Variance (Anova) to determine if the different species had different response due to different treatments. Post hoc investigation was carried out with the Fisher LSD test with an individual error rate with critical value at P<0,05.

Results

Under a slow decline in the soil watertable there was no difference in seedling survival and root lengths (most of the replicates reached the bottom of the pots), but there was a slight difference, not statistically significant, in roots dry biomass ($p<0.09$) (Fig.6).

Under a more rapid rate of decline there was still no difference in seedling survival between species but there was a statistically significant difference in root dry biomass ($p < 0.05$) and length ($p < 0.01$) (Fig.7/8). The Fisher LSD test showed that mean root dry biomass of *A.saligna* (Fig.9) was statistically higher and that mean root length of *Eucalyptus marginata* was statistically lower compared with the values of the other species (Fig. 9a: *B.attenuata*).

Discussion

Only under manipulated rapid decline of soil moisture root development did differ significantly between the species.

In permanent transect assessed in 1939 and 1999 in Kings Park, Banksia species (Fig.2) were the main one to show declined in populations number and in dominance; this manipulative experiment for this group does not point out the rate of root growth under drying conditions being an important factor for the lack of establishment of the species in Kings Park bushland over the 60 year period. However presence of A. saligna and D.sessilis, which have increased their abundance in most of the transects, may be less discriminate by lower moisture availability compared to the other species due to their ability to increase root length (Fig.7) under more rapidly drying soil conditions. The result for E.marginata is puzzling as it is generally considered to be able to develop deep roots in seedling phase.

This experiment could not fully simulate the extent of drying in the soil in Kings Park over summer. However the difference in root growth between the different species could help explain why seedlings of some species may not be performing as well now as they might have been under conditions of a slightly higher rainfall regime in the past.

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Fig.5

Fig.5a

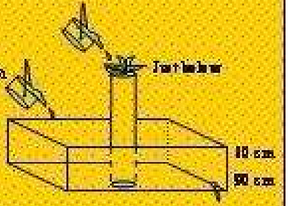


Fig.6

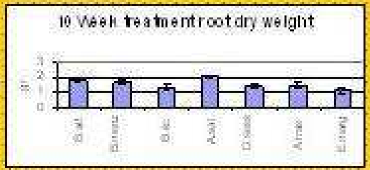


Fig.7

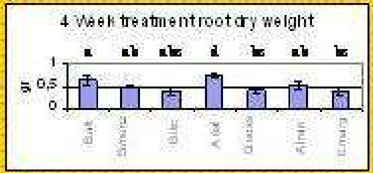


Fig.8

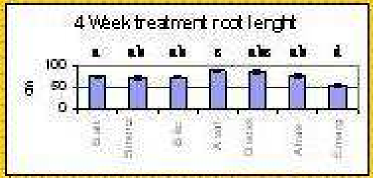


Fig.9

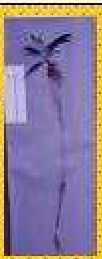
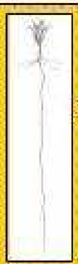


Fig.9a



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46th IAVS Symposium 8-14 June 2003, Naples Italy

Appendix V Photos

Kings Park bushland in the city of Perth

B. attenuata tree

B. attenuata inflorescence

B. attenuata infructescence

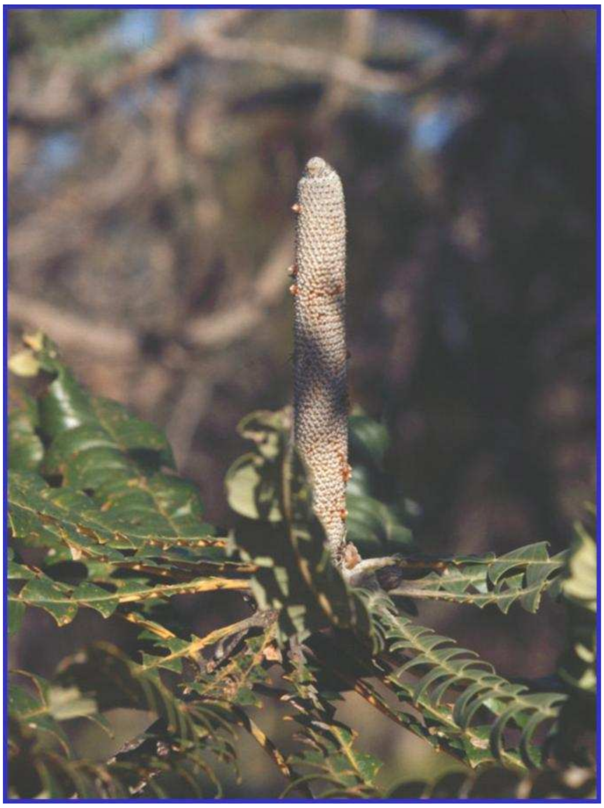
B. menziesii inflorescence

B. menziesii losing flower parts

B. menziesii infructescence

B. menziesii open follicles and aluminium tag

B. grandis inflorescence

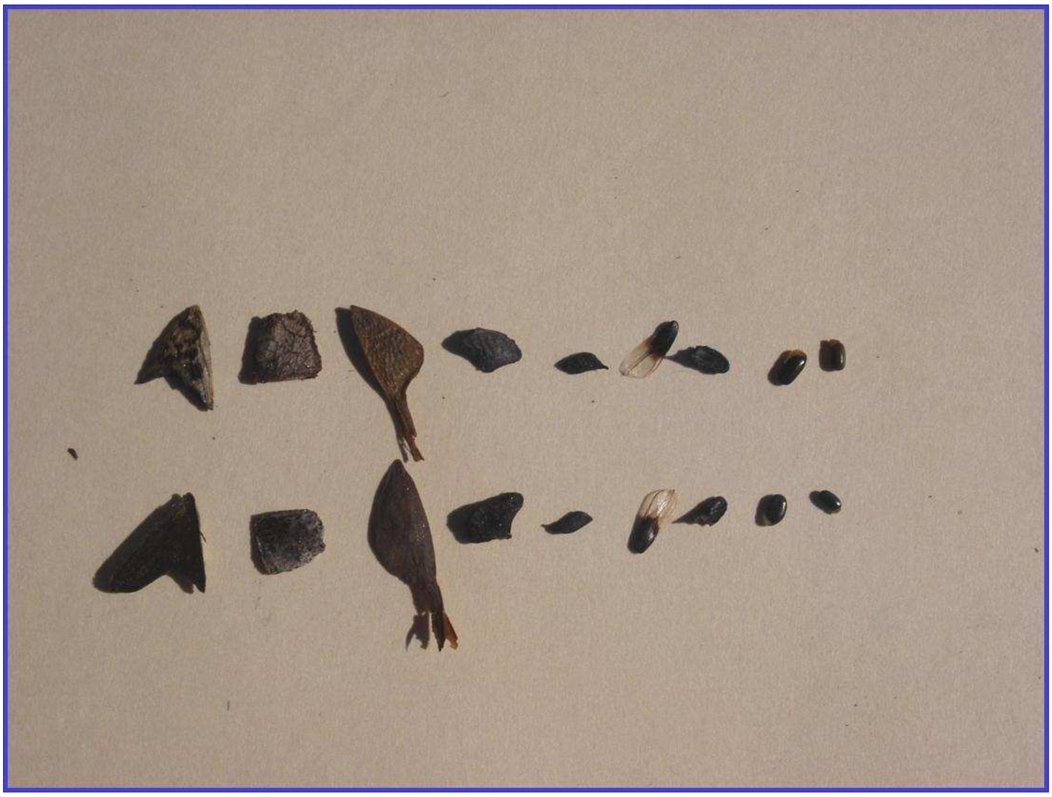


B. grandis developing infructescence

B. ilicifolia inflorescence

B. ilicifolia follicles

B. ilicifolia follicle, separator and seed



Seeds of all the investigated species

B.attenuata, B. Menziesii, B.grandis, B. ilicifolia, D. sessilis, A. fraseriana, E. marginata, A. saligna, A. pulchella

The experimental unit (EU) for the post-dispersal seed predation experiment

Seed germination experiment with vertebrate exclosure treatment

Infructescences with sign of bird predation

Banksia spp. Seedlings in trial

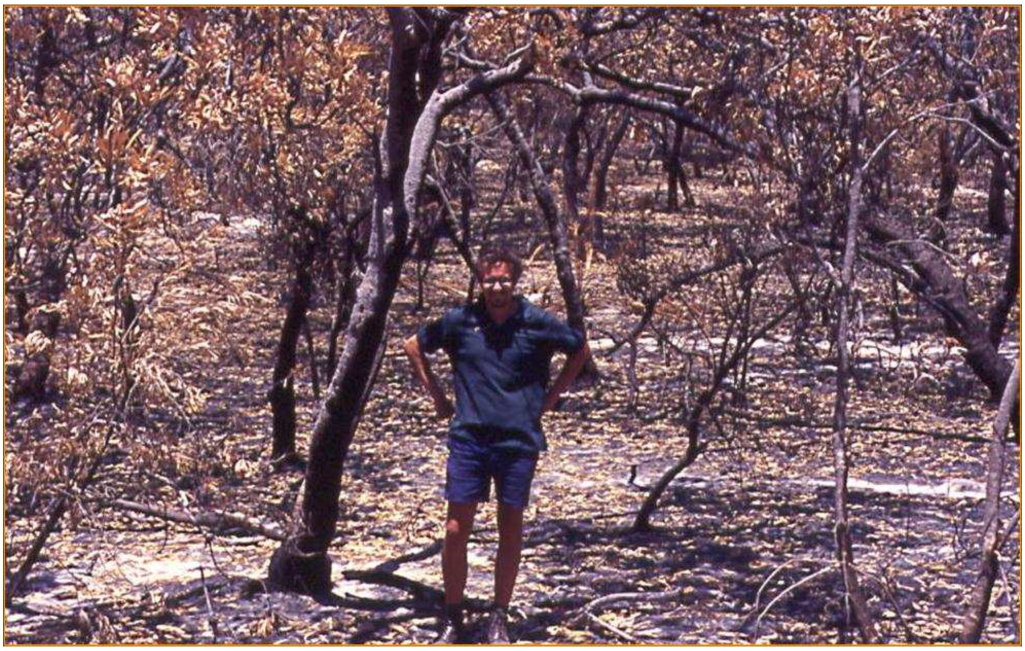
B. attenuata germinant

B. menziesii germinant

Tunnel house with the germination experiments

Thick understorey of *Dryandra sessilis*

Post-fire site



the author