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PLANT POPULATION DYNAMICS UNDER VARYING FIRE REGIMES.

by

ROSS ANDREW BRADSTOCK

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy.

School of Biological Sciences, The University of Sydney.

May, 1985

Volume 1
STATEMENT OF ORIGINALITY

This thesis contains the results of an original study, except where otherwise indicated. It has not been previously presented for publication or examination at this, or any other, university.

ROSS BRADSTOCK
THESIS SUMMARY

The aim was to study the effects of differing combinations of fire frequency, intensity and seasonality on the population dynamics of four proteaceous species; *Banksia ericifolia*, *B. serrata*, *Petrophile pulchella* and *Isopogon anemonifolius*. These species contrast widely in their habit and mode of recovery from fire, but are found to broadly co-habit in fire-prone woodlands, forests and scrubs in the Sydney area. As well, these species all store a seedbank above ground in serotinous cones.

Simple quantitative models were derived and used to predict changes in abundance of each species under varying fire regimes. The aim was to compare the responses of these woody species, with the emphasis on contrasts between species with differing modes of recovery and habits. The results were interpreted in the light of current hypotheses which relate survival in plants with differing modes of recovery from fire to particular fire frequencies. In this study equal emphasis was placed on the effects of seasons and intensities of fire.

The study set out to examine fire-regime effects in all stages of the life cycle. The methods used were demographic in that changes in abundance within life-cycle stages and in the transfers between stages were measured under the influence of differing fire regimes. It was considered that such an approach was necessary to understand and test the comparative responses of these species to differing fire regimes.
Examination of the responses of established plants to burns indicated that *B. ericifolia* and *Petrophile* rely on seeds for recovery (obligate-seeders) whilst *Isopogon* and *B. serrata* resprout. However, at ages in excess of 20 years *B. ericifolia* individuals may survive fires if crown scorch is not complete.

Recovery and survival of *Isopogon* and *B. serrata* were strongly dependent on sizes of either the aerial stems or lignotubers. Young juveniles lacking a lignotuber are killed by low-intensity fires in both species and the acquisition of a lignotuber of fire-tolerant size may take over a decade in either species (after seedling emergence). Death rates of lignotuberous individuals varied with size and fire intensity in either species. There was a possible influence of time since fire in *B. serrata* and *Isopogon* with higher mortality at longer (13-year) and short (2-year) fire-free intervals compared with intermediate (5-year) intervals. These effects were dependent on the size and reproductive status of plants.

Survival of all species between fires was high and calculated half-lives indicated life-spans of established plants in excess of 50 years. In *B. serrata* growth analyses and modelling of stem diameter increments indicated that frequent fire (<10 year cycle) may suppress stem development and prevent the setting of cones. Studies of serotinous seedbanks were performed to estimate losses and gains in accumulated seeds through time and numbers of seeds were modelled through time for stands of each species. These indicated that *Isopogon* may store the most seeds and *B. serrata* the least, although the rates of contributions and losses from differing sources and at differing times varied widely.
between species.

Studies of the release of seeds indicated that in all species this was strongly dependent on fire, but that seed-release in unburnt conditions became significant in terms of numbers of viable seeds released in old (>20 years since fire) stands in all species. Survival and emergence of seedlings in all species was enhanced by the removal of vegetation cover. No effect of heating the soil was apparent, although litter enhanced survival in B. serrata. Predation of seedlings in unburnt conditions was severe. In burnt conditions it was comparatively minor.

A model of the control of post-fire emergence by soil moisture and ambient temperatures was developed and tested and used to predict the likely patterns of emergence after burns in differing seasons. These predictions showed that maximal emergence of available seedbank in all species is likely to occur after hot late-summer-autumn fires which promote bulk seed-release in winter. Post-fire seedling survival in all species was highly varied and was found to be adversely effected by both high and low levels of soil moisture. It was concluded that survival may be enhanced by burns that produce emergence in winter. In all species, seedling deaths are concentrated in the first 100 days after emergence.

The overall responses of species across all life-cycle stages were synthesized in several modelling exercises which showed that under predictable high-intensity, late-summer-autumn burns, stability in numbers of established populations could be maintained at a minimum fire frequency of eight years in B. ericifolia and Petrophile and at a frequency in excess of 10 years in the resprouting species B. serrata.
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I wish to specially thank my Supervisor Dr. Peter Myerscough for all his help and advice during my candidature. Thanks and gratitude are also due to Dr. Keith Mullette, Chief Scientist, N.S.W. National Parks and Wildlife Service, for his more than generous allowance of time during 1984-1985, to finish this work after I had commenced employment with the Service. I would also like to thank the various heads of the School of Biological Sciences for allowing me to work in the School and the University of Sydney for granting me a Postgraduate Studentship. Many people have helped during all stages of my work and my thanks go to all of them. Of these a few deserve special mention:

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and also died during "droughts". Site effects were also apparent within species. A common index of soil moisture was calculated for the year covering observations using the WATBAL model. Moisture average data were related to mortality, and the results indicated that at high and low moisture, seedlings in the cotyledonary stage died, whilst most mortality in larger seedlings occurred at low moisture (droughts). Hence the relationship between water availability and survival is complex, but it was concluded, using data from a 52-year average, that the qualitative risk of mortality in newly emerged seedlings was higher in Summer than in Winter. Hence fires timed to produce emergence in Winter were on average likely to produce higher survival of seedlings. This reinforced the result of the analysis of emergence in relation to season of fire.

The above analyses of responses to fire in various phases of the life cycle were synthesized using simple quantitative models. The effects of various high-frequency fires were modelled in each species, with the aim of defining the maximum fire frequency at which constancy in population size could be maintained. In the obligate seeders, B. ericifolia and Petrophile, the maximum frequency of fires at which constant numbers in stands could be maintained lay between 8 and 12, and 8 and 18 years respectively. The lower limits were defined using the highest measured estimates of emergence, seedling survival and growth in seedbank. The upper limits were defined using the lowest measures of the variables. As it was concluded that high-intensity fires in
Summer and Autumn would on average favour seedling emergence and survival, such fire regimes could be maintained at frequencies close to the maxima in which species without depleting population sizes. Other combinations of season and intensity of fire may on average be less favourable, and the corresponding maximum frequency of fire at which they could be maintained may lie more toward the higher values for the intervals given above.

In the resprouters, *B. serrata* and *Isopogon*, frequencies of fires of less than 10 years, regardless of their intensity or season would tend to limit recruitment by killing young juveniles resulting from emergence after each preceding fire. Also, in *B. serrata*, fire frequencies less than 10 years would inhibit the development of smaller lignotuberous plants by killing their stems and continually forcing them back into the mode of basal sprouting. A proportion of the population would therefore be suppressed and may remain immature under such firing. As mortality in both species, through fires, far exceeds that measured in unburnt stands, regardless of fire intensity, frequent fires will hasten the demise of established plants and may inhibit recruitment. In both *B. serrata* and *Isopogon*, if fires of high intensity occur at a frequency of less than or equal to once a decade, populations may decline to low levels or extinction in the long term. If the fire cycle is lengthened recruitment will occur as enough time will be available for recruits to gain fire-tolerant lignotubers and for suppressed lignotubers to grow fire-tolerant and
reproductively active stems. In both species, a single fire-free interval of about 20 years may ensure large-scale recruitment. The primary juvenile period in both these species of resprouters may exceed 20 years.

Comparisons between obligate seeders and resprouters indicated therefore that obligate seeders may be favoured over resprouters in the long term by high-intensity Summer or Autumn fires at a frequency of 8 to 10 years. At frequencies of fires of around 15 to 30 years, all species will survive at potentially very high abundances, regardless of their modes of recovery. At longer intervals between fires, the fate of populations may be fixed by the relative life-spans of individuals, which in all four species may be between 50 to 100 years, and by changes in vegetative cover and levels of predation. It is likely that, in the absence of fire, enough seedlings may survive such that populations of the species persist but at greatly reduced abundance.

Overall, the contrast between obligate seeders and resprouters can be seen as a trade-off between the length of the primary juvenile period and the ability to grow a fire-resistant lignotuber. In resprouters with a long primary juvenile period, young recruits grow a resistant lignotuber before flowering. In obligate seeders, the absence of such an organ is correlated with a much reduced time to maturation. In the case of the species studied, very frequent predictable high-intensity fires in Summer or Autumn may favour the
and Isopogon. Changes in fire intensity and seasons may alter the minimum fire frequency at which constancy in numbers can be maintained. At fire frequencies in excess of 10–15 years, populations of all species may turn over in a manner that maximises potential rates of increase in numbers. At fire frequencies in excess of about 30–50 years, seed shed will be adequate to provide replacement of individuals through attrition, however seedling predation may be the factor that determines recruitment levels in unburnt conditions.

The comparative responses at high fire frequencies between resprouters and obligate seeders can be viewed as a trade-off between a shortened primary juvenile period (obligate seeders) and a longer juvenile period in resprouters where resources are diverted into developing a fire-resistant lignotuber.
COMMON ABBREVIATIONS USED IN THIS THESIS

Anova  Analysis of variance
M.S.  mean square
S.S.  sum of squares
F  F ratio
d.f.  degrees of freedom
t  value for Students t-test
G  value for G-test of independence
\( \bar{x} \)  mean of samples of x.
\( \bar{y} \)  mean of samples of y.
p  probability
n  no. of sample units
S.E.  standard error
\( > \)  greater than
\( < \)  less than
\( s^2 \)  variance
S.N.K.  Student-Newmann-Keuls Test
r^2  regression, co-efficient of determination
\( \sum \)  sum of
mm  millimetres
cm  centimetres
m  metres
D.B.H.  diameter at breast height
O.D.  oven dry
M.S.D.  moist soil days
S.S.D.  sprout-stem diameter
S.S.H.  sprout-stem height
The cohort of seeds formed $t$ years after the onset of maturity in a population seedbank or numbers of seeds at $t$ years after maturation in a population.

The initial cohort of seeds produced in the first year of maturity in a population.

Proportion of intact viable seeds retained in cones $i$ years after the formation of those cones.

Years.

Degrees Celsius.
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1.1 Introduction

The effects of fire on vegetation can be understood on the basis of knowledge of the responses of individual species (Gill 1975, Noble and Slatyer 1977, 1980, 1981). Gill (1975) showed that individual adaptive traits (to fire) had to be evaluated against the whole plant life-cycle in order to understand the way a species survives and reproduces under periodic disturbance by fire. This theme has been explored further by Gill (1981a,b,c). Hand in hand with this concept has been the consideration that fire operates in a manner that can be described by combinations of seasons of fire occurrence, intensity, frequency and other characteristics such as fire type. Combinations of these components are called fire regimes and their actions have been extensively reviewed for differing ecosystems and regions of the world (e.g. Kozlowski and Ahlgren, 1974, Mooney and Conrad 1977, Mooney et al. 1981, Gill, Groves and Noble 1981, Wein and Maclean 1983).

The problem of understanding fire regimes and their effects on plants can be approached from many levels, the species approach (sensu. Gill 1981a, b) being one. However the utility and rapid acceptance of schemes such as those of Noble and Slatyer (1980, 1981) and Connell (1979) for understanding, describing and predicting vegetation dynamics from the basis of life-history attributes of individual species, under regimes of disturbance,
has stimulated further interest in the species approach to fire. As an example, Rowe (1983) has related a classification of species responses in boreal forests based on Noble and Slatyer's (1980) system to categories of differing length fire-cycles.

Many fire studies which attempt to deal with whole units of vegetation have concentrated on following a single fire where pre-fire data were absent (e.g. Jarrett and Petrie, 1929, Cremer and Mount 1965, Siddiqi, Carolin and Myerscough 1976, Baird 1977) or present (e.g. Purdie 1977a,b Purdie and Slatyer 1976, Posamentier et al. 1981), in order to characterize post-fire succession and the general impact of fire. An outcome of these studies has been the generation of hypotheses about the effects of variations in fire frequencies, seasons and intensities (e.g. Purdie 1977a, b, Posamentier et al. 1981, Baird 1977). The testing of these hypotheses can be done in major long-term manipulations of vegetation under varying experimental fire regimes (Trabaud 1974, Van Loon 1969, Hoare pers. comm., unpublished and described in Bradstock 1981). These studies involve major investments in time, manpower and money. Another alternative is to test the effects of fire regimes on vegetation using the techniques of population biology, namely, demography (Harper 1967, Harper and White 1974, Harper 1977). These techniques offer a "short-cut", in that through short-term studies of the whole life-cycles of plants predictive knowledge of population dynamics is gained (Harper 1977, Solbrig 1980).
Such a study is presented here, the aim being to test the effects of varying fire regimes on the life-histories of a group of broadly co-habiting species. The reasons for the choice of more than one species was to see if significant elements of a vegetation type (Hawkesbury Sandstone) follow similar or different pathways in relative abundance under various fire regimes (see Gill and Groves 1981). Such comparisons between species were desired for two reasons. Firstly, data enabling predictions of vegetation dynamics in fire-prone areas of the Sydney Region (where this study was done) are still inadequate yet pressures for imposing and containing certain fire regimes are strong (Boughton 1970, Luke 1971, Richmond 1975, Weir 1978, Anon 1980). Zedler (1977) and other workers such as Walker et al. (1981) have advocated the adoption of a detailed population approach to solving management-oriented fire/vegetation problems.

Secondly, studies in the Sydney region (Beadle 1940, Evans 1962, Siddiqi, Carolin and Myerscough 1976) have indicated that in the fire-prone Hawkesbury Sandstone vegetation, woody species may recover from fire in a variety of ways, through either vegetative regrowth of burnt plant parts or through reliance on seed or both. The appearance of seedlings of many species is common in the post-fire environment. The presence of the ability to survive and regrow is more variable, in the Hawkesbury-Sandstone vegetation. Species which rely solely on
recovery from seeds have variously been called obligate seeders whilst those which survive fire and regrow have been called resprouters (Naveh 1975, Purdie and Slatyer 1976). A feature of the Hawkesbury Sandstone vegetation is the large number of dicotyledonous species which rely on seed only for recovery from fire. A recent study (Benson 1984) has documented this, and other workers (Clemens and Franklin 1981, Siddiqi, Carolin and Myerscough 1976) have provided data which suggests that many species in the Sydney Region are strongly reliant on seed-only regeneration from fires. A selected comparison of the numbers of obligate-seeding and resprouting dicot species in Australian sclerophyll forest/woodland/shrubland vegetation is given in Table 1.1. The results of this comparison (Table 1.1) suggest that obligate seeders have a high prominence in the vegetation of this region.

Another feature of the vegetation in the Hawkesbury Sandstone is that many species (of both categories of recovery) retain seeds in above-ground storages: (Beadle 1940) that is, enclosed in fruits held for long periods on branches. Such seed and cone characteristics in coniferous species have been called serotinous (Lotan 1967, Gill 1981c), and angiosperm species which display degrees of serotiny in woody fruits (e.g. Kruger 1977) may be said to have seedbanks (Harper and White 1974, Harper 1977) stored above-ground. Other species may store seeds in the soil and their response to fire in terms of germination and establishment have been extensively studied (Floyd 1966, 1976, Christensen

It can be concluded that variations in modes of recovery and positions of seed-storage have great prominence in the Sydney Region in sclerophyllous fire-prone vegetation. How do plants exhibiting differing combinations of these factors respond to differing fire-regimes? An answer to this question is vital to an understanding of vegetation dynamics in relation to fire which is in turn vital to any useful attempt to manage vegetation, especially with respect to fire (Kessel 1979, Gill 1977, Good 1981).

Attempts at modelling vegetation responses subject to recurrent fire have been reviewed by Noble and Slatyer (1981). One such method devised by Noble and Slatyer (1977, 1980, 1981) relies on a qualitative model of key responses in differing life-cycle stages of the component individual species of any vegetation type. These responses are termed "vital attributes" (Noble and Slatyer 1977, 1980, 1981) and they are essentially a qualitative summary of demographic characteristics of species. The system devised by Noble and Slatyer (1977, 1980, 1981) was principally
aimed at modelling vegetation changes under differing frequencies of disturbance, such as fire. Some attempts at implementing this method where enough relevant data are available, have been made (Cattelino et al. 1979, Malik and Gimingham 1982, Rowe 1983). Other workers have approached aspects of plant response to recurrent fires of differing frequency in a broadly similar (e.g. Le Houerou 1977) way, or else by using comparative judgements between species of qualitative traits in the life-cycle (Keeley 1977a, Keeley and Zedler 1978, Keeley 1981, Hodgkinson and Griffin 1982, Bell et al. 1984). A concern of these workers and of Noble and Slatyer (1977, 1980, 1981) has been to examine the differing influences of fire-frequency on species that arise from possessing differing modes of recovery from disturbance, as dictated by differing life-cycle traits. One result of such work was the formulation of an hypothesis by Keeley and Zedler (1978), and Keeley (1977a) which specifically related the relative degree of co-occurrence of obligate seeding and resprouting species in the Californian chaparral to differences in fire-frequency. Specifically, Keeley (1977a) and Keeley and Zedler (1978) proposed that moderately high frequencies of fire favoured resprouting species over obligate seeding shrubs whereas at frequencies of fire in the order of once in 100 years obligate seeders would be favoured over resprouting shrubs. Keeley (1981) tentatively generalised his conclusions on the selection of obligate seeders in mediterranean-type South African shrublands where obligate seeders and sprouters coincide within genera. He emphasised
that these adaptations may reflect high predictability of fire in the environment, though not necessarily frequent fire and may be correlated with the moisture status and cover of sites, citing the examples given by Specht (1981) as support. Other workers such as Hodgkinson and Griffin (1982) have attempted analyses of qualitative life-cycle characteristics (in arid Australian shrubs) and have embraced the hypothesis of Keeley (1977a) that shrubs which resprout may be favoured over seeders, if fire recurs at 5-10 year intervals. Similarly Bell, Hopkins and Pate (1984) have offered this hypothesis as an explanation for the relatively large numbers of resprouting species present in the sand plain flora of south Western Australia. Noble (1981) has also discussed the general applicability of this hypothesis.

It can be asked whether this hypothesis has generality away from the regional and species context for which it was derived. It can also be asked how considerations of other fire-regime components may affect the types of classifications of species responses or qualitative models of vegetation change based on species attributes.

A recent study by Malanson and Cleary (1982) in coastal sage scrub vegetation in California demonstrated that due to the lack of survival of seeds in fires and their ability to establish in open unburnt conditions, resprouting shrubs are prevalent in areas with a naturally
low fire frequency. Malanson and Oleary (1982) discussed
the proposition that by altered establishment requirements
and capabilities these shrubs may diverge from the model
offered by Keeley (1977a). Clearly differences in life-
history characteristics and region may be important.

Zedler (1977), in analyzing the qualitative life-
history attributes of species in stands in California,
containing *Cupressus forbesii* (Tecate cypress) found that broad
categories of attributes representing strategies could be
defined. Zedler (1977) encountered difficulty in account-
ing for some of these species strategies in the light of
their observed distribution, noting that some species with
prolific sprouting and seed production established poorly
in post-fire conditions. Because of the limitations and
scope of this kind of classification of life-histories
Zedler (1977) concluded that:

"It will require much more than this crude
table to predict which of these species
may be expected to increase or decrease in
response to different types of manipulation.
But with respect to fire even this limited
presentation makes it clear that species
will respond quite differently."

Examples of similar studies of this type given
above go further to varying degrees, in the kind of detail
they offer with regard to classification of species life-
history and fire-frequencies. Gill (1981b) has put these
studies into some perspective by discussing how knowledge
of species behaviour in increasing detail may offer
greater predictive power as to likely fire-regime effects. Gill (1981b) concluded that the 'species replacement' and 'species classification' approaches may give insight into the effects of frequency and intensity of fires. These qualitative life-history studies effectively fall into those categories though in some cases, such as Keeley (1977b) Keeley and Zedler (1978) and Hodgkinson and Griffin (1982) attempts at quantifying some trends and responses to fire in individual life-cycle stages were attempted. Where quantification of trends has been attempted the studies may be called "demographic".

Gill (1981b) stated that the use of "demographic models" as opposed to the "species-replacement" models allowed effects of further components of fire regimes and other environmental factors to be tested. Gill (1981b) defined the demographic approach as one that: "sets out to determine the numbers of seeds, seedlings, juvenile and mature plants in a population and to then study or predict how these numbers may be affected by fire." This study set out to take such an approach so that the response of a group of co-habiting species to variations in fire frequencies, intensities and seasonalities could be understood. An attempt was made to study the whole life-cycles of plants in a quantitative manner as defined above. Knowledge of this kind would effectively allow the consequences of fire-caused variations in numbers in any particular lifecycle stage to be judged across the whole
life-cycle. As an example, Keeley (1977 b) showed how, in differing species of the shrubs Ceanothus and Arctostaphylos, fluctuations in inputs to the soil seed bank and overall seed bank size could be related to the numbers of seedlings produced after-fire in ways that differed between species. Traits such as relative degree of reliance on seed regeneration (Keeley and Zedler 1978, Hodgkinson and Griffin 1982) can be assessed from the point of view of seed outputs, seedbank size (as done by Keeley 1977 b) and variations in germination and establishment caused by factors other than fire. Keeley (1981), after an extensive review, concluded that species' life-histories need to be closely studied in relation to their environment so that the role of fire regimes and adaptive traits could be clearly defined. As Gill (1981 b) has suggested this may be done most incisively by fully using a demographic approach. Here I present a multi-species demographic study, which seeks to contrast species within and between the modes of recovery: that is resprouters and obligate seeders. This study asks several questions: do widely varied fire regimes (combinations of season, intensity and frequency) affect the abundance of four cohabiting species in differing ways? If so, in what part of the life-cycle do these fire regimes have their major effect, and does this differ between species and or general modes of recovery? Thus, this study is not concerned only with the mode of recovery but the response across all stages of species-life-histories. Gill (1981a,b) has given a classification of modes of
of recovery which will for convenience be referred to here. As outlined previously, species in the study area may be found with seedbanks stored in serotinous fruits or cones. A decision was made to centre the study on these species as they are prominent in the flora and they provide a readily accessible pool of seeds for quantitative study. Aside from some studies of a preliminary nature (Carpenter and Recher 1979, French 1983), intensive studies of the dynamics of these above-ground seedbanks have not been made.

1.2 Problems with and features of demographic studies of long-lived plants.

Much of the reported work on plant demography has concentrated on short-lived perennial or annual species (reviews in Harper 1977, Solbrig et al. 1979, Solbrig 1980, Silvertown 1982) in which the life-spans can be followed directly within the confines of a short-term study. Despite this, complete studies which have covered all life-cycle stages of plants are rare, even for short-lived herbaceous plants, with some exceptions such as for several Ranunculus species (Sarukhan 1974, Sarukhan and Harper 1973, Sarukhan and Gadgil 1974) and Viola sororia (Solbrig et al. 1980, Solbrig 1981) and Poa annua (Law 1981). The life-spans of plants can't be directly observed in their entirety for longer-lived plants such as woody shrubs and trees, hence many demographic studies such as Crisp 1978, Crisp and Lange 1976, Hett 1971, Hett and Loucks 1971, 1976,
Yarranton and Yarranton (1975) Schlesinger and Gill (1978) have concentrated on particular life cycle phases, namely seedling mortality and recruitment and survival of adult plants. Other attempts to cover and model changes in the whole life-cycle have been made by measuring rates of change both within and between life-cycle stages and applying models of population change such as the matrix model of Leslie (1945) (e.g. Hartshorn 1975, Enright and Ogden 1979, Werner and Caswell 1977, and Bierzychudek 1982). Models other than the matrix model which utilize demographic and physiological growth data have also been developed (Noble and Slatyer 1981, Shugart and Noble 1981). The basic method of these studies was adopted here: that is the whole-life cycles of plants were studied and changes both within life cycle stages and transfers between stages were measured in relation to fire regimes. Despite their utility, the use of the above models was not attempted. However in the future they may be explored with the data produced here. Rather, simpler calculations of rates of change are presented in this thesis.

The demographic study of life-cycle stages in long-lived plants relies on the short-cut method of simultaneously examining differing stages in spatially separate populations. This was done here.
1.3 The study species and study area.

The Hawkesbury Sandstone vegetation, its general processes and environment has been described by Pidgeon (1937, 1938, 1940, 1941) and Hannon (1956, 1958). It is subject to recurrent firing (Beadle 1940, Christensen et al. 1981), particularly the Shrublands and Woodlands and Open-forest types (Specht 1970). As noted above a feature of the woody plants is the large number of obligate seeders (Table 1.1) and numbers of species with serotinous seedbanks (Beadle 1940, category I(A) in Gill's 1981a,b, classification). For these species there would appear to be no persistent seedbank of dormant seeds in the soil.

The species chosen in this study were mentioned in the studies of Beadle (1940) and Siddiqi, Carolin and Myerscough (1976). They are:

(i) **Banksia ericifolia** L.f.
(ii) **Banksia serrata** L.f.
(iii) **Petrophile pulchella** (Schrad.) R.Br.
(iv) **Isopogon anemonifolius** (Salisb.)

Nomenclature is as given in Beadle et al. (1982) and George (1981) and these species are generally referred to in this thesis in the abbreviated forms; B. ericifolia, B. serrata, Petrophile and Isopogon.

All species co-occur to varying degrees in the particular study area chosen; Brisbane Water National Park
(Figure 1.1) to the immediate north of Sydney. The vegetation types in this Park have been mapped and described by Benson and Fallding (1981). The vegetation types and soils in which the species occur according to Benson and Fallding (1981) are listed in Table 1.2. The level of co-occurrence between species is broad (Table 1.2), however, the range of types in which each species was studied was narrower (Table 1.2). In each species the study was concentrated in stands where in the case of *B. ericifolia* and *Petrophile* the species were dominant, (Table 1.2). These were considered to be optimum for the species, and plants heavily suppressed by other species in their stratum were not examined. Hence competitive relationships between some of the species, for example in *B. ericifolia* where dense stands cause domination of small *B. serrata* or *Isopogon* bushes, (see: Siddiqi 1971), though common, were not studied. Thus study sites for each species (though with many exceptions in *B. serrata* and *Isopogon*) tended to be separate, though directly adjacent. Siddiqi (1971) investigated the edaphic factors controlling plant distributions in nearby coastal heathlands and characterized *B. ericifolia* as a dominant of wet sandy heath. *Petrophile* would seem to also favour this habitat, often occurring in wetter areas of open-forest with *B. ericifolia* and *Hakea teretifolia* (Benson and Fallding 1981) in dense alternating patches. These were the type of stands examined here. *Petrophile* may also extend further into Open-forest and Open-woodlands
which were the habitats where B. serrata and Isopogon were studied.

The complex geological and edaphic factors present in the general study areas (Benson and Fallding 1981) causes the particular vegetation types in which these species were studied, to be closely juxtaposed. The relative flammability of differing stands has not been assessed however, it is apparent to any casual observer that when fires occur that similarities in broad levels of severity and evenness of burning occur across this range of sites. Therefore assessments of reactions to common fire regimes of each species were justified.

A description of each species follows:

(a) B. ericifolia

The species is described by George (1981) as a shrub or small tree, single-stemmed, non-lignotuberous, bark up to 0.5 cm thick, reaching a maximum height of 6 metres. Flowering is in Autumn to Winter, and seeds are set in infructescences, here referred to as cones, consisting of aggregations of follicles each containing usually 1 seed. George (1981) has classified this species as being dependent on fire for the release of seeds from follicles. The mechanism for this has been explored in the closely related species Banksia ornata (see Doust 1983) by Gill (1976). Further general studies of seed release
and effects of fire on the species are given in Bradstock (1977) and Bradstock and Myerscough (1981), and this work showed the species to be dependent on a fire cycle between 5 - 30 years. Bradstock and Myerscough (1981) also discussed possible interactions between fire intensities and seasons. The species' response to fire can be classified as I(a) (Gill 1981b). Figure 1.2 illustrates differing stages in the life-cycle of B. ericifolia.

(b) B. serrata

George (1981) describes this species, when mature, as a single-stemmed tree up to 16 metres, though existing in some coastal habitats as a shrub up to 3 metres, with bark up to 3 cm thick, flowering in Summer. The species has a well-developed basal swelling (lignotuber) prominent in younger and small plants (Beadle 1940) and is capable (George 1981) of epicormic regrowth, as well as lignotuberous regrowth. The population studied in this project were generally smaller than the maximum height value given by George (1981), rarely 9 - 10 metres and commonly averaging 4 - 5 metres. The species was claimed by George (1981) to release seeds in both the presence and absence of fire from follicles in the infructescences. However casual observations in the study area suggested that the degree of dependence on fire for seed release was similar to B. ericifolia. The species can be classified as VI(B) (Gill 1981,b). Figure 1.3 illustrates aspects of the life cycle of B. serrata.
(c) Petrophile

This species is described as an erect shrub to 3 metres high, Spring-Summer flowering with achene fruits contained in bracts aggregated into cones (Beadle et al. 1982). Taller plants were sometimes observed in old (20 + years) stands in the study area. Plants are single stemmed. No lignotuber was observed on any individual, though Beadle (1940) claimed the opposite. It is possible, as the nomenclature of this species has been revised several times, that Beadle (1940) may have referred to the very similar species Petrophile sessilis. No individuals were ever observed to survive fire as Beadle (1940) has claimed.

The small achenes in Petrophile are released when the bracts forming the cones open. This mechanism was observed initially to be substantially dependent on fire (as did Beadle 1940) though not to the same extent as in the Banksia species. The achenes are referred to as "seeds" in this study. The species was therefore classified as I(A) (Gill 1981,b). Figure 1.4 illustrates the life-cycle stages of Petrophile.

(d) Isopogon

This species (I. anemonifolius var. anemonifolius) was described by Beadle et al. (1982) as being a Spring-flowering shrub to 2 metres in height with globular cones, composed of bracts, enclosing achenes, which dehisce to allow fruit release. Effectively the cone disintegrates
and as with the other species, to a greater extent this seemed to be reliant on fire. The species is multi-
stemmed (Fig. 1.5) in adult form having a large plate-like lignotuber largely below the ground surface (Fig. 1.5). Other stages of the life-cycle are illustrated in Fig. 1.5. Achenes are largely referred to here as seeds. Stems are easily killed by fire, however, where lignotubers are developed, the species readily resprouts. Therefore it is classified as possibly V(B) (Gill 1981,b).

In summary, I selected for study broadly co-habiting species, though individual study sites for each were chosen. The species were chosen so that contrasts in life-form and habits, within the broad categories of obligate-seed and resprouting regenerative ability, were made. These contrasts were greatest in the sprouters between B. _serrata_ (thick bark, single stem tree/shrub) and _Isopogon_ (low, thin, multi-stemmed shrub). The principal contrast between _B. ericifolia_ and _Petrophile_ was in the thickness of bark present in older plants. Hence the study provided contrasts within the I(A) category of Gill (1981,b). The study also contrasted the demographies of the closely related _Banksia_ species. This was the basis of Keeley and Zedler's (1978) work, their rationale being to provide an explanation of within-genus divergence (over evolutionary time) and co-existence between sprouting and obligate seeding habits.
1.4 *Ecological versus evolutionary studies.*

Harper (1977) stated that an objective of plant demography was concerned with:

"the selective processes which .... lead to ecological and evolutionary change."

The use of demographic studies to address both ecological and evolutionary questions is common (e.g. Horn, 1979, Solbrig 1980) though others such as Mack and Pyke (1982) have questioned the degree to which generalizations can be made on the basis of the varied and opposing trends found in their long-term studies of the grass *Bromus tectorum*. Attempts to generalize, *a posteriori*, about events and processes which are untestable have been criticised by Hickman (1979) and Harper (1982). Studies such as for e.g. Keeley 1977a, Keeley and Zedler (1978), Naveh (1975), Wells (1969) have attempted to characterize fire adaptations in plants on an evolutionary basis whether these be simple morphological characteristics or suites of characters forming life-cycle traits. The difficulty of doing this has been discussed by Noble (1981) and Rowe (1983) who conclude it is impossible to know whether these traits were derived either singly in the presence of fire or interactively or fortuitously with other factors. The general adaptationist approach has been comprehensively criticized by Lewontin (1978) and Brady (1979, 1982) whilst Harper (1982) has discussed the confusion that currently surrounds the use of the concept of adaptation.
With regard to fire the basis for judging primitiveness of characters, essential for framing evolutionary hypotheses in closely related species, has been given little attention, despite examples such as Wells (1969). Decisions about primitiveness are not generally objectively tested as hypotheses in these types of studies. Rather, reliance is placed on classical taxonomic classifications usually framed from a sample of floristic and morphological characters. An objective method of testing character states such as cladistics (Platnick 1979, Eldridge and Cracraft 1980) is absent from the methods of evolutionary ecologists whose studies seek ultimate (sensu Harper 1982) explanations from ecological data.

Cladistic analysis of the genus Banksia (Doust 1983) using a broad range of morphological and floristic characters revealed that of the co-occurring species in the Sydney Region, B. serrata, B. aemula and B. ericifolia had close affinities, whilst other species such as B. oblongifolia were more closely related to Western Australian species. However, my prime concern in this study is with providing "proximal" rather than "ultimate" explanations (Harper 1982) of species behaviour. Auld (1984) has discussed the difficulty of testing evolutionary hypotheses from ecological data, emphasizing that the significance of traits within life-cycle stages must be carefully judged against the whole life-cycle before any "ultimate" explanations are attempted. I have adopted a similar conservative approach with these species.
1.5 Fire regimes in the study area.

(i) Fire intensity

The classes of fire intensity defined by Cheney (1981) have all been observed in the study area in Open-forests, Woodlands and Scrubs where the vegetation reaches the nominated heights in Cheney's (1981) classification. A problem exists in these vegetation types, in that the prominent shrub components are not formally considered in some widely used models of fire behaviour (McArthur 1967, Noble et al. 1980). These shrubs and small trees are readily observed as prominent components in most conflagrations and are often consumed completely (except for stems and large branches). There is an urgent need to modify existing fire-behaviour models (Noble et al. 1980, Rothermel 1972) to suit these vegetation types. Sampling methods developed in similar vegetation in Western Australia (Peet 1971, Sneeuwjagt 1973) may provide a basis for their quantification, as a first step in this process. The experiments on fire behaviour begun by Cheney (unpublished report) need to be completed.

(ii) Fire seasons and seasonal occurrence of fires.

Fire seasonality in the region of the study has been defined by various methods, for example, the climatic averaging method used by Walker (1981). Generally the fire season is defined as being contained within the Summer
months (Luke and McArthur 1978). Some sources such as Luke (1961) add fire as an occasional risk in Autumn and Spring and as being non-existent in Winter. Actual records of fire incidence show that the fire season is much wider (Table 1.3). Records of fire since the mid-1960s in Brisbane Water National Park, where much of this study was contained, showed that fires have occurred in all months of the year with a wide season of most frequent occurrence stretching from Spring to Autumn (Summer inclusive) (Table 1.3). Clearly, irrespective of source of ignition, whether deliberate, accidental or "natural", the contemporary risk of fire in the vegetation studied spans the greater part of the year. This study was done during a severe drought, during which conditions of high fire danger in the field were noted irrespective of season. This occurred when fuel moisture became low. An example, extreme fire danger was forecast on several days in early August 1980 (Winter) for the Sydney region (Bushfire Council of N.S.W. pers. comm.).

This study was based on the premise, that a fire risk in any season existed and that the full range of seasonal possibilities were to be considered.

(iii) **Fire frequencies.**

Fire histories in the park date back reliably to 1964. However old, (<1964) unburnt stands have been reduced severely in extent due to recent large fires. Fire cycles
below or around 5 years are not uncommon in areas where pyromaniacs are active, and I have been able to identify several sites in the vegetation types studied which have been burnt 3 times since 1964. The emphasis on prescribed burning of large blocks for hazard reduction by National Parks and Wildlife Service personnel has changed in recent years (Tegart, pers. comm.) to a policy of strategic strip perimeter burning which may have an overall effect of lengthening the fire cycle in the hinterlands in the future.

In summary, a wide range of variation is found within the individual fire-regime components. As well as the likely combinations of low-intensity Winter burning (prescribed or unprescribed), and high-intensity Summer fires, less obvious combinations were observed to occur or have occurred, such as low-intensity midsummer fires (the result of a midnight backburning operation) or high-intensity Winter fires (August 1980) in severe-drought conditions. It was considered that a wide range of variations existed and this study endeavoured to explore these.

1.6 Definition of main themes and layout of the study.

Harper (1977) provides some diagrammatic models of plant life-cycles, and as none of these directly represent species with above-ground seedbanks, a modified version using similar life-cycle stages is presented in Figure 1.6.
Questions of age and life-cycle stage have been explored by Gatsuk et al. (1980). Flexibility is necessary to account for the differing characteristics of individual species. In the cases studied here, commonly used techniques for determining age through ring counts in stem cross-sections could not be usefully employed. Whorl counts on stems in *B. ericifolia* (Morris 1975, Bradstock 1977) may be useful up to ages of about 10 years and were feasible in *Petrophile*. However, these species can also be aged from knowledge of fire-histories of sites, and in all cases this was the method used to determine either age or the time since last fire. Records of fire in the study area were available back to 1964. In stands unburnt before this year, varied estimates of age were tried in relevant studies (see Chapter 4 particularly). In *B. serrata* an attempt at determining maximum age was done using radio-carbon dating of lignotuber wood in two very large plants. Details of this are given in Chapter 9.

Within the life-cycle stages given in Figure 1.6, estimates of age at which crucial processes occur are presented in the relevant chapters. Generally though, an arbitrary definition was applied to discriminate between seedlings and established plants. Seedlings in this thesis are defined as plants less than 3 years of age. Within the established phase in the lignotuberous species, *B. serrata* and *Isopogon*, a further division was made between young juveniles and juveniles, the former being plants either without or with lignotubers too small...
to be fire-resistant. In all species there is no discernible vegetative propagation of ramets (Harper 1977). Individuals in all stages constitute genetically distinct units or genets and it is fluxes in genets that are addressed in the thesis.

This study was concerned with rates of change in numbers within life-cycle stages and transfers between stages. Within-stage studies of survival and additions of new individuals were complemented in some cases by studies of growth in size, as size rather than physiological age may be more important in determining survival and reproductive output (e.g. Werner 1975).

The effects of fire on these processes can be resolved into a number of areas of study with respect to changes within and between life-cycle stages. A simple model outlining these is presented in (Figure 1.7). The study involved consideration of the fire survival of genets (Figure 1.7), within life-cycle stages. Considerations also of the transfer of genets between stages were based on their dependence or otherwise on fire regimes (Figure 1.7). Other considerations of growth and changes in numbers within life-cycle stages in the absence of fire are important in that they determine the levels of abundance when or if a fire occurs (Figure 1.7). The general themes produced by the model in Figure 1.7, are summarized in Table 1.4 in their order of presentation in the thesis.
CHAPTER TWO: FIRE EFFECTS ON ESTABLISHED PLANTS.

2.1 General

Introduction

Studies on the survival and recovery of established plants after burning were carried out to determine the effects of:

(i) plant size
(ii) life-cycle stage and plant maturity
(iii) the length of the interval between burns
(iv) differing fire intensities and levels of inflicted damage
(v) differing burn times or seasons of burning.

An understanding of population response was regarded as being dependent on these effects and would allow, in particular the formulation of a model that would discriminate between individuals and predict their fates. In addition if information on determinations of modes and rates of recovery in survivors were also included, variations in the response of the population in relation to fire frequency could be predicted. This is done in a later chapter.

As a preliminary to the main body of work, an outline of species responses is provided. These impressions were gained from general observations at the outset
of the study. These observations were used to decide the direction of further studies in each species.

**Banksia serrata**

This species was observed to resprout from epicormic buds on branches, stems and lignotubers and in all cases the origin of recovery was above-ground. Because of the uneven-aged structure of most populations and the wide range of size classes and forms present, the position or mode of resprouting was likely to depend on interactions between fire intensity and size. In fires of low-scorch height and presumably of low intensity (Cheney 1981, van Wagner 1972) large individuals were seen to be relatively unaffected whilst small plants suffered complete scorch or worse. Higher scorch height, and presumably intensity, was noted to affect progressively larger proportions of populations. The fire-tolerant nature of *B. serrata* as suggested by these observations warranted inspection of the degree of insulation and dissection of the resprouting mode into its varied components. These lines of study are described below.

**Banksia ericifolia**

This species was noted by Gill (1981 d) and Bradstock and Myerscough (1981) as being generally susceptible to fires, though Ingwersen (1977) observed survival through fire in large stems and subsequent suckering of
new growth from burnt parts. Stricker (pers. comm.) has also noted such recovery and he added that this seemed to occur in sandy sites where the stem bases were buried and insulated from fire allowing new growth to effectively arise from or below ground-level. In my experience any definite survival of plants directly burnt was usually restricted to the edges or patches of fire where low flame heights gave partial scorching of the foliage. However, resprouting in plants totally scorched (as used in Gill's (1981, b) classification) or from burnt parts in partially scorched plants was not observed. In general, survival but not resprouting was most common in large individuals under low flame and scorch conditions. Where the flames were high enough to reach into the foliage of these trees (usually flames of height one metre plus) to ignite the lower branches the nature of the leaves and their orientation and distribution is such that eruption of flaming in the entire crown occurs. The foliage offers an ideally ventilated fuel matrix which under a wide range of weather conditions will burn in this way. A similar effect in south-eastern Australian sandy heath has been described in general by Cheal (1981). Therefore plant survival is often limited to the fringes of burns such as roads, tracks or clearings often where backburns or back-fires have occurred or amongst areas of broken terrain such as sandstone outcrops and cliffs where the even passage of fire-fronts have been broken up.
Survival and size were considered to be possibly related in large old individuals through a presumed presence of bark thick enough to provide insulation on the lower stems (George (1981)). As stated, though, re-sprouting was not observed in burnt plants.

**Isopogon anemonifolius**

Stem development of the usually multi-stemmed individuals rarely exceeded more than a metre in height or a centimetre in diameter of each stem. Fire-affected stems were in all cases virtually completely killed irrespective of the level of general scorch in the surrounding vegetation. Inspection of stems revealed bark to be usually less than a millimetre in thickness and hence further considerations of recovery and survival in stems were not made. Rather, the vigorous recovery observed from ligotubers, at below ground level, warranted further attention.

**Petrophile pulchella**

A similar response in Petrophile was observed though by comparison with Isopogon, stems can achieve greater heights and diameters. Bark thickness as with Isopogon was rarely greater than a millimetre in the larger stems (~ 2-3 cms diameter). As with B. ericifolia some partially scorched stems were seen to survive but only rarely. As opposed to B. ericifolia, deaths of large individuals whose crowns remained partially intact after
burning, were frequently observed and this was attributed to the presence of thin bark at their bases. Resprouting in five individuals which were artificially defoliated was observed to be vigorous and sustained. Because of the thin nature of the bark further analyses of both bark thickness and fire survival was not attempted, the species being considered to be sensitive to fires of all severities, in all size classes.

In summary, further studies were planned for Banksia serrata, Isopogon anemonifolius and B. ericifolia. In Banksia serrata analysis of stem survival and recovery and lignotuber response was planned. As a first step, bark thickness in relation to stem size was analyzed in the Banksia species to provide a basis for predicting the sizes of stems likely to be vulnerable to burning and for comparison with plants burnt in real fires. In Isopogon efforts were concentrated on the survival and response of lignotubers. In Banksia ericifolia, studies on survivors of burns were performed to investigate sources of vegetative recovery and their vulnerability to fire, in relation to plant size.

Measurement and manipulation of fire intensity

Gill (1981a,b) acknowledged that problems may arise in relating quantitative measures of fire intensity such as the Byram measure (Byram 1959) to the effects on plant parts. Such use of the measure is particularly difficult where plant sizes vary. In such cases data are sought on
survival in populations.

Plant ecologists working with fire, have been criticized by Alexander (1982) and other authors cited by him for their lack of perception (and measurement) of fire intensity and behaviour. Both Alexander (1982) and Rothermel and Deeming (1980) decried the lack of quantitative descriptions of fire intensity in ecological studies that prevent meaningful comparisons between burns and observers in effects of fires on plants. Despite these criticisms the best designed and measured experimental fire studies may encounter difficulties in standardizing and applying fire intensities. For example, Noble (1982) used standard quantities of added straw fuel for comparative studies on the effects of varying the season and frequency of burns in mallee *Eucalyptus*. He reported that there was variation between the fire intensities, presumably due to differing weather conditions, and that this would have been confounded with stem survival between treatments. Another difficulty is that quantitative fire-intensity measures are often averages or indices of what is essentially a complex and varied set of events. Gill (1981 b) raised this problem and discussed its nature within particular fires in terms of variation in their intensity and behaviour, and emphasized the possible importance of these variations in population survival. As an example, Walker *et al.* (1981) found no positive correlation of Byram fire intensity with shrub mortality in *Eucalyptus populnea*
woodlands, with higher mortality being found in areas burnt under low-intensity back-fires than under high-intensity head-fires.

One method of analyzing fire effects on stems is through studies of the insulating capabilities of bark of differing trees. Vines (1968), Hare (1961 a,b 1965), MacArthur (1968) described studies where bark thickness, internal temperatures of the stem and measurements of fire intensity have been simultaneously carried out. Mostly this type of study has been concerned with comparing species' fire-susceptibility through quantitative and qualitative comparisons of bark (e.g. Gill and Ashton 1968). However both Vines (1968) and MacArthur (1968) related within-species variations in stem-size to bark thickness and these were related to variations in stem survival and damage. Workers studying fire in semi-arid and arid lands of eastern Australia have attempted to relate differential shrub and tree survival to variations in size and fire-related damage (Walker and Green 1979, Wilson and Mulham 1979, Hodgkinson 1979, Walker et al. 1981, Hodgkinson and Griffin 1982). Hodgkinson and Griffin (1982) emphasized the need for the presence of regenerative buds protected by either bark on above-ground parts or else by soil, if on roots, if active vegetative recovery is to occur in woody plants. Plants may also survive if their crowns are incompletely killed by fire and some live branches remain with green foliage, provided insulation on the lower, burnt parts of the stem.
is adequate to ensure survival of the vascular tissues at the level of heating sustained. Such a phenomenon was noted by Walker and Green (1979), Wilson and Mulham (1979) and Hodgkinson and Griffin (1982).

One difficulty with using real fires for the direct determination of population survival lies with the danger and impracticability of trying to light high-intensity fires, hence observations such as Vines (1968) were carried out in either fires of low intensity or in heavy slash fires. An alternative approach found in the literature, both with respect to stem and bark studies (Gill and Ashton 1968), Hare (1961a,b,1965) and in rootstock or whole shrub studies (e.g. Kayll and Gimingham 1965 and Leigh et al. 1978, Leigh and Holgate 1979), is to use artificial heat sources such as propane burners. A particular advantage of such apparatus is that they should allow estimation and standardization of two of the variables given by Rothermel and Deeming (1980) as being useful for quantitative description of fire intensity. These are residence time and heat output per unit area.

This kind of apparatus was adopted in this study as the extensive areas of land and the necessary logistics needed for comparative experimental burning were not available. However application of artificial heat sources to established plants was limited in scope to those plant parts which could be evenly and instantaneously covered by the
equipment. Therefore, studies of lignotubers only, were considered amenable to this kind of treatment. Manipulations of fire intensity in relation to differing stem sizes were more difficult. An indirect approach to understanding the survival of stems in relation to varying fire intensities was taken. The relationship between bark thickness and stem diameter in the *Banksia* species was investigated and interpreted in the light of experimentally-determined internal temperature changes at the vascular cambium, under heating. A quantification of possible vulnerable stem sizes was sought from this approach.

The survival of the stems of the *Banksia* species in relation to their size was then examined in the aftermath of fires in the study area. As quantitative data on intensity for these fires were not available, populations were sampled at the high and low extremes of fire damage in *Banksia serrata*. In *B. ericifolia*, populations burnt in fires yielding low scorch and leaf damage only were examined. For *B. serrata*, data on overall plant mortality were also collected. Variations in bark moisture in *B. serrata* were also followed in the field to investigate the influences of site and season on this variable and its possible role in stem insulation.
2.2 Rises in internal stem temperatures under an artificial heat source in *B. serrata*.

**Introduction**

Measurements were sought on internal temperature changes under heating in stems of a range of sizes so as to:

(i) define the relationship between bark thickness and temperature change;

(ii) identify the level of stem size that may be susceptible to damage induced by heating.

A propane gas torch was used as a heat source, applied to stems in the field.

The insulation properties of bark have been extensively investigated by Martin (1963a,b), and many authors have demonstrated the relationship between thickness of bark and its role as an insulator as measured by the rise in internal stem temperatures under heating. Martin (1963,b) demonstrated that the critical temperature for death of cells varies with time of exposure for given temperatures in a semi-logarithmic manner.

By comparison, other authors such as Vines (1968) and Kayll (1966) have used fixed estimates of critical temperature for cell death when considering the fate of vascular tissues in studies of heated stems. An instantaneous value of 60°C at the cambium was used by both
these authors as a critical temperature. For convenience, this value was adopted here as a working level of critical temperature.

While much of the impetus of such work has been to investigate the likely damage to wood in species of commercial importance under varying fire intensities, the method has potential for identifying the population consequences in terms of stem damage — size relationships within any species.

**Methods**

Stems were selected covering a range of diameters at around breast height. Wedges of bark were removed at this point and in the opening a horizontal hole was drilled from one side toward the opposite side of the stem. The length of the hole was judged, by measurement of the bark thickness and calibration of the bit, so as to terminate approximately at the cambium on the opposing side of the tree. Several trial runs were made and excavated by chisel to measure the success of these estimations. As they were within 2mm of the cambium in each case, this method was adopted. The hole was of a diameter just large enough to accommodate chromel-alumel thermocouple wires sheathed in resin. The wires were 1 mm thick and were exposed at the tip junction. The wires were rammed hard up against the end of the hole after insertion to force the tip junction into the tissues. The exiting...
wires were sheathed in aluminium foil as was the cut generally. A cold reference junction made from an ice-filled thermosflask was used and voltage in the thermistor was read from a digital multimeter on a 0 - 100 millivolt scale. A second thermistor encased in a metal sheath was placed on the bark surface adjacent to the inner probe and fastened with metal clips.

Details of the gas burner and the regulator settings used are given in Appendix 1. The torch was hand-held in all treatments with the flame tip just touching the bark adjacent to the estimated position of the inner thermistor. Heat was applied for four minutes in four stems and eight minutes in two stems. Temperatures (voltages) were scanned in each probe every twenty seconds using a switch incorporated in the wiring. Measurements were maintained for up to six minutes after the cessation of heating.

When cooling had occurred the treated area was chiseled carefully away to reveal the tip of the inner probe. The bark thickness was measured to this point on a squared off cut. The placement of the tip in relation to the cambium was noted.

Results and Discussion.

Table 2.1 provides details of the stem and bark measurements and location of the probes.
Figure 2.1 showed that the differences in stem size and bark thickness affected the internal temperature measured during heating. Regression lines for various periods of heating were formulated (Figure 2.2) and these illustrated the relationship between rise in temperature over the initial temperature in relation to bark thickness. It can be seen firstly that a difference of 10°C in initial pre-burn temperature will substantially alter the range of bark thickness which will be of adequate size to prevent internal temperatures reaching the critical level, for any given time of heating. The data indicated (Figure 2.2) that the range in bark thicknesses, (estimated by extrapolating the regression lines as done in Fig. 2.2.) that could be considered vulnerable to temperature rises of greater than 30°C were from 0 – 10 mm, for up to 2 minutes heating and up to around 15 mm for 3 minutes heating. Such a level of temperature rise may be critical in Summer.

As the readings were taken on a colder than average day in Winter, a rise of 40°C (see Table 2.1 for measured initial internal temperatures) can be regarded as the maximum needed to reach 60°C+ at any time of the year.

2.3 Relationships between stem diameter, bark thickness and heating in the Banksia species.

Aims and Introduction

In order to relate the measurements given above to the stem sizes likely to be vulnerable to given amounts
of heating, it was necessary to determine the relationship between stem size (diameter) and bark thickness. The aim was to formulate a general model for each Banksia species from which the sizes likely to be killed by varied exposures to flaming combustion could be predicted. Vines (1968) pointed out the possible uses of such a model for the predictions of stand sensitivities to fire. The first step in such a model was to investigate whether a general relationship between the variables could be found within each species.

The relationships between bark thickness and stem diameter have been discussed by several authors. McArthur (1968) in presenting data for two species of Eucalyptus showed how bark thickness was related to age and stem size. His data showed increasing thickness with increasing stem size but he noted that this relationship may break down in old trees of E. rossii in which bark thickness may decrease with stem size. He also noted that the form and position of trees can affect the relationship. Gill and Ashton (1968) presented regression data for such relationships in three Eucalyptus species, showing that the slopes for each species were highly significant statistically. These equations related reciprocal values of both variables. Gill (1981,b,c) further noted that the nature of within-species variability of this relationship has had little investigation.
The initial aim here was to explore this variability within species. Initial studies in *Banksia serrata* used a range of sites which were last fired at differing times. Data were also assembled within sites last fired at the same time in two differing sample stands in order to compare possible spatial influences. In *Banksia ericifolia* the initial study compared old populations at differing sites, with measurements at differing heights on the plants, forming the basis of the comparison.

**Methods and Results**

(i) *Banksia serrata*

Bark thickness and diameters of sample stems were recorded in three populations, with two stands in each being measured. The last recorded burns were respectively for the populations 1976, 1968 and unrecorded (20 years +). Stands within "ages" were adjacent to each other. Stands chosen were for each of the two more recently burnt populations, located in flat Open-forest on fairly deep soils. Those of indeterminate age were located on mildly sloping sites of more-variable soil depth and overstorey.

Within each stand, twenty-five stems were selected representing the range of sizes present. A wedge approximately 15 x 15 centimetres in diameter was removed from each stem at around breast height (1.6 metres). Height
of wedge removal was standardized at this point on all stems. Straight erect stems only were used to avoid complications arising from gnarled forms. Before wedges were removed stem circumference was measured to the nearest 0.5 millimetre using a metal tape, in stems greater than about 4.0 centimetres in diameter. In smaller stems, diameter was measured using calipers to the nearest millimetre.

Wedges were extracted with a hammer and chisel. Cuts were made on four sides perpendicular to the bark surface. The bark thickness was measured on the wedge at two points, each roughly 0.5 centimetre from the upper and lower edges.

**Results**

Regressions for each site were developed using diameter as the independent variable and bark thickness as the dependent variable (Table 2.2). Regressions using a logarithmic transformation of the variables and reciprocal values were also formulated, however while the latter gave $r^2$ values similar to the equations using untransformed data, the fit of calculated lines in small stem sizes was inferior and they are not considered here. Both variables were analyzed in units of millimetres.

All sites gave equations with high $r^2$ values and highly significant slopes. However equations varied between stands and populations in the slope and intercept.
values (Table 2.2). Comparisons of these values were made using analysis of covariance (Zar 1974). The results (Table 2.3) showed that differences in slopes were non-significant but that differences between intercepts were highly significant. In particular, the value for site 6 (Table 2.2) was of a differing sign.

As the equations tended to overestimate bark size at small stem sizes, data for stems less than 10 centimetres D.B.H. were analyzed separately for each sample. The results (Table 2.4) showed a similar pattern to those given above in terms of the significance of site (Table 2.5) differences, though intercept values were ordered differently amongst the samples.

(ii) Banksia ericifolia

Methods

The methods of stem measurement and wedge extraction and measurement described above were used, but the sampling points within stems and sites varied. As noted earlier, resprouting from burnt or scorched parts was not observed though survival can occur. It was decided to concentrate measurements only on the lower stems of very large individuals in old populations as these were the usual survivors if partially or lightly burnt in low ground fires.
Three sites were chosen, one being 25 years old and the others being of indeterminate but older age. Five stems in each were chosen representing a range of the largest sizes of straight erect individuals present. Measurements of diameter and wedges were drawn at points on the stem above-ground of 20, 50, 100 and 150 centimetres.

Results

Within each site, equations were constructed from between-stems data at each height (Tables 2.6). These were initially compared between sites within heights (Table 2.7). The results of analysis of covariance showed that at heights of 20 and 50 cm slopes and intercepts were not significantly different, whilst at the other heights, slopes differed significantly. Site data at each of the lower heights were pooled (Table 2.8) and combined equations were compared (Table 2.8) but proved to have significantly different intercepts.

Discussion and Conclusions

The results for both species indicated that a general equation at least within the categories of age and sites sampled could not be adopted to describe the relationship between bark thickness and stem size.
In Banksia serrata, a trend for similarity existed amongst equations developed for all stem sizes sampled in the sites most recently burnt. Differences between intercepts were apparent in the "oldest" site and it was therefore concluded that the time since last burn and site factors either separately or in interaction may influence the relationship. Generalizations and site comparisons concerning stem size and fire susceptibility as a function of bark thickness would need to be framed on the basis of individual site equations. It can be concluded that survival or levels of damage of stem and branches in fires of given sizes will be affected to some degree by sites. Variations in sizes were viewed by examining the predicted range of bark thicknesses generated for given stem sizes by the sets of equations. Values of stem diameter from 1 to 10 cm were fed into the equations for each species (Tables 2.9 and 2.10). The contrasts between the equations for all stem sizes and stems < 10 cm diameter, in B. serrata can be readily seen in terms of predicted bark thicknesses at small diameters (Table 2.9).

For B. serrata the heating experiment showed that bark thicknesses (Figure 2.2) up to 15 mm allowed possible lethal rises in temperature if heating was applied for three minutes. As this was considered to be the maximum likely duration of combustion or "burn-out time" (McArthur and Cheney 1966) (See discussion below in next section), the range of possible, vulnerable diameters can be read
from Table 2.9. A value of around 8.0 cm was the maximum indicated from Table 2.9. This was therefore considered to be the maximum stem diameter at which fire-induced cambial death could be inflicted. For lesser durations of heating (2 and 1 minutes respectively) values of maximum stem size of 6.0 and 4.0 cm were given by Table 2.8. Mean values for each heating level can be computed from substituting the critical bark size values into each equation. These will fall within a centimetre lower than each of the maxima given above.

A similar procedure was applied for Banksia ericifolia. Direct heating effects on internal temperatures were not carried out. However Martin's (1963a) work on between-species comparisons of bark thermal diffusivity suggested that differences in the capabilities of species' barks to transfer heat are negligible. Hence, from the heating observations in B. serrata maximum stem sizes for 3, 2 and 1 minutes heating (Table 2.10) were respectively 20 cm+, 18.0 cm and 9.0 cm. As considerable variability existed between equations, within and between heights and sites, the ranges of stem values corresponding to the critical bark thickness were wide (≈ 5-6 cm), indicating the potential for varied response in terms of damage to the cambium under heating both within and between stems.

Comparisons between the species highlighted the importance of bark thickness in determining possible
survival differences at given sizes, with the thinner-barked *B. ericifolia* contrasting most strongly in terms of likely vulnerable stem diameters at all levels of heating.

Further work in *B. serrata* was aimed at checking these predictions in burnt plants at varying levels of fire severity.

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2.4 Measurement of bark moisture content in *B. serrata*.

**Aims and Methods**

Martin (1963 a) demonstrated that bark thermal diffusivity, which is the variable crucial to temperature rises within heated stems (Gill 1981.b), may be effectively constant under a wide range of moisture contents in several pine and hardwood species. This comes about through inverse compensatory effects on the components of thermal diffusivity (Martin 1963 a). Nevertheless, other authors such as Vines (1968) have attempted to relate variations in bark moisture to empirical measurements of internal temperature rise in stems. Vines (1968) concluded that moisture variations can have a secondary effect, after diameter, on stem tolerance to heating, indicating that moist bark by increasing thermal conductivity (a component of thermal diffusivity) will allow higher cambium temperatures to be reached under heating than in dry bark. Hence Vines (1968) concluded that dry
bark is a better insulator. Vines (1968) conclusions were based on comparisons of seasonal differences in heating of various Eucalyptus and willow (Salix). Differences in the time taken for an internal rise of 40°C, for stems of varying bark thicknesses, within species were attributed to seasonal moisture differences in the order of 15 - 35%.

As Banksia serrata was generally observed to be the principal species, amongst those dealt with here, to exhibit post-burn epicormic regeneration, it was decided to investigate variations in bark moisture content through time in order to view possible influences of seasons or other external factors. As well, variation in sites was included as a factor. As this study was generally conducted in stands characteristic of "better" sites in the range that the species occupies, it was decided to contrast data from a poorer site to see if habitats may affect bark moisture statistically. The presence of any statistical difference between sites and sample dates required biological interpretation as to the likely effects on heat transfer and cambial temperature.

Bark moisture was sampled in two sites, the first was characteristic of those used throughout this study for the species, being flat and on deep soils with an overstorey of low-open-forest. The second was on an upper slope, the plants being between large sandstone outcrops on shallow soils of varying depth.
A pool of seven large adjacent trees in each site was chosen and on each sampling occasion five wedges were drawn randomly, one per tree. Sample trees were rotated between the various sampling occasions. The wedges were taken at between one and two metres above-ground and repeated extractions were spaced laterally and vertically at random, with no two extractions being closer than about 7-8 cm. The bark wedges were wrapped in aluminium foil and weighed then dried at 105°C for 48 hours. Proportions of moisture as oven dry weight of bark were calculated.

Sampling commenced in October 1981 and was carried through at irregular intervals until June 1983. In all, eleven paired samples were drawn in this period covering all seasons.

**Results and Discussion**

The data were analyzed using analysis of variance with times and sites as factors. The results were non-significant for times but significant for sites (Table 2.11). It was apparent (Figure 2.3) that the shelf site gave consistently lower means.

Comparisons of the absolute values and differences between site means showed that the average difference was
around 20% oven dry moisture (Figure 2.3). Further studies of the direct effects of such moisture differences on heat transfer and internal temperatures under heating, were not pursued. Rather it was inferred from Vines' (1968) results that such a difference between sites may be of some importance. As the work that is described here in succeeding sections within the species, was narrowly confined to the "better" site type, it was concluded that possible seasonal effects of fires, caused by moisture differences were unlikely. Moisture trends through time showed no obvious relationship with either rainfall or season in general (For rainfall data see Appendix 2).

Lower average moisture contents in bark in the poorer site may be interpreted as providing greater fire resistance in such sites. Whether a correlation between fire prevalence (either severity or frequency) can be demonstrated in such sites is of interest, but such a relationship was not examined further.

2.5 Survival and resprouting in B. serrata after fires in the field.

Aims and Methods

Studies in burns were carried out to investigate hypotheses relating the severity of burning to:

(i) overall levels of plant mortality,
(ii) plant mortality in differing size classes,
(iii) levels of stem damage in burns in relation
to size,
(iv) modes of recovery in relation to (iii).

As conventional quantitative measurements of fire intensity were not available (burns were either unplanned or occurred without my prior knowledge), the studies were structured so that sites representing both extremes of fire-caused damage were sampled. These can loosely be expected to represent "high" and "low" intensity fires that typically burn stands of the type studied.

Conclusions were sought on levels of mortality and the changes in sizes and configurations of survivors, as determined by mode of recovery, that would allow predictions of fates of populations of known size structure in some detail.

A. Mortality and Modes of Recovery

The hypothesis that mortality was affected by level of fire severity was tested by comparing a range of samples drawn from differing burns at each level. Because differing burns were used, an additional hypothesis, namely, that the time of burning affected mortality, was investigated.

In each individual plant sampled, the presence or absence of any resprouting was noted along with its origin.
The data were used to test the hypothesis that mode of recovery was related to the sizes of stems and lignotubers. Resprout origin was divided into basal and epicormic modes in each case arising from aerial stem buds, in the first instance on the basal swelling of the lignotubers and in the second on the stem proper or the branches. The presence of basal resprouting implied that the stem was dead above the lignotuber.

The proportions of individuals in various stem size classes that resprouted basally or epicormically were compared between severity levels to test the hypothesis that fire severity may influence resprouting mode. Specifically the proposition that high-severity fires may cause greater levels of stem deaths over a wider range of stem sizes was tested.

Site selection and sampling

Measurements were carried out in the aftermath of unplanned fires, hence pre-burn knowledge of the condition of populations present was unavailable.

Estimates of mortality attributed to burning were based only on the samples identified after burning and were therefore biased toward identifiable size classes. Another possible source of bias may have been the presence of dead individuals before the burns.
This was dealt with in several ways. Firstly long-dead mature individuals tended to have cones with open empty follicles on their branches. Dead (post-fire) plants were checked for scorching on the interior of follicles which were open. Freshly opened follicles had a very distinct appearance and could be easily distinguished. Hence any plants displaying scorching in large proportions of opened follicles were excluded. These were few. On large trees this was checked using binoculars. Secondly, observations in unburnt populations showed that plants above a metre or so in height, after dying, tended to show physical signs of decay within a year or so of death. Generally stems toppled over and bark was shed in patches. Hence, plants found burnt in an obvious prone position or which had charring in missing patches and cracks in bark on extensive areas of the stem were not recorded. The final point in relation to pre-fire mortality was that mortality observed in unburnt established populations rarely exceeded about 1% per annum, hence the chances of attributing mortality, in a plant recently dead before each burn, to the fires was low. An adjustment can be made to the data for this quantity, but as it would have been likely to be even amongst samples, analyses of burn mortality were made on unadjusted data.

The original aim of sampling was to obtain a balanced design of high and low-severity-sites in burns of differing times. High and low severity sites however were only available together in each of two burns. How-
ever further burns were sampled which occurred in differing years and seasons which offered sites of one or the other severity. As the pair of burns which offered sites of both levels of severity occurred at contrasting times, the opportunity was taken to specifically test burn-time effects and interactions of time and severity of burns on mortality. The addition of further sites burnt in differing fires provided further contrasts within levels of fire severity.

The choice of sites, aside from levels of fire severity was made on structural characteristics of the vegetation as well as on aspect and position. A further criterion in the choice of sites was the presence of B. serrata in relatively high abundance in a wide range of sizes from tree forms downward. Site were standardized in aspect being either on ridge-tops or extensive level areas and were flat or slightly sloping ( < 4°). All were chosen on comparatively deep soils free of outcropping parent material. The presence of a dominant canopy of mixed Eucalyptus species and Angophora costata was common to all and a final consideration was that within the level of burn severity each site was as evenly burnt as possible as judged from the level of damage and scorch present in the crown and understorey. This type of site was representative of the maximum development of vegetation in which the species was found and hence was likely to yield maximum fire intensity under appropriate conditions. The sites chosen to represent the severe level of damage were examples showing the greatest level of damage
observed in the area, with regard to height of scorch and leaf and branch consumption. In contrast, in sites chosen to represent low severity of damage, lowest levels of scorch observed in terms of height and understorey damage, generally, were within a scorch level of less than 2 metres. Initial samples were drawn from sites burnt in March 1980, August 1980 and December 1980, each being sampled at about fifteen months post-fire. Sites showing each type of severity were available from only the December burn. Generally each of these fires was of apparently high intensity, however an area of low damage was located in the December burn where a night back-burn had been lit for fire-control purposes. In the December burn, two replicate populations at each level of severity were sampled. In the March burn, a pair of replicate populations in an area of high severity were sampled, whist in the August burn restrictions forced by the small area burnt and topography limited the sample to a single population burnt with high severity.

Further samples in burns were obtained as the study progressed. The severe drought that was in progress, provided numerous periods of high fire danger and in the study area several small fires of generally high intensity, occurred. Samples were taken from two burns; occurring in July 1981 and May 1982. The latter fire provided sites of differing severity and accordingly a search was made for suitable samples at each level. Two replicate populations were sampled in each in this burn.
The July burn was of low severity and replicated samples were recorded in it.

In each site, a ten-by-ten-metre area was located in the chosen population of *B. serrata*. This was intensively searched and further squares were added as they were exhaustively sampled until the population was adequately sampled or the burn or site criteria were considered to have changed. All individuals of *B. serrata* that could be found were measured for basal (lignotuber) diameter, diameter at breast height (D.B.H.) and were classified by resprouting mode. Dead plants (according to the criteria given above) were defined as those which had failed to resprout or in which resprout shoots had died completely.

**Results**

In the high severity sites, the distribution of recovery modes in relation to the two measures of size revealed a consistent pattern amongst sites (Tables 2.12-2.18). In the smaller individuals (small stem around 1.0 cm D.B.H, and lignotuber < 20 cm) recovery was from basal sprouts. Individuals with larger stems (4 - 8 cms) within these ranges of sizes tended to recover from epicormic shoots, as did all larger surviving individuals.

A further breakdown of the numbers of epicormic resprouters and basal resprouters in the fires of high
severity (Table 2.19) showed that variability in the proportions of basal to epicormic sprouters in some size classes, existed between sites. In samples from each of the December 1980 and March 1980 burns, complete stem death was more commonly found in larger D.B.H. classes than in other samples and burns. In the smallest sizes stem mortality was absolute.

Modes of recovery in the low-severity burns (Tables 2.20 – 2.25) showed firstly that relatively few of the larger plants suffered complete scorch. This level of damage was concentrated in small sizes (stems and lignotubers). The ratios of basal to epicormic (fully epicormic sprouters plus incompletely scorched plants) in small stem size (D.B.H.) classes (Table 2.19) showed that no complete stem deaths occurred above a size of 2.0 centimetres. In smaller stems, basal sprouting occurred with 100% scorch. The data (Table 2.19) showed that instances of stem survival (this occurred where less than 100% scorch occurred) were present in some sites.

The mean proportion of basal resprouters in high- and low-severity burns were compared for the 1.0 – 2.0 cm D.B.H. class (Table 2.19). No significant difference in angular transformed means was found. As complete stem death and basal recovery were absent in larger D.B.H. classes in low-severity samples (Table 2.19) no formal comparison was possible.
The proportions of plant mortality appeared to be related to the level of fire severity (Table 2.26). As well, the sizes of dead plants appeared to differ between levels of fire-severity (Tables 2.12 - 2.25). Within the high-severity samples mortality was widely distributed amongst stem-lignotuber size combinations. Individual trends occurred in some populations. In the December 1980 (II) sample (Table 2.13), a wide range of sizes were recorded in dead plants as opposed to the December 1980 (I) sample where mortality was biased toward large plants (Table 2.12). In the May 1982 (II) sample, bias was toward smaller sizes (Table 2.17).

In the low-severity burns, mortality was concentrated in plants that were substantially scorched, (Tables 2.20 - 2.25), these being the smallest members of the populations in each sample. Larger, partially-scorched plants suffered no mortality with one exception in the May 1982 (I) sample.

The proportions of mortality in the samples appeared to be related to the level of fire severity (Table 2.26). Analysis of variance was attempted for the balanced data set for December 1980 and May 1982 burns, however, the Cochran's Test for heterogeneity of variances of the angular-transformed data, proved to be significant and the analysis was not performed. Instead mortality between all samples within severity levels was compared using a non-parametric test. A two-way G test of independence of the
frequency of survivors versus deaths was employed (Table 2.27). The results showed that within severity levels, survival differences were non-significant, though a trend existed, especially in high severity burns for heterogeneity between samples (Tables 2.27 & 2.28). As a result, samples at each severity level were pooled and a G-test of survivors vs. deaths between severity levels was made (Table 2.29). This showed a significant difference was present, with mortality being greater in the high-fire-severity group. Formal tests of size differences in dead plants between severity levels were not made.

Discussion and Conclusion

The results indicated that plant mortality was principally affected by the level of fire severity and not by the time of burn, though possible interactions could not be tested. Differences in mortality between severity levels appeared to derive mainly from the selective deaths of large individuals in high severity sites. Exposure to substantial or total crown damage increased the risk of mortality in these sizes. Subtraction of the deaths of large individuals from the high severity samples would have left little difference between the two levels of severity in mean mortality.

Possible sources of bias and error in the estimation of probabilities of deaths at each fire severity level warrant further discussion. As noted above, deaths occurring
approximately one year prior to each burn stood a good chance of being scored as fire-induced. Biases toward either severity level seemed unlikely, hence a general correction for one year's mortality can be justified for either figure. Values for this correction are discussed in later chapters. Possible errors and biases between severity levels were likely to be due to a number of causes. Though sampling was standardized at a time of about 15 months post-burn in each sample, differences were apparent in the amount of ground cover and litter present between severity levels. The high-severity sites were generally more open and easily searched. Balanced against this was the likelihood that very small individuals (lignotubers < 10 cms, height < 1.0 metre) may have been damaged to an extent that rendered them unidentifiable after the high-severity fires. It was felt that this later bias may have been the more important of the two and as a consequence the high-severity estimates of mortality may be underestimates particularly amongst smaller sizes.

Overall, the contrast between mortality at the two extremes of fire severity implied that fires which damaged plants at a level of intermediate severity may cause an intermediate level of mortality. By structuring the study so that maximum opposing extremes of fire severity were examined, the task of relating measured fire intensities in similar sites may be simplified.

The analysis of stem survival (whole stem death versus partial stem death) between levels of fire severity
showed that whilst striking physical differences in appearance may exist between populations burnt at either extreme the consequences for stems in small D.B.H. classes are not all that dissimilar. The principal difference lay in a higher toll of stems in high-severity samples between 4 - 8 cm D.B.H. (Table 2.19), no stems being completely killed in this range in the low severity samples. Effectively, stems either less than 1.6 metres height or less than 1.0 centimetre D.B.H. can be assumed to be completely killed in any fire, whilst a fixed amount of approximately 50% will die in the class from 1.0 - 2.0 cm D.B.H. Presumably in fires of intermediate severity, at sizes up to 8.0 cm D.B.H. the probabilities of total stem death will grade between zero and the values given for the high-severity sites in Table 2.19.

2.6 **Further measurements in epicormic resprouters.**

**Aims and Methods.**

Measurements of critical diameters in stems were made to compare the predictions made from bark measurements as to the likely stem diameters which would be vulnerable to heating. Though the samples were drawn from specific extremes of fire severity, variations in the amount of damage to individuals occurred both within and between samples within severity levels. The data discussed above effectively provided an average view of likely mortality
and resprouting mode with respect to size at the given fire severity levels. Accordingly, some indication was sought as to the average maximum size (diameter) of stems on parts of stems and branches which had been killed, under the influence of samples and fire severity levels. In addition the hypothesis that lignotuber size may have affected the position of resprouting, was tested.

Gill (1978) showed that the uppermost point of resprouting on stems of *Eucalyptus dives* was related to levels of fire severity. Furthermore he showed that the diameter at this point was also affected in a manner such that in the higher-severity samples (crowns consumed versus crowns scorched) mean diameters were larger whilst the mean heights at this point were lower than in the samples with less severe damage. Effectively, larger proportions of the stems were killed in trees showing complete crown consumption. The distal sprouting point can be regarded as an indicator of the cut-off between stem death and survival and measurements there provided an estimate of maximum stem sizes at which vascular death occurred.

For convenience here, the diameter at this point is referred to as *sprout stem diameter* (S.S.D.) and the height as *sprout stem height* (S.S.H.) The specific hypothesis that lignotuber size affected S.S.D. was tested, by calculating correlation co-efficients between these latter variables. Acceptance of the hypothesis would have implied that lignotuber size in addition to bark thickness may be a
determinant of the minimum diameter of the stem from which sprouting can occur.

As overall levels of damage differed between the general samples drawn from burns of high severity, from partial to full crown consumption, calculations were only performed on plants homogeneously damaged and from a limited range of S.S.H., from high-severity sites.

As a part of general sampling outlined in the previous section, the S.S.D. and S.S.H. for all epicormic sprouters were determined along with the level of damage: that is crown fully scorched versus partially consumed, versus fully consumed, on each plant. These measurements were made in high-severity sites where the distal sprouting point occurred below 3 metres above ground. Estimates of these variables were made on trees which sprouted above three metres but these are not considered here.

In low-severity burns, as most of the populations were incompletely scorched, attempts to define the maximum vulnerable stem diameter could not be made. Rather, measurements were made on branches which had been fully scorched, in a manner analogous to that used on high-severity stems. A problem arose in that many small branches often existed on an individual. A judgement was made by eye, of the largest branch diameters at distal resprouting points and these were measured. The largest value was recorded. This is referred to as S.B.D. (sprout branch diameter). Heights was also recorded at this point.
In summary the following hypotheses were analyzed:

(1) Comparisons between sites of stem D.B.H. of epi-
cormic sprouters in high-severity burns were made,
to test if the samples of stems sprouting below 3.0
metres differed significantly in size.

(2) Comparisons of S.S.H. and S.S.D. in high-severity
samples were made to test for differences in
average maximum critical stem size and implied
variations in average fire intensity between
samples.

(3) Correlations between lignotuber size and S.S.D.
in several sites were calculated to test for the
effects of lignotuber size within stands. Ligno-
tuber size was chosen as a measure of plant size
independent of stem size.

The initial analysis was tested as a pre-requisite for the
second. S.S.D. and S.S.H. could not be meaningfully com-
pared if mean stem sizes were heterogeneous. Implied
variations in fire intensity could not be made from S.S.D.
and S.S.H. data extracted from samples of differing mean
size as bias may occur simply as result of differing stem
sizes at a given level of heating. The analyses tested
the hypothesis that fire intensity between samples within
the high-severity damage level did not vary. Rather than
attempting to relate these estimates to independent varia-
tions in fire intensity (e.g. crown damage) as Gill (1978)
did, the aim was to view and compare the average level of
S.S.D. and S.S.H. and implied fire intensity between samples, so as to provide some indication of their variability within the category of fire severity sampled. The calculation of correlations between S.S.D. and lignotuber sizes was made in several samples, for plants suffering 100% leaf consumption only.

For low-severity burns, analyses similar to the first two listed above were performed. Sprout branch height (S.B.H.) was not compared, however, as branch heights were strongly related to stem size, hence heights of maximum S.B.D. were not determined purely by heating phenomena.

Major assumptions underlying between sample comparisons of S.B.D. and S.S.D. were that surviving buds were either located immediately adjacent to the critical point measured on stems or were consistently and evenly spaced between stems such that errors in measured diameter as estimates of the critical diameter would be consistent between stems. Evidence from small and moderately sized stems defoliated in a later experiment suggested that active buds were sufficiently closely and evenly spaced along large and small stems and branches to minimize error from this source.

Results

Correlation co-efficients inter-relating lignotuber size and S.S.D. are given in Table 2.30. The co-efficients
were calculated only from those burns where a reasonably sized sample of plants of varying lignotuber size which had suffered total foliage consumption, was present. In the remaining samples, foliage consumption was partial. The results (Table 2.30) showed that no significant effect of lignotuber size on S.S.D. (or vice-versa) could be detected.

For stands burnt with high severity the analysis of variance of epicormic stem D.B.H. (below 3 metres) showed that means between samples were homogeneous (Table 2.31). Comparisons of S.S.D. and S.S.H. (Table 2.32) showed that heterogeneity occurred amongst samples. The December 1980 (I) sample showed both highest S.S.D. and lowest S.S.H. means and these were significantly different from a number of the samples (as determined by S.N.K. test, Table 2.32). The March 1980 (II) sample displayed a similar trend.

Comparisons of stem D.B.H. for the epicormic branch sprouting samples from low-severity burns (Table 2.33,a) showed that larger means were present in the May 1982 (I) and December 1980 (II) samples. Mean S.B.D. values did not vary significantly (Table 2.33,b).

Discussion

Correlation analysis revealed that the distal sprouting point was unlikely to have been affected by plant size, at least in high-severity burns. Hence measurements of S.S.D. were regarded as estimates of maximum stem size as determined
solely by the heating phenomena that surrounded each stem. Amongst the high-severity samples, homogeneity in stem D.B.H. of epicormic sprouters, sprouting below 3.0 metres, demonstrated that the fires had selected out similar groupings of stem sizes. This was interpreted as showing that heating phenomena on average were similar in their broad effect (0 - 3 metres) on resprouting position, between samples. It was concluded that epicormic resprouting will generally occur below three metres in stems of from 1.0 to about 11.0 cm D.B.H.

Within this broad range of height, differences between sites in S.S.D. and S.S.H. were interpreted as the result of variations in heating or fire intensity. Sites with the highest S.S.D. tended toward lowest S.S.H. (Table 2.32), these being the "hottest" sites. Whilst variations between sites caused by differing bark-stem size relationships cannot be ruled out, the inverse nature of the variables suggests the above conclusions. These sites also tended to be those (Table 2.30) selected for the correlation analysis as they had the largest samples of plants with total leaf consumption, indicating probable higher fire severity.

Aside from highlighting variations in probable fire intensity within the high-severity level these comparisons served to estimate the range of maximum sizes of stems suffering damage and death. These values fell into the range of sizes suggested by the regressions of bark thickness under three minutes of artificial heating (Figure 2.2, Table 2.8, Table 2.32).
It was concluded that estimations from the bark regressions and heating experiment could be used as a reasonable guide for predictions of likely critical ranges of bark thicknesses and stem diameters across a broad range of fire severity.

The comparisons on S.B.D., despite differences in mean sample D.B.H., showed no significant differences. It was concluded that heating effects were reasonably homogeneous within the severity level, despite possible influences through differences in branch height and stem size between samples. For the low-severity samples the mean S.B.D. values were generally of the order of 1.5 - 2.0 cm (Table 2.33-b) which accorded with the results of the artificial heating experiment (Figure 2.2) and indicated that flaming combustion was most likely of very short duration.

2.7 Observations and experiments on survival in B. ericifolia under burning.

Introduction

It was noted above that B. ericifolia was regarded as being fire-sensitive. Where survival was observed to occur burning was low in height as judged by scorch, and patchy in extent, so that crowns of bushes were incompletely and variably destroyed. Often in these situations, instances
of flare-ups can be found which result in small-scale incineration of clumps of bushes, whilst neighbouring bushes remain lightly scorched within a few metres. These burns occur in mild weather and/or in moist ground-level fuels, as is the case often in the months outside Summer, or at night in the hotter months. Where weather and/or moisture conditions are more conducive, irrespective of season, stands usually burn fiercely and completely. Flaring into the crowns in older stands (>10 years) would appear to be governed by conditions controlling combustion rate and flame height at the ground as well as the continuous presence of potential fuels in the zone between the litter and lower branches. In younger stands the development of the bushes is usually such that foliage forms a continuum between ground level and the tops of plants and stand destruction is usually complete in any fire. Such is not the case in older, less dense stands where gaps between lower branches and potential ground fuels occur, paving the way for the effects outlined above.

The prime concern was to examine the relationship between degree of damage, possible resprouting and size in the aftermath of these light patchy burns. Effectively, fire severity in these stands can be regarded as a binary phenomenon. Either complete crowning and stand destruction occur or else a patchy burn results. Of particular interest, were the observations of Ingwersen (1977), noting resprouting from burnt plant parts. This appeared to be conspicuously absent in the study area.
Bark regression data showed that considerable portions of the lower part of larger stems were likely to be resistant to heating. Observations were therefore initially focussed on individuals of varying stem sizes (basal diameter, at 20 cm above ground) which had suffered 100% scorch but in which leaves had not been consumed, in order to see if stem size played a part in determining possible vegetative recovery.

Results and Discussion

A burn in July 1981 was used for this purpose. A mildly burnt stand of _B. ericifolia_ was located and sampled. Plants in three basal size classes were tagged. Sizes were 20 - 25, 19 - 15, and 11 - 15 cm. Plants in smaller size classes were located but had suffered more severe levels of damage and hence were not used. Within the samples used some consumption of lower leaves was found to have occurred. However as this was consistent between classes, possible interactions in severity of heating with size were considered unlikely. The numbers of plants used in each class were respectively 6, 12 and 10.

Tagging was done three months after the fire and further checks were made at three-monthly intervals for a year. At no time was any sprouting observed on any plants. No evidence of any resprouting prior to tagging was found.

It was concluded either that:
(i) Whilst internal vascular tissues may be shielded, epicormic buds may be insufficiently shielded from very light heating; or (ii) Heating throughout the sizes of plants used was sufficient to kill the stem close to the base.

Experiments on _B. ericifolia_ resprouting.

**Aims and Methods**

It was decided to contrast plants totally, with those partially defoliated to compare resprouting and its dependence on the presence of live foliage in the absence of burning. To test for the initial dependence of resprouting on vascular activity, basal ringbarking treatments were incorporated as a factor in the design.

As the results for this experiment became obvious a further experiment was added. Within four large bushes, two equivalent-sized branches with maximum diameters around 5 cm were selected and marked. The plants were defoliated (including the selected branches) and one of the selected branches was lightly heated with a propane gas torch. The flame was played as evenly as possible over the branch from its tip to base with no part of the branch receiving more than about 30 - 45 seconds exposure. Very light charring occurred such that the treated branches appeared similar to scorched plants in the aftermath of real fires.
For the defoliation experiment samples of five plants were each subjected to one of the following combinations of treatments, these being: ringbarked, full vs partial defoliation and unring-barked, full vs partial defoliation. Defoliation was done with secateurs with foliage bearing minor branches and twigs being cut at their base. Ring-barking was done below the first major branching axis in each stem, the cuts being made deeply into the heartwood. The cuts were treated for several minutes with the flame of a propane torch until lightly charred. In all cases stems were between 15 and 20 cm diameter in a population of old but unknown age. Observations on resprouting and plant survival were carried out for nine months until the plants were destroyed in a fire.

Results and Discussion

Defoliated plants irrespective of degree of leaf removal or stem ring-barking, were all observed to begin resprouting within six weeks of the commencement of the trial in October 1982. Resprouting occurred mainly from cut, twig ends in the crowns but occasionally from buds at the junction between both small and large branches. Resprouting from low levels on the stems was rare though one or two instances were noted in all treatments. Over the severe 1982/83 summer the new shoots and leaves on all ring-barked plants died and the plants remained dormant until the stand was burnt and were regarded as dead. Two unring-barked, completely defoliated trees also "died" in
this period, though one subsequently recovered again in the Autumn of 1983. This was the status at the time the stand was burnt in June 1983.

In the paired burnt/unburnt-branch trees, resprouting was absent in the burnt branch and present on cut twigs in the unburnt branch in all cases. Sprouts generally were sustained throughout on the unburnt branch though some individual sprouts died over the summer.

Discussion and Conclusions

The results showed that sprouting will occur irrespective of the presence of live vascular tissues at the stem base or of a live leaf crown. The evidence from the ring-barked plants suggested it is probable that the lack of resprouting in totally scorched plants after burning was probably not due to stem death at or near the base in large plants but rather death of buds on smaller branches on the upper branches through heating. The results in general showed that:

(i) In small twigs and branches buds are most active. This source of resprouting was removed under light heating;

(ii) Resprouting from larger branches was infrequent and was also negated by light heating;

(iii) Resprouting from buds low on the stem or the stem base was absent.
Survival, was therefore, concluded to be dependent, after fires, on the escape of some part of the foliage at least in large stems. In turn it would appear that the larger (taller) a plant is, the chance of retaining a partially unburnt crown would be higher than in short plants. Below a critical stem diameter size, bark thickness must be inadequate for insulation. Experience of low-severity fires with B. serrata (see preceding section) suggested that the sizes of small branches killed corresponded to bark thicknesses of around 1 mm. If a similar level of heating is assumed, substitution of this value into equations (Table 2.9) shows that critical stem sizes are likely to be small (1 - 2 cm). It was concluded that the relationship between scorch height and plant height is likely to be the principal determinant of which individuals survive. It should be noted that critical stem size is likely to rise, with scorch height. Whether heating occurs which is sufficient to kill a plant of a given height without totally scorching the crown, could not be determined, however the very low heats involved in the patchy low-severity burns would appear to differ little in their effect on stems than that predicted.

As the spatial distributions of fuels in any stand are likely to vary, the relationship between plant height and survival in any stand will be mediated by fuel conditions around the plant. The likelihood of flare-ups under low fires is difficult to predict and their observed presence means that predictions of stem survival under
simulated fires of a given arbitrary scorch level will overestimate likely overall survival and be inaccurate in the predicted range of sizes of survivors. Nevertheless, such a method may be considered a useful initial step in predicting post-fire stand structure and identification of likely survivors.

One further feature observed in these data concerned the probability of plants which survived one fire surviving another. Bushes which survive fires, through retaining the top of their crowns appeared to have a reasonably high chance of surviving further burns of low-intensity (low-scorch) as their lower branches and leaves were shed leaving a large fuel-free gap between the ground cover and crowns of the bushes. Such an effect may have important consequences for stand dynamics of the species under repeated high-frequency fires. The chances of this happening would therefore rise with increasing age so that in old stands, scattered individuals may be left in the aftermath of low-scorch fires, thereby creating an uneven age-structure and providing a source of seedbank during the juvenile period of the post-fire seedling generation. These stand structures can be observed after such events in the study area.
2.8 Experimental studies of resprouting and survival in *B. serrata* and *Isopogon*.

**Introduction and Aims**

An experiment was performed to:

(a) test the effects of burning at different seasons (burn-times) within a given year on the ability of plants to successfully resprout;

(b) test the effects of varying levels of damage inflicted by differing quantities of heating and cutting on resprouting ability;

(c) test the effects of varying times since the last burn on resprout success;

(d) to view possible interactions in these factors particularly with regard to their effects on plants of contrasting size and status of establishment and maturity.

Identification of effects of burn-times and intervals and levels of damage on the ability to successfully resprout was considered an essential part of the unravelling of fire-regime effects on populations. Whilst the previous section related size and mode of recovery in *Banksia serrata* to levels of fire severity, the causes of mortality induced by burning, whether through failure to resprout or through death of shoots were only generally analyzed and discussed. Further specific comparisons were sought in burn-times, intervals and levels of damage sustained.
This study was restricted in that the seasons of treatments in differing years and sites within levels of differing age since the last fire could not be replicated due to restrictions on resources and suitable sites. Hence the conclusions must be tempered by possible interactions between weather events and the differing seasonal treatments and site characteristics and possible burn intervals.

Plants were damaged artificially in various different ways to judge the effects of physical removal of plant parts in the absence of heating as well as in its presence. Differing levels of heat were planned to test the effects of varying fire intensity, the amounts of heat inputs and rates being measured and controlled.

Various hypotheses with respect to the effects of these treatments were tested in terms of resprouting ability (frequency and percentage of individuals that resprouted) and overall success (frequency and % of survival of resprouted individuals). In the previous section a range of sizes was surveyed to test the average effects of severity and times of fires. Here these effects plus "age" (time since last fire) were tested within groups of plants of specific sizes, and responses were broadly compared between groups. Each size of plant chosen corresponded with a particular potential reproductive status within the established life-cycle stage. Variations in size within categories of reproductive status occur but were not addressed in this part of the work. However the work provided an overview of the treatment effects across the established life-cycle stage.
Effects of fire seasonality and age.

Inherent effects of season may be difficult to interpret after fires because confounding effects of variations of fire intensity with different seasonal weather conditions cannot be entirely excluded. The approach taken above with *B. serrata* to some degree overcame this. Differences in the seasons of fires may affect both the survival of individuals or plant parts and the vigour and sustainability of vegetative recovery. Vines (1968) and Kayll (1966) suggested that differences in internal stem temperature between seasons may cause differences in stem damage and survival for a given level of heating or fire intensity. The potential for such an effect in both *Banksia* species was demonstrated above. Stems would appear to be more prone to death in Summer. A similar effect may apply to subterranean or semi-subterranean organs such as lignotubers. As an aside, it is worth noting that the differences in fire intensity or applied heat needed to overcome seasonal internal temperature differences may be a useful and biologically relevant measurement.

Other causes of mortality attributable to seasonal effects may occur when the insulation of vascular tissues and buds is adequate but the physiological state of the plant is such that recovery is weak and unsustainable or even inhibited. Such an argument was put forward by Curtin (1967,a) who proposed that new active growth may be more susceptible to heat than older "hardened" growth. Curtin
(1967 a) also added that regenerative capacity of tissues was related to the amount of stored food reserves available. As an example, Floyd (1967) suggested, on the basis of findings of other workers, that Autumn scorching in *Eucalyptus regnans* trees resulted in death because new leaves would not be produced until Spring.

Such possible effects have been implied by other studies using cutting and defoliation treatments either in combination with burning (e.g. Noble 1982, Miller and Miles 1970) or alone Cremer (1973). These studies showed that trends varied amongst the woody species tested.

Cremer (1973) showed that various *Eucalyptus* tree species and associated understorey species, treated as young seedlings gave more vigorous sprouting after Autumn treatments compared with Winter or Spring treatments. Site conditions and plant age in further treatments affected the results with older plants showing little recovery. Noble (1982) reported seasonal effects on survival in mallee *Eucalyptus* species, with greatest mortality occurring under Autumn treatments. Miller and Miles (1970) showed that differences between burning and cutting treatments in their effects on the mass of sprouted material may alter markedly with season.

Seasonal conditions may interact with site factors (e.g. Naveh 1975) and the age of the plant may affect the outcome of burning. However age is not easy to determine in many woody species which do not possess annual growth rings.
Size is not necessarily correlated with age (Harper 1977) and cannot be used as a sole indicator. The approach used here was to select certain combinations of plant size and reproductive status. The sizes used represented a broad range of those present in the established phase of each species. Effects of the treatments on plants of sizes intermediate to those used here could be inferred from comparisons of the responses of the extremes used here. Similarly, a range of reproductive status was covered, these levels of reproductive status being deliberately confounded with size.

Levels of reproductive status examined were mature, juvenile and young juvenile. The sizes of plants in each category were respectively: those presenting the threshold above which individuals are often mature: those at which plants were never observed to be mature: recent unburnt recruits. A full discussion of size and maturity is given in the next chapter (Chapter 3).

Within these stages plants were selected within a narrow size range in order to minimize variations caused by differential effects of bark thickness or storage of reserves in differently sized organs. Sources of artificial heat were employed as the various heating treatments and were applied in all classes. Contrasts were sought in response to two levels of heating, these varying in both the rate of heat input and length of time of heating. These treatments were necessarily restricted to lignotubers from
which aerial parts had been removed. Contrasts between
the heat treatments with cut but unheated lignotubers
and intact control plants were also included in the design.
In the mature Banksia class, these being tall shrubs (up
to 4-5 m height, with stems around 5-6 cm D.B.H.), further
treatments were performed to examine the effect of progres-
sive levels of damage to the aerial parts above the ligno-
tuber. As burning large aerial parts of the whole plants
in these cases, was impossible or impractical, the effects
of differing levels of fire damage were simulated by first-
ly complete removal of all leaves (defoliation) and secondly
removal of the entire crown. This latter treatment was done
by sawing off the stem at the main branch axis, usually
around 2 metres above ground. The treatments therefore
represented the effects of fires of progressively greater
severity.

\[
\begin{array}{c|c|c|c|c|c}
\text{100\% Leaf} & \leq & \text{100\% Crown} & \leq & \text{100\% Stem} & \leq \text{100\% Stem death}<\text{100\% Stem death}
\end{array}
\]

\[
\begin{array}{c|c|c|c|c|c}
\text{(unburnt ligno-} & \text{tubers} & \text{death} & \text{(Low heat} & \text{Treat-} & \text{ment})
\end{array}
\]

It should be noted though that additive effects of heating
and defoliation or crown death were unable to be tested.
The latter three treatments allowed the effects of stem
removal and progressively greater heating to be evaluated.
These were performed on individuals in the juvenile class
in Banksia serrata and in mature and juvenile classes in
Isopogon. For small juveniles in both species, the treatment
which applied the greatest amount of heat (high heat treat-
ment), was omitted.
Restrictions were imposed by the size of populations available and logistics which severely limited the choice of sites in the study area. In particular the equipment used, necessitated that work had to be carried out in sites adjacent to good roads. Of the available sites, a number were located, of similar aspect and vegetation structure and these varied in time since last fire (ages) though in each, perusal of fire records showed a history of frequent fires (5 - 10 year interval) over the preceding two decades. Numbers of plants particularly Banksia and mature Isopogon were inadequate in all of these sites for the performance of a fully replicated experiment within ages. Of the four available sites which were located in the study area, two were chosen which were directly adjacent and which were homogeneous in soils (yellow earths), vegetation and aspect and fire history, except time since the previous fire. The times since burning were respectively five and two years at the end of 1981. A further site was used, located some ten kilometres from the others. The site was of similar aspect (flat ridge-top) and generally similar vegetation structure and soils, but differed in that the previous burn had occurred 13 years before.

The design could be construed as a three-factor design without replication for each species reproductive status class, with ages (time since last burnt) fire/cutting treatments and seasons as factors. Therefore, the data were analyzed in a way which initially tested age effects, then bulked like ages as effective site replicates to test heating/cutting and seasonal effects.
This was done by non-parametric testing of the independence of survival frequency. As the samples sizes which could be accommodated (5 individuals per cell, per replicate) were low, the Fisher Exact Test as recommended by Zar (1974), was used, with the procedure given by Ghent (1972) for calculation of 2 x 3 table probabilities being employed. Hence the analysis provided a test of age effects within heating/cutting treatments but did not directly test hypotheses relating these three factors in interaction.

Whilst effects of time since last burn, commonly called "age"* have received some attention in the literature (Köyill and Gimingham 1965, Miller and Miles 1970, Noble 1982, Zedler et al. 1983), considerable further effort is needed to understand fully the effects within and between species. Miller and Miles (1970) concluded that declines in vegetative output from burnt plants with increasing "age", as indicated by their own studies and that of Köyill and Gimingham (1965) in Scottish Calluna, did not have an inherent physiological basis but occurred as a consequence of stand dynamics in reducing stem number and potential resprouting points within individuals. Briefly tests of "age" would involve where possible, replication of sites within ages and preferably within sites, within-ages replication should ideally be present in a nested design. This was unfeasible here both as a single experiment or in integration with season and plant treatments as additional factors.

*"age" or "year old" whenever used in the remainder of the chapter implies "time since fire".
Young juveniles were defined as plants which had arisen since the last burn and as these could be identified and found in adequate numbers in the 5-year site, treatments were applied in two replicates on each two occasions (two seasons) only.

Methods

(i) Heat treatments and seasons of burning.

Heat treatments were applied on three occasions: November 1981, late February-Early March 1982 and August 1982, broadly representing the late Spring, Summer and Winter seasons each of which have an appreciable record of fire occurrence in the area (See Chapter 1).

For this experiment, as elsewhere in the thesis where heat sources were used, two types of burners were employed. Details of these and their outputs and operational settings are given in Appendix 1). They are referred to here as small and large burners and the treatments delivered by each are called respectively low and high. Both burnt liquid propane gas (L.P.G.), the large unit running on a mixture of this fuel and pressurized oxygen.

A crucial component of the heat treatments was the time of heating. As there were no direct data on residence or burn-out times for the vegetation types under study, estimates were made based on personal observations and
calculations. McArthur and Cheney (1966) provided a formula for burn-out time for fuels of known weights. This was used to derive an estimate from the maximum measured fuel weight (including shrubs) for a site of over twenty years age (Appendix 1). The estimate was rounded to three minutes and was used for the high treatment. A lesser time of two minutes was adopted for the low treatments. In both cases the heat source was set at a constant rate throughout this time. Gas regulator settings and bottle valves were kept constant as were the bottle sizes used. (See Appendix 1). Variations in flame behaviour occurred due to variations in bottle pressures and levels as supplied but these were regarded as being minor in comparison to the overall heat outputs.

For the high treatments a box constructed from stainless steel sheet was used to enshroud the lignotuber, both to concentrate heat on the plant and protect the operator (Fig. A1.1). For the low treatments the heat was applied without any enclosure, the burner being moved over the treated area in an even motion at a constant height. The box covered a square area of a size 0.5 x 0.5 metre and a similar area was treated (containing the lignotuber) in the low heat burns.

For the lignotuber treatments in *Banksia* in all size classes the stem was removed one centimetre above the top of the basal swelling. For crown removal the stems were lopped at the lowest major branch axis, whilst defoliations
were carried out with secateurs, leaves being removed in clusters from fine branches (≤ 0.5 cm diameter). In *Isopogon* stems arising from each lignotuber were pruned at ground level.

**Plant selection, site preparation and monitoring.**

In *Banksia*, individuals of moderate size (lignotuber about 20 cm diameter, stem about 6 cm D.B.H.) were chosen from amongst the range of possible mature sizes. These represented the maximum size of stems likely to suffer substantial damage in high-severity fires (see previous sections). In *Isopogon*, the mature individuals chosen were by contrast the largest plants present in the range of sizes (circa 25 - 30 cm average lignotuber width).

For juveniles, well established individuals in both species which had been present before previous fires, as evidenced by charred bark in *Banksia* in all sites, were selected. In *Banksia* these were individuals with stems either <1 cm D.B.H. or less than 1.6 metres in height with lignotubers between about 8 to 12 cm diameter. In *Isopogon* these were small inconspicuous plants with largely underground basal swellings around 5 cm in width.

Treatments of young juveniles were not commenced until February 1982 and the second treatment was held over until August 1983, rather than August 1982, in order to judge the effect of one year's growth on survival. Sizes were at the time of first treatment in *Banksia* about 30 cm
height and lignotuber about 1.5 cm width whilst in *Isopogon* heights were around 5 cm and no swellings at the stem bases could be observed.

For each seasonal treatment in each age and class within the species, a fresh sample of controls was tagged from the pool of plants selected for treatment. Treatments were randomly allocated within the pool.

Standing vegetation around selected plants was cleared within a radius of about 2.0 metres and litter was raked back to the mineral soil in this area, leaving the lignotubers on stems exposed. All heat treatments were timed using the second hand of a wristwatch.

Inspections of the treatments were made every second month for 12 months - and in each plant the presence or absence of resprouting was noted. Death of resprouts was recorded. At no time was any significant grazing damage apparent. On plants scored as non-resprouters the likelihood of error through removal of all shoots by grazing was small as bud eruption through the bark in both species was striking and unmistakeable. All recorded deaths of resprouters were attributable to observed failure of shoots. No deaths were found or recorded due to total disappearance of shoots.
Results and Discussion

For both species, the results can be discussed in two forms. Contrasts existed between the total number of plants which resprouted and those which had resprouted and were still alive at the end of 12 months. That is, deaths of resprouted plants occurred to varying degrees amongst species and classes of reproductive status (Tables 2.34 - 2.39).

(ii) Banksia serrata

In mature Banksia (Table 2.34), the effects of stem removal on both total resprouting ability and survival were marked. Resprouting ability was lowest in the February and August compared to November in the two heat treatments. Differences in survival (Table 2.34) evened out the differences in the numbers of live resprouting individuals present 12 months after treatment. The 2-year old class showed the least initial response (Table 2.34), though again differences between ages in survival evened total response out.

Analysis of live resprouts at 12 months (post-treatment), between ages within cells (heat/cutting versus season, treatments) were carried out (Table 2.40(a)) and these showed that the frequencies of live resprouted individuals did not differ significantly. Some heterogeneity existed in the low heat/November treatment (Table 2.40(a)) principally due to the low value for the 2-year age class. Analysis of variance (Table 2.42(a)) of all treatments using all values
for all ages as replicates was done. Differences in mean percentage survival were tested (data were angular transformed). The results showed a significant effect of heating and cutting (Table 2.42(a)). Removal of leaves or the total crown had no significant effect on survival, whilst removal of stems significantly decreased survival (Table 2.42(a)). Differences between heat treatments were non-significant, however heating further significantly decreased survival over stem removal. (Table 2.42(a)).

In juvenile Banksia, the initial effects on the ability to resprout were mainly confined to the high heat, February 2-year age class, where fewer individuals initiated regrowth (Table 2.35). At the end of 12 months mortality of resprouted individuals was widespread in all the treatments, being particularly severe in the 13-year age class (Table 2.35). Tests for age effects on survivors within treatment cells (Table 2.40(b)) showed that a trend to heterogeneity was present in the low-heat, August and cut, November cells due to low survival of 13 year-old plants. Values were non-significant, hence analysis of variance of % survival was done (Table 2.42(b)) using all data. The results showed again a significant effect, only, of heating/cutting, though differences between means were less clear-cut than in the mature class. Survival was decreased by stem removal and low heating though not significantly, whilst high heating caused a significant decline compared to the control (Table 2.42(b)).
In young juveniles (recruits) all burnt individuals in the initial (February, 1982) treatment failed to recover (Table 2.36). Cut individuals resprouted vigorously and survived to 12 months (Table 2.36). For the August 1983 treatment, several burnt individuals recovered, whilst recovery in defoliated plants was complete (Table 2.36). No deaths occurred in the controls. Formal analysis was not carried out.

(b) **Isopogon**

In mature plants, resprouting was strong in all treatments (Table 2.37) except in 2-year old plants in the low-heat February treatment (Table 2.37). Survival of resprouted plants was variable and at 12 months after treatment large declines had occurred in live numbers in the 13-year-old age class and to a lesser extent in 2-year-old plants. (Table 2.37). Analyses of survival frequencies (Table 2.41(a)) showed that trends to heterogeneity (though non-significant) occurred in all treatment categories in the February class, due mainly to high numbers of deaths of resprouted plants in the 13-year-old site. Whilst values were non-significant, it was decided to eliminate this source of bias and an anova was carried out on percentage survival using data from 2-and 5-year-old plants only (Table 2.41(a)). The results (Table 2.43(a)) showed that declines in survival caused by the treatments were non-significant.

In juvenile **Isopogon** a marked affect of high heating on the ability to resprout was readily apparent (Table 2.38).
The frequencies of survival at 12 months after treatment were not significantly different between ages, though a trend in the low-heat, February cell due to high mortality in resprouted 2-year-old plants was present (Table 2.41(b)). An anova was carried out using all age data (Table 2.43(b)) and the results indicated a strong effect of high heating on mean % survival. Low heating and cutting caused declines in % survival which were not significantly different from the control (Table 2.43(b)).

In young juveniles burnt and cut plants showed almost total mortality (Table 2.39). No analysis was performed.

Discussion

(a) Banksia serrata

The effects of ages differed between the mature and juvenile classes. The overall trends were for high mortality of resprouted 2-year-old plants in the mature class, and high mortality in 13-year-old resprouted juveniles. Some effect on the ability to resprout was apparent in both classes in 2-year-old plants. Overall, though survival tended to be optimum in 5-year-old plants. The reasons for this are unclear but may be possibly due to the availability of resources or the activity of buds at these differing fire-return intervals.
The overall analyses of survival showed that the impact of high heating was greatest in terms of comparative within-class survival in mature plants. These resprouted less and mature resprouts tended to have lower ability to survive than juveniles. Whilst the removal of the stem showed an independent effect on which heating was added, crown removal or defoliation in mature plants had no significant impact. It was concluded therefore that possibly the most significant real fire-effect would be caused if stems were totally killed in mature plants. As this was found to be fairly rare in the size class of stems represented in the mature class, in high-severity fires (see previous sections), it would appear that the diminished regenerative capabilities of the lignotuber in mature plants has little practical significance.

Lacey (1983) noted that lignotubers in Eucalyptus may be most important as a survival mechanism in young (presumably) small plants and that the lignotubers often merge into the stem as growth in single-stemmed species advances. Such was also the case in B. serrata. As Mullette (1978) has noted in Eucalyptus gunnifera plants with a mallee habit, the above-ground parts are more severely affected by fire than in larger tree-forms. An analogy can be drawn here between the degree of damage sustained by small lignotuberous juveniles and larger trees in the relative amount of damage suffered in fires. Juvenile plants of the size used in this experiment suffered total stem death in both high- and low-severity burns (see previous sections). Therefore
the capacity of the lignotuber to produce viable resprouts is more crucial (Lacey 1983). Whilst its capabilities were less hindered, comparable to other treatments, than in mature plants, the production of viable resprouts by individuals was progressively reduced by increasing levels of heating, possibly due to the increased mortality of buds or meristematic tissue.

A model is provided in Figure 2.4 that summarizes the effects of the experiment in relation to levels of fire severity, in terms of average mortality. The values given are derived from the experiment for the strictly defined sizes of plants given. For high-severity fires, the usual maximum effect as verified in the field (in previous sections) is for destruction of the crown to occur. Therefore the mean survival value given in Figure 2.4 is an average of the percentages achieved under defoliation and crown removal treatments (12 months after cutting). For low-severity fires a value of zero is given. These values are comparable in magnitude for mature plants of this size and larger measured in burns of extreme severity in the field (Tables 2.12 - 2.18). The model has an important assumption. Heating either along the stems or at the bases in mature plants was not carried out hence the possible interaction between the varied crown treatments and heating was not assessed. The model assumes no such interaction is present, though an additive effect of heating on stem removal was found. The comparability of the estimate in Figure 2.4, with the data from burns suggests that if any interaction is
present it may have a negligible effect on survival.

The model assumes no effects of seasons of fire or return intervals on overall survival in mature plants. These criteria were supported by both the field burns and experimental data.

Another assumption was that the experimental heat levels corresponded to levels of fire intensity at all given severity extremes. The congruence between these measures in discussed in Appendix 1.

For juveniles, the mortality averages given in Figure 2.4, were derived, for both severity levels, from the experimental data on survival. Pooled data for the high-heat treatments were averaged to give the high-severity estimate, whilst low-heat data were averaged to give the low-severity value. The value for the high-severity estimate was substantially larger than that found in juveniles in real burns as was the low-severity estimate (see previous sections). The reason for this is not clear. Sizes of juveniles burnt in real fires were varied and if mortality is strongly dependent on size in lignotuberous juveniles, this may account for the difference between burns and experiment. This result may also mean that all dead plants were not located after real burns and that the measured levels of mortality are sizeable underestimates as a consequence.
The model for juveniles assumes no effect of seasons but notes that a decline in survival may occur with increasing fire-return intervals. (Figure 2.4). This accords with the experimental results.

In young juveniles, the differences between the few heated plants that resprouted and those that did not were related (Figure 2.5) to the size of the developing lignotuber. Sectioning of the basal swelling revealed little difference in internal stem size between plants with small and large swellings. The prime difference lay in the thickness of the bark. Beadle (1940) presented a diagrammatic section of a young B. serrata plant in which the bark was labelled "cork" and which similarly showed that for a lignotuber approximately four times the average width of those treated here, the bulk of the swelling was composed of this cork.

It appeared that survivors had attained a level of lignotuber size, which gave bark of a thickness suitable to provide adequate insulation to buds and vascular tissues for the level of applied heating. The results indicate the minimum size of lignotubers in young juveniles needed for the acquisition of fire tolerance, at least to fires of low severity or intensity (Figure 2.4). The consequences of growth and size are further examined in relation to fire tolerance in Chapter 3.

(b) **Isopogon**

The effects of age in combination with season were present in treated mature plants, there being lower survival
due to death of resprouts in 13-year-old plants. Much of this was concentrated across heating/cutting levels in the February treatment. This treatment coincided with end of the Summer growth period. In juveniles some decreased survival was recorded in 2-year low-heat, plants, due again to death of resprouts. It is possible that opposing trends with size and reproductive status may occur with respect to fire-return intervals.

Other than these "age"-related trends, it was concluded that there was little effect of seasons or of heating levels over cutting in mature plant survival. In juveniles, heating at high levels decreased survival over that of low heat and cutting or cutting alone. It was therefore concluded that juvenile Isopogon plants were susceptible to increases in fire severity both on a comparative basis to low heat levels within the class and also compared the response of mature plants. This sensitivity is due to the small size of the basal stem swelling (plants in this class were usually single-stemmed) and the thin bark on it. Some protection in individuals is given by partial burial of this swelling, though the degree of burial varies.

The results for young juveniles showed that these plants were too small to survive low heating, having no discernible basal swelling and stems whose width is measured in millimetres. The growth in small juveniles during the study was small and further testing was not done. It was concluded that disturbances including burning are likely
to result in either total or high mortality in young juveniles at the absolute age tested (≈ 5-6 years). A further discussion of growth in *Isopogon* young juvenile recruits is presented in Chapter 3.

In comparison to *B. serrata* the ability to tolerate fire, as indicated by increased survival, increases with size. That is lignotubers are larger in larger mature plants and possibly have more potential regenerative buds in more protected positions. This correlates with the fact that there is no relative difference in the degree of damage to above-ground parts suffered in mature and juvenile phases, unlike *B. serrata*. Hence the lignotuber is as vital to survival in mature plants as it is in juveniles. Growth adds an advantage in mature plants.

The progressive decline in survival in heated plants over cut plants parallels the results found by Hodgkinson (1979) and Hodgkinson and Griffin (1982) who suggested that in rootstock-resprouting shrubs, heating possibly causes mortality in some buds close to the soil-surface which are less well insulated. Such an effect may be possible in *Isopogon* and at larger sizes presumably more buds and meristems are present in better insulated positions.

A model of *Isopogon* response to burning along the lines given for *B. serrata* is presented in Figure 2.6 incorporating these conclusions.
Further concluding comments.

The reasons for the above results and conclusions, particularly when survival at 12 months is considered, appear to be straightforward. Differential susceptibility between the classes of plants used in both species, to high levels of heat, (except in mature *B. serrata* lignotubers) may be due to simple differences in size and hence protection afforded to potential regenerative buds. However the differences inherent in the ability to resprout and maintain live shoots across the treatments suggest that far more complex factors may govern the overall resprouting processes.

Sections of lignotubers of *B. serrata* were stained and examined microscopically. Bamber (pers. comm.) indicated that large quantities of starch were present in the sapwood parenchyma in a manner similar to that described by Bamber and Mullette (1978) for *E. gummifera* lignotubers. The conclusions of Bamber and Mullette (1978) that lignotubers offer a store of regenerative buds well stocked with food reserves may apply here. The deployment and fluctuations in reserves may affect responses either within or between species (Zedler et al. 1983). However the way in which this occurs is not clear.

One step in any further investigations may, as Noble (1982) suggested, be to implement a thorough study of the carbon-economy in these woody organs (lignotubers). Further studies using greater between-and-within-age and seasonal replications would also be useful.
Summary

Studies of survival in established plants showed that size-related variations in all three species (i.e. B. ericifolia, B. serrata and Isopogon) affected either the level of damage sustained in fires, the ability to resprout and/or the ability to maintain viable resprouts. Banksia ericifolia was shown not to be a resprouter, but may survive fires when individuals are large enough to escape 100% crown scorch in low-intensity fires. The proportions of individuals at given ages and levels of fire scorch were not estimated but have been observed to be small but significant in the aftermath of some fires. This point is examined further in the next chapter.

In Banksia serrata and Isopogon, seasons of fires were shown not to have an overall effect on survival, however the proportions of plants that do resprout are affected by increasing levels of fire severity. The magnitude of this effect is generally inversely proportional to size and potential reproductive status. The effects of fire-return intervals varied with combinations of species, size and reproductive status.
General Introduction

Survivorship is commonly presented as a relationship between the logarithm of the numbers of survivors over time. Deevey (1947), after Pearl and Miner (1935), described three types of survivorship (Figure 3.1) which have come to be called respectively, Deevey I, II and III. Plant demographers have placed considerable emphasis on categorizing their survival data into this system. The type II survivorship model of Deevey (1947) has useful properties in that it can be described by an exponential function expressing survival as the decay in numbers over time.

\[ y = y_0 e^{-rt} \]  \hspace{1cm} \text{(equation 3.1)}

where \( y \) = numbers surviving at time \( t \).
\( y_0 \) = the initial numbers at time zero.
\( r \) = the decay constant
\( t \) = time.

Effectively the value \( r \) is the rate of decline in numbers and can be taken from life-tables (e.g. Caughley, 1977) of cohorts of individuals or directly calculated from plotting survival data and fitting the appropriate semi-logarithmic regression.

\[ \log y = -rt + b \]  \hspace{1cm} \text{(equation 3.2)}

where \( b = \log y \).

Models for other types of Deevey's (1947) survival categories
have been fitted and explored in plants of varied life-history for both short- and long-lived species covering both seedling and established phases, as summarized in reviews by Harper (1977), White (1980) and Silvertown (1982). These reviews have shown a mixture of the Deevey types, however the Deevey Type I survival has been rarely documented. Of relevance are the results of studies of long-lived perennial woody plants which show mainly Type II and Type III survival curves. (e.g.: Ashton 1976, Hartshorn 1975, Sarukhan 1980, Hett and Loucks 1976). My previous work in B. ericifolia (Bradstock, 1977) demonstrated that species survival in established plants (> 1 year old) was constant (Type II) irrespective of broad categories of ages. This study was only done over a limited period (6 months), and the data may have been similarly limited in scope. An understanding of survival in the established phase was needed so that abundance in each species could be estimated and modelled at any given time and the likely survival and lifespans in unburnt conditions and carry-over of individuals after possible fires, at differing times could be assessed. Beside these changes in numbers within the established life-cycle stage, reproductive processes such as flowering, pollination, fertilization, fruit and seed maturation, need to be understood (Solbrig, 1980). However time was insufficient to study these individual events fully, though other workers (Carolin 1961, Blake 1971, Carpenter and Recher 1979, and Recher 1981) have examined these in some of the study-species and in closely related genera and species. However, the broad relationship between
the endpoint of these reproductive processes, that is cone formation and the size and age structure of the population of the study species was sought, so that the basic trends in inputs to the seedbank could be estimated. A discussion of seedbank dynamics and the consequences for varying fire regime effects on post-fire seed abundance is given in later chapters.

The effects of fires on reproductive ability have been discussed by Gill and Groves (1981). Some studies such as that performed by Gill and Ingwersen (1976) have demonstrated that flowering may be stimulated by burning, though Gill and Groves (1981) concluded that this response may be limited generally to monocotyledons. Pyke (1982) reported that inflorescence and fruit production in Telopea speciosissima and Lambertia formosa peaked 2 years after fire and declined thereafter.

In my study the ability to set cones was not examined experimentally by burning plants (e.g. Gill and Ingwersen 1976) but was estimated from a series of populations at differing ages in the two resprouting species. These included populations burnt just prior to the commencement of sampling, so that trends such as noted by Pyke (1982) could be detected.

An analysis of size and growth allowed mortality and fecundity to be related to possible fire-induced changes of population structure in E. serrata and Isopogon. Whilst in
Petrophile and *B. ericifolia*, ages of populations and individuals could be estimated from fire records, in the resprouting species, populations were composed of individuals from differing generations and sizes. Size may not in *B. serrata*, be related to age, due to effects of firing on stem survival (see previous chapter). Some workers (eg: Werner 1975, Werner and Caswell 1978, White 1980) have used size rather than age as a basis for studying and discussing survival and reproductive output in established plants, where estimates of age were either unavailable or spurious.

Therefore, in both *B. serrata* and *Isopogon*, the emphasis was placed on studying survival, growth and cone-outputs through time in relation to size of plants and time since fire. This was done so that the transfer of individuals from young-juvenile $\rightarrow$ juvenile $\rightarrow$ mature classes could be estimated. The effects of differing inter-fire intervals could then be tested to see what impact there may be on these transfers, in accordance with the relative differences in fire sensitivity found in Chapter 2.

Overall, this work enabled:

(a) the nature of basic inputs to the seedbank (cones) to be related to either time since fire or age;
(b) the numbers and sizes of established individuals to be related to time since fire or age.
These data are crucial to considering fire-frequency effects and some discussion is given of these at the end of the chapter. Previous studies of fire have often examined resprouting as an attribute simply scored as present or absent (e.g., Purdie and Slatyer 1976). Others have classified the relative amount of resprouting between species (Keeley and Zedler 1978, Hodgkinson and Griffin 1982, and some of these studies have considered the fire-survival in differing stages of establishment (Bell et al. 1984, Hodgkinson and Griffin 1982). Other studies have examined the sizes of stems in relation to the ability to survive and resprout (Hodgkinson and Griffin 1982, Walker et al. 1981) as was done here in Chapter 2. I have attempted here to integrate the relationships between size, growth and fire survival, so that the demographic effects of fire, especially fire frequencies, on the established life-cycle stage could be judged.

3.2 General aims and techniques.

Studies in established populations addressed several basic questions, though the form of approach varied between obligate seeders and resprouters. For obligate seeders the null hypothesis was tested:

(i) that age had no effect on mortality in established plants.

by contrast, for resprouters (B. serrata, Isopogon), the hypothesis was;
(ii) that time since last fire had no effect on the mortality of plants.

For these species sampled individuals were present before the previous fire in any given site, though in the older samples some may have originated after the last burn.

The object of both hypotheses was to test the constancy of the mortality rate (Deevey II survival) through time between fires and to estimate and compare lifespans between species. If mortality was constant with age or time, half-life calculations could be made using the exponential decay function given above. This was done wherever possible by pooling death proportions over the whole study period from non-significantly different samples and calculating a combined mean mortality proportion. This was then expressed as an average rate over the sampling period and the half-lives were calculated from this estimate. Calculations of life tables for samples are not presented here for the sake of brevity.

Growth data for increments in stem and height diameter and lignotuber diameter, where applicable were calculated on a relative basis using the formula generally applied (Evans 1972) to the analysis of weights of plant parts. The formula in the form used here was:

\[ \bar{R} = \frac{\log_e S_2 - \log_e S_1}{t_2 - t_1} \]  

\hspace{1cm} (equation 3.3)

where \( \bar{R} \) = mean annual relative growth rate
Extensive use was made of this method in modelling stem size changes in *B. serrata*. In each species the null hypothesis that plant size had no effect on reproductive success (the ability to set cones) was examined. Effects of growth on cone-set were examined in the two obligate seeding species (*B. ericifolia* and *Petrophile*) along with possible effects on mortality. In these, density effects on growth and mortality were also tested.

In *Banksia serrata*, growth in small-stemmed individuals was studied to view the time needed to grow a fire-resistant stem in basal resprouters. The effects of stem size and lignotuber size on growth in stem dimensions were tested for this purpose.

The data on survival, growth and reproductive output allowed an assessment of the effects of size on survival and reproduction (cone-set) in each species. Variations in fire frequency were then briefly examined and their likely effect on comparative population structure and abundance predicted and compared between species.

### 3.3 Banksia ericifolia

**Aims and methods.**

Contrasts were sought between early-mature, mature and old-mature plants in order to test hypotheses concern-
ing mortality and maturity. These categories represented ages of around 5, 15 and 20 plus years respectively. Times to first flowering and fruit-set were observed to be variable within areas of known homogeneous age. Variability appeared to be related to site conditions.

For the young-mature category of plants a group of populations arising from fires in the mid-1970s were available, covering an array of sites contrasting in plant stature and reproductive status. Sampling was carried out to contrast populations of high and low stature. These corresponded with the "high" and "low growth" forms discussed by Morris and Myerscough (1983) in their analysis of density-related self-thinning. These forms also corresponded with fast and slow times to first cone set, respectively, and subsequent sampling showed that soil depth may be an important factor in delineating plant stature and time to maturity. On sites of low growth, the distance to underlying rock varied between 30 - 45 cm (depth). In high growth sites rock was not encountered below 1 metre. Three ages were sampled in young mature plants, these originating from fires in Summer 1976/77, 1975 and 1974. Comparisons of mortality both between site-types within ages and between ages were sought.

Older mature sites were chosen on deep soils in burns which occurred in 1968 and at an unrecorded date prior to 1964. For young mature plants site-types are referred to as deep- and shallow-soil sites.
Sampling

Comparisons in mortality were sought between random samples in stands typical of the species, that is where the species was a dominant or main co-dominant in the shrub stratum and where the overstorey was sparse or absent.

The sampling was random in that plants were tagged along transects in randomly chosen quadrats. The position of transects was decided subjectively to sample what appeared to be a typical dominant stand within the age-class. In the two older ages, two transects were each placed in spatially separate stands within the populations. Stands were chosen to be as similar as possible. These were 200 and 500 metres apart for the 1968 stand and the stand of unknown age (< 1964). For young mature ages, single transects were placed in each site-type. In all cases sufficient quadrats were selected to give a minimum sample of 50 plants per transect. Quadrat sizes were 1 x 1 metre and 0.5 x 0.5 metre in old and young ages respectively.

Plants were initially tagged and measured at the end of 1980 - early 1981. Height to the top of the foliage was recorded, this measurement being preferred over stem height as it provided a more relevant way of comparing possible size-fruiting effects between individuals and populations as fruiting was generally dependent on the available number of branch axes or whorls in the shrub crowns.
Censusing was carried out twice yearly until late 1983, with heights being recorded annually along with new fruits for the 1981, 1982 and 1983 flowering seasons. In 1983, the diameters of the bases of individual stems were measured.

A setback occurred soon after the commencement of the study when a fire destroyed a transect from each of the 1974 and old (<1964) samples. A replacement for the 1974 deep soil transect was located in a stand burnt in 1973 but time prevented relocation of another "old" sample.

Results

(a) Mortality in young-mature plants.

In both site types, mortality was strongly concentrated in the summer of 1982/83 (Figure 3.2a,b) with the exception of 1975 and 1977 samples where some mortality occurred in 1981/82. As overall mortality within ages was substantially higher on shallow soils, no formal comparisons were made. However effects of density were tested within the shallow-soil sites as wide variations existed within samples (Figure 3.3). Such variations (Figure 3.3) within deep soils, were not present but the reason for this is unclear. Density effects (Table 3.1) were non-significant indicating that plants sampled at greater than or equal to 20 per square metre suffered similar frequencies of mortality to those sampled at lesser densities. Between sites (ages)
comparisons of overall mortality revealed no site/age effects of significance (Table 3.2).

Effects of growth in relation to mortality were tested in shallow soil samples (Table 3.3). The hypothesis that dead plants were less vigorous in the year preceding death than survivors was tested using growth data for 1981/82 for plants which succumbed in 1982/83. A significant result was obtained (Table 3.3) for the 1977 sample whilst a trend for depressed mean growth rate existed in the 1974 mortality sample, but was non-significant (Table 3.3). Little difference between survivors and dead plants was found in the 1975 site.

Sizes of dead plants were generally small to medium relative to the distributions present in each sample (Figure 3.4a-h). Dominants did not succumb.

(b) Mortality in older mature plants.

The levels of mortality were similar to those sustained in young mature samples. Again deaths were concentrated in the summer of 1982/83 (Figure 3.2,b). Sizes of dead plants were either small or medium relative to the ranges present (Figure 3.4,d-h). As mortality was low further formal analyses were not performed other than a comparison of overall proportional deaths between young-mature, deep-soil samples and old-mature samples (Table 3.4). No significant difference was found and hence the hypothesis that mortality was constant with age was accepted.
Measurements of basal diameter as well as height were made (in 1983) to estimate the proportions of the populations with thick, potentially fire-resistant bark. These measurements were done in the two oldest sites and the frequencies of individuals (out of 50) in size classes above 9 cm and 6 - 9 cm (diameter) are given in Table 3.5.

(c) **Growth and fruiting in survivors.**

In all populations the average of the annual mean relative growth rate in successive years did not appear to be related to size (full data are not presented for the sake of brevity) though the mean relative growth-rate varied in differing years within and between individuals to a substantial degree. Comparisons of mean relative growth-rate in height in young-mature plants showed no significant variation with density of the plants. (Table 3.6).

The ability to set cones varied in relation to mean relative growth-rate in height in young-mature populations (Table 3.7). Successful mature plants in the 1976 (deep soils) sample showed a significantly lower average mean relative growth-rate in height than immature individuals (Table 3.7). No significant effects however, were noted in other deep-soil samples. Successful cone set was not observed in any tagged plants on shallow soils, though some flowering occurred in all years and a few cones were set on adjacent plants. In the 1968 sample cone-set did
not affect the rate of growth (Table 3.7). As data for growth of individuals over 4 metres height were not collected in the old (< 1964) sample no such analysis was made.

Yearly fluctuations in plants setting cones occurred (Figure 3.5) with a tendency for a greater activity in 1982 being marked in most sites (Figure 3.5). Individuals tended not to set cones in successive years except in the oldest sample. In general, in all samples (Figure 3.4), the reproductively active plants during the study were of dominant to medium size in relation to the respective size distributions. The pool of reproductively active plants amongst the samples as judged by the proportion carrying cones overall (Figure 3.4) appeared to reach a peak at an early age. It would appear that from this pool as time passes a proportion are active in any given year and that relatively few plants matured at older ages (Figure 3.4). Average cones per plant in each sample (all plants) showed a trend to increase with age (Figure 3.6) indicating that retained cones accumulated with age. The average number per plant added during the study (Figure 3.6) was greater at older ages reflecting the greater yield in mature bushes in those samples. This reflected a size effect of the dominants in the older samples, these being the principal cone-producers with large, highly branched crowns, compared to younger plants.
Discussion

The results showed that the rate of survivorship was constant with age (Deevey II model) in populations on deeper soils. The mean average annual death rate of all samples was 0.9 ± 0.3% per annum. Half-life calculations using the exponential model of decay (equation 3.2) were made for both deep and shallow soil samples. Values of 74.9 and 6.2 years were obtained respectively, the latter being derived from a shallow soil death rate of 10.5 ± 1.7% per annum. These measures contrast with the earlier measure of about 10 years made by Bradstock (1977).

The possibility of senescence at very old ages boosting the death rate could not be excluded, however the Deevey II model was accepted as a reasonable approximation of survivorship over the life span of the species on deep soils.

The overall pattern of survival on shallow soils was unknown, the above estimates being derived from the measurements taken in the young samples. It is possible that the mortality rate may decline in older stands in these sites. A Deevey III model would then more adequately represent overall survival trends. Nevertheless, the contrast in expected life-spans on differing soil depths was outstanding.

Mortality measurements in this study were possibly biased by the exceptionally hot and dry summer of 1982/83 (See Appendix 2). The above half-lives may be, as a conse-
quence, underestimates. Many of the dead plants observed in this period and others appeared to have wilted or shed many leaves before death.

The relationship between size (height) and mortality varied between samples (Figure 3.4). The overall view (Figure 3.4) was that mortality was concentrated amongst small- to medium-sized plants, in each sample. With the exception of the 1977 and old (≤ 1964) samples which showed negatively and positively skewed size distributions respectively, sizes were roughly symmetrically distributed (Figure 3.4). Deaths occurred amongst the most abundant sizes or smaller sizes, larger dominants being free of mortality. As average growth was largely independent of size, the shapes of the size distributions were largely unchanged during the study, along with the relative sizes of individuals. It was therefore concluded that the factors which determine population structure during establishment may be of prime importance in determining which individuals survive and reproduce during the life-span of each generation.

Actively mature plants (those setting cones with seeds) during the study tended to be dominants, therefore reinforcing the importance of the above conclusion.

The high reproductive output in the (≤ 1964) oldest stand came about through the high cone output of fewer mature plants compared to younger stands suggesting that in these stands a shrinking pool of mature dominants is res-
ponsible through time for additions to the seedbank. Actual amounts of viable seeds available at any time during the development of stands will be dependent on these cone inputs as well as cone losses and the survival of retained seeds. These variables are examined in the next chapter. However at the level of cone inputs, it was concluded that the number of seed-bearing cones may grow, at least, at a constant rate with age.

The analysis of stem diameters in the older stands showed that only a small proportion of the samples had exceeded the minimum size of 9.0 cm, needed to survive heating for 1 minute (see Fig. 2.1, Table 2.10 in Chapter 2). It would appear that an age much greater than 15 - 20 years is required before a sizeable number of stems achieves this minimum degree of fire tolerance. The proportion of 0.14 stems per sample in the <1964 may be used as an indicator of the maximum number of individuals in any old population that may survive a low-severity fire if the crowns remain intact (see Discussion in Chapter 2).

3.4 Petrophile pulchella.

Aims and Methods.

A similar contrast in ages to B. ericifolia was sought in the study in Petrophile of mortality and reproductive output. Measurements of growth, size and cone-set were performed in a similar manner.
Populations of Petrophile did not appear to exhibit the variations in size related to site conditions found in B. ericifolia and sampling was not divided into differing habitat classes. Paired transects in stands burnt in 1977, 1975, 1974, 1968 and < 1964 were set up and samples of a minimum of fifty plants per transect were tagged and measured in late 1980 - early 1981 in 1 x 1 metre quadrats. An exception was the 1975 site where because of extremely high densities, smaller quadrats (0.5 x 0.5 metre) were used in some instances and the numbers sampled were higher.

Transects were more closely spaced than in B. ericifolia in all sites except the oldest, being around 20 - 30 metres apart, but were laid out using similar criteria. Unfortunately a fire destroyed one of the pre-1964 transects during 1981 and the data presented for that age were drawn from a single transect only.

Results

(a) Mortality in young-mature plants.

Deaths were concentrated in the sampling periods covering mid-1981 and 1982/83, to varying degrees in all samples (Figure 3.7). However, the most striking feature was the massive mortality in the 1974 sample (both transects) during 1981 which was tentatively attributed to competing effects of vigorously growing co-habiting sedges, principally, Restio species. These co-habitants were either absent or
considerably less dense in other sites. Density variations were widest in the 1975 sample (Figure 3.8), and testing for density effects on mortality was carried out on these data (Table 3.8). No significant effect was found, and comparisons between the proportions of overall average annual mortality for the 1975 and 1977 samples were (Table 3.9) similarly non-significant.

Sizes of dead plants (Figure 3.9) were generally small to medium relative to the sample distributions (1974 samples are not discussed further).

(b) Mortality in older-mature plants.

Levels of mortality on an overall annual average basis were of a similar order to those in young-mature populations (Figure 3.7, Table 3.10). Dead-plant sizes were small or medium in relation to the ranges present (Figure 3.9,c, d).

(c) Growth and reproductive output.

In young mature plants, positive correlations of growth rate and size were apparent only in high-density samples (data not presented here) from the 1975 site. Height growth for $<1964$ plants was not calculated because plants were too tall. Comparisons of means for all plants in the low density quadrats and individual high density quadrats
were not carried out due to heterogeneity of variances (Table 3.11). An informal comparison however suggested that plants exhibited greater relative growth at low densities (Table 3.11).

Cone-set in the 1975 low-density plants significantly depressed the mean relative growth rate (Table 3.12). Few high-density plants set cones during the study. In the 1977 populations no significant effect occurred, whilst for the 1968 sample a trend existed for lower relative growth rate in reproductively active plants but this was non-significant (Table 3.12). As virtually the entire population sampled in the old (\(<\ 1964\) site set cones, no such comparison was made. In all samples (Figure 3.9c,d) at all ages the majority of mature individuals (cone-set during the study) were either large- or medium-sized within the size distribution present. During the study, variations in the number of plants fruiting between years occurred (Figure 3.10), though no consistent trend was present amongst sites. Few plants set cones in successive years (Figure 3.10).

In the 1968 transects the pool of mature plants (Figure 3.9,c) expanded by ten during the study. In the oldest (\(<\ 1964\) sample (Figure 3.9,d) the pool remained static. As cone production in the (\(<\ 1964\) site outstripped that in younger plants (Figure 3.11), the disparity in the number of cones present per sampled plants, at the beginning of the study, widened during its course.
Discussion

The hypothesis that mortality was constant with age was accepted and hence the Deevey II model, as with *B. ericifolia*, provided an adequate representation of survivorship in Petrophile. Accordingly the mean average annual death rate over all samples (except 1974) was $2.8 \pm 0.9\%$ per annum and half-life calculation using the exponential model (equation 3.2) was made yielding a value of 24.7 years. The comments made for *B. ericifolia* as to bias in death rates caused by the extreme weather (see Appendix 2 for rainfall data) during the study may equally be applied in Petrophile. As with *B. ericifolia*, deaths appeared to be related to symptoms of moisture deficiency.

Sizes of plants were symmetrically distributed in all samples, except the 1975 transects (Figure 3.9,b). As with *B. ericifolia*, deaths were concentrated in the most abundant or smaller size classes. This trend was pronounced in the 1975 sample where the size structure was negatively skewed (Figure 3.9,b). Conclusions presented for *B. ericifolia* as to the effects of size on growth and the determination of the size-class hierarchy were applicable to Petrophile.

The mature pool of plants and the mean annual rate of sample cone production expanded with age hence the seedbank (ignoring losses) is likely to grow at an increasing rate through time in this species, though in the unlikely occurrence of continued absence of fire this rate would presumably steady and finally decline and then become negative as the maximum life span of individuals was reached.
3.5 Banksia serrata

Aims and Methods.

Studies of mortality and growth in this species were aimed not only at testing patterns in mortality and cone-set through time after fire, but were also directed toward estimating the time needed for small plants (see previous Chapter (2)) to reach a size where their stems were fire-resistant. In turn, the effects of size of stems and lignotubers, and times since fire on the ability to set cones, were tested. The aim was to define the likely combination of sizes of these variables which were indicative of mature individuals and the time after burning at which maturity was achieved.

The results of the previous chapter indicated that substantial numbers of individuals in any population may be forced to recover from basal resprouts after burning across a wide range of fire-severity levels. Hence studies of growth and recovery through time were aimed at defining the time needed for the formation of fire-resistant stems, in basally resprouting individuals. As recovery may be influenced by the size of various organs such as the lignotuber, growth data were tested to determine size effects of the lignotuber and stem on the rate of growth in stem diameter and height, at various times since fire. As in the previous chapter, a single measure of stem size (diameter at breast height, D.B.H.) was used. On this basis a growth model was formulated to predict the times after fire at which...
stems may achieve a size which is fire-resistant.

(a) **Mortality and Maturity.**

The hypothesis that time since fire has no effect on mortality was tested amongst five samples from differing burns. Years of fires in these samples were 1980, 1976, 1974 and some time prior to 1964 (≤ 1964). Within each sample, 50 plants were tagged in each of two spatially separate replicates. Only plants which were present before the previous fire were tagged. As these could only be identified with any certainty in the three sites most recently burnt, it is likely that a few smaller individuals in the two samples least recently burnt, may have been of post-fire origin. Samples were drawn in each location from a 20 x 20-metre quadrat initially, though in all cases further plants were added from the immediate surrounds to make up the numbers. Tagging and measurement of height (up to 4 metres only, higher plants were estimated) and D.B.H. was done in early 1981 and subsequent checks on survival were done twice yearly until mid-1983. In 1982, lignotuber (or basal) diameters of all individuals were measured. The seedbank of all individuals was assessed in 1981 and counts of cones from the 1981/82 and 1982/83 flowering seasons were made.

(b) **Growth in tagged plants.**

In September 1981 a study of D.B.H.-growth in all tagged plants was begun. Plants were remeasured, using calipers where the stem was less than 4.0 cm D.B.H. and a tape above that size. The point of measurement was marked by a drawing pin. Plants were remeasured in November 1982
and September 1983, though due to losses in the marker pins the sample sizes were diminished. Heights also, were re-measured annually (where applicable). In summary, size and growth data were used to test the following null hypotheses.

(i) That mortality was unrelated to size.
(ii) That cone production was unrelated to size.
(iii) That cone production was unaffected by time since fire.
(iv) That height growth was unrelated to lignotuber size.
(v) That stem growth (D.B.H.) was unrelated to stem or lignotuber size.

As basal resprouters were present in some numbers in the 1976 and 1974 samples, growth measurements in these individuals were of particular importance in formulating a model for prediction of stem-fire tolerance. As many individuals in this category were below 1.6 metres (breast height), at the outset of the study, emphasis was placed on measuring both height growth in these and stem growth in larger plants.

As numbers of tagged basal resprouters in the 1980 samples were low, an additional set of measurements were performed on plants burnt in a variety of sites from 1980-1982. These were made in mid-1983, to specifically test the effect of lignotuber size on the measured height of the resprouted stem in each individual at differing times after burning, up to about 40 months. Data were assembled in a static time series of sites from differing burns in
order to assess the overall effect of lignotuber size on height growth through time during these early stages of recovery. The relationships between early growth and lignotuber size were then incorporated into a growth model.

The burns which were sampled, occurred in March 1980, August 1980, December 1980, July 1981 and May 1982. Contrasts between severity-levels were made in all burns, though the criteria for judging severity as given in the previous chapter were considerably relaxed in order to obtain samples of adequate size. Measurements of height were made from ground level to the top of stem.

(c) Growth modelling

As stated, the aim was to estimate the time taken for recovery in that portion of the population most heavily affected by fire: the basal resprouters. Whilst epicormic sprouting may occur at varying points on a stem according to the degree of damage inflicted, in effect those plants that resprout only at the base were assumed to be those with the greatest amount of growth and development needed to attain a reproductively active and fire-resistant aerial stem. In a situation of high fire-frequency, these plants were envisaged as being prevented from setting seed if continually forced to regrow stems under repeated burning. The aim of assembling a simple growth model was to predict the likely critical time needed for recovery, to
progress to the point where a stem was of sufficient size to withstand high-severity fires. This size was defined from Table 2.26 of the previous chapter as being \( \geq 2.0 \) cm D.B.H. At this size the average proportion of stems surviving completely was around 50\% irrespective of the level of fire severity (See Table 2.26). The model followed several steps aimed principally at predicting firstly the effect of lignotuber size on growth up to 1.6 metres (breast height) and then incorporating stem size and lignotuber size as predictions of stem size growth until the above D.B.H. limit was exceeded. To achieve the above predictions, effects of lignotuber size on height from the March 1980 data were used to generate expected heights at age 3.5 years. Height growth equations for the 1976 and 1974 samples were then used to predict heights over a hypothetical period of three years using the above predicted heights (at 3.5 years after fire) as a starting point. Where stems achieved a height of 2.0 metres, stem D.B.H. was assumed to be 1.0 cm (this was verified in the field), and further growth was projected for a maximum hypothetical period of three years or until a value of 2.0 cm D.B.H. was generated, using stem growth data from the 1976 and 1974 samples. The method involved several major assumptions and limitations that are dealt with below in the discussion.

(d) **Growth of juvenile recruits.**

The development and dynamics of seedlings up to around three years of age is dealt with in a later chapter. The work presented in this chapter was largely orientated
toward both older immature and mature plants subject to previous burning. However studies of juvenile recruits in the previous chapter showed that they may be eliminated by burning at around 5 - 7 years of age. It was therefore necessary to study their growth to estimate the age at which they acquire fire tolerance and survivorship. The time for recruits to acquire fire tolerance is a crucial factor in overall recruitment, and in situations of sustained high fire-frequency may influence the maintenance of abundance in populations. Expressed in another way, the growth of recruits and their achievement of fire tolerance, may be crucial in determining the minimum sustained fire frequency under which abundance in a population may remain constant or expand.

Populations of unburnt juvenile recruits of known age greater than 3 years were difficult to find. However a sample was available in the 1976 burn used for mortality and growth studies, though the plants studied were in an adjacent area of the site, to that where survival and growth studies of larger established plants were carried out. The controls used in the experiment in Chapter 2 plus some extra plants were monitored from August 1982 to March 1984, for both height and lignotuber growth, with an intermediate measure being taken in August 1983. Calipers were used to check lignotuber diameter.

The data from the previous chapter showed that fire susceptibility in juvenile recruits appeared to relate to the size of the lignotuber, with recruits with a lignotuber
diameter of around 4.0 to 5.0 cm, showing survival under low heating. This size range was therefore used as an estimate of minimum size of lignotubers required to survive low-intensity fires. Survival through high-intensity fires would require thicker bark and a range of larger diameters may have to be achieved (possibly $\geq 7 - 10$ cm.).

Results

(a) Survival

Mortality in all samples was low and varied in timing (Figure 3.12). As deaths were few, formal comparisons between samples were not carried out. Rather the data supported the hypothesis that time since fire had no effect. Deaths were spread in relation to size (Table 3.13(a) - (h)) but were too few to allow any conclusions to be drawn as to size-survival relationships.

In the 1980 samples, flowering and cone-set commenced during the second flowering season (1982/83) after burning. In resprouting species this interval is called the secondary juvenile period, Gill (1975). A secondary juvenile period of this length was observed generally in the species regardless of burn season. Successful cone-set occurred in a more limited range of larger-sized plants than in the samples in which the time since the last fire was longer, though strict comparisons between the 1976 and 1974 samples and others may not be possible as these appeared to have been
burnt at a lower level of severity. The overall chance of successful cone set (all samples other than 1980 combined) (Table 3.13 (c) - (h)) indicated that a minimum stem size-class of 1 - 4 cm and lignotuber size-class of 11 - 15 cm were necessary for maturity. (These minima were only found in the <=1964 samples). These values were adopted as general estimates for the threshold of maturity.

The annual average number of cones produced per actively mature plant (ie. plants setting fruit during the study) showed (Figure 3.13) no obvious trend with time since last burn and was effectively regarded as being constant.

(b) Growth in tagged plants.

As noted above, markers for diameter measurements were lost in some numbers, hence only growth data for those individuals which were available for two consecutive years (1981/82 and 1982/83) are presented in the analysis.

All growth data (stem and height) were calculated on a basis of mean annual relative growth, using the formula given previously, to allow comparisons of individuals of widely differing size.

The increment in stem diameter (mean annual relative growth) as an average of the two annual measurements. Figures 3.14 (a) - (e)) was related to the sizes of stems and lignotubers (Table 3.14) firstly as sole independent variables
in bivariate regressions and jointly in multiple regressions (Table 3.15). In the former analysis regressions were significant for both independent variables for all except the 1964 sample, though co-efficients of determination \( r^2 \) were low (Table 3.14). When entered together, overall significance of the equations was similar (Table 3.15), as were co-efficients of determination, but lignotuber slopes were non-significant. Hence it was concluded that stem growth was independent of lignotuber size when considered in conjunction with the effects of stem size.

Height growth in the 1976 and 1974 basal resprout samples was not found to be related to lignotuber size. Data were pooled to produce an average overall annual growth estimate for populations burnt at those times (Figure 3.15).

The results expressed as regressions for the series of samples taken in varied sites after burning (up to 42 months post-fire) are summarized in Table 3.16. Regressions of height against time since burning were calculated (Table 3.16) for each sample, using the logarithm of height averaged over time (months) since burning (i.e. log average height per month). This variable was an estimate of the rate of growth of the resprouted stems.

Comparisons of selected equations drawn from burns at similar times (Table 3.17) showed significant site/fire severity effects and on this basis a pooled formal model of height growth over the post-fire time-span of the samples was not calculated. However a series of averages of all raw
height data in a series of lignotuber size classes at various times after burning is presented (Figure 3.16) to illustrate the overall trends in resprouted stem growth in basal resprouters. The effects of lignotuber size (Table 3.16, Figure 3.16) were positively correlated with height: that is large diameter tubers produced taller stems up to this time after fire. Most equations (Table 3.16) were significant though $r^2$ values were variable. Because of differences between equations (Table 3.17) it was concluded that rates of height were affected by sites and fire severity levels. The average rates of growth were highest in the samples taken at the largest time since fire (see comparative sizes of slopes in Table 3.16) and lowest in the samples taken soon after burning. Weather events may also have affected the results, particularly in the 1982/83 Summer (low rainfall - see Appendix 2) when the "youngest" samples were commencing resprout growth.

(c) Growth modelling

The average heights at 42 months generated by the relevant equations (Figure 3.16) were used as a starting point for further growth simulation. Statistical differences existed between mean height growth equation intercepts at this time after burning (Table 3.17). The predicted height-values generated by equations from samples taken at 37 and 42 months however showed little difference in practice, and therefore the average values for stem height in differing sizes of lignotubers given in Figure (3.16) were used as a starting point in the model. Figure
(3.16) shows that plants with large tubers were reaching an average maximum height in excess of breast height (1.6 metres) and therefore estimates of diameter increment (D.B.H.) over further time could be simulated.

Further height growth (after 42 months) was projected where applicable using the pooled growth estimate (for 1976 and 1974 data) over three years or until a stem height of 2.0 metres was achieved. (Table 3.18). Where a value substantially in excess of this was achieved over a year, the above critical height was assumed to have been reached midway through the year (Table 3.18). Further growth-stimulations after the height of 2.0 metres (1.0 cm D.B.H.) was reached, were carried out using the stem growth equations (bivariate lignotuber equations) for the two 1974 samples and the 1976 sample. The lignotuber equations were used for consistency with other parts of the model. Growth was therefore modelled solely on this variable.

The results of simulations over consecutive years are given for each equation in Table (3.19). As there was little difference between the predictions for each equation the overall results were averaged and summarized as the extremes of predicted overall times needed to achieve a stem D.B.H. just in excess of 2.0 cm, (Table 3.20).

The positive effect of lignotuber size in shortening the time to achieve fire resistance was obvious (Table 3.20). Also marked was the potential for variations in fire-frequency to differentially select and force certain individuals back into
a basal resprouting mode (Table 3.18).

(d) **Growth in the lignotubers of young recruits.**

Though the sample size was small and unreplicated spatially, no mortality was recorded in juvenile recruits. Mortality was therefore assumed to be similar to larger established plants.

Expansion of lignotubers (Figure 3.17) in the 1976 recruit sample was unrelated to size. Mean relative growth rate in the 6 months to March 1984 as opposed to the full year previous, was such that if the rates were maintained over a full year the 82/83 rate would be exceeded. (Figure 3.17). On the basis of the average rate (0.199 p.a.) for the two measured growth periods, growth was simulated over 3 consecutive years (Figure 3.18). The results (Figure 3.18) showed that over 50% of the sample had by then achieved a minimum lignotuber diameter of 5.0 cm. As this was considered to be the minimum fire-tolerant size, the exercise showed that the minimum age of fire-resistance for half the recruit population was 11 years (Figure 3.18).

**Discussion**

Several major assumptions were inherent in the growth model. The major limitation was that estimates of lignotuber growth in the tagged non-seedling samples were not made. As lignotuber size can reasonably be expected to change over the fairly lengthy simulated time spans given
in Tables (3.18 - 3.20) it is necessary to consider the sensitivity of the model to various possible changes in the observed populations. Observations of lignotubers up to 42 months post-fire suggested that expansion as indicated by cracking in the charred outer-bark was possibly limited to less than a centimetre (diameter) over a three-year period. Observations in the less recently burnt stands suggest neither a rapid increase nor decrease in this approximate rate. The net effects in the model of an increase in lignotuber size of this magnitude (~1 cm) may balance out with the effects of stem growth over various stages of recovery. Whilst growth in lignotubers in the early stages will hasten height growth (see Figure 3.16), it will tend to decrease stem D.B.H. growth in the later stages covered by the model. (Figure 3.15). Expansion of the lignotuber by a centimetre in larger individuals in the initial stage may have the effect of possibly shortening the time to reach a height of 2.0 metres by up to half a year. A similar rate of expansion however may more than cancel out this advantage if maintained for several years in the model. Hence the times given in Table 3.20 to achieve fire resistance in stems can be seen as possible overestimates. More importantly, the values given for lignotuber size will have increased, and further consideration of repeated cycles of burning must take into account such an effect and the feedback in terms of growth. The extent to which the morphology of individuals can be driven toward a form consisting of a large lignotuber with a thin weakly developed stem, as may be postulated under a continual high frequency of burn-
As with the obligate seeding species, the rate of mortality was found to be constant between samples. Though time since fire was not analogous to age, the results indicated that no significant changes in mortality occurred as the time since the last burn increased. The plants composing each of the samples were likely to be of widely varying ages. The results cannot directly be used to represent likely survivorship of an even-aged cohort and calculation of a half-life for the samples may be biased in an unknown manner for this reason. However as mortality seemed unrelated to any of the size measures and by inference, to age, the half-life estimate of the samples (86.3 years, based on a death-rate of $0.8\% \pm 0.3$ per annum) may be therefore a reasonable approximation for recruits, juveniles and mature plants. Taken in conjunction with the mortality data given in the previous chapter, the long-term survivorship pattern following a fire of uneven-aged samples of *B. serrata* would be adequately described by the Deevey III model (Figure 3.1) with the initial death rate during and immediately following fire differing in the differing categories of plants within the established life-cycle stage.

Output of cones from mature trees was unaffected by time since last fire. No attempt was made to compare sites
in order to generalize about the effects of tree size on cone outputs or the size of the pool of mature plants due to possible fire-severity differences being confounded with time-since-last fire. However observations suggested that the largest trees set fruit earlier after fires than the smaller plants, possibly because higher branches suffered less fire damage. At later times after fire, large trees appeared, in a number of sites, to produce greater quantities of cones. Therefore if a population remains unburnt the chance of a large proportion of individuals reaching large sizes would exist and reproductive output of stands, during long fire-free periods may increase. Conversely high fire frequencies would not only prevent or delay individuals from reaching a mature size but would impose frequent checks through unproductive flowering seasons (those in the years immediately following fire) on the overall reproductive output of the population.

The varied size structures of the samples presented in Table 3.13 (a) - (h) may be partly viewed as the outcome of the fire histories at each site if the predictions offered by the growth model are realistic. From the model, fire cycles of less than ten years if maintained may substantially suppress the growth of smaller plants and maintain a proportion of the population in a form with weakly developed stems. The size of this proportion in any sample would depend on the size class structures present at the outset of such a series of fire cycles.
A population with plant sizes similar to those found in Table 3.13(h) (<1964(b)) would, if subjected to an extremely high-frequency fire cycle, have relatively few plants suppressed in form. A population such as in Table 3.13 (c) (1976 (a)) on the other hand may be largely held in its existing suppressed state under a 5 - 6 year repeated fire rotation, allowing little movement of individuals into possible mature size classes. The population represented in Table 3.13 (c) (1976(a)) was burnt in 1971 and 1966 according to National Park records dating from 1964, suggesting that arguments provided by the growth model may be partially substantiated by examination of past fire histories.

The effects of low fire frequencies are further compounded by their impact on young juvenile recruits as indicated by the fire-tolerance experiments (Chapter 2) and growth observations. These results indicated that an inter-fire period of 10 - 15 years may be required before the bulk of seedlings have achieved a tolerance to at least low-severity fires (Figure 3.18). Further time may be needed to acquire tolerance to high-severity fires.

1.6 *Isopogon anemonifolius*.

**Aims and Methods**

Hypotheses concerning mortality were similar to those given for *B. serrata*. Populations burnt in 1980, 1977, 1974 and pre-1964 were sampled, coinciding in the main (with one
exception) to *B. serrata* samples. In 1977 and 1974 areas, three sites were present with substantial numbers of young juvenile recruits dating from the previous fire. Samples of these were monitored.

Measurements of growth were restricted to height, whilst estimates of lignotuber size were made in 1982. In large individuals the lignotuber forms a plate-like structure similar to that illustrated by Beadle (1940) for *Lambertia formosa* and *Eucalyptus botryoides* (Lacey 1983).

The pattern of radial stem growth from the fringes of the lignotuber, illustrated by Lacey (1983) is closely followed in *Isopogon*, though size and stature of stems is somewhat smaller than in *Eucalyptus botryoides*. The model of stem response to fires proposed by Lacey (1983) would also appear to apply in *Isopogon*. In this model Lacey (1983) proposed that small plants initially have a single stem that is killed by fire, and that subsequent growth and fires result in continual replacement with multiple stems arising from an enlarging lignotuber. The presence of small single-stemmed lignotuberous juveniles and larger multi-stemmed adults in *Isopogon* is evidence that such a pattern of growth under repeated firing may hold in this species.

In *Isopogon* the lignotuber edges are usually defined above-ground by the ring of stems arising from the lignotuber. As the lignotuber is usually covered thinly by soil and litter, an estimate of size without disturbance was made
by measuring the shortest and longest widths as marked by the points of emergence of stems from the soil surface. The averages of these two figures are presented as estimates of size. Generally tuber shapes were oblong-elliptical in larger plants and less regular compact forms in smaller plants.

Cone production from 1980/81, 1981/82 and 1982/83 was monitored and outputs at differing ages were compared.

Results
(a) Mortality
Amongst established plants (Figure 3.19) deaths were only recorded in a 1980 sample. Mortality amongst the juvenile recruits occurred in all samples and tended to peak in the Summer of 1982/83 (Figure 3.19).

(b) Fruiting in survivors.
Height growth analyses are not presented principally because the measurements were of limited use in describing growth for this spreading multi-stemmed species. However the results confirmed the overall impression that pre-fire stature of burnt plants was generally regained within 3 years. Measurements of growth and survival of individual stems may have been appropriate however time prevented such a detailed study. Correlations between lignotuber size and cone production were investigated but as shown in the example in
Figure 3.20, these proved to be of limited use. By implication, fruiting was also independent of stem numbers in each individual. The minimum size of mature lignotuber varied between 5 and 10 centimetres, with no apparent site/fire time effects (Figure 3.21). Mean annual fruiting in mature plants during the study (Figure 3.22) peaked in the 1976 samples, other sites showing only slight differences. The hypothesis of constant cone production, with time since last fire, was therefore rejected. Cone production in all samples was greater in the 1980/81 and 1982/83 seasons, than in 1981/82. These results contrast with the findings of Pyke (1982) in Telopea and Lambertia species. Lignotubers in juvenile recruits were either absent or minimal in size ($\leq 0.5$ cm diameter of swelling).

Discussion

The absence of mortality in established and previously burnt plants at a time of two years or more after burning, in contrast to the young recruits, suggested that the overall survivorship pattern for a cohort in the species, after establishment, may follow the Deevey III model. Mortality was concentrated in the period prior to recruitment into the pool of lignotuberous plants: that is in juvenile recruits. The average annual death rate for all samples was $0.48 \pm 0.008$ and from this value a half-life for juvenile recruits of 14.1 years was calculated.

Significant mortality also occurred in recently burnt plants, as shown in this (1980 sample) and the preceding
chapter. This was concentrated in the year after burning.

The growth of lignotubers in established unburnt juvenile recruits was imperceptible during the study and if such a rate was maintained it would appear that plants may have to reach an age of at least 15 - 20 years before a degree of fire tolerance is achieved in any cohort. Whether growth proceeds at a constant or changing rate was unknown.

As reproductive output appeared to peak at an intermediate time after burning, additions to the seedbank are linked to the cycle of recovery and growth after fire in plants with moderate to large lignotubers.

3.7 General Discussion and Conclusions.

Comparisons of species half-lives indicated that obligate seeders were likely to be less long-lived than resprouters. The potential effect of soil depth on death rates and the initiation of cone-set in B. ericifolia may serve to highlight the importance of understanding varied populations across a species' habitat range (Andrewartha, 1984).

The time taken to first cone-set in the obligate seeders (primary juvenile period, Gill 1975) varied from 5 to 9+ years for B. ericifolia, 5 to 6 years for Petrophile, in the tagged samples, though in the populations studied in general some plants were observed to have matured earlier.
These values fall within the ranges for woody shrubs given by Gill and Groves (1981) Kruger (1977, 1979) and Bell et al. (1984). Fire intervals less than or equal to the ranges given for Petrophile and B. ericifolia will cause local extinction or drive abundance to very low levels due to the lack of accumulated seedbank. Cone accumulation (Figures 3.6 and 3.13) in young populations is such that fires at ages slightly above the given ranges will have a strong depressing effect on the potential abundance in the succeeding generation. These questions are more fully explored in the next chapter. It should be noted that variability in maturation of populations may partially stem from variations in establishment times of plants after fires in differing populations. Rainfall events may cause wide differences in germination time after fires, as will be shown in a later chapter.

High fire frequencies may affect resprouting species in two differing ways. The responses of established previously burnt plants and unburnt seedlings may differ. Isopogon and B. serrata contrasted in the established phase in that Isopogon plants quickly re-established their aerial habit and reproductive capacity (secondary juvenile period) within three years of burning. In B. serrata, though flowering and cone-set were observed within a similar period after fire in large plants, recovery was heavily dependent on plant size. The most severely affected burnt plants (basal resprouters) were shown to require (Table 3.20) between 6.5 and 9+ years to regrow a fire-resistant and likely mature
stem. Achievement of this stem size can be likened to the breaking of a barrier to continued reproduction and rapid recovery and maturity after further fires. Exposure of populations to fire cycles that will maintain a proportion of plants below this size barrier will limit seedbank accumulation by preventing any inputs from them, though they may persist. This phenomenon was noted by Curtin (1967,b) who concluded that frequent firing may change the size composition in stands of lignotuberous Eucalyptus by suppressing the development of plants of small sizes, through the continued destruction of aerial parts. Some woody plants may respond in such circumstances as annual or biennial burning by producing rhizomatous growth as described by Lacey (1974) for Eucalyptus porrecta. However Lacey (1974) noted that a minimum stem height was needed for flowering and fruiting to occur and that this took several years. Necessary fire-free periods of this length were few (Lacey 1974).

The acquisition of fire-resistance in established young-juveniles in both resprouters was estimated to be dependent on longer fire-free intervals than those critical for the recovery of basal resprouters. In contrast, Henry and Florence (1966) found that tolerance was acquired in some Eucalyptus seedlings to annual burning. That is lignotubers were sufficiently developed within a year after emergence to withstand some heat. Henry and Florence (1966) found that in some species, lignotubers 1 inch (diameter) in size were present within a year of emergence. However Henry
and Florence (1966) noted that the survival of small lignotuberous spotted gum (*Eucalyptus maculata*) was less than other species under annual burning and that this may cause eventual shifts in species composition.

The lesser sensitivity of large established *Isopogon* plants as characterized by their more rapid recovery was contrasted with the apparently slower growth and formation of lignotubers in seedlings. The length of the primary juvenile period in *B. serrata* and *Isopogon* is unknown, but in the absence of fire would be related to rates of growth in stem and lignotuber size.

The net effect of repeated growth in short fire cycles of between 5 and 10 years in resprouters compared to obligate seeders was that in both species recruitment was likely to be prevented and that in *B. serrata* a proportion of the population would effectively be suppressed with consequent effects on the accumulation of seedbank. As mortality was found to be heightened during and immediately after fire in comparison to the inter-fire periods in both resprouters, a sustained short fire cycle would cause a higher overall average death rate than in unburnt populations. In *Isopogon* fire can be seen as the major source of mortality in lignotuberous plants. Such effects are discussed and modelled extensively in the final chapter (Chapter 9) of this thesis.

The chief comparative difference between resprouters and obligate seeders therefore lies in their relative sensi-
tivity to a succession of frequent fires. The resprouting habit will confer resilience in such conditions even though populations of either of B. serrata or Isopogon may go into a pronounced decline, due to decreased survival of established plants and the elimination of fire-intolerant recruits. It may take a long period to drive this decline to extinction. However a single fire-free interval of a length that will allow the acquisition of fire tolerance in juvenile recruits and for the release of fire suppressed established lignotubers (in B. serrata) will allow either species to rebound and build up established numbers. Fire cycles of intervals that are on the threshold of causing these barriers in Isopogon and B. serrata may be comfortably tolerated by the obligate seeders (B. ericifolia and Petrophile). However both obligate seeders are subject to possible site extinction under a single very short-fire interval, which would have no long lasting effect (if it is a one-off occurrence) in either resprouting species.

These scenarios are more formally discussed in the final chapter in the light of data on emergence and seed-bank accumulation examined in the following chapters. The overall findings in this chapter are summarized in Figures 3.23, a-d, representing the changes in numbers from recruits to juveniles to mature plants, through time in all species, in the absence of fire.
CHAPTER FOUR: STUDIES OF SEEDBANK

4.1 General Introduction

As indicated in Table 1.4 in Chapter One, the theme of Chapters 4 and 5, are respectively the size and nature of seedbanks through time, and releases of seeds from storage both in the presence and absence of fire. These themes are related in that one of the determinants of seedbank size (Figure 4.1) will be losses caused by seed release. Other losses are summarized in Figure 4.1. The prime input into seedbanks comes from the annual production of seeds after each flowering season (Figure 4.1).

The significance of the sizes of seed storages in relation to the quantitative study of post-fire seedling abundance have been studied by Christensen and Kimber (1975), Keeley (1977, b), Shea et al. (1979), Auld (1984) for species with soil-stored seedbanks and Ashton (1976, 1981) and Gill (1981 a,b,c) for *Eucalyptus regnans* which retains seed in capsules on the canopy and *Banksia ornata* with woody cones. Available seed numbers in the seedbank may or may not directly affect abundance of post-fire seedlings as shown by Keeley (1977 b) and in turn the abundance of seeds may or may not directly reflect immediate numbers from inputs of fresh seeds from recent flowering seasons. As well as the numbers of seeds, other factors such as the distribution of seeds with respect to soil depth (in soil-stored seedbanks) may determine the numbers which emerge as seedlings (Shea et al. 1979, Auld 1984, Keeley 1977 b). Hence the numbers of seeds and characteristics of the seedbank will
in concert determine the numbers of seedlings which emerge following a fire of given intensity.

For the canopy-retained or above-ground seedbanks, the principal factors which will determine available seeds at the time of fire are:

(i) size of seedbank - number of viable seeds in fruits.
(ii) rates and amounts of post-fire seed-release from fruits.
(iii) survival of seeds in fruits during fire.

The first of the above points is explored in this chapter whilst the other two are each explored in the two subsequent chapters.

Various workers have contrasted differences in the degree of seed storage in serotinous or close-cone species. (Gill 1976). Lotan (1967), cited in Gill 1981 c) demonstrated variations within Pinus contorta in numbers of seeds retained in the cones. Lotan (1967) correlated these variations with plant and stand age and other site characteristics related to fire risk, noting that the highest degree of serotiny occurred in the most xeric and hence most fire-prone sites. Other gymnosperms which are reliant on fire for release of seeds from cones in southern California have been discussed by Vogl (1967) and further discussions of relative degrees of serotiny have been provided by Gill (1976 and 1981 c).
Variations in the degrees of seed storage between Banksia species which possess woody cones has been discussed by Gill (1976), and comparisons of the mechanisms of seed release in Eucalyptus, Hakea and Banksia, were presented by Gill (1981a), who concluded that the former two are less reliant on heat for seed release and are more prone to release seed in the absence of fire. In Banksia species, further comparisons of the degree of serotiny have been attempted by George (1981), who classified the relative dependence of species on fire to trigger seed shed. George (1981) classified B. ericifolia as dependent on fire and B. serrata as partially dependent.

These discussions are useful in relating the seed retention habit to fire and the likely availability of seeds in post-fire conditions or otherwise. However, external assessments of numbers of seeds missing from cone-bracts or follicles, whilst providing some measure of the numbers and circumstances surrounding seed release, are only partial descriptors of the amount and nature of these above-ground seedbanks. Meaningful comparisons of seedbanks within and between species may need to take into account both absolute numbers at given ages and rates of accumulation of viable uneaten seeds (Figure 4.1), if seed numbers are to be related to seedling numbers in the presence or absence of fires. The significance of predation in woody fruits has been briefly reviewed by Gill (1981a, c) but attempts at incorporating losses due to this (see French 1983, for Hakea species) and seed release
in unburnt conditions have not previously been made, but such a study is presented here.

**Introduction - measurements of seed survival and seedbank.**

A study was done to estimate the size of seedbanks in each species and the way these may change through time. In Chapter 3, basic data on trends in cone production were identified with respect to plant age, size and time since last fire. The data indicated, as did general observations, that cones and hence seeds in all species accumulate through time (or with age), on the branches. The accumulation of seeds and fruits can be termed a seedbank (sensu: Harper 1977), though the origin of this term was generally related to seed storages in the soil. Many studies of soil-stored seeds have described the general species composition (eg. Carroll and Ashton 1965, Major and Pyott 1966, Thompson and Grime 1979). Other studies have documented changes through time in the composition and abundance of soil-stored seeds (Roberts and Dawkins 1967, Roberts and Feast 1973, Cook 1980).

Various models which describe the changes through time in soil seedbanks have been proposed (Cohen 1966, Schaffer and Chilcote 1969 and Roberts 1972). Here, such a model was desired so that nature of the canopy-retained or serotinous seedbanks could be modelled through time and the effects of variations in fire cycles on the potential abundance in post-fire generations, judged.
Models of seedbanks.

Schaffer and Chilcote (1969) proposed that the total buried seed population(s) at any given time could be represented on a percentage basis:

\[ S = P_{\text{ex}} + P_{\text{end}} + D_g + D_n \]  \hspace{1cm} (equation 4.1)

where

- \( P_{\text{ex}} \) = % seeds in a state of exogenous dormancy.
- \( P_{\text{end}} \) = % seeds in a state of endogenous dormancy.
- \( D_g \) = % of seeds undergoing germination \textit{(in situ)}.
- \( D_n \) = % of seeds which have lost viability.

Roberts (1972) expanded this model by arguing that the terms \( D_g \) and \( D_n \) were made up of further terms, such that:

\[ D_g = D_{gd} + D_{ge} \] \hspace{1cm} (4.2)

\[ D_n = D_{ni} + D_{na} + D_{np} \] \hspace{1cm} (4.3)

where

- \( D_{gd} \) = % of seeds germinating deeply and failing to emerge.
- \( D_{ge} \) = % seeds emergent.
- \( D_{ni} \) = % of seeds never viable.
- \( D_{na} \) = % of seeds of seeds made inviable by ageing.
- \( D_{np} \) = % of seeds rendered inviable by predators.
In order to adapt such a model to the characteristics of the species and the canopy-retained or serotinous seedbank the relevance of each term had to be assessed.

Losses due to germination in the serotinous seed-banks \( (D_g) \) were assumed not to occur inside closed follicles. Rather, in an unburnt state, seed losses from cones were casually observed by the presence of a proportion of opened, empty follicles/bracts in the species studied. Losses due to inviability, including predation \( (D_n) \) could be observed in casual inspections of seeds and cones. In related genera within the Proteaceae, Scott (1982) demonstrated in Western Australian Banksia species that insect infestations in conflorescences may inhibit the amount of seeds formed in the subsequent infructescences. In the South-African species Protea barbigera, Myburgh et al. (1974) found that losses of seeds occur during fruit maturation due to insect predation. Myburgh et al. (1974) also found that seed numbers in fruits were low several years after maturation compared to one year after maturation. They concluded these differences were due to progressive predation through time, though other losses, due, for example, to seed shed, were not discussed.

The dormancy status of seeds in the species studied \( (P_{\text{ex}} + P_{\text{end}}, \text{induced or innate}) \) appeared to be low, and authors such as George (1981) have concluded that seeds are ready for germination immediately on extraction from cones in Banksia, and will readily do so if kept saturated.
for a number of weeks. Hence dormancy was thought to be relatively unimportant in the Banksias, but was unknown in Petrophile and Isopogon. Seeds were therefore saturated in water in all species, and the amounts of germination compared to samples subjected to the tetrazolium test (International Seed Testing Association, 1976). The aim of this exercise was to see if the absolute, potential numbers of seeds viable (tetrazolium test) equalled the numbers germinating in water with no scarification or heating. If germination under the two methods was not significantly different it could be argued that dormancy was not effective.

Methods

Tests were done on at least two replicates of 50 seeds per treatment per species. Seeds were extracted mechanically by using a hammer and chisel in the Banksia species, and by allowing Petrophile and Isopogon cones to open after several weeks drying at room temperatures. Seeds from cones of differing ages were tested in Petrophile and Isopogon. The ages of cones were designated "young" and "old" for Petrophile and "young" and "medium" for Isopogon. In the Banksia species seeds from "medium" cones only were tested (these age descriptions are discussed and fully defined in the next section). Seeds were placed for germination on a laboratory bench in distilled water, whilst seeds subjected to the tetrazolium test were placed in a 1% solution of tetrazolium in petri-dishes. The dishes were wrapped in aluminium foil and the seeds were allowed to
soak for 48 hours. After soaking, the seeds were washed in distilled water. The seed coats or achene cases were removed and seeds were scored as viable if no more than 30% of the area of cotyledons distal to the radicle were unstained (necrotic). If necrosis either proximal to or on the radicle was present, the seed was scored as inviable. Seeds was set in water for 10 weeks to germinate, germinations being scored as radicle extension through the seed coat or achene case of > 1 mm. Experiments were commenced in May 1981.

Results and Discussion.

For each cone-age-class in each species there was no significant difference in viable seeds scored between methods (Table 4.1). It was concluded that innate or induced dormancy was not present in any of the study species. Later (see Chapters 6 and 7) it was found that high ambient temperatures induced dormancy in either all or a large proportion of seeds in the species studied. However, under Winter conditions, as existed at the time of this initial test, germination was optimal. Further determinations of viability described below were therefore conducted under cool temperatures conditions in an environmental cabinet.

A Model for serotinous seedbanks.

The above results showed that innate or induced dormancy could be discounted as a factor in any model
describing seedbank numbers through time. Rather seeds in cones were effectively in a state of enforced dormancy (Harper 1957, Mott and Groves 1981), that could be broken by removal from cones and exposure to water. Similarly Siddiqi (1971) reported that no heat stimulus was needed in several Banksia spp. including B. ericifolia and he reached a similar conclusion as to the requirements for germination. Hence the following model (after Roberts (1972)) was proposed to describe at any point of time the overall proportional make-up of the serotinous seedbank(s) expressed as percentages. (See Figure 4.1).

\[ S = P_{\text{enf}} + D_r + D_{\text{ni}} + D_{\text{na}} + D_{\text{np}} \]  

(4.4)

where \( P_{\text{enf}} \) = % of viable seeds held in enforced dormancy in cones.

\( D_r \) = % of seeds released from cones.

\( D_{\text{ni}} \) = % initially non-viable.

\( D_{\text{na}} \) = % lost viability with age

\( D_{\text{np}} \) = % seeds eaten or damaged and inviable.

These quantities were investigated in cones of differing ages so that trends through time could be measured. Time-related trends were therefore based on a chronosequence of cones of differing age since fruit maturation, sampled simultaneously. Trends with time were estimated in the following components:
In each, the null hypothesis was tested that declines did not occur with increasing age. At each cone-age, the respective components were assembled to assess the proportion of viable stored seeds remaining. This was done on a per-cone basis, and assumed that the numbers of follicles/bracts in each cone represented the number of seeds present at the time of completion of fruit maturation. It was assumed that there was one seed per follicle/bract. In both Banksia spp. and Petrophile, this was invariably the case. A modified method was used for estimating cone losses through time in Isopogon, as bract numbers were difficult to count and only a minor proportion of bracts enclosed filled achenes.

The results of this analysis yielded a view of seedbank in a single hypothetical cohort of cones through time since fruit maturation. As was shown in Chapter 3 and illustrated in Figure 4.2, annual inputs of cones occur as a consequence of annual flowering seasons in all species. Effectively the seedbank is composed of a pool of cones, made up of differing generations of cones or precisely, differing age-classes of cones (Figure 4.2). At any time after a fire, these age-classes or cohorts of cones can be

* losses due to cones falling off are present (Figures 4.1, 4.2) but rates measured in the study were very small and hence these losses aren't further considered here.
described in terms of their seed content as:

\[ C_0 + C_1 + C_2 + C_3 + C_4 \ldots C_t \quad (4.5) \]

\[ C_t = \text{the cohort of seeds, formed} \]
\[ \text{in the year "t" after the} \]
\[ \text{onset of post-fire maturity} \]
\[ \text{in the population (year 0).} \]

At any time the total seedbank can be expressed as a function of the remaining viable seeds in each cohort:

\[ S_t = d_t C_0 + d_{t-1} C + \ldots d_1 C_{t-1} \quad (4.6) \]

where \( S_t \) = numbers of seeds at \( t \) years
after the first crop of seeds
produced by the plants
\( C_t \) = numbers of seeds formed in a
cohort \( t \) years after
maturation
\( d_t \) = % of seeds in the cohort remain-
ing after subtraction of
losses through seed release,
inviability and predation.

The values of \( d_t \) are determined by the losses due to \( D_r \), \( D_p \) and \( D_n \) (from above, 4.4) at time \( t \) and the remainder is equal to \( P_{enf} \) (4.4, above); that is the number of viable uneaten seeds held intact in cones. If the numbers of seeds produced in cohorts from year to year are assumed to
be constant then, after a fire in any population:

\[ S_t = t.C_0 \sum_{i=1}^{i=t} d_i \]  \hspace{1cm} (4.7)

On this basis, the components of \( d_i \) (4.7) were estimated so that trends in \( d_{(i)} \) through time could be evaluated and simulations of whole seedbank numbers \( S_t \) through time estimated. Simulations were based on these simplistic assumptions above, as well as situations where variations in \( C_t \) (4.6) were used.

Calculations of \( d_i \) (4.7) were made by assessing each of the components of (4.4) in cones as stated, and for each cone-age in the age series of cones used, a value of \( d_i \) was calculated by multiplying the proportions of samples unaffected by losses through \( D_n' \), \( D_{np} \) and \( D_n \) (4.4):

\[ d_i = (1 - D_r) (1 - D_{np}) (1 - D_n) \] \hspace{1cm} (4.8)

where \( d_i \) = proportion of unreleased seeds per cone \( i \) years after maturation, intact and viable.

Values of \( d_i \) gained from samples of cones at given cone ages were used as estimates of the intact viable seeds remaining in each whole yearly crop of cones and therefore cohort of seeds in the \( i \)th year.
The trend in seed numbers in each cohort of seeds was tested by using the values of \( d_i \) at given ages and fitting the exponential decay model suggested by Roberts (1972) for this purpose:

\[
S = S_0 e^{-gt} \quad \text{(Roberts, 1972)} \tag{4.9}
\]

where

- \( S_0 \) = initial seed numbers
- \( S \) = survivors at time \( t \)
- \( g \) = rate of survival (called germination constant by Roberts, 1972)

Values of \( S \) at differing ages were estimated using values of \( d_i \) for the appropriate sampled cone-ages and were plotted logarithmically (natural logs) against time and a seed-cohort death or decay rate estimated. The function is identical to the model of survival used in Chapter 3 for established plants. Therefore seed cohort half-lives could be estimated. Values of the seed decay rate \( g \) derived from the regression equations (4.9) were used in the calculation of \( S_t \) (4.7).

The simulations produced by (4.6) and (4.7) were evaluated by examining real trends in \( C_t \) in each species as a function of variations in both annual numbers of cones and seeds per cone produced.

Both the numbers of cones produced and the numbers of ripe seeds set per cone are the principal variables
that determine yearly seed cohort size \((c_t)\). In both the simulation exercises performed later in this chapter overall trends in seedbank were modelled as a function of \(c_0\): that is the seed cohort size produced at the time of ripening of the first seed crop produced after fire. In all species this occurs one year after the first flowering (i.e.: cessation of \(1^\circ\) or \(2^\circ\) juvenile period) in populations. The measure of \(c_0\) was a convenient base-line on which to model trends in seedbank and the ultimate exercise in this chapter examines the effects of changes in \(c_t\) relative to \(c_0\) as determined by changes in numbers of cones and seeds per cone produced at differing ages or times after fire.

Seed numbers per cone were contrasted between samples within stands of a given age (or time since fire) as well as between stands of differing ages (times since fire). In this way trends in \(c_t\) with age (or time since fire) could be tested as well as the effects on \(c_t\) of variations within ages or times. Similarly determinations of the components of \(d_1\) were tested for within- and between-stand variations. French (1983), found that significant heterogeneity existed within sites in the amounts of viable and predated seeds in Hakea species. She concluded that these results hindered the degree to which generalizations through time could be made within the chronosequences of stands sampled.

In summary, the following procedures were followed:

(i) Cones from varied stands of plants of differing ages or times since fire were collected. Collections
were replicated within sites. Samples of cones were collected in each stand sampled in differing estimated cone-age classes. The sites and stands sampled were those described in Chapter 3.

(ii) Mean percentages of seeds, in each cone sample, left intact, viable and unreleased and mean losses due to release, inviability and to predation and dessication were estimated.

(iii) Tests were made of the effects of site-ages/times since fire and of spatial variations (within sites) on means of the above components in (ii), within cone-classes.

(iv) The significance of losses of seeds due to each individual component in cones over time since fruit ripening was tested using the sequence of differing cone ages as a time series.

(v) Survivorship was estimated in an idealized seed cohort using equation 4.9. The significance of the model used in equation 4.9 was tested and the decay rate (g) estimated.

(vi) An application of the seed decay rate (g) was made using equations 4.6 and 4.7 where values of $d_i$ were calculated from the survivorship equation (equation 4.9). Seed cohort size ($C_t$) was held constant such that any $C_t$ was assumed to equal $C_0$.

(vii) Real variations in the components determining seed cohort size ($C_t$) were evaluated and trends in $C_t$ were modelled as a function of real estimated $C_0$. 
(viii) The results of (vii) were applied to estimate actual seed numbers at differing ages or times since fire.

The general aims of this exercise were to estimate the trends in numbers of seeds (seedbank) over time (age or time since fire) and to compare these trends between species as a basis for judging the relative responses to varying intervals between fires. The amounts of seeds available at any given time will directly affect the potential levels of recruitment of seedlings in any post-fire generation.

The importance of quantifying potential seedling abundance as a function of available seedbank was emphasized by Sagar and Mortimer (1976) and Cavers (1983). The processes that limit seed abundance may largely shape established plant abundance. Ultimately (see Chapter 9), seedbank sizes proved crucial in determining the comparative responses of the species studied here to differing fire regimes. Whilst the mechanisms that control seedbank size were not studied in detail the relative importance of the varied factors which determine losses of seeds is highlighted.

4.2 Cone Sampling.

Methods

(i) Cone aging.

As stated above, estimation of the seed-decay rate
(g) (4.9) was based on the presence of cones of differing age as determined by their physical appearance in each species. Whilst further division may be possible in each, three classes of cone age were used in the species studied: for convenience these were termed "young" "medium" and "old". "Young" cones were cones of known age set during the study, whilst "medium" cones were chosen to represent cones of about 5 years of age at the time of sampling, and "old" cones in the stands which contained them were selected both by position on the plant and appearance, as those likely to be the oldest in the stand. During the study, the appearance of "young" and "medium" cones tagged for the estimation of seed release was constantly checked in order to confirm the approximate age given for the "medium" samples used in the seed-bank work. The age given above was hence considered a reasonable estimate.

Seedbank samples were drawn in 1983, though batches of cones marked in 1981 were used for seed release and seeds/cone estimations. Generally, in all species, at any given time cones from the two previous flowering seasons could be reliably recognized and this form of aging was used in the study. Ages of "old" cones could not be as reliably determined. In Petrophile and B. ericifolia, these were drawn from the < 1964 and 1968 stands sampled for survivorship (See previous Chapter). Assuming that the oldest cones present were the first cones formed in the 1968 stand and that these were borne circa 1975, the age of these was assumed to be 9 years. In this stand for
both species, these were the lowest cones on the plants, other scars from missing cones in a similar position being infrequent. In the stands older than < 1964, the "old" cones sampled, occupied similar positions on the plants but the number of old cones lying on the ground and frequent scars on the bottom stems and branches indicated that a proportion of the oldest of the cones had fallen from the plants. As the age of the stands is indeterminate but likely to have been 30 + years, a variety of estimates of age for these "old" samples were used in the formulation of seed decay rates for these species.

In *B. serrata*, "old" cones were sampled in stands burnt in 1976 and last burnt before 1964.

In the former, these pre-dated the fire, whilst in the latter these were assumed to be unburnt. Only "old" cones from the 1976 stand without any charring were removed. As the 1976 stand was previously burnt *circa* 1965 by an extensive wildfire it was assumed that the "old" sample must have been set subsequent to that year. An age of 15 years was therefore estimated for this sample and as the cones from the < 1964 stand were of similar appearance, this age was accepted as an estimate for that "old" sample. The age may be an underestimate, but further estimates were not explored in the seedbank calculations as with *B. ericifolia* and *P. pulchella*. For *Isopogon*, cone survival through fires was unlikely hence "old" samples drawn from stands last burnt before 1964 were cones which had originated
after the respective burns. However observations of cones considered "young" or "medium" at the commencement of the project in 1980/81 suggested that an "old" appearance may be acquired between a cone age of 5 - 10 years. Considerations of measured cone disintegration supported this conclusion. Further discussion of cone age in this species is given below.

(ii) Cone collection - all species.

Sampling of cones was done in the same stands used for survivorship and cone-production studies (See Chapter 3). All cones collected were taken from live branches in all species. In Banksia ericifolia and Petrophile, two spatially separate replicates were drawn each from opposing ends of the paired transects. In B. serrata and Isopogon, spatial replicates were taken from samples of plants approximately 50 metres apart. In these species, some plants tagged for survivorship studies were sampled. In Petrophile, additional cones were extracted from a stand not used for the survivorship study. This was the 1973 stand used for B. ericifolia sampling. Samples of Petrophile cones were drawn from groups of plants roughly 50 metres apart.

In all species within each spatial replicate, 10 cones per cone-age class were harvested from a group of 3 or 4 adjacent plants, except in the younger sites where up to 10 plants were required. Cones representing the two older cone-age classes were matched in appearance as
closely as possible. Upon removal, all cones were taken to the laboratory, where in the case of the Banksia species they were heated at 200°C for 10 minutes in a forced-draught oven to facilitate follicle opening. This treatment was shown by Bradstock (1977) not to adversely affect seed viability in B. ericifolia and was reasonably assumed to apply in B. serrata. Petrophile and Isopogon cones were left unheated for one and two weeks respectively before seeds were extracted.

(iii) Seed extraction and sampling.

In all species other than Isopogon, follicle counts (Banksia spp.) or bract counts (Petrophile) were done on arrival in the laboratory with both total and open, empty, fully formed follicles/bracts being recorded for each cone.

Where unopened follicle/bract numbers exceeded 20 in a cone in any sample in these species, a subsample of 20 randomly chosen follicles/bracts on each cone was examined for predation and/or seed condition. Where the seed was absent or visibly damaged in a fully formed follicle/bract, predation was scored. Intact seeds taken from cones of Banksia spp. were examined for malformation or desiccation of the embryo. Intact seeds in any sample from Banksia or Petrophile were then pooled according to their spatial replicate within cone-ages/sites, and additional seeds required for tests of viability were extracted from unsampled follicles and, after inspection for desiccation or malformation, were added to the appropriate pools.
In *Isopogon*, seed counts for each cone were carried out as the cones were mechanically disintegrated (after drying for a fortnight) using forceps. Predation was noted by the presence of drilled passages in a few cones, but the extent of losses of individual seeds could not be fully determined. Hence all seeds with visibly full embryos were counted for each cone and pooled according to replicates as above.

Seed viability was tested in all species in replicates of 50 seeds, each of which was placed on Whatman "42" filter paper circles, in Petri dishes, in an environmental cabinet, running on a 12/12 hour night/day cycle of 5/15°C. Seeds were kept moist and scoring of germinations was done for 8 - 10 weeks. In all species, germination was defined as radicle extension of \( \geq 1 \text{ mm} \) through the seed or achene surface.

Two replicates of seeds were tested for viability within each spatial replicate of cones sampled, per cone-age class.

(iv) **Data analysis.**

(a) *Banksia* spp. and *Petrophile*.

Effects of sites and replicates within cone-age classes for all components of the seedbank model, namely the % of intact, % viable and % unreleased seeds per cone, were tested using a hierarchical analysis of variance (Zar 1974). All data were angular-transformed before analysis and Cochran's testing for homogeneity of
variances was performed before each anova was calculated.

The intact-seed estimate was made up of the sum of losses due to predation and desiccation/malformation. After the analysis of site and replicate effects, regression equations were calculated for each component using the varying known and estimated cone ages of each class to test hypotheses of time effects on trends in each component. Regression took the form of \( \log_n \% \) seed survival (dependent variable) on age (independent variable).

(b) Isopogon.

Seed-release data used for analysis in this species were collected differently. Seed release in Isopogon tended to be on an all-or-nothing phenomenon, in that whole cones disintegrate in the field over a short period. Whilst the number of disintegrated cones in a population could be counted, it was impossible to determine the age of individual remains and thereby derive a rate of disintegration through time. Hence observed seed-release (cone-disintegration) data were used in the seedbank calculations in Isopogon, though similar measurements were made in the other species studied and are dealt with in a later section of this chapter.

Disintegration was measured in samples of tagged cones from February 1981 to March 1983 in the stands used for survivorship studies. A sample of twenty cones per cone-age-class was tagged in each stand giving 2 replicates per site, these being the 1977, 1974 and \(<1964\) sites.
In all sites "young" (1980/81 flowering season) cones and "medium" cones (~ 3 years old) were tagged. In the < 1964 site older cones ("old") were tagged (these being the oldest cones present with an estimated age of about 10 years). The cones were checked after one year and were subsequently harvested (see previous section) in 1983. Where possible, one cone per plant was tagged.

As was noted above, some evidence of insect borers was found in a few of the harvested cones, however an estimation of losses of seeds was not possible. Therefore predation was treated as being absent from the retained seed-bank in this species. Estimates of seed release and viability were prepared for analysis in the same manner as in the other three species.

Results

(a) Banksia ericifolia.

Desiccated or malformed seeds were absent in one-year-old ("young") cones; very few (<1% seeds/cone) in "medium" cones; and numerous (15 - 20%) in "old" cones. Hence, the proportions of the intact seeds (Figure 4.3 (a)) were appreciably lower only in this last cone-age-class. Anovas of intact seeds revealed significant between-site effects (Tables 4.2 - 4.4) in "young" and "old" cones only. A significant between-sites difference was also apparent in the proportion of viable seeds present in "old"
cones (Table 4.4). As a consequence, the 1976 "young" cone values were omitted from further calculation of regressions (Table 4.5).

Ages for "old" cones from the <1964 site, entered into regressions for all components, were 15 to 20 years. Calculations of further separate equations using a 9-year value but omitting the 1968 "old" percentages were justified on the basis of anova results but were not done.

Regressions for all components (Table 4.5) varied in significance, with moderate to high co-efficients of determination. Regressions for both viability equations were non-significant.

(b) Banksia serrata.

Desiccated or malformed seeds were absent in "young" cones, but were present in variable quantities both between replicates and sites in "medium" and "old" cones (0 - 30%). Anovas of intact seeds (Figure 4.3 (b)), (Tables 4.6 - 4.8) in these older cone classes proved to be non-significant, as between-cone variations within samples were great, due to heterogeneous predation and desiccation of seeds. Formal analyses of the components in "young" cones were not considered necessary, due to the small between-replicate and site variations present (Figure 4.3 (b)). Similarly no analysis of % unreleased seeds in "medium" cones was performed. The heterogeneity
between sites and replicates in viable unreleased seeds in "old" cones was significant (Table 4.7) and, as a consequence, regressions of both viable and unreleased seed components (Table 4.8) were calculated using the highest and lowest values for each from the "old" cone class. These gave a range of regressions between which others calculated with alternative values, would fall. Regressions of viability were significant but equations for intact and unreleased seeds were non-significant, though in all cases r² values were high (Table 4.8).

(c) Petrophile pulchella.

Due to the woody nature of the achene in Petrophile, the condition of the embryo could not be judged without dissection, hence desiccated or malformed seeds were not scored and the proportions of intact seeds (Figure 4.4 (a)) were estimated from the visible evidence of predation. Previous examination of Petrophile seeds by dissection had revealed large proportions with malformed or aborted embryos and these were reflected in the viability estimates (Figure 4.4 (a)). Viability proved to be variable between replicates in most sites, though differences were non-significant (Tables 4.9 - 4.11). The mean percentages of intact seeds also were variable (Tables 4.9 - 4.11) with inter-site differences being significant in all cone classes and inter-replicate differences being significant amongst "medium" cones. Analyses of unreleased seeds were not performed for "young" and "medium" classes as site and replicate differences were minimal (Figure 4.4 (a)).
Regressions were calculated using alternate values of 9, 15 and 20 years as the age of the <1964 samples (Table 4.12). For intact seeds, due to the heterogeneity of variance amongst "medium" samples, separate regressions were calculated using the samples with the highest and lowest means respectively (Table 4.12). One equation is presented for viable seeds to demonstrate the viability was effectively constant with cone age (Table 4.12). For intact seeds, 9 and 15-year equations only were significant, whilst for the unreleased seeds, all equations were non-significant (Table 4.12). Hence significant age effects were dependent on estimated "old" sample ages in opposing trends in differing components.

(d) *Isopogon anemonifolius.*

Viability varied little between samples and cone-ages (Figure 4.4 (b)) and as a result a formal analysis was not performed. Cone disintegrations were concentrated in the second year of observations, possibly due to the severe drought conditions. Whilst it appeared that the rate of disintegration was higher in "old" cones an average, annual cone-disintegration (seed-release) rate was calculated by pooling all data and dividing by two. The value was 3.07% per annum.
Discussion

The measurements of seed losses due to the various factors showed no consistent influence of age or time since fire across cone-classes or species, though heterogeneity between and/or within sites was present in all species. This heterogeneity had the effect of altering the age-based regressions in Petrophile and B. serrata. As definite trends in site/age effects in "young" or "medium" cones were not detected, possible biases due to these sources, when data were applied to the seedbank model would be minimized. In all cases, calculation of alternative regressions using significantly different between-or within-site values provided a range in age trends for each component. The only exception was the exclusion of the 1976 site data for intact seeds in "young" B. ericifolia cones. This result may support an hypothesis for lower levels of seed predation in young versus older populations in this species.

Non-significant age trends (and very low $r^2$ value) in Petrophile viability indicated that losses may be concentrated soon after seed formation or may be random in time.

Whilst equations were mixed in significance between and within components, in most cases the majority of variance was accounted for (high $r^2$ values). Hence it was concluded that whilst the null hypotheses of trends in components could not be rejected the trends were strongly developed
where high $r^2$ values were present. Therefore simulations of seedbank accumulation in time were made and variations due to differing site/cone-age effects were incorporated.

The aim was to generate a range of estimates for each species covering the alternatives thrown up by the analyses.

In all species, measurements of predation were assumed to have estimated losses incurred after fruit maturation: that is after follicles and seeds were fully formed. However it is possible that some scored losses may have occurred during the maturation period. No attempt was made to calculate these losses during this period, which lasts for about 1 year in the Banksia species and Petrophile and about 6 - 9 months in Isopogon. Similarly influences of predation at the flowering stage on seed set as shown by Scott (1982) were not studied. Possible influences at this stage are identified in following sections and the actions of insect predators in relation to time since fire may be significant. Auld (1983) studied the importance of insect seed predators in leguminous species in south-eastern Australia species. Auld's (1983) conclusion, that changes in predator abundance may have vital effects on seed formation and seed survival is relevant to the study species here also, particularly with regard to time since fire. Further study of insect abundances and their controls as Auld (1983) suggests are needed. Relative judgements about seed release in unburnt conditions derived from the data presented here contrast with the conclusions presented by George (1981) for the 2 Banksia species. Amounts of seeds released are
strongly dependent on cone-age, as recognised by Gill (1976), and any conclusions based on individual percentage figures for a species may be misleading without reference to the sampled cone-age, or overall rates of seed-release as cones age.

In both Banksia species measurements in "medium" and "old" cones greatly exceeded the 3% empty follicles measured by Gill (1976) in "old" (age unstated) B. ornata cones. The mechanism of follicle opening in B. serrata and B. ericifolia may vary from that proposed by Gill (1976). This is discussed in the next chapter.

4.3 Calculation of seed decay rate (g) and simulations of seedbank accumulation ($S_t$)

**Introduction and Methods.**

The proportion of seeds of a cohort left intact ($d_i$) at any time (i) after maturation was defined above as being the product of the proportions uneaten, remaining viable and unreleased.$(equation (4.8)). The model for seed survival (equation (4.9)) was applied using the regressions of calculated values of $d_i$ for differing cone ages. From these regressions estimates of $g$ (seed survival rate in cones) could be made for each species and the half-lives of cohorts of retained seeds calculated. These survival regressions were used to simulate overall seedbank accumulation ($S_t$) through time.
(i) The "survival" of seeds in cohorts.

Here as implied in equation (4.8) "survival" is defined as retained viable seeds. Homogeneous replicate and site data were used to derive values of $d_i$ at each cone-age in the respective species. Regressions of the logarithm ($\log_n$) of percentages of survivors ($S_t$) at the differing cone ages, on estimates of age in years were calculated. Regressions were calculated within species for separate sets of $d_i$ calculated from heterogeneous site/age data. A data pair of $\log_n 100\%$ at age zero was included in all these calculations. It was assumed that seed ripening was complete at time zero (one year after flowering) and that the initial numbers of seeds were those available and intact irrespective of any pre-ripening losses. The assumption of 100% survival in both Banksia species was that aborted seeds were absent though in most cases a few were present. As well, no seed release or predation of ripe seeds was assumed at time zero. This assumption was followed by an adjustment in Petrophile where only a minor % of achenes were found to contain viable, fully formed embryos. Morrison (pers. comm.) found that viability was maximal one year after the completion of cone-set, hence the mean viability scored from "young" cones was regarded as the maximum value likely. Values from other cone-ages were rescaled as a % of "young" cone viability. Generally "young" cone viability in Petrophile was around 30% of bract numbers (potential achene no.) in cones. Whilst no trend in unscaled viability with age was found in Petrophile, individual means declined slightly
with increasing cone-age (Figure 4.3) and were included in the seed-survival calculations, rather than a pooled general mean.

In *Isopogon*, a modified approach was used. As viability was found to be effectively constant, regardless of age (no decline in old cones) calculations were made of the proportion of retained viable seed \(d_i\) from the product of the proportion viable \((1-D_n)\) constant, \(v\) and the proportion unreleased \((1 - D_r)\) in each successive year after fruit formation, for 25 years, using 2 regimes of seed release. The formula used to calculate \(d_i\) in any year \(n\) after maturity of fruits was:

\[
d_i = v^n \cdot (1 - D_r)^n
\]  
(4.10)

(definitions given in text above).

(ii) Seedbank simulations.

The seedling "survivorship" equations for cohorts were applied to simulate seedbank accumulation. At any given time after the onset of maturity (either after a primary or secondary juvenile period, sensu Gill (1975)) in a population of the species studied, individual cohorts of seeds set in differing years will co-exist. The numbers of seeds in each cohort will be determined by the time since seed set and at any given time the overall seedbank \(S_t\) will be equal to the sum of surviving seeds in each cohort present (equations 4.6 and 4.7). This general method was used to simulate patterns of seedbank accumulation \(S_t\) in
each species. Three separate simulation exercises were performed.

Firstly seedbank \((S_t)\) was modelled using a fixed seed cohort size; that is the seed cohort size \(C_t\) did not vary from the initial value \(C_o\). The results are presented as seedbank in units of \(C_o\). The second exercise simulated an increase in \(C_t\) through time at a fixed linear rate from the onset of maturity, with increments equivalent to 0.1 units of \(C_o\) per annum being added to the original \(C_o\) (ie: year 0 = 1.0\(C_o\), year 1 = 1.1\(C_o\), year 2 = 1.2\(C_o\), etc.). This calculation was done in each species, using the survival regression equation which yielded the lowest rate of seedbank increase in the initial simulation.

The third exercise was also done using this survival regression and simulated the effects of fluctuating cohort size. Again the fluctuations and resultant \(C_t\) values were scaled against \(C_o\). In this case the cohort size \(C_t\) fluctuated around a mean value of one unit of \(C_o\) in a regular cycle of plus or minus 0.5 units of \(C_o\) per annum. (ie: year 0 = 1.0\(C_o\), year 1 = 0.5\(C_o\), year 2 = 1.0\(C_o\), year 3 = 1.5\(C_o\), year 4 = 1.0\(C_o\), etc.). This was done to approximate likely yearly fluctuations in real stands. One component determining \(C_t\), mean cone numbers set per annum, was found to either remain steady or rise with "age" across the chrono-sequences of stands of species in Chapter 3. The second of the above simulations approximated the rising influence of numbers of cones set in \(C_t\), through time.
Results

Values of $d_i$ for all species other than *Isopogon* used for calculation of seed survival regressions are given in Figure 4.5. In *Isopogon* regressions were calculated using a constant annual depletion rate of 1.0% for inviability and for a constant rate of seed-release (cone disintegration) of 30% per annum. An additional model of survival was calculated using an increased rate of seed-release after 10 years. In this case the rate of seed-release was doubled in a stepwise manner at 10 years (cohort age). This simulated the observed trend at or above this seed cohort age (Figure 4.4). Regressions for seed survival in all species gave high $r^2$ values (Table 4.13). In both *Banksia* species, intercept values (time zero) and values at 1 and 2 years from the regressions were equal to untransformed values of greater than 100%. Half-lives of seeds varied substantially between equations in *Petrophile*, however values (Table 4.13) for both *Banksia* species fell substantially below the range for *Petrophile* and *Isopogon*. This reflected the substantially higher rates of seed-cohort decay in the *Banksia* species (Table 4.13).

(ii) Seedbank accumulation ($S_t$).

Due to presence of untransformed cohort regression values greater than 100% (Table 4.13) at 0, 1 and 2 years in the *Banksia* species, calculation of amounts of seedbank ($S_t$) at these times in cohorts was not done. Rather values of 100% were substituted. Estimates of
survival were included where necessary at cohort ages which yielded values less than 100%, when substituted into the equations.

For a constant cohort size the seedbanks \( S_t \) in each species tended to level off at or toward a plateau value of \( C_0 \) that varied according to species (Figures 4.6 - 4.9). The most striking features were the earlier times that constancy in seedbankswas achieved in the Banksia spp. and the greater output, in terms of units of \( C_0 \) in Petrophile and Isopogon (Figures 4.6 - 4.9).

The effect of increasing cohort size was to push the seedbank plateau back in time so that over the time modelled (up to 30 years after the commencement of flowering) each species effectively showed a sustained linear rate of increase in seedbank (Figures 4.10 - 4.13). Outputs in units of \( C_0 \) were greatly enhanced over the previous simulation.

The effect of fluctuating cohort size compared to constant size was a slight overall increase in seedbank size in all species (Figures 4.14 - 4.17) but the shape of the curves were similar. The calculated times to levelling off in the Banksia spp. was unchanged (Figures 4.14 and 4.15).
Discussion

Higher rates of predation and losses due to inviability were found in seed cohorts of the Banksia species compared with Petrophile and Isopogon. These caused high seed cohort decay rates \((g)\) and shorter seed half-lives in the Banksia species. These results were reflected in the simulations of seedbank accumulation \((S_t)\), especially where cohort size was constant. It could be argued from that exercise (constant cohort size simulation) that a decline in cohort size after 10 - 15 years would cause an overall decline in seedbanks in the Banksia spp. and bring about an earlier levelling off in seedbanks of Isopogon and Petrophile.

The overall effect of a constant cohort size in relation to varying intervals between fires was that potential abundance (available seeds for germination) in any successive post-fire generation was most strongly influenced in the Banksia spp. If a primary juvenile period of five years is assumed in B. ericifolia then a constant seedbank size in either species was achieved 10 - 15 years after burning. As the secondary juvenile period in B. serrata was shorter (\(\sim 2\) years) then the plateau would be reached in this species at a correspondingly earlier time. Potential abundance following fires after this would be unaffected by the timing of fire. With increasing cohort size, potential abundance rose with time to the next fire in all species.

Effects of fluctuating cohort (around a constant overall mean) size were minimal in that patterns of seedbank accumu-
lation ($S_t$) and potential abundance in relation to the timing of fire were unaltered over the steady cohort-size simulation.

The differing equations compared within species in the constant cohort simulation had varied effects between species. In both Banksia species, effects on the maximum amount of seedbank accumulated were relatively small as were the effects on times to achieve constant seedbanks. In Petrophile, contrasts in the sizes of seedbanks were more marked between the estimates given for the varied equations, as were the effects on the shape of overall patterns of accumulation. The major effect, however, was on the sizes of seedbanks, and hence potential abundance, rather than patterns of seedbank accumulation over the time-span simulated, though in Petrophile over a larger time-span, contrasts between equations in the times taken to achieve seedbank constancy may be significant (Figure 4.8).

Based on these simulations, it was decided that reasonably realistic calculations of numbers of seeds in seedbanks ($S_t$) could be made. It was necessary, though, to examine first, real fluctuations in seed cohort size ($C_t$) and possible effects on it of factors such as stand age or time since fire. These results would allow realistic modelling of cohort sizes through time to be carried out. Data from the stands studied and described in Chapter 3 were used for this purpose.
4.4 Variations in seed cohort size ($C_t$) and the calculation of numbers of seeds in seedbanks ($S_t$).

Introduction

The size of cohorts of seeds produced in a stand in any year will be affected by:

(a) the number of cones produced per mature plant.
(b) the number of seeds produced per cone.
(c) the number of mature plants per stand.

Variations in each of these quantities were examined in relation to differing sites/ages and between differing flowering years. In each species, long-term seed cohort size was modelled quantitatively on the basis of these measurements, and estimates of actual seedbank accumulation ($S_t$) were compared. In this way the relative abundances of seeds in each species could be realistically compared at differing times since fire.

(i) Variations in seed and cone outputs.

Methods

To test the hypothesis that seed numbers per cone were unaffected by differing flowering seasons, cones were collected from spatially separate localities within some of the sites described in Chapter 3, in 1982 and 1983. Cones from at least two flowering seasons within each species were removed. The dates of the flowering seasons are given in
Figures 4.18 - 4.21. Ten cones per sample were removed and the details of the position and numbers of samples were identical to those described in the seed survival section. In some cases, data from cones used for seed survivorship studies were utilized. Total bract/follicle numbers in Petrophile and Banksia spp. were scored, as were total seeds per cone in Isopogon upon cone disintegration. Tests for (within-species) within-site, between-replicate differences in mean seeds per cone were carried out initially, and where no significant differences were found replicates were pooled and a two-factor analysis of variance was performed to test for differences in mean seeds between flowering seasons and sites/ages.

Data for yearly cone production in the sample stands described in Chapter 3 are also presented, on a raw and comparative basis (cones/mature plant).

Results

In all species (Table 4.14), between-replicate differences in mean cone set (Figures 4.18 - 4.21) were non-significant. Hence, pooling of replicates and analysis of variance were done in all species (Table 4.15 (a) - (d)). Trends differed widely between species, in that no significant differences between ages/sites or flowering seasons were present in B. serrata (Table 4.15 (b)); in B. ericifolia (Table 4.15 (a)) seasons were significant but ages/sites were non-significant and in Petrophile and
Isopogon significant interactions were found between the variables (Tables 4.15 (c) & (d)). Numbers of seeds per cone expanded with age in Petrophile and declined in Isopogon in an individual season (Figures 4.20 & 4.21).

Both raw and comparative measures of cone production in all species showed substantial fluctuations between differing years. Within-species trends were apparent with a season of high productivity occurring across most sites in 1982 in B. ericifolia; 81/82 in Petrophile (older sites only); 82/83 in B. serrata; and 82/83 in Isopogon (Figures 4.22-4.25).

In B. serrata and Isopogon trends in cone outputs per mature plant (Figures 4.23 and 4.25) were tested between times since fire and flowering seasons. Results of analysis of variance indicated no significant effects of either flowering seasons or times since fire in B. serrata (Table 4.16). In Isopogon (Table 4.17) a significant effect of time since fire was found. The mean value for the 1977 sites was significantly higher than for all other sites (no differences occurred between these).

Discussion

Differences in seed outputs between sites (ages or times since fire) and flowering years in all species other than B. serrata may be due to a variety of causes, some of which may be correlated with site characteristics such
as age and sizes of plants. Other direct effects such as through rainfall or other climatic variables have been identified by Morrison (pers. comm.) in Petrophile and Acacia suaveolens and may have been in operation here. As no detailed attempt was made to study these factors their influence will not be further discussed in detail. One possible influence however may be insect predation which may vary annually or in interaction with sites. Such fluctuations in insect predation may affect the numbers of seeds set.

Similar effects may be responsible for variations in numbers of cones produced in differing years and sites. Overall trends in cone production in both B. ericifolia and Petrophile were not statistically compared between years or sites because of problems with lack of replication. However trends in the overall sample or stand averages in both species indicated few differences between sites up to and including the 1968 site data. However the 1964 average data in both species were substantially larger than at lesser ages. (Figures 4.22 and 4.23). In both species in stands where cone-set occurred for the first time, numbers of cones produced (Figures 4.22 and 4.23) were few. Mean annual cone production per sample in both species was accepted as rising with age though the rate of rise was not progressive or linear. In the previous chapter it was shown that the numbers of mature plants in the samples increased in Petrophile to a larger degree than in B. ericifolia particularly in the 1968 sites. Therefore the species were producing cones in differing ways within samples
with either static or expanding pools of mature plants providing cones. It was concluded that modelling of seedbank should be carried out on a simple total stand basis (cones produced per stand).

A principal drawback with the method of using a range of chronosequences of stands to model a dynamic process was that flowering and fruiting processes in either species in the type of even-aged stands studied may be strongly influenced by density and in turn by consequent pathways of stand dynamics, in interaction with site-specific factors. The patterns of stand cone production discussed above were therefore explored as wide variations in the seedbank calculations. That is, alternative calculations based on a relatively small rise in cone-production in the initial ten years following the onset of species maturity and a larger rise to the levels found in the oldest stands were done.

In *B. serrata* and *Isopogon*, the numbers of cones produced per mature plant (Figures 4.24 and 4.25, Tables 4.16 and 4.17) were differentially affected by flowering years and times since fire. Overall average trends were accepted as being constant with time since fire in *B. serrata*, though a trend existed for higher values in the 1974 sample. In *Isopogon*, cone production was consistently higher in the 1976 sample (per mature plant) and it was accepted that a rise and decline may occur with increasing time since fire. These conclusions were adopted for the calculation of seedbank sizes. As discussed in the previous chapter, comparisons of
cone-output were best done on a per-mature-plant basis so that stands of widely differing size structure could be meaningfully contrasted.

Trends in numbers of seeds (per cone) and cones in differing years were related in some cases. Variations in seed numbers per cone in *Isopogon* B. ericifolia and Petrophile were positively correlated with seasons of greatest cone output (Figures 4.18, 4.20 - 4.23, 4.25). Highest mean seeds per cone were produced in years of highest cone production. This phenomenon if consistently repeated would have the effect of widening fluctuations in overall seed cohort size. The annual fluctuations in cone-production (both per mature plant or stand) were substantial (Figures 4.22 - 4.25) and in most cases exceeded the simulated fluctuation of ± 0.5 units of $C_0$ carried out in the previous section. This result plus the above correlated fluctuations in seed set indicated that overall fluctuations in annual seed-cohort-size may substantially exceed the simulated level.

In summary, this analysis of trends in the components of seed cohort size showed that:

(i) In *B. ericifolia* annual fluctuations may be large but that outputs of seeds per cone may rise with age. The principal variable causing changes in mean annual seed cohort size was the output of cones per stand with differing ages. Seeds per cone fluctuated yearly, however, as space and age
effects on this variable were absent, mean long-term trends were considered to be absent with respect to age.

(ii) In *Petrophile*, a similar conclusion was reached, though seeds per cone may rise in older stands in some years. This reinforced the trend for a rise in seed cohort size with age.

(iii) In *B. serrata* seeds per cone were fixed in time and space. Cone output per mature plant fluctuated yearly, however trends in both yearly fluctuations and effects of sites (times since fire were non-significant). Therefore a constant output with increasing time was assumed.

(iv) In *Isopogon*, cone-production (per mature plant) peaked at around 5 - 6 years post-fire and declined in older stands to a level equivalent to that occurring immediately after fire (1980 stands, Figure 4.25). The number of seeds per cone declined in old stands to levels around 50% of that found in young stands (age = time since fire). Seasonal fluctuations in seeds/cone occurred in a manner that accentuated this decline.

(v) Numbers of plants per stand in *Banksia serrata* and *Isopogon* both actively mature during the whole study (Chapter 3, Figures 3.15 and 3.23 and Figures 4.24 and 4.25) were not directly related to age due to size structure differences in the samples.
However, amongst the stands in *Isopogon*, there appeared to be little change in the average number of plants setting cones in any year with respect to time since fire (see Figure 4.25; numbers calculated by: Total cones produced – cones produced/mature plant).

The conclusions were used to calculate amounts of seedbank ($S_t$) at differing ages or times ($t$) since fire. In these calculations yearly fluctuations in cone numbers and seeds/cone were largely ignored and models of seed cohort size ($C_t$) were constructed using the trends in average data summarized above. The prior simulations showed that in a simplified situation regular fluctuations had little effect on seedbank size. Whilst the fluctuations were of greater amplitude than those simulated, the frequency and pattern of variations through time could not be fully understood from the results of this study. The outcome of the early simulation was therefore used as a justification for not attempting to incorporate yearly fluctuations into these calculations.

(ii) **Calculations of numbers of seeds in species seedbanks ($S_t$).**

**Introduction and Methods.**

The general trends in seed cohort sizes are summarized above. These were used to estimate the patterns in numbers of viable seeds accumulated through time in hypothetical stands equivalent to those described in Chapter 3 (ie: $\sim$ 50 plants per stand). The methods of calculating
these seedbank sizes were identical to those used earlier in this chapter. That is, calculations were based on estimating the sum of remaining seeds in individual cohorts present at any time after the onset of maturity in each species, using equations 4.6 and 4.7.

Trends in seed cohort size ($C_t$) used, are defined in Tables 4.18 - 4.21. In Petrophile and B. ericifolia, expansions in $C_t$ with age were due principally to increases in stand cone-outputs (Tables 4.18, 4.20). In the calculations of B. ericifolia seedbank, numbers of seeds/cone (Table 4.18) were set at a constant, defined by averages of all stand data for 1981-1983. In Petrophile values for <1964 cones from the 1981/82 season were not used to calculate this average.

In B. serrata and Isopogon, values of $C_t$ (Tables 4.19 and 4.21) changed according to variations in differing components. In B. serrata, seeds/cone and cone production per mature plant were held constant at values equal to the overall annual stand averages (Table 4.19). A rise in $C_t$ with increasing time since fire was modelled due to an expansion in the number of mature plants in the hypothetical stand employed in this exercise. This was done to represent the situation in unburnt stands where growth in individuals will progressively result in an ever-increasing proportion of plants reaching a reproductively active size.

In Isopogon variations in $C_t$ were modelled from changes in seeds/cone and cones per mature plant (Table 4.21).
The numbers of mature plants were held constant with respect to time since fire. A decline in numbers of seeds/cone was used in the calculation (Table 4.21) and a rise and fall in cone output (per mature plant) were used (Table 4.21).

In all species calculations of seed numbers \( S_t \) were carried out for a post-maturity period of 25 years, with the first cohort \( C_0 \) being produced at time zero. Tables 4.18 - 4.21 document the changes in the components of cohort size used over this period and the actual numbers of seeds/cohort \( C_t \) used in the calculations. Changes in overall cohort size \( C_t \) as used for the calculations are given for this period and are expressed in units of \( C_0 \) (Figures 4.26 - 4.29). Initial cohort sizes \( C_0 \) are noted in Tables 4.18 - 4.21. In all species equations of seed survival which gave highest and lowest estimates of \( S_t \) were used. In B. ericifolia and Petrophile, alternative estimates of growth in \( C_t \) were also calculated (Tables 4.18 and 4.20, Figures 4.26 and 4.28) using differing estimates of annual cone outputs per stand. As discussed in the previous section, annual cone production rose little in stands up to and inclusive of the 1968 samples. However \(<1964 \) samples produced many more cones. Therefore, in each species, trends in \( S_t \) were calculated over 10 years (post maturity) (Tables 4.18 and 4.20) (Figures 4.26 and 4.28) that were representative of cone outputs in the samples over this age span. As well, changes in \( C_t \) which progressively reached the levels of cone-output found in \(<1964 \) stands were also calculated (Tables 4.18 and 4.20). In both species these produced
estimates of $C_t$ (based on cone-production) that outstripped those observed in younger stands. As given above, in all cases, numbers of seeds per cone were held constant, though in Petrophile average seeds numbers per cone were divided by 3. This was done so that seeds per cone estimates matched the real numbers of viable achenes found in most samples (see previous sections).

After calculations of trends in $S_t$ (expressed as units of $C_0$) were complete, seed numbers were calculated by multiplying the actual estimates given of seeds per initial cohort ($C_0$) (Tables 4.18 - 4.21) at the appropriate times since fire or ages.

**Results and Discussion**

In all species except Isopogon, actual numbers of seeds (Figures 4.30 - 4.32) increased with age or time since fire. In Isopogon the alternative seed "survival" equation incorporating a doubled rate of seed release after 10 years (Figure 4.33) caused a drop in $S_t$ (expressed as $C_0$ and as estimated seeds) at later times since fire.

Overall amounts of seeds were greatest in Isopogon, followed in decreasing order by Petrophile or B. ericifolia depending on the estimate (Figures 4.30, 4.32 and 4.33). Banksia serrata seed numbers were the lowest especially at later times, though they were roughly equivalent to Petrophile abundance in the lowest estimate at 5 years after stand
maturation (Figures 4.31 and 4.32).

In all species regardless of estimate it can be seen that potential stand replacement levels of seeds (∼ 50 seeds) are reached very soon after maturation (Figures 4.30 - 4.33). Real levels of stand replacement however must take into account potential losses during emergence and establishment and hence larger amounts of seeds are needed. This topic is explored further in the last chapter, however it can be concluded that levels of seeds several times the abundance of established plants in stands were, quickly achieved in all species (Figures 4.30 - 4.33).

Over the periods modelled, seedbank sizes in B. ericifolia, B. serrata and Petrophile continued to increase with increasing time. In Isopogon apart from the discussed fall in numbers, seed numbers tended to level off to a greater degree in the alternative calculation than in other species. In all species it can be concluded that seed numbers and hence potential abundance in succeeding generations rises with age or time since fire.

The trends in seed cohort sizes which form the basis for these estimates are assumed to represent the processes that have occurred in the sample stands. Their generality within and between species is unknown. Changes in trends may occur if any component of Cₜ varies widely in species. The prolific seed production estimated in
**Isopogon** may be an overestimate if realistic considerations of seed predation are introduced into the model for that species. In both **Isopogon** and *B. serrata* potential increases in $C_t$ through the growth and maturation of post fire recruits may continue well past the period considered here. Expansions or maintenance of seedbanks ($S_t$) will occur accordingly, though thinning through mortality may balance or temper such trends.

In *B. ericifolia* and *Petrophile* at greater ages than presented here, gross changes in reproductive behaviour and stand structure may be possible due to senescence. In both species declines in seed storages may be possible due to deaths by senescence of old dominants causing both losses in stored seeds and decreases in yearly cohort sizes. Whether this occurs in a gradual manner or en-masse could not be determined due to the lack of available intact senescing stands. Observations on scattered old senescing plants suggested that reproductive activity may be maintained at high levels right to the time of death. Further measurements in older stands of all species may be needed to reliably extrapolate the trends in seedbank size to greater ages or times since fire.

In summary, this study showed that seedbank size is determined by a number of differing factors (Figure 4.1) each of which exhibited differing trends within species. The species with highest potential storages, **Isopogon**, was not the species with the highest seed "survival" (as
judged by retained seed half-life). Whilst various assumptions have been made in order to simplify calculations the estimates contained in Figures 4.30 - 4.32 are presented as reasonable approximations of trends in stands of around 50 plants similar to the study stands.
CHAPTER FIVE : STUDIES OF THE RELEASE OF SEEDS

5.1 General Introduction.

This chapter deals with the transfers of seeds from their woody storages to the soil surface. The role of fire is examined to view the effect of:

(i) its presence or absence on the numbers and rates of seeds released from cones,
(ii) variations in its intensity on the numbers and rates of seeds released.

Some discussions of serotinous seedbanks have concluded that they may contribute to the exploitation of burnt conditions by allowing seeds to be released en-masse (e.g. Naveh 1973, 1975).

Such seed-falls after various fires have been documented in species by Specht et al. (1958), Cremer (1965), Christensen (1971), Vogl (1967), Kruger (1977) and Kilgore (1981) amongst others.

Variations in serotiny have been discussed in the previous chapter in terms of the components which determine the amounts of seeds stored in cones through time. Factors such as predation and seed viability in relation to cone age were shown to be important along with amount seeds retained in cones.
Seed-release, especially as triggered by fire, as a characteristic of cone serotiny, needs to be viewed from the perspective of differing cone ages, site effects and age (or time since fire effects), as was done in the previous chapter, so that meaningful conclusions as to the role of fire in seed-release and comparisons within and between species can be made. George (1981) attempted to generalize about the dependence of follicle-opening and seed shed, on fire, in differing Banksia species. Presumably the basis for his conclusions was the relative amounts of open-empty follicles observed in cones of differing species. As was shown in the previous chapter, the proportions of open-empty follicles may vary according to cone-ages and perhaps in some circumstances, sites. As George (1981) did not specify the ages of cones from which his measures may have been taken, little can be concluded from his comparison. Such considerations must be made when measuring seed release under all circumstances.

Gill (1981 a,c) has reviewed both the mechanisms and the significance of the storage of seeds in woody fruits. Gill (1981 a,c) drew the distinction between species such as Banksia ornata which appears to be almost totally dependent on fire to initiate seed release and species of Eucalyptus and Hakea which release greater proportions of seeds in unburnt conditions and which may differ in the mechanism of release.
In Banksia ornata, Gill (1976) studied the mechanisms controlling the opening of follicles and concluded that it is related to both the strength of wood and moisture content in the follicles. High temperatures cause the wood in the follicle abscission zone to weaken and also lower the moisture content, causing follicle opening (Gill 1976). Bradstock and Myerscough (1981) argued that such a mechanism may apply in B. ericifolia cones. As noted in the previous chapter, Gill's (1976, 1981a) estimates of opened, empty follicles in B. ornata populations (∼ 2%) are much lower than those measured here, especially in older cones of B. ericifolia and B. serrata. Gill (1976) stated that moisture contents in old B. ornata follicles declined to a level of 10% from 90% found in young follicles. Differences between B. ornata and the species studied here in the amount of unburnt seed release may have been due to differences in follicle moisture. This point and the dependence of heat applied through direct contact with flames or through indirect means were studied, along with direct observations of seed release in unburnt stands.

Investigation of the significance and role of serotiny within and between species must not only address questions on the amounts and proportions of seeds held in cones but also on the rates of seed release under both burnt and unburnt conditions. In turn these quantities may influence the numbers of seeds available through time for germination and ultimately the abundance and structure of the population.
Alternative regressions of seed release against cone age (derived using a series of observations from differing cone-ages) from the previous chapter (Table 5.1) indicate that little difference was found between the rates (slopes) of seed release in *B. ericifolia*, *Petrophile* and *Isopogon* in unburnt stands. Alternative rates were somewhat higher in *B. serrata* indicating that the degree of serotiny, in terms of the ability to retain seeds for long periods after cone-set, is least well developed in this species. However comparisons of amounts of seed release (% open empty follicles, Figures 4.3 and 4.4) in "young" and "medium" cones in all species shows that *B. serrata* seed losses are equivalent or even less than those in the other species. The calculated rates of seed release were therefore strongly influenced by trends in "old" cones and of the age estimate of these in *B. serrata*. This example illustrates that single measures at one cone age are inadequate to determine levels of serotiny.

Studies of observed rates of seed release under both burnt and unburnt conditions were therefore initiated so that seed availability at the soil surface could be estimated. In a previous study of *B. ericifolia*, massive seed release from cones was shown to be triggered by burning, and, in turn, the rate of seed-release was affected by variations in recorded fire temperature (Bradstock and Myerscough, 1981). It was hypothesized that the timing of seed release, as dictated by heating levels (fire intensity), in relation to rain, may be of importance in deter-
mining the proportions of seeds which emerge. Whilst emergence and its controls are discussed in a later chapter, rates of seed-release were studied here in differing cone-ages under differing heat treatments.

Further measures of seed release in unburnt stands, as a function of cone-age, were carried out to check and complement the essentially static measurements used to derive the rates given in Table 5.1. From this exercise, the amounts of viable seeds released in the stands described in Chapters 3 and 4 were calculated. These calculations provided estimates of changes in seeds available through time for inter-fire emergence and establishment of seedlings. These were needed to evaluate the possible contributions of recruitment in unburnt conditions.

In summary, two lines of enquiry are presented below. Firstly, hypotheses regarding the effects of burning and/or heating cones on seed-release are tested and presented. Secondly, direct observations of seed-release in unburnt conditions are presented and discussed in relation to measures given previously (Chapter 4), and are used to calculate likely availability of seed in stands of differing age in unburnt conditions. As well, an analysis of cone/follicle moisture contents is presented.
5.2 Aims and methods — burnt and unburnt seed-release.

(i) Effects of fire on seed release.

This study was carried out in two strands. Initially a series of observations after a burn in May 1982 were commenced in order to monitor the effect of extremes in fire-severity, cone position and differing sites.

Observations were made in two separate sites which were as similar as possible. Considerations of cone-age were made in B. ericifolia and Petrophile, by sampling cones at two differing heights on bushes. In B. ericifolia old cones tended to be found low down on bushes (Bradstock and Myerscough, 1981) whilst the bulk of young cones were located in shrub-crowns in both species. Such a differentiation was not possible in B. serrata or Isopogon.

Sampling was done to contrast extremes of fire-severity, observations being made on bushes with minimal scorching to less than a metre above-ground and on bushes where all leaves were consumed and all remaining parts were heavily charred. Independent samples at both extremes were available in B. serrata, B. ericifolia and Petrophile, however in B. serrata numbers of available cones were biased toward the high-severity level. Low-severity samples in Isopogon were unavailable.

The design of these observations confounded effects
of cone-age and fire severity, in that within each fire-severity level heating appeared to have been greatest close to the ground (see also discussions in Chapter 2). It was concluded that definitive conclusions on post-fire seed-release patterns in relation to variations in cone-age and fire-intensity could not be derived from these observations, and therefore a separate experiment with controlled artificial heat sources was performed. The field observations though provided detailed, benchmark descriptions of seed release after real fires and a comparative basis on which to judge the experimental results.

The heating experiment was designed to test the following null hypotheses, in a situation where unequivocal and unconfounded combinations of cone-age and heating could be applied:

(i) That variations in the time of heating had no effect on the amount (percentage per cone) of seeds released.

(ii) That variations in the type of heating had no effect on the amount of seeds released.

(iii) That cone age had no effect on the amount of seeds released.

Included in the comparison of heating treatments was an unburnt control in each species. All shrubs/branches containing treated and control cones were ring-barked, after being
initially manually defoliated (see Methods), this being done to simulate the effect of total shrub/branch death in a fire. Therefore the treatments represented the responses of cones from plants or branches killed by fire. Seed release from heated cones or branches in an un killed condition may differ. Cone ages used in the experiment were "young" and "medium" as defined in the preceding chapter. "Old" cones were not available in sufficient numbers for inclusion. Heating treatments of three differing kinds were performed. Firstly a direct flame was applied to cones. The second was the exposure of cones to a stream of heated air (heat convected and conducted to cones). The third involved a mixture of these treatments. Exposures were 0.1, 0.5, 1.0 and 2.0 minutes for the direct flame treatments, 1.0, 2.6 and 5.0 minutes for the indirect heating treatments and 0.1/1.0 (direct/indirect) and 1.0/2.5 minutes for the mixed treatments.

(ii) **Seed release in unburnt stands.**

Observations of seed release were made in unburnt stands and the effects of both stand-age or time since fire and cone-age were measured. As discussed in the preceding chapter these measures were used to calculate amounts of viable seed release at differing ages and times since fire. As well, these direct measures of seed release for unburnt plants were compared with the rates measured indirectly (Table 5.1) and served as a
base-line comparison to the rates measured in post-fire observations and experiments.

**Methods**

(a) **Seed release experiment.**

The heat source used was a hand-held propane burner (described in detail in Appendix 1). The direct flame treatment was applied to each cone from the base, with the burner nozzle held at between 5 - 10 cm from the cone so that most of the cone surface was evenly enclosed in the flame.

Convected heating was done using a box constructed of galvanized sheet steel. The box was L-shaped, with the torch being placed in one end and the cone in the other. The cone was protected from the flame and direct radiated heat. Heat was forced along the horizontal leg of the box and up the chimney and over the cone. Mixed treatments (direct flame plus convected heat) were done by immediately placing the cone after the flame treatment into the box, and applying heat.

In *B. ericifolia*, treatments were spread across five trees, each being completely defoliated and ring-barked at the base. In *B. serrata* eight trees were used. Each minor branch containing treatment and unburnt control cones was ring-barked, the remainder of the plants being left intact. For *P. pulchella*, ten bushes
were used, each being ring-barked at the base. In Isopogon, ten bushes were also used; branches containing treatment cones had their bark peeled away at the base.

For B. ericifolia and Petrophile, five replicates (cones) were used for each treatment (1 per tree), so that treatments were spread amongst sample trees. Similarly in B. serrata and Isopogon, four replicate cones were used.

Seed release in Banksia and Petrophile was scored as open empty follicles, fresh ones being marked on each visit by white typing correction fluid. (Open follicles, present prior to treatment were initially marked). In Isopogon the amount of cone material missing having disintegrated and fallen away, was estimated at each visit as a percentage of the whole cone. In B. ericifolia and Petrophile, observations were maintained for about 11 months (November 1982 - September 1983), whilst in B. serrata and Isopogon observations were made for approximately 6 months (from April 1983 - October 1983).

(b) Seed release observations.

Observations were made in two spatially separate areas. In each, B. ericifolia and Petrophile stands were located which were burnt at extremes of fire severity, as judged by the fire-scorch height and degree of charring on branches and cones and proportions of leaves consumed. Old
bushes of either species were located which had been completely incinerated and severely charred. By comparison, bushes on which scorch and leaf death occurred only up to about 0.5 metre above the ground surface, were also located. The 10 lowest cones on between 5 and 10 individuals of each of these species were located in each case. A further 10 cones at the top of the same plants were located. These represented "old" cones and "young"-"medium" cones respectively according to the definitions presented in the preceding chapter.

In B. serrata, at each of the sites a selection of large individuals were tagged and cones were numbered and classified according to the severity of scorch on their surface. In Isopogon, difficulty was found in locating bushes that showed extremes of scorching. Observations were made only on bushes which were severely scorched.

Observations were commenced five days after burning in all species, individual sample plants having been located immediately after the burn. On each visit, open empty follicles/bracts were marked with white typing correction fluid and counted. Open follicles/bracts at the commencement of the study were marked where charring was present on the inner surfaces and excluded from calculations. In Isopogon, % cone disintegration was estimated at each visit. Percentage cone disintegration in Isopogon was assumed to represent % seeds released in both experiment and post-burn observations. Seeds were assumed to be evenly distributed within cones.
(c) Seed release in unburnt stands.

Observations in Isopogon were described and used in the last chapter and are not dealt with further here. In the other species, observations on the rate of seed release were mounted in at least two stands. In B. ericifolia and Petrophile, samples of "young" "medium" and "old" cones were tagged in the 1968 and ≤1964 stands used and described previously. In B. serrata, observations on all three cone classes were made in the 1976, 1974 and ≤1964 stands.

Samples in each species were tagged in mid-1981. The number of open empty follicles/bracts in each species were counted and marked in each cone at the commencement of the study. Cones were harvested and recounted in mid-1983. By necessity, in B. serrata, numbers of cones were unevenly spread amongst individual plants within sites. In the other species, where possible, one or two cones per cone class were sampled on individual plants.

5.3 Results and discussion - fire effects on seed release.

Results

(i) Seed release experiment.

B. ericifolia

Compared with seed release from "medium" cones, that from "young" cones was greatly diminished. (Figures 5.1 and
Analyses of variance were carried out on "medium" cone data to test for differences between treatments in mean cumulative percentages of seeds released per cone at 30, 92 and 330 days post treatment (Table 5.2 - 5.4). No significant differences were found at any of the sampling times, though means at 30 days were close to being heterogeneous (F ratio 0.10 > p > 0.05). Hence the proposition was accepted that heat treatments had no effect on the overall rate of seed release. Prior to 30 days (Figure 5.2 (a)), mean seed release from the 0.1 minute, flame (direct heat) treatment, lagged behind the others. By comparison to the heat treatments the mean seed release from the controls (Figure 5.2 (a)) was substantially lower, reaching a maximum of 6.5% at the end of observations.

For young cones, statistical analysis was not performed as the treatments caused only a small amount of mean seed release. Again the proposition was accepted that differences between treatments had no effect on seed release.

B. serrata

No mixed heat treatments were performed due to a lack of suitable cones.

Two-factor analyses of variance were carried out on percentage seed release (per cone) data to determine the significance of differences caused by cone-age and heat
treatments. These were performed on cumulative seed release data collected at 20 days and 140 - 150 days (final observations) (See Figures 5.3 and 5.4).

Results for the 20-day anova showed a significant effect of treatments (Table 5.5). As data for control (unheated) cones were excluded from the analysis due to obvious differences in % seed release (Figures 5.3 and 5.4), the differences were between heating treatments only. Student Newman-Keuls testing (Table 5.5) revealed that mean % seed release under the 2.0 minute flame treatment was significantly greater than all other treatments, between which there were no significant differences. Anova results for the final observation showed (Table 5.6) that differences between heat treatments were less clear-cut but that the 2.0-minute flame treatment again caused significantly greater seed release than most other treatments. Means for 1.0 and 0.1 minute flame treatments were similar to the 2.0 minute flame treatment indicating that over the period sampled, the direct heating treatments as a group, may have promoted greater seed release.

As with _B. ericifolia_, unheated controls (branches ring-barked) produced comparatively low overall levels of seed release (Figures 5.3 and 5.4).

**Petrophile**

As with the _Banksia_, analyses of variance were
carried out on data of cumulative mean seed release (Figures 5.5 and 5.6) at various times after treatment (30, 90 and 335 days). Results (Tables 5.7 - 5.9) gave significant interactions within the 30- and 90-day samples, suggesting heterogeneity of means amongst cone-classes and heat treatments. Data from unburnt controls were excluded from these anovas but were included in the anova of the final observations (335 days). S.N.K. tests showed that overlapping similarities between means existed with no consistent trend in either cone-age or heat treatment apparent in either 30- or 91-day observations. Analysis of the final observations (Table 5.9) revealed a significant effect of cone-age. Mean seed release for 'young' cones was significantly greater than medium cones. This result was due to the inclusion of 'medium' cone control data (Figure 5.6 (a)) the mean of which was substantially lower than other treatments. Therefore whilst individual heat treatments such as high-mixed heating in 'young' cones versus 1.0 minute indirect heating had different effects on seed release in the intermediate phase of seed release, no consistent pattern with regard to type of heating, duration or cone-age emerged. Over the duration of the observations all treatments had a similar effect on cones of both ages, other than the unheated control in medium cones.

**Isopogon**

Problems were encountered with the longer heat treatments in *Isopogon*. These tended to burn through the stems
near the base of the cone causing the cone to fall off in the middle of the treatment. Hence treatments were restricted to 0.1, 0.5, 1.0 minutes, direct flame for "young" and "medium" cones. A consistent pattern (Figures 5.7 a & b) emerged with respect to heating and cone-age, "Young" cones disintegrated more rapidly for any given level of heating than "medium" cones and a progressive increase in disintegration rate with increasing exposure to direct heat occurred (Figures 5.7 a & b).

The indirect heat treatment gave a result intermediate to the two longer direct heat treatments in both cone classes. The trends were considered clear-cut, hence no statistical analysis was performed. Responses in unheated controls varied between cone classes in that "young" cones (Figure 5.7a) disintegrated at a more rapid rate.

(ii) **Seed release observations.**

Data were treated in a similar manner as above. That is, where feasible, analyses of variance were performed at various times (~30, 90 and 450 days, post fire) to determine site and cone-position effects on the mean percentage of seeds released up to those times.

*B. ericifolia*

For cones burnt at the high-severity level (Figure 5.8), variances of sites and heights (transformed data) proved heterogeneous at 34 days and the anova was not performed.
However, differences between means for high and low cones in both sites were marked (Figure 5.8) and mean seed release in site I was, overall, higher than in site II. Anovas for 91 days and the final (450 days) readings were performed (Tables 5.10 and 5.11) and these showed that a significant difference between height means (Table 5.10) existed at 91 days. High cones had released more seed than low cones. No differences attributable to site on cone position at 450 days were significant (Table 5.11).

For low-severity cones (Figure 5.9) anovas were carried out at 91 days and 450 days only, because at 34 days most cones had not released any seed (Figure 5.9). At 91 days, differences between heights were significant with greater mean seed release having occurred in low cones (Table 5.12). At the final reading, site differences only, were significant with a higher level of mean seed release having occurred in site II (Table 5.13). Contrasts between fire severity levels (Figures 5.8 and 5.9) were obvious at all times. Cones burnt at the high fire severity level released more seeds.

**B. serrata**

A balanced set of observations with respect to sites and fire severity was unobtainable in this species. Cones burnt at high levels of fire severity greatly outnumbered lightly burnt cones at both sites (Table 5.14). Comparisons
between mean seed release at the differing levels were not made statistically, however differences (Figures 5.10 and 5.11) were pronounced. Comparisons within severity levels between sites (Table 5.14) were non-significant at the high-severity level. In cones burnt at low levels of fire severity significant site effects were present at 34 and 91 days post fire but not at the time of the final observations (450 days) (Table 5.14).

It was concluded overall that high levels of fire-severity increased seed release.

**Petrophile pulchella**

For high-severity cones (Figure 5.12) significant heterogeneity amongst the site/height treatments was found at 91 and 34 days (Table 5.15 and 5.16). S.N.K. tests (Tables 5.15 and 5.16) indicated that low cones in site I released significantly less seeds up to these times. However at the time of final readings no significant site or height effects were present (Table 5.17).

As with *B. ericifolia*, low-severity cones showed obvious lower levels of seed release than high-severity cones (Figures 5.12 and 5.13) and formal comparisons were not considered necessary. Analysis of variance at 91 days indicated significant site effects with higher seed release in site II (Table 5.18). At the time of final readings, site effects were non-significant but
height effects were (Table 5.19) significant. High cones had released more seeds than low cones (Tables 5.19).

**Isopogon**

Differences between sites were significant initially (34 days) (Figure 5.14) (Table 5.20), however at later times these proved non-significant (Tables 5.21 and 5.22). As the range of cone positions was found by experience in unburnt vegetation to be of little use in indicating cone-age, initial attempts to partition differences according to this criterion were abandoned. As well, variations within *Isopogon* bushes were small in comparison to within-height class level variations in both *Petrophile* and *B. ericifolia*. Hence as with *B. serrata*, cone-age effects if significant were confounded with site influences.

**Discussion**

Patterns of seed release within species particularly within the observed natural burns were varied and complicated with regard to cone position and site effects. Between-site variations in fire severity, within-severity levels in *B. ericifolia* and *Petrophile* made definite conclusions on some site and severity effects difficult. Site differences in *Petrophile* and *Isopogon* at initial and intermediate times during the observation period were reduced to non-significant levels by the end of the study,
and in the Banksias were mostly non-significant throughout. Their influence in Petrophile and Isopogon was largely attributed to fire-severity variations (within-severity levels) that could not be avoided in the sampling procedure. This was because sampled cone-height positions were held constant within species, as were overall sizes of the sampled plants in B. ericifolia, Petrophile and Isopogon. Hence, intrinsic site influences on seed release were considered unlikely, though detailed experimentation using controlled heat sources at differing sites would be needed to fully resolve this question. In all cases, the broad comparison between what were perceived as normal observed extremes of fire severity, as judged by post-fire damage, proved clear-cut. In all species (excluding Isopogon where no comparison was possible), cones burnt at the high level of severity released seeds faster and generally released more seeds (except in B. serrata) over the duration of the observations. (Figures 5.8 - 5.13).

Effects of cone position differed between Petrophile and B. ericifolia. Where differences were significant, in Petrophile, greater seed release was found at both severity levels from high cones. In B. ericifolia, trends differed according to severity level with high cones releasing more seeds at the high-severity level and the reverse applying at the low-severity level. In both species, these trends were found only at the intermediate observations (Tables 5.10, 5.13, 5.16 and 5.18), not at the times of
final readings. Hence cone-age as implied by position affected the initial rate of seed release in the first 100 days. It is possible that the mechanism of follicle/bract opening in both species is affected by age. In *Petrophile* and *B. ericifolia*, at the high level of fire severity, initial rates of opening may be slower in old (low) cones. The turn-around in *B. ericifolia* at low levels of severity suggests that the degree of damage to cones may interact with the opening mechanism and cone-age in a way that changes rate. Old (low) cones may initially open more readily when slightly heated, but at the most severe levels of fire, damage sustained by old cones may interfere more with the mechanism of follicle opening than in young (high) cones. Such an interaction was not present in *Petrophile*.

The contrast outlined above between probable extremes of fire severity and cone-age though somewhat incomplete provided an estimation of the ranges of seed release patterns likely in each species. However before considering these, the results of the heating experiment can be viewed in their context, particularly the effects of cone-age and types of heating.

In *B. ericifolia*, the heat treatments did not cause significantly differing rates of seed release, though the unheated, cut control had a lower amount of seed release. By comparison, in the other species, heat treatments
affected seed release in a manner both dependent on species and cone age. In Petrophile, some of the longer heat treatments in "young" and "medium" cones caused significantly lower seed release at intermediate times, though significant differences at the final observation were solely between cone ages. This result was consistent with the observations in the natural burn where high cones (young cones) showed consistently higher levels of seed release. In B. serrata, cone ages did not affect seed release, however the highest direct heat treatment (2.0 minutes) consistently sustained higher levels of seed release. In B. ericifolia, the choice of one-year-old cones was unfortunate in that these appeared to be not quite ripe at the time of treatment. Seed release may have been retarded because follicles may not have been fully developed and hence the opening mechanism may not have responded normally. In Isopogon, patterns of release were strongly dependent on cone age.

Overall, the heating experiment showed that species respond in quite differing ways, both with regard to the type and amount of heating and cone-age response. The importance of the type and duration of heating can be summarized as being low in B. ericifolia, and high in the other species. The experiment allowed these conclusions to be made without possible confounding influences of unknown heating variations and cone positions/ages.
Except at the lowest level of fire severity in the natural burns and the cut/unheated controls in the experiment, the shapes of the seed release curves of all species were positively skewed. Whilst variations in initial rates have been discussed above, the bulk of seed release in all species occurred relatively quickly. Times for release of 50% of seeds for each species were estimated from the averages of treatments found not to be significantly different and are presented in Table 5.23. These facilitated comparison of the range of rates of release within and between species. Strict comparisons between the values derived from the experiment and those from the natural burn may be difficult because the observations in each were not synchronous but overlapped in time. Differing weather during each observation period may have caused separate responses in each. In spite of this possible source of variation, ranges of times varied substantially within and between species.

Differences particularly between heating of cones in the low-heat treatments in the experiment and the low fire severity levels in the burn may have accounted for some of the variations in the rates and amounts of seed release. In the burns, many cones selected for low-severity observations were unscorched and showed little signs of any other heating. In the heating experiment, all cones in all species ignited, even in the lightest, convected, indirect heat treatments, though the Banksia
species burnt more fiercely on ignition due to the prevalence of floral remnants on the exterior of the cones. It may be concluded that the cones sampled at low-severity levels suffered less heating and consequently took longer in all species other than *Isopogon* to release 50% of their seeds.

In summary, several points may therefore be emphasized:

(i) Effects of cone age and heating variations, largely affected the initial rates of seed release, though there were exceptions.

(ii) Cones either unscorched and unheated or possibly heated at levels below those used in the experiment (low-severity treatments in the natural burns may fall into this category) released significantly less seed in the long term (> 1 year post-burn) at lower rates in all species other than *Isopogon*.

(iii) Effects of cone age were variable but young cones in *Petrophile, Isopogon* and in some cases, *B. ericifolia* may release seeds faster than old cones. Cone-age effects appeared to interact with heating effects in *B. ericifolia*.

(iv) Initial rates of seed release appeared to be least sensitive to a broad range of heating levels (other than very low heating) in *B. ericifolia*. Other species showed more sensitivity, reflected in the values in Table 5.23.
(v) Generally higher levels of heating produced faster initial seed release in those sensitive species, but it may be possible particularly in Petrophile that threshold effects may be present beyond which increments in heating may have no further effect.

(vi) Initial seed release (see Table 5.23) is fastest in B. serrata, followed by Isopogon, B. ericifolia and Petrophile under high levels of heating, in order. At lesser levels of heating, differences between all species other than Petrophile are less wide.

The consequences of these varied seed release patterns in terms of seedling emergence are dealt with in a later chapter.

Results and Discussion

5.4 Seed release in unburnt stands.

B. ericifolia

Data for both stands (1968 and ≤ 1964) in all classes were similar (Figure 5.15). A 2-factor analysis of variance was performed on the data for "young" and "medium" cones to test the effects of cone age and site on mean % seed release. Neither factor (Table 5.24) proved significant. Mean percentage seed release in "old" cones did not differ between sites (t = 0.764, df. = 21, p > 0.20). It was concluded that seed release was unaffected by cone-age in the ages covered by "young"- "medium"
cones but that seed release was greater in "old" cones (Figure 5.15).

**Petrophile**

Mean seed release appeared to vary amongst sites and increased with cone-age in Petrophile (Figure 5.17).

T-tests for comparisons of sites within cone-ages in "medium" cones ($t = 0.457$, df. = 67, $p > 0.50$) and "old" cones ($t = 1.21$, df. = 23, $p > 0.20$) however proved non-significant. A comparison in "young" cones was not done as only a single cone in each sample exhibited seed-release. In Petrophile, release of seeds tended to be an all-or-nothing process with either a substantial proportion of bracts opening on a cone or none at all. It was concluded that % seed release increased with cone-age.

**B. serrata**

In this species, seed release was variable between sites amongst "medium" and "old" cones (Figures 5.16). A t-test was performed between "old" cone means for <1964 and 1977 sites ($t = 1.557$, d.f. = 44, $p > 0.10$). These were not significantly different. Data from the 1974 site were not analyzed as only a single cone released seeds. It was concluded that mean seed release rose with cone age in a manner partially dependent on sites (Figure 5.16)
Discussion

For B. ericifolia, B. serrata and Petrophile the results contrasted with the model of seed release accepted for results from an age series of cones. In that case straight-line regressions of the logarithm of seed release versus time were significant indicating that the hypothesis of a constant mortality could be accepted. In both cases, actual observations of seed release indicated a varied increasing rate with cone-age, implying for any cone that the annual seed release rate may rise with time since fruit set. The magnitude of this discrepancy between the methods of measuring seed release and their results is illustrated comparatively in Figures 5.18 - 5.20, for all three species. The trend in the data from static seed release measurements was similar in that fitted regression lines in all cases had y intercept values greater than 100% (Figures 5.18 - 5.20). This occurred because mean "old" cone values in general biased the slope of the line toward higher values than would have been generated by mean "young" and "medium" cones in all species (Figures 5.18 - 5.20). Nevertheless, the trend was greatly pronounced in the measured seed release data by comparison and the assumption of a constant rate of release could not be made on that basis.

Possible biases due to the circumstances surrounding the direct seed release observations may have been present.
The drought conditions that prevailed during the period of measurement may have accelerated the release of seeds, from old cones in particular. Further measurements in differing years would obviously be required to resolve the effect of such influences.

Site effects on seed release in Petrophile and B. serrata, contrasted generally with the results of the cone age-class analysis, where site differences in the percentage of unreleased seeds were generally non-significant (See previous Chapter).

The main ramification of the seed release data was that the estimates used for seedbank simulation and estimation may be biased in that the seed-release rates may realistically rise with cone-age in all three species. The consequences of this would be that overall rates of increase in retained seedbank as simulated and levels of calculated seedbank in the Banksia spp. and Petrophile as simulated, may be reduced.

As stated above, another aim of this section was to provide estimates of the magnitude of viable seed release in unburnt stands. The disparity between seed-release measurements given by the differing methods prevented any general attempt at estimating seed release using a combination of data. Rather "actual" estimates based on the direct measures of seed release during 1981 - 1983, viability
estimates for differing cone ages made in each site, and
the measured size of the cone population on an age-class
basis in 1981 in each species, are presented on a stand basis.
(Tables 5.25 - 5.28) (Approximately 50 plants per stand).
The principal assumption made in their calculation
involved the lumping of all cones into one of the three
age classes used for viability measurement. Cones were
classified and counted as being in the nearest age-class.
Whilst this may have caused some biases it was felt that
possible errors may be somewhat self-cancelling. Seed
release rates (Tables 5.25 - 5.28) used were average annual
figures gained by halving the measured percentages released
during the two-year period in each appropriate species/site
combination.

In the obligate seeders, Petrophile and B. ericifolia,
the magnitude of estimated annual seed release of sample
stands rose with age across the age-sequence of sites pre-

tented, along with the numbers of accumulated cones
(Tables 5.25 and 5.27). Overall in all species the outputs
of viable seeds could be considered as significant, regard-

tless of age or time since fire, whether on a stand basis
as depicted or on a seeds-per-established-individual basis.
In all species potential establishment in unburnt conditions
may rise as a function of available seeds (Tables 5.25 -
5.28) with age or time since fire.

This conclusion reinforced the importance of tracing
the fates of released seeds in unburnt stands as well as
determining the factors governing establishment of seedlings under these conditions.

5.5 Measurements of Follicle Moisture.

Aims and Methods.

In all species seed release, whether measured "statically" or directly, rose with cone-age. As noted earlier Gill (1976) found that follicle moisture content declined with follicle age and he attributed the small amount of seed release observed in unburnt conditions (concentrated in old cones) to this decline.

A series of measurements were undertaken to see if cone-age correlated with moisture. Such measurements were repeated on several occasions within the same sites to test temporal variations.

In all species other than Isopogon "young", "medium" and "old" cones were examined. In Isopogon only "young" and "medium" cones were studied. In the Banksia species individual follicles were removed from cones and studied whilst in Petrophile and Isopogon removal of individual bracts was not feasible. Instead, whole cones were subjected to analysis.

Moisture contents of follicles and cones were determined gravimetrically by heating the parts in an oven at
105° for 48 hours. Moisture was expressed as a percentage of oven-dry weight of cone or follicle material. In the Banksia species the follicles were removed using a hammer and chisel. The cones were harvested in contrasting seasons: January, March and July 1983. Five cones per species cone-age class were harvested on each occasion.

Results

Analyses of mean cone or follicle moisture were performed to test for between cone-age and sample date differences (Tables 5.29 – 5.33). Results varied between species (Tables 5.30 – 5.33). In B. ericifolia, moisture contents in follicles of all cone-ages tended to be significantly higher in July than at other times (Table 5.30). In B. serrata, a similar trend existed except that the January "young" cone value significantly exceeded all other values (Table 5.31). In Petrophile values in January outstripped those on other occasions and comparisons were dispensed with (Table 5.29). A comparison using the March and July values revealed significant differences between sample dates and cone-age class in cone moisture (Table 5.32). Cone moisture was higher in July than March and was significantly higher in "young" versus "medium" cones. In Isopogon (Table 5.33) no significant differences were found.
Discussion

No simple relationship between cone-age and follicle/cone moisture was evident in any of the species. It appears that temporal variations in the Banksia species and Petrophile may override any differences due to cone-age. In Petrophile, there was greater similarity in cone-moisture content between "young" and "old" than medium cones in March and July.

In the Banksia species there was no apparent decline in follicle moisture with cone-age as reported by Gill (1976) for B. ornata. Aside from follicle opening and seed shed caused by branch deaths, it would appear that the progressive release of seeds found with increasing cone age may be controlled by a mechanism other than moisture. In the Banksia species this may be due to a breakdown in the wood strength across the follicle abcission zone with age. Some similar structural decline may cause bract opening or disintegration in Petrophile and Isopogon. Further studies are needed to test this hypothesis.

5.6 General Summary and Conclusion.

Rates of seed release were found to be more rapid in plants affected by fire in some manner, than in unburnt plants. In unheated cones borne on fire-killed branches, in all species, seed release was more rapid than in unburnt
cones retained on live branches. In heated cones seed release rates were shown to be broadly dependent on the amount of heating. Generally in cones subjected to high levels of heating initial seed release was more rapid than in the aftermath of low-heat levels.

In all species, the calculated amounts of viable seeds released annually in unburnt conditions would appear to become high in old stands, especially those greater than about 20 years of age or time since last fire. This parallels the rise in stored seedbank.
CHAPTER SIX: THE EMERGENCE AND SURVIVAL OF SEEDLINGS IN BURNT AND UNBURNT CONDITIONS.

6.1 General Introduction

This chapter contains a study to determine effects of burning on released viable seeds and on emergence and establishment of seedlings from them. As well as determining the influence of the presence or absence of fire on changes in numbers in the transfer between seed and seedling life-cycle phases and in the early seedling phase, the effects of variations in fire-intensity were also examined.

Studies such as Went et al. (1952) and Christensen and Muller (1975 a,b) have listed the factors which may control the emergence and establishment of seedlings in relation to fire. Some of these may be categorized, in relation to emergence and establishment of seedlings, as direct or indirect. Direct effects may include the influence of:

(i) heat on seed viability
(ii) heated soil on seed viability
(iii) heated soil on seedling emergence and survival
(iv) the presence of ash on seed viability and the emergence and survival of seedlings.

Indirect effects may include influences of changed site conditions at the soil surface due to:
(i) the removal of vegetative cover
(ii) removal of litter
(iii) interactions with factors such as numbers of predators.

The effects of heating seeds in "hard" seeded species such as legumes, have been extensively studied (Stone and Juhren 1951, Floyd 1966, 1976, Martin et al. 1975, Shea et al. 1979, Auld 1984). Heat, through burning is an important agent for the breaking of dormancy in hard-seeded species with soil-stored seedbanks.

The effects of heating seeds retained in above-ground seedbanks have not been as well examined, though Ashton (1981) discussed the fortuitous survival of seeds of Eucalyptus species stored in woody capsules, during high-intensity crown-fires. Ashton (1981) concluded that the thin wooden walls of the capsules may provide just enough insulation to prevent lethal temperatures either being reached or else sustained for periods long enough to cause inviability of seeds. Siddiqi, Myerscough and Carolin (1976) reported on the effects of heating seeds of several Banksia species (including B. ericifolia). They defined combinations of temperature and exposure combinations likely to cause inviability. Bradstock (1977) attempted to relate survival of seeds in B. ericifolia cones exposed to differing time-temperature combinations in a muffle furnace, to maximum temperatures measured in the field during fires. From this work it appeared that fire would cause little inviability in mature seeds in cones in the field.
Chemical inhibition of germination and survival (allelopathy) has been extensively postulated and in some cases demonstrated such as in Californian chapparal (Muller et al. 1968, McPherson and Muller 1969, Christensen and Muller 1975 a,b). The effects of soil borne micro-organisms and chemical conditions related to them, have been ascribed an inhibitory role in germination and growth of seedlings, such as in the example of *Eucalyptus* species (Florence 1981, Ashton and Willis 1982). Fire may play a role in these and other examples by changing or removing or reducing the sources of direct inhibition whether these be soil- or plant-borne (Warcup 1981). The presence of inhibitors in unburnt plant material has been postulated as being important in some southern Australian sclerophyll vegetation by Withers (1978) and Purdie and Slatyer (1976), though definitive isolation of chemical elements in their studies was not done. Mott and Groves (1981) have pointed out the possible difficulty in discriminating between removal of sources of inhibition and other effects caused by the removal of plant cover by fire. Nonetheless, experimental manipulations of factors such as plant cover (eg: Burrel 1981, in *Leptospermum laevigatum*) may pinpoint sources of effects and clarify the role of fire even if the primary sources of inhibition of emergence and/or survival are not identified.

The presence of ash has been suggested as a beneficial effect of fire particularly in relation to and in conjunction with soil nutrient enrichment and microbial changes postulated for post-fire conditions (Florence 1964, Cremer and
Mount 1965). Experiments examining the effects of soil heating, sterilization or the presence of ash in *Eucalyptus* seedlings of various species (Florence and Crocker 1962, Attiwill 1962, Wellington 1981) have indicated a positive effect on growth and survival through each of these components. Siddiqi, Myerscough and Carolin (1976) indicated that the availability of nutrients was enhanced in burnt coastal heathland but that the uptake by young seedlings of several *Banksia* species was such that little benefit in the short-term was achieved in their growth. The seedlings could not utilize the higher levels of elements such as phosphorus.

The removal of cover independent of burning and the subsequent modification of the environment at the soil surface in terms of changes in available light, water and levels of temperature may strongly affect the emergence and establishment of seedlings. Miles (1974 a,b) and Goldberg and Werner (1983) have noted the generality of the requirements for seedling establishment through the removal of established cover, in the literature and have demonstrated the effects of varied gap sizes in experiments. On the other hand, the presence of litter or ash may provide physical barriers to seeds, shed from canopy borne fruits in both burnt or unburnt conditions. The role of seed removal by ants has received increasing attention in Australia (Berg, 1975, Rice and Westoby 1981). The burial of seeds by ants and its consequences in interaction with heat from fires in breaking dormancy have been examined particularly in
legumes (Shea et al. 1979, Auld 1984). The species studied here were not reported by Berg (1975) or Rice and Westoby (1981) to be taken by myrmecochorous ants. All four species lack appendages or elaisomes which are usually present in other species favoured by myrmecochorous ants. However the potential effects of harvesting seeds by ants or other predators may be:

(a) destruction of seeds
(b) burial or storage of seeds in positions from which effective emergence was impossible.

The interaction of fire with predation of seedlings has been shown by Christensen and Muller (1975 a,b), Whelan and Main (1979), Leigh and Holgate (1979) and recent experimental studies (eg: Mills 1983) have highlighted how predator preference may alter the numerical balance in establishing seedlings of co-habiting species. In this study, as mortality in seedlings in both burnt and unburnt areas was heavily concentrated in the initial three months after emergence (see Chapter 8), the emphasis was placed on examining predator effects soon after emergence.

Therefore the work here covered a broad range of the above aspects of possible fire-induced or related effects. These can be classified as heating/substrate effects, vegetative cover effects, predation and seed removal in unburnt and burnt conditions and effects on seed viability and longevity.
6.2 Aims

(a) Heating, substrates and vegetative cover.

The factors were studied in a series of glasshouse (and laboratory) and field experiments. Heating versus non-heating, differing amounts or levels of heating, the presence of litter and ash, differing types of ash and the presence of differing amounts of vegetative cover were all examined.

The initial glasshouse experiment addressed heating, ash and litter (substrates) effects on soils specific to each species. That is, those factors were examined in the presence of possible soil-borne intraspecific effects on emergence and survival. Levels of heating employed, were a straight heated versus unheated comparison, whilst the presence and absence of litter and ash singly and in combination were examined. The response measured was percentage emergence of seeds sown, using a three-factor analysis of variance, though short-term observations of seedling survival (up to two months post-emergence) were done. The null hypotheses tested on soils typical of each given species were that:

(a) Prior heating had no effect on the percentage of subsequent emergence of seedlings.
(b) The presence of litter had no effect on emergence.
(c) The presence of ash had no effect on emergence.
Tests of ash and litter effects were designed to be intraspecific. In each species, plant material was taken from stands and was tested against seeds of that species. Following preliminary observations from this initial glasshouse experiment, two experiments in the field were commenced. One of these, referred to as the heating/substrate experiment also addressed the above hypotheses with the additional aim of testing differing extreme levels of heating. This was done to see if variations in fire intensity may be important in seedling emergence and survival. Enhancement of emergence survival and growth has been attributed to high levels of soil heating or baking after high-intensity fires over those encountered after low-intensity fires, independent of direct heat stimulation of seedling emergence, by enhanced mineralization of elements and altered activity of soil micro-fauna and flora (eg: Florence and Crocker 1962, Florence 1964 in Eucalyptus pilularis). This experiment was also designed to examine mortality as well as emergence over a longer period than in the glasshouse.

As specific effects of the experimental factors appeared to be absent in the laboratory and because there were constraints on suitable sites and resources, the experiment was not run separately in sites specific to each species but rather in a site where all species were generally present. Experimental plots were not located under bushes of a particular type but rather distributed randomly.
A two-factor design was used with types of substrates (levels of ash and litter) and heating as factors. "Unheated" and "bare" treatments were incorporated as levels of these factors. The ash/litter mixture used in the laboratory was tested on two differing levels within substrates. Ash levels used were a "hot" treatment, and a "cool" treatment which contained a mix of ash and partially burnt litter. "Hot" ash consisted mainly of fine white ash and charcoal produced by lengthy firing of plant biomass and litter. This represented the aftermath of high-intensity burning. "Cool" ash used the same raw materials, however the total fuel was not allowed to fully burn leaving a mixture of burnt and partially burnt material similar to that produced by low-intensity burns in the litter. The material used for ash had components of litter and live biomass from all the four study species as did the unburnt litter mixture. Hence possible inter- and intra-specific effects within these components were tested for.

The levels of heating used were chosen to test extremes that could be applied to the soil by hand-held gas apparatus. These represented possible widely differing fire intensities (See Appendix 1). They consisted of high- and low-heat treatments.

In summary, null hypotheses tested in the heating/substrate experiment were:
(a) That levels of heating of the soil surface had no effect on subsequent emergence and survival of seedlings arising from seeds deposited on the burnt surface.

(b) That differing substrates had no effect on the emergence and survival of seedlings.

A second experiment in the field tested the effects of unburnt vegetative cover on emergence and survival of seedlings. This experiment was restricted to testing intraspecific effects directly under the canopies of established bushes of each of the study species. This was done in plots directly adjacent to the heating/substrates experiment. The experiment tested the selective removal of shrub cover and shrubs plus ground cover and litter. Hence the null hypothesis was that the presence of vegetative cover in unburnt sites had no effect on seedling emergence and establishment.

(b) *Predation of seeds and seedlings, the longevity of seeds and effects of heating on seeds.*

Two field experiments were performed to examine the possible removal and/or predation of seeds and predation of newly emergent seedlings. Further experiments were designed to measure any possible decline in the viability of released seeds in both field (burnt and unburnt) and laboratory conditions and effects of heating on viability.

The experiments on seed removal/predation utilized several differing structures to exclude and examine the
effect of various possible predators. A perspex box of shallow depth open on one side, without a bottom was used primarily to see if removal of seeds occurred, in both burnt and unburnt areas. The boxes were designed so that seeds were protected from disturbance by wind as all the study species seeds were found to be readily susceptible to wind generated movements. Also the boxes provided shelter from rain, which was another source of unwanted disturbance, but which in all cases also caused fairly rapid germination (see later in this and the following chapter). The opening available to animals once the boxes were in place was less than 2 cm on one side, hence it was likely that only ants, other small insects and possibly some small reptiles had access to the seeds.

The experiment involving open perspex enclosures was performed in both burnt and unburnt areas in two treatments where the tops of the boxes were either covered with wire mesh (~3 cm opening, "chicken-wire" type) or left unmeshed. The aim of these comparisons was to determine if access to virtually all potential predators (unmeshed boxes) resulted in higher levels of predation on seeds and/or seedlings than restricted access (meshed boxes) which excluded probably most vertebrates except small reptiles.

By performing both experiments in burnt and unburnt areas the dependence of levels of predation on burning could be assessed.
The seed-longevity study was also performed in burnt and unburnt sites. Seeds were placed on the mineral soil surface in bags of nylon mesh in a large perspex box with a removable lid and cut-outs in the sides for ventilation. Concurrently a similarly sized sample was placed in a desiccator in the laboratory. At intervals of 4 - 6 weeks samples were removed from each storage and germinated. The aim of the experiment was:

(a) To test if a decline in the viability of released seeds occurs.
(b) If a decline is present, whether it was affected by the characteristics of storage.

In the burnt site a light layer of ash and mineral soil was sprinkled by hand over the seeds. In the unburnt site a layer of litter was placed over the seeds. The boxes were used to prevent the seeds from wetting and possible germination.

The effects of heating were studied by comparing populations of seeds taken from adjacent burnt and unburnt stands in each species. Cones from fixed positions on plants in each stand were harvested and seeds extracted and germinated. Burnt cones were taken from sites subjected to a high-severity fire in December 1980, within a week of the fire. Unburnt cones were taken at the same time. The rationale behind the method was that potential inviability was likely to be maximal under high-severity fires.
6.3 Heating, substrates and vegetative cover.

Methods

(i) Effects of heating and substrate-glasshouse.

Soils from under established bushes of each species were collected to a depth of ten centimetres, after the litter and any standing ground cover were removed. Litter and plant material were separately bagged.

Soils were spread to a depth of 5 centimetres in large plastic trays (approximately 50 x 25 cm). The heat treatment was applied on the soil using a propane burner to an area approximately 15 x 35 cm within each tray. A heat shield with a cut-out of these dimensions was used to apply these treatments and prevent ignition of the surrounding plastic. Aluminium foil was used to further shield the tray edges. The propane burner used was relatively small (Appendix 1) and its use here involved heating for 1.5 minutes at a gas consumption rate of 0.03 kg/minute.

The ash was produced by burning vegetation and litter harvested at and adjacent to each point of soil collection. Therefore ash and litter treatments contained those elements that were specific to the sites of each species. The ash was made by burning the plant material in a metal
garbage bin. Some extra heat was deployed using a propane burner so that all the material was thoroughly burnt. The ash-litter mixture was made by mixing a sample of normal litter thoroughly with ash in roughly equal proportions by volume.

Soil surfaces were prepared by completely covering the treated area with ash or litter. Due to the different bulk density of litter the effective depth of coverage was deeper than with ash.

Fifty seeds per tray per species were scattered on the prepared surfaces. Soils and seeds were kept saturated throughout the period of observation and care was taken to prevent seeds from being washed away from the treated areas. Emergences were noted on average about three times weekly.

Initially, the experiment was performed in a glass-house but rodents destroyed the seeds mid-way through the experiment. Subsequently, the work was repeated on a laboratory bench with trays being arranged randomly under normal room fluorescent lighting for about 12 hours per day.

Due to limitations of space, one tray per treatment was used. Replication was carried out by repeating the experiment immediately after the initial run was concluded. Emergents were marked by match sticks and
survivors were counted at the conclusion.

(ii) Effects of heating and substrate - field experiment.

Differing heat treatments were applied using the large and small propane burners described in Chapter 2 and Appendix 1. An initial trial experiment was commenced in May 1982 after a prior attempt in early 1981 had failed due to the washing away of planted seeds. As an additional test, in the winter of 1981 trials of freshly emerged seedlings (raised in the laboratory) planted in the field, were performed. These proved unsuccessful and a full germination experiment was therefore planned.

The 1982 trial and the main experiment were conducted on a level site in 11-year-old vegetation near Pearl Beach, adjacent to some of the sites used for the heat-treatment experiments on lignotubers, described in Chapter 2.

The methods for both the trial and main experiment were similar, with two important exceptions. In the trial a single heating treatment only was applied, and mesh enclosures were not used. The results of the trial are not further discussed in this chapter, though the data for seedling emergence are discussed in the following chapter. Seedlings in the trial were heavily grazed after emergence, hence no analysis of their sur-
vival in relation to the treatments was possible. No evidence of extensive seed predation or removal from the plots was found, therefore data on emergence in the heated quadrats was analyzed in the following chapter in relation to soil moisture.

Quadrats were prepared as cleared 1.0 x 1.0 metre squares. Their location was at random in the chosen site. All species except B. ericifolia were common in the site, this species being represented by scattered individuals.

I selected quadrat sites by throwing a tape measure over my head from various points along lines on the site perimeter. At the point of landing of each throw, all vegetation was cleared in a radius of about 2 metres using a brushhook. A motor mower was then used to cut-off remaining ground cover at ground level. All cut and mown vegetation was raked and collected in bags along with the litter from each clearing. The preparation resulted in an evenly cleared surface. Treatments were allocated randomly amongst the cleared plots, with a single quadrat being positioned in the centre of each.

Heating was applied in 0.5 x 0.5 metre squares, so that four consecutive applications had to be made to successive quarters of each heated quadrat. The amounts of heat applied were identical to those described for the high- and low-heat treatments given in Chapter 2 (also Appendix 1) in that burner settings and the duration
of the applications were the same. Litter treatments were applied by evenly spreading a mixture of all collected litter on each quadrat. Elements of litter from all four species studied were present in the mixture.

Ash was produced by burning the harvested vegetation and litter in an open 200-litre drum. The fuel was stirred to ensure that it burnt evenly. Again materials from all study species were present in roughly equal amounts in the ash mixture. After the initial burning, the remaining ash was divided and one half was subjected to further combustion with a propane burner until it consisted mostly of a fine whitish powder. Extra biomass was added and burnt so that enough of this "hot" ash was available. The other half of the ash was mixed with fine litter material so that the mixture contained unburnt, partially burnt and completely burnt material. This was the "cool" ash.

After ash or litter had been applied to the selected quadrats and heating had been completed a plastic fence was erected around each quadrat. Four one-metre high wooden stakes were hammered in at each corner of the quadrats and plastic sheeting ~ 80 cm wide was wrapped around these stakes to form a tight fence. The sheeting was pinned to the stakes and the bottom edge was buried to a depth of about 5 cm using a spade. The sheeting fence provided a barrier to prevent wind and water from moving seeds outside the quadrat. The sheeting was placed
so that its edge lay within the treated squares of soil surface. One hundred seeds of each species were scattered in each quadrat in mid-November 1982. After four weeks, a mesh-cage made of chicken wire was erected around each quadrat, the top edges of the wire being crimped over and tied so that quadrats were enclosed from above. The cages were opened during subsequent sampling days.

Observations on the emergence and survival of seedlings were carried out over a year. New emergents were marked with a matchstick and mapped. A check was made repeatedly to see if seeds were being removed or eaten but no obvious losses were seen.

(iii) Effects of unburnt vegetation in the field.

Quadrat sizes were identical to those used in the heating/substrate surface experiment. Bushes of each species adjacent to the above experiment were chosen. B. ericifolia quadrats were located underneath "old" (estimated 20 + years) bushes in an adjacent stand. All other bushes were either eleven year-old resprouts or in the case of Petrophile eleven year-old genets.

Quadrats were pegged as described above but more difficulty was encountered in neatly caging and fencing these pots containing vegetation due to the presence of standing stems and branches, hence fences and cages especially in the uncut plots were larger than in heating/substrate surface plots. Cages could not be completely
closed in these plots, but the wire was bent over and attached to any branches or limbs present so that large herbivores had little chance of access. In the plots where shrubs were removed all shrubs over about 1-metre high were cut at ground level in a circle of about 2 metres radius. The quadrats were positioned in this circle. In the bared plots all vegetation was removed by cutting and the use of a motor mower as described above for the heating/substrates experiment.

Two replicates of each treatment per species were set up. In each quadrat, one hundred seeds of the same species as the overstorey bushes were scattered at the same time as the heating/substrate surface experiment.

Results

(a) Heating and substrate effects - glasshouse.

Mean emergence of all species (Figure 6.1) except *B. ericifolia* was found, by analysis of variance of the angular transformed data, to be unaffected by any of the treatments (Table 6.1). In *B. ericifolia* a second order interaction between ash and litter was significant (Table 6.1 (a)). S.N.K. tests between means were all non-significant. Whilst the result was difficult to interpret, the means of three treatments (Figure 6.1 (a)) were substantially different from the others. Both the burnt and the litter treatments gave
lower mean emergence (Figure 6.1 (a)) than the bulk of treatments whilst the burnt-bared treatment gave a substantially higher mean. There was a trend present that indicated that on burnt and unburnt soils emergence was inhibited by the presence of ash or litter (but not in combination) compared to when both were absent. The level of third order interaction ($p = 0.078$) hinted that such a trend may have been more strongly developed in the burnt treatments.

In all species, only a few deaths occurred over the two months or so seedlings were kept in the trays. Hence it was concluded that there was no apparent effect of any treatments. Seedlings were not kept longer due to the possibility of the limited soil depth in each tray causing widespread mortality.

(b) Heating and substrate experiment - field.

Percentage emergence and mortality a year after the seeds were planted are given in Figures 6.2 and 6.3 respectively. Analysis of variance of mean angular-transformed emergence percentages was done in B. ericifolia, Petrophile and Isopogon (Table 6.2). In all cases, main factor effects and the interaction were non-significant, though a trend existed particularly in Petrophile toward an effect of substrate-surfaces. In this species, a trend existed for lower emergence in the
litter treatments (Figure 6.2). In B. serrata analysis of variance of emergences was not performed as the variances in transformed data were heterogeneous, having yielded a significant Cochrans Test value. Comparisons of transformed main effect means (Figure 6.4) indicated that possible significant differences occurred between substrate levels with highest emergence occurring in litter treatments and lowest in bare-soil treatments.

Analysis of variance of transformed mean percentage mortality was performed in all species (Table 6.3). Except for B. serrata, effects of treatments and the interaction proved to be non-significant while in B. serrata the heating effect was significant (Table 6.3) and there was a trend toward an effect of substrates (Table 6.3). S.N.K. tests indicated that transformed unburnt and high-heat mean mortalities were significantly different from the low heat mean (Figure 6.3). Mortality was greater in the low heat treatment. This result was due (Figure 6.3 (b)) principally to high mortality in seedlings in low-heat, hot-ash treatments. As only a few seedlings emerged (Figure 6.2 (b)), the mortality result was biased by low numbers and the result was not taken as conclusive evidence of an effect of low-heating on mortality. The trend in survival amongst substrates in B. serrata was for fewer deaths in the litter treatments (Figure 6.3 (b)) and whilst this result was influenced by the result from the low-heat-hot-ash
treatment, it was more broadly based (Figure 6.3 (b))
in all the levels of heating.

(c) Shrub and understorey experiment.

Data for emergence and mortality for all species
are given in Figures 6.5 and 6.6. The effects of removing
shrubs on mean (angular-transformed) percentage emergence
and mortality were examined using the analysis of variance
(Tables 6.4 and 6.5). Emergence in all species (Table 6.4)
was not significantly affected by the treatments though in
Isopogon no emergences occurred in one intact quadrat.
Mortality was significant only in Petrophile (Table 6.5 (c),
Figure 6.6 (c)) where deaths in the bared quadrats were
less than in those with vegetation. In B. ericifolia a
trend to higher mortality in the intact plots versus the
cut plots was indicated (Figure 6.6 (a), Tables 6.5 (a),
\( p > 0.05 \)). Similar trends to these were present in
B. serrata and Isopogon but were less strongly developed
(Figure 6.6, Table 6.5). Analysis of mortality in
Isopogon was restricted to a shrubs-removed-versus-bared-
plots comparison as only a single quadrat registered
emergences in the intact treatment (Figure 6.5). This
comparison was made with a t-test (Table 6.5), and showed
no significant difference between them.
Discussion

Emergence

In all species except *B. ericifolia* the results of both glasshouse/laboratory and field experiments were consistent in that heating and substrates did not significantly affect emergence. In *B. ericifolia*, the depressing effect of litter and ash in the laboratory was not registered in the field. For *B. serrata*, some effect of substrates may have been present though the significance of the trend to higher emergence in the litter treatments was not tested. In *Petrophile*, heterogeneity between substrates was strongly indicated with lower emergence on litter in the field.

A comparison of the glasshouse and field trials was tempered by several differences. Firstly, the glasshouse work used soils specifically taken from beneath bushes of the same species as the seeds laid on them. Hence, as discussed in the introduction, species responses were measured in the presence of possible soil-borne indirect influences. Secondly, watering in the glasshouse was done so that the seeds were kept close to saturation, irrespective of substrate. In the field differences in moisture occurred both within the differing layers of ash and litter and in the respective soils underneath and in bare soil (Figure 6.7), due to their differential mulching and evaporation characteris-
tics. Moisture input was solely from rainfall, as no attempt was made to minimize substrate-related moisture differences through watering. The data in Figure 6.7, were taken from observations during the trial experiment in 1982 on burnt soil. They indicate that whilst little or no advantage in % oven-dry (by weight) moisture existed under litter in wet periods, that the top 5 cm of the soil under litter may not dry out as much as under ash or when the surface is left bare.

Under conditions of constant saturation it would appear that either litter or ash singly (but not in combination) may provide some barrier either to water uptake or radicle extension into the soil in B. ericifolia. Whether this is specifically related to a soil effect cannot be determined because of the above limitations and differences between experiments. In B. serrata, the possible trend to greater emergence in litter and lesser emergence on bare soil in the field may be due to the higher levels of moisture sustained in soil under litter (Figure 6.7). In Petrophile, the opposite result may have been due to the radicles of seedlings being unable to reach the soil after having germinated on the litter bed. This was observed in many instances in the experiment. Hence the enhanced moisture conditions could not be exploited in this species.

The results of the experiment in species-specific standing vegetation plots were clear-cut. Removal of vegetation alone did not appear to influence emergence.
Combined with the results from the laboratory, this result showed that on soils underneath bushes of each species that intra-specific emergence was unaffected by the following treatments, prior to deposition of the seeds:

(a) removal of shrubs of that species,
(b) total removal of all vegetation,
(c) total removal of vegetation and litter in _B. serrata_, _Petrophile_ and _Isopogon_.
(d) heating (from an artificial source),
(e) the presence of ash in _B. serrata_, _Petrophile_ and _Isopogon_.

For _B. ericifolia_, the following hypotheses can be advanced.

(i) Ash or litter form some physical barrier to emergence.

(ii) Some component in the litter or ash may constrain emergence by chemical or biological means.

The latter hypothesis is unlikely in that the ash/litter appeared not to depress emergence.

On soils that may be occupied by each of the study-species but at sites not located under particular bushes, but at random, the following summary may be made:
(a) different levels of fire intensity (provided by different heating treatments) had no comparative effect between themselves or the unheated treatment,

(b) the presence of differing types of ash had no effect compared to bare soil,

(c) the presence of litter may have opposing affects between B. serrata and Petrophile whilst it had no effect in comparison to ash or bare soil on emergence in the other species.

For B. serrata, the following hypotheses may be put forward to account for the result:

(i) Litter may create more favourable moisture conditions for B. serrata than either ash or bare soil.

(ii) Litter has some stimulatory effect on B. serrata seeds.

The evidence available (eg: Figure 6.7) favoured the first hypothesis.

In Petrophile, the hypotheses that may be considered are:

(i) Litter may create a physical barrier to the emergence of germinated seeds by preventing them from penetrating the soil effectively.

(ii) Litter may have some other inhibitory effect on emergence.

Observations supported the former hypothesis.
Mortality

Due to the limited depth of soil in the trays used in the laboratory, mortality was not monitored over a lengthy period. In the short time, (~ 2 months), seedlings were present there was no apparent influence of the treatments.

In the field, on soils specific to each species, the progressive removal of the vegetation significantly influenced mortality in Petrophile, though similar trends also existed in the other species.

Due to a small number of replicates used it was accepted that survival was enhanced in bare versus covered quadrats in all species, though by varying degrees.

In Petrophile, the crucial factor (Figure 6.6 (c)) appeared to be the removal of the ground cover, as mortality was significantly less on the bared soil than that on surfaces where the covers of litter were left intact or those from which vegetation and shrubs were removed. In B. ericifolia this trend occurred with shrub removal, there being little difference between the mortality in the bare and shrub-removed treatments (Figure 6.6 (a)).

In summary, the removal of vegetation had varied effects on mortality of seedlings growing underneath the canopies of established bushes of the same species.
In quadrats, non-specific to each species (heating/substrate experiments), mortality was unaffected by any treatment except in *B. serrata*. Evidence for a significant effect of heating was discounted due to the low numbers present in one sample, however the strong trend toward fewer deaths in litter may be due to a greater sensitivity in this species to either the enhanced levels of moisture under litter or perhaps some protective effect afforded to seedlings from raindrop damage or other disturbance.

In summary, it was concluded that in this experiment:

(a) heating levels had no intrinsic, direct effect on mortality compared both between themselves and with an unheated treatment in all species,

(b) the presence of ash and litter had no effect on mortality except in *B. serrata*.

**Overall summary and conclusions.**

In order to assemble a unified view of the effects of heating, vegetation removal and substrates on emergence and mortality of seedlings, the differences in soil/site criteria between experiments had to be either assumed to be negligible or else bridged. In an effort to test for possible effects of soil between the field experiments, the data for unheated-bare soil emergence and mortality were compared in each species. Treatment preparations,
Planting times and the observation period were identical, so this comparison was used as a baseline. Results of t-tests (Table 6.6) showed that no significant differences in emergence were present. A significant difference in mortality (Table 6.6) was found in Petrophile, there being more deaths in the heating/substrates experiment.

On this basis it was assumed that soil/site differences could possibly be set aside in order to generalize from a combination of the experiments. It could be argued that soil/site specific interactions between heating or added substrates (ash or litter) may occur, however only a complete experimental comparison would confirm this possibility. The roles of fire (heating), plant cover and substrates are summarized for each species below.

B. ericifolia

Emergence of seedlings was not dependent singly on the presence of plant cover or heating. Hence fire as either a direct agent or the soil or as an indirect source of removal of cover has no effect on emergence. The effect of litter or ash in depressing emergence in the laboratory would be self-cancelling after fire as litter would be either reduced and mixed with some ash (no effect on emergence) or else removed and replaced by ash. As this effect was absent under natural watering conditions in the field it can be concluded that any effect of fire through the presence of ash or litter is absent. Emergence
is independent of these factors.

The survival of seedlings can be concluded to be dependent on fire. Fire in its indirect role as a remover of cover enhances seedling survival. Direct effects of fire such as soil heating and creation of ash did not enhance or lower survival, nor did indirect effects such as the removal of litter. Variations in fire intensity may influence survival by differential removal of levels of plant cover. This would therefore be the central role of fire in determining the emergence and survival of seedlings in *B. ericifolia*.

*B. serrata*

Effects by fire on both the emergence and survival of seedlings were identified. The principal action of fire appears to be one of reducing emergence and survival by either fully burning or partially removing litter. Whether the presence of litter alone underneath established vegetation promoted emergence was not tested. However, it would appear that as the mechanism was moisture-related, the effect of fire in removing litter was accepted as general, regardless of the degree of plant cover. Emergence may be enhanced in unburnt conditions, where a substantial litter cover exists.

Mortality was reduced in the presence of litter.
The presence or absence of fire would therefore appear to have the most crucial effect in *B. serrata*, through its indirect role in determining the presence or absence of litter.

**Petrophile**

The principal influence of fire in this species is through the removal of vegetative cover and litter. Survival of emergent seedlings is enhanced through the indirect effect of fire in removal of shrub and ground cover and litter. As with *B. ericifolia*, variations in fire intensity may, through differential removal of cover, influence the course of seedling survival.

**Isopogon**

The effects of fire in this species would be indirect through their role in removing vegetative cover, as with *B. ericifolia*. Data from the shrub cover experiment suggested that emergence may tend to be restricted in fully covered quadrats (comparisons were non-significant, Table 6.4, but at higher levels of replication a significant trend may be likely). Similarly the survival of seedlings seemed to be affected by the presence of vegetative cover. As with *B. ericifolia* variations in fire-intensity may influence survival and emergence through differential removal of plant cover.
In all species, these conclusions related to results gained from the presumed exclusion of large, non-insect herbivores. Possible losses in seeds and seedlings due to predation or removal are examined below. Conclusions relating the presence of vegetative cover may be specific to the degree of cover in the experimental sites, as a function of site age or time since last burnt. Whilst responses to varied levels of cover or age were not extensively studied, it may be hypothesized that in those species susceptible to the effects of cover (B. ericifolia, Isopogon and Petrophile) seeding emergence or survival may be related to stand age or density as determinants of cover. The experiments suggested an apparent absence either of ash-bed effects or inhibitory substances in the soil, though the results gained by the removal of intraspecific cover leave questions open as to the possible role of chemical influence stemming from the vegetation, or alternatively shading effects.

6.4 Predation of seeds and seedlings, seed longevity and effects of heating on seeds.

(i) Seed box experiments.

Seeds were arranged on filter paper circles under perspex boxes in a burnt and an unburnt area. The boxes were 10 x 10 cm in size with sides 3.5 cm high. One side was left unenclosed. The boxes were pressed into the soil, a small cut being made with a light spade for the edges.
Filter papers each containing 20 seeds of each species were placed in the boxes, and a plastic rain shield was erected over the open side of each box. Six replicates spaced at ten-metre intervals were placed in each area. In the unburnt area, boxes were placed in reasonably clear inter-shrub spaces. The boxes were placed near the heating/substrate experiment described earlier. The burnt area was located about three kilometres from these. The area was burnt in July 1982 and the experiment was commenced in November 1982.

Observations of seed numbers remaining in the boxes were made 1 and 12 hours after placement and at 2, 5, 10, 24 and 57 days.

(ii) **Seed enclosure experiment.**

Seeds were placed in open-topped and bottomed perspex enclosures in a burnt and an unburnt area. These enclosures were placed in an undisturbed site about 400 metres from the heating/substrate surface experiment. The sides of the enclosures were embedded approximately 1 cm into the soil. Enclosures were 30 x 40 cm in size with sides 12 cm high. Caged treatments were covered with wire mesh (mesh diameter ~ 3 cm) whilst controls were left open. Enclosures in burnt and unburnt areas were placed in inter-bush spaces adjacent to bushes of like species to the enclosed seeds.
Within each enclosure 50 germinated seeds of a species were placed. Seeds with radicles longer than about a millimetre were used. The radicles were buried in the soil surface using forceps. The soil surface was saturated prior to planting and again immediately after planting using a watering can and a very fine spray attachment. Seeds were moved in some enclosures by watering however the effect was similar to that anticipated and observed under heavy rain. The enclosures were on average watered twice weekly. The experiment was commenced in late May 1982, the burnt treatments being placed in an area burnt earlier in that month. Commencement times for differing species were varied, with *B. ericifolia* and *B. serrata* being started about a fortnight earlier than the other species, due to differences in germination times. Emergent seedlings were marked using matches and mapped within enclosures.

(iii) **Seed longevity experiment.**

Twelve batches of fifty seeds were placed in each storage as described in the introductory section above. On removal each batch was placed on a filter paper circle in a glass petri-dish. Germination was carried out on a laboratory bench at room temperature in a non-heated or air-conditioned room. Seeds were kept saturated with water and germination was scored as radicle elongation of $\geq 1$ mm. Scoring of germinations in each batch was done for about 10 - 12 weeks, after first watering.
(iv) Seed heating experiment.

As given above, burnt cones were selected from plants burnt at high levels of fire-severity in December 1980. For each species a separate site was located. In each of *B. ericifolia*, *Petrophile* and *Isopogon*, around twenty cones were collected from about five bushes. The cones taken were the highest on the respective bushes. The procedure was repeated in the closest available unburnt stand. Generally the cones taken were about 2 to 3 years old. Care was taken to select unburnt stands with bushes of the same stature and age as the burnt stands.

The procedure for cone selection in *B. serrata* was less readily controlled than in the other species, though an attempt was made to collect from branches of bushes and trees of a similar size between burnt and unburnt sites. Collections in all species were made within a few days of the burn.

Seeds of all species from burnt cones were readily extracted after drying in paper bags at room temperature in the laboratory for several weeks. Seeds from unburnt *Petrophile* and *Isopogon* cones were also able to be readily extracted in this way. I had already determined (Bradstock 1977) that mild heating of *B. ericifolia* cones (150°C for 10 - 15 minutes) had no effect on seed viability and facilitated seed removal. This treatment was used to extract seeds from unburnt *B. ericifolia* and *B. serrata* cones.
Extracted seeds were bulked for each treatment then placed in batches of fifty on filter paper circles in Petri dishes and germinated using distilled water on a laboratory bench. Germination was defined as radicle emergence of greater than 1 mm. Four replicates per treatment (burnt or unburnt) per species were used.

Results

(i) Seed box experiment

No movement of the seeds of any species was found in the unburnt area. After 57 days, all seeds were intact. In the burnt area, no movement had occurred after 12 hours, but in two replicates after 2 days some Petrophile seeds had disappeared and after 5 days in 3 boxes all Petrophile seeds had disappeared. In the other remaining box, no Petrophile seeds were removed.

Further batches of 20 seeds were each located near the 3 disturbed boxes on the soil surface. These were shielded with a crude plastic sheeting fence and watched constantly for several hours after placement in order to identify the animals responsible for the seed movements. No seeds were taken however during this time or at the end of the following day. A heavy rain shower then disturbed these batches and no further seeds were laid out.
(ii) **Seed enclosure experiment.**

In both areas *Isopogon* seedlings were the first to emerge (Figures 6.8 - 6.11). Within a month of planting hypocotyls of all the other species could be seen to have penetrated the soil. However in the unburnt areas between the 17/6 and 27/6 (Figures 6.8 - 6.11) extensive predation of both germinated and ungerminated seeds and emergent seedlings occurred, resulting in the virtual destruction of all seeds or seedlings in each species in both meshed and unmeshed enclosures.

No damage of this kind was observed in the burnt area, and the presence of mesh appeared to have no effect on emergence and mortality in any species. (Figures 6.8 - 6.11).

(iii) **Seed longevity experiment.**

In *B. ericifolia* and *B. serrata* differences with respect to both types of storages and times of withdrawal were absent (Figure 6.12 (a), (b)). The overall trend in *Petrophile* and *Isopogon* differed in that trends existed for apparent declines in viability mid-way through the storage period. These were later attributed to temperature conditions experienced in the laboratory during Summer (high temperatures suppressed germination - see Chapter 7). Differences between viability at the commencement and end of storage were negligible as were the effects of storage type.
(iv) **Seed heating experiment.**

The viability of seeds was compared using t-tests of mean numbers germinated, between treatments (Table 6.7). Differences in each species proved non-significant. It was concluded that burning of the cones at high levels of fire-severity had no effect on seed-viability.

**Discussion**

**Predation and removal of seeds and seedlings.**

Removal or destruction of seeds contrasted between burnt and unburnt sites. Predation of seeds (mostly in a germinated condition) was virtually absolute in the unburnt site in all species. The predator was unknown, and was small enough to gain access to the seeds through the mesh. It did not disturb either meshed or unmeshed enclosures. Aside from the contrast between burnt and unburnt areas, it would appear that variations may occur in unburnt areas. Predation occurred in the enclosures at the same time as the first heating/substrate was run. No obvious removal or destruction of seeds was observed after close scrutiny in this experiment, which was placed in an adjacent site. Several months later though, most emergent seedlings of all species in the uncaged pilot trial were destroyed by a predator. Predation of seeds or seedlings in unburnt areas may be varied according to the time taken for a predator to
locate them or in turn the searching ability or density of predators. Several aspects of the experiment may have affected the patterns of predations. Firstly in the unburnt areas the clumped nature of the seeds and seedlings may have ensured that once a box was located, total destruction by a predator would follow. As well, the boxes were generally located in open inter-shrub spaces and therefore may have been more easily found. Rates of predation for scattered individuals in more well covered microsites may differ from those measured here. In conclusion, seeds and young seedlings (up to 2-3 months after emergence), present in open clumped sites are likely to suffer a high level of predation in unburnt areas. By comparison, the risk in burnt areas is very low.

Effects of time since fire, both in the short and long term, on the chance of being eaten are unknown.

Where general access to seeds was heavily restricted (seed box experiment) removal of seeds occurred only in *Petrophile* in burnt areas. Removal though not complete was significant, though both the source of movement and fate of the seeds were unknown.

**Seed heating and longevity experiments.**

The experiments unequivocally demonstrated that seeds held at the soil surface in both burnt and unburnt sites were not subject to declines in viability over
14 months nor were seeds held in cones heated in a high-severity fire. Any seed losses due to fire in the short and long term must be concentrated after release from fruits. Fruits were effective insulators in the study species.

6.5 General Discussion and Conclusions.

The two chapters that follow deal specifically with post-fire seedling emergence and survival. In view of the results from the preceding chapter which indicated the levels of viable seed release in unburnt stands, it is necessary to discuss the likely fate of such seeds. Data in Chapter 5 showed that seed release may become significant in old stands (considerable times since fire). What are the fates of these seeds?

In both *B. ericifolia* and *Petrophile* the presence of cover was shown to be in some way detrimental to seedling establishment. In *B. serrata* and *Isopogon* seedling establishment was less affected or perhaps even enhanced in some unburnt conditions (eg: presence of litter in *B. serrata*). Therefore predation may be the crucial determinant of survival in these species, whilst in *B. ericifolia* and *Petrophile* its role is additional to that of cover.

Whilst destruction of seedlings in the enclosure experiment was virtually complete in all species, seedlings
growing individually may undergo comparatively fewer losses. It is likely that some emergents will survive in some unburnt situations even though a majority will be eaten. The opportunity to study the long-term survival of seedlings in unburnt conditions arose on several occasions and the results are briefly considered here.

In Petrophile, in the <1964 stand, seedlings which had freshly emerged were found in more open areas covered mainly with sparse leaf litter in early 1981. A sample of 23 of these was tagged and censused on subsequent occasions up until 1983. The average annual death rate was 19.6% which yielded a half-life of 3.5 years. Desiccation seemed to be the prime cause of death. In B. ericifolia, a cohort which arose in May 1983 in the <1964 site was followed for 9 months. The 23 seedlings which were originally tagged had declined to 3 by the end of the period. Many of these disappeared and the tags were dispersed indicating a high level of predation. Other B. serrata, B. ericifolia and Petrophile seedlings were found in sites under bushes which had been defoliated for cone-heating experiments in 1982. These were tagged and monitored for 10 months in 1983. Of the 41 B. ericifolia seedlings tagged, 14 died and again the evidence suggested predation was the main source of mortality. In Petrophile 37 seedlings were tagged, of which 20 died. Many of these were intact at death, indicating a substantially lesser role of predation. In B. serrata, only 8 seedlings were
found of which 7 died, all of which appeared to have been eaten. No adequate sample of *Isopogon* was located. Whilst these latter set of results were artificial in that they were drawn from the fringes of partially disturbed conditions, they indicate both the sources and rates of death in sites which have not been burnt for over a decade. In all species mortality was high and the conclusion that predation may be a crucial determinant of post-emergence survival is supported.

In summary, it is suggested that whilst mortality is high in these examples, post-fire seedling attrition (many instances given in Chapter B) may reach similar levels, though through differing causes. It may be concluded that the principal limitation on seedling establishment up to old ages may be the lack of seeds in all species, and in *B. ericifolia* and *Petrophile* and less strongly in *Isopogon* and *B. serrata* by the presence of cover. Whilst some authors have suggested in *Eucalyptus* species (Wellington 1981, O'Dowd and Gill 1984) that fire satiates seed predators by providing masses of seeds, in the study-species here, fire may satiate seedling predators, as seed predation appears to be unimportant.

The fates of surviving seedlings, further on in their lives in unburnt stands may be an altogether different story.
CHAPTER SEVEN: THE EFFECTS OF MOISTURE AND VARIED TEMPERATURES ON SEEDLING EMERGENCE AND PREDICTIONS OF SEEDLING EMERGENCE AFTER BURNS IN DIFFERING SEASONS.

7.1 General

Introduction

Numerous studies in a variety of vegetation types and localities have dealt in some way with comparisons either multiple or pair-wise, experimental or observational, between fires at different times, but few detailed analyses have been presented on the direct consequences of variation in time (or season) of burn on post-fire germination and establishment of seedlings. The focus has been primarily on vegetative recovery, in relation to time of burn.

The limited number of studies available which actually relate seedling response to time of burn are varied in their depth of analyses of causes. Orme and Lege (1974) compared emergence of Ceanothus sanguineus (Redstem ceanothus) in Idaho (U.S.A.) shrublands after prescribed burns in Spring and Autumn. In each case, emergence was delayed to the following Spring, cold stratification being required to break dormancy. The Autumn burns gave consistently higher levels of emergence, and this was primarily attributed to consistently higher intensity of fires in Autumn (drier fuels, higher unburnt temperatures) stimulating the breaking of dormancy of the hard
seeds of this species, large numbers of which are stored in the soil. These authors noted that whilst the bulk of emergence occurred in the Spring following each fire, small amounts of emergence occurred in subsequent years. No seasonal effects other than those affecting fire intensity were invoked as reasons for differential emergence between different times of burn. Kruger (1977) commented that the season of occurrence of fire in South African fynbos can be unrestricted under dry conditions. He cites the work of Jordaan (1949) and (1965) where it was suggested and shown in Protea repens (Proteaceae), an obligate-seeding shrub, that burning in Winter was unfavourable for regeneration as opposed to Summer burning. Jordaan (1982) showed that regeneration from seed after an April burn in P. repens and P. burchellii, a similar shrub, was limited, whilst in a cohabiting shrub species Leucadendron rubrum a more prolific response was recorded. The latter result was attributed to seed dispersal from a neighbouring unburnt area, something which presumably did not occur in the Protea species. The unfavourability of the period April - June for germination and hence recovery was attributed to a lack of available ripe seed (Jordaan 1949; loc. cit.) though Kruger (1977) notes that Lombard (1971) reported that Protea repens in stands of 10 - 12 years of age carried viable seeds stored in serotinous capitula that were four years old. Kruger noted that serotiny may be variable and this may account for his observations of P. repens regenerating elsewhere by seed after Winter burns. Interactions with other
variables controlling emergence are not discussed.

Purdie (1976) noted possible interactions between moisture and seasonal control in the emergence of leguminous seedlings following a fire in open forest in N.S.W., Australia. She hypothesized that the germination of *Dillwynia retorta* was limited to Winter by seasonal factors other than moisture and showed that co-habiting *Daviesia mimosoides* and *Acacia genistifolia* were less restricted and more immediately responsive after the burn to moisture. She concluded that differential outcomes may be possible after Spring and Summer fires respectively, the former favouring *Daviesia* and *Acacia* establishment over *Dillwynia* which would be delayed for up to six months, thus conferring some growth advantage on the former species. In turn, Summer burns would cause more synchronous timing of germination between species. Purdie concluded that seasonal factors as determinants of post-fire emergence and establishment of seedlings are likely to vary widely, hence the outcome after any given burn is likely to be the result of a unique combination of circumstances making generalizations and predictions about fire seasonality effects difficult.

In South Australian shrublands, Specht (1981) related the level of post-fire seedling density observed in the obligate seeding shrub *Banksia ornata* to the length of the Winter wet season. He thus indicated that this evidence of variability in emergence and survival
may be related to available soil moisture after a fire.

In Northern Australia, studies of grasses and their emergence after fires in varied seasons, have suggested that emergence may be influenced by rainfall in both a positive and negative way (Norman 1969). The time of exposure that seeds experience after the removal of overlying cover was found to be critical in tropical species (Norman 1963). In this region of Australia late dry-season burning was considered optimal for seedling emergence as it removed cover and directly stimulated seeds, just before the onset of high levels of moisture in the wet season. Wet-season fires can markedly affect grassland composition in this region (Stocker and Sturtz 1966, Stocker 1966) by destruction of individuals of such species as Sorghum intrans during its period of development just prior to flowering. This effect was noted in a wider context in the review of Tothill (1971).

Burbidge (1943) in her study of post-fire succession in Australian semi-arid Triodia pungens (spinifex) vegetation noted that the process of germination was related chiefly to soil moisture and:

"not to any particular period of the year"

though successful establishment of seedlings depended on the formation of a root system that enabled the plant to withstand the subsequent summer, something only possible in seedlings emerging early in the year.
Though knowledge of emergence at various times following burns is limited, the examples given above, highlight the varying interactions between time since a fire and available moisture, seasonal controls, viable seed availability and general site conditions in determining germination.

In this study a set of questions were formulated and investigated to gain a detailed understanding of seedlings in relation to the seasonal timing of fires. These were:

(1) What factors control emergence? Do these particular factors operate in a way that limits emergence to a particular season;
(2) How do these factors affect the level or amount of emergence (percentage of seedbank emerged)?
(3) How do the above factors vary with time of occurrence of a burn. If so, can the effects of burning in different seasons be predicted?

As discussed in the first chapter, burns occur across a wide range of seasons in the study area. This study was based on the premise that the full range of seasonal possibilities were to be considered. In any case the nature of seed release after fire in all the species studied (Chapter 5) dictated that newly released seeds after any given burn would be exposed to a range of differing seasonal conditions.
Rainfall averages for the Sydney region (Table 7.27) indicated that the distribution of rain is quite uniform throughout the year, though as Leeper (1970) noted the effectiveness of this may be limited in Summer. Nevertheless, efforts to determine the effects of rain and moisture on emergence were not confined to a single part of the year, as was done by Specht (1981), rather an attempt was made to study possible relationships in all seasons. In relation to the first of the questions given above, the themes that were studied are illustrated in Figure 7.1. As implied in Figure 7.1, the ultimate aim of the exercise was to model the effect of temperature and moisture interactions on emergence, and to examine and generalize soil-moisture conditions for seedling emergence from this model using simple climatic data for a relatively large sample (~50) of years. Bradstock and Myerscough (1981) showed that seeds of B. ericifolia faced periods of fluctuating moisture conditions between the time of their release and emergence of seedlings from them. Bradstock and Myerscough (1981) suggested that optimal timing of the bulk of seed release with high rainfall would yield high levels of emergence. These conclusions were based on an overall informal correlation of emergence with rainfall. Hence further studies needed to investigate fully the effects of soil moisture availability. Bradstock and Myerscough (1981) showed that emergences of seedlings in B. ericifolia differed between two burns in a way that suggested that ungerminated seeds lying on the ashbed (due to low rainfall)
were possibly subject to heavy losses through inviability or predation. Data presented in the previous chapter suggest this is not the case in this species following fire, though seed removal in Petrophile could have such an effect in that species. Therefore this part of the study was done to see if moisture variations governed by differing seasonal conditions (Figure 7.1) could account for variations in emergence of seedlings.

In summary, this work addressed the following themes as implied in Figure 7.1. Namely:

(a) The relationship between available soil moisture and seedling emergence in differing seasons;
(b) The relationship between rainfall and available soil moisture in differing seasons;
(c) The relationship between emergence and seasonal temperature variations;
(d) The implied interactions between these factors.

Control of emergence of seedlings by moisture and temperature.

Much of the focus on the direct control of germination and emergence by available moisture has been on arid and semi-arid zone species. The review of Mott and
Groves (1981), treats Australian examples of these studies, emphasizing the importance of considering interactions between moisture and other variables, such as temperature, an approach also deemed crucial by Angevine and Chabot (1979). Of particular interest is the importance Mott and Groves (1981) placed on the possible consequences of alternating cycles of wetting and drying and the hitherto dearth of Australian work done on this phenomenon. In one of the few detailed studies done, Watt (1974 and 1978) showed that for some grass species seeds could be brought to an intermediate state or threshold of germination by small intermittent increases of soil moisture and that subsequent optimal moisture conditions would yield high germination. This process was considered to be of importance on heavy clay soils where imposition of matric stress on seeds was rapid even after heavy rain, effectively limiting the possibility of germination and emergence after any single rainfall event. Though Mott and Groves (1981) pointed out that this process would be of importance in the arid and semi-arid zones, it would seem that it would be no less useful to consider it in higher rainfall areas, where rain may be more reliable and/or predictable but where nevertheless wet and dry spells continue to alternate. Anderson (1982) drew attention to this conceptual problem by his claim that the arid zone may be quantitatively but not qualitatively different from temperate areas, hence species may have similar traits between the areas in relation to qualitatively similar stresses or phenomena.
Other workers have approached the problem of wetting and drying effects both from the point of view of rates of germination and emergence and overall success in establishment (Heydecker et al. 1975, Berrie and Drennan 1971, Hanson 1973, Mott 1973, 1974, 1978, Akalehiywot and Bewley 1980, Baskin and Baskin 1982). The study of Baskin and Baskin (1982) represented an attempt to relate the results of experimental study of germination, emergence and establishment to the ecological circumstances of a species in the field. The general conclusions of these studies were that small rainfall events are cumulative in their effects on germination and, if imbibition time is taken into account, rates of germination and emergence are little different than for seeds exposed to continual high moisture. Baskin and Baskin (1982) were able to argue that enhancement of germination and possible survival of seeds exposed to wet spells may occur in Summer in the annual *Cyperus inflexus*, an inhabitant of north eastern U.S. forests. Furthermore, their study showed interaction with other factors such as temperature stratification and light requirement in the process.

It was consequently considered necessary in this study to look at not only the minimum duration of soil moisture for single periods necessary to stimulate emergence (e.g. Mott 1973, 1974, Silcock 1973) or given levels of emergence (Watt and Whalley 1982) and the variance of these periods in relation to other factors, but to investigate the effects of multiple periods of levels of
high moisture interspersed with dry spells. If possible, it was desired to judge the effects of varied length and frequency of such cycles. Because of the considerable differences substrates can impose on germination patterns in interaction with moisture and other variables (eg: Harper and Benton 1966, Kaufmann and Ross 1970, Watt 1974), it was resolved to examine moisture and temperature effects in both glasshouse and laboratory situations where soil and artificial substrates were used.

Previous work on temperature control of germination by Sonia and Heslehurst (1978) in four Banksia species, including B. serrata suggested that temperature optima for germination could be defined, (sensu Thompson 1970), and that, for B. serrata these suggested that in the Sydney area germination would be curtailed by temperature in mid-Summer and mid-Winter. Their model was based on mean maximum and minimum data for Sydney and hence was an indirect assessment of likely field conditions. Extrapolation alone of likely emergence on temperature data can be misleading without considering interactive factors. Winkworth (1973) and Watt and Whalley (1982) have emphasized that detailed measurements of microclimatic conditions at the soil surface are necessary before predictions and extrapolations of experimental results can be made in the field.
7.2 General Aims and layout of the study.

As implied in Figure 7.1, the model adopted required the estimation of soil moisture under varied inputs of rain and heating and evaporation. Examples of studies using a broadly similar soil-moisture model, such as Noble and Crisp (1980) or Preece (1971), have involved the use of functions relating moisture input, evaporation and evapotranspiration in order to predict moisture patterns and seedling emergence. These have required the use of computer packages such as the WATBAL package (Keig and McAlpine 1974) used by Preece (1971). The aim of this study was to examine the effects of the above factors on seeds and soils in a variety of situations in the field, glasshouse and laboratory to initially define their action. After this was done, a decision was made as to how best to integrate the results into a specific model of soil moisture that incorporated the elements in Figure 7.1.

A simple attempt at using a moisture and temperature model to predict the incidence of years with periods favourable for germination of seedlings of Banksia ornata and other South Australian heath species was performed by Specht et al. (1958). In this case, Specht et al. (1958) defined a temperature optimum for B. ornata (15°, 20° and 25° constant temperature treatments) and related the occurrence of these in the field to the yearly occurrence of heavy rainfall events sufficient to cause an inch or more of soil moisture storage. On
average in one out of four years (based on 48 years data), Specht et al. (1958) showed that optimal temperatures and rainfall sufficient to yield the moisture storages given above did not coincide.

This general method was used here, except that questions of comparisons of moisture and temperature in differing seasons, as a function of burn-time, were investigated. The work described below was oriented towards developing such comparisons and relationships between temperature, soil moisture and emergence, and can be split into 2 categories: glasshouse/laboratory studies and field studies.

(a) Glasshouse/Laboratory studies.

The effects of varying cycles of wetting and drying in soil on seedling emergence were tested under contrasting seasonal conditions in a glasshouse experiment. The seasons used were Summer and Winter. In each season, a set of six treatments plus a control were used. The treatments consisted of three different watering frequencies and two different watering intensities. The results were approached in two ways. Firstly, a comparison was sought between the overall levels of emergence and rates of emergence in watering treatments and seasons, the null hypothesis being that variations in watering and seasons had no effect on seedling emergence. Secondly, as a way of summarizing trends in soil moisture caused by differing wet and dry cycles and possible levels of emergence in a
form applicable and comparable to measures taken in the field and derived from climatic data, the relationships between percentage emergence and average soil-moisture data were examined in the four species.

The treatments used were:

**Watering intensities:** once weekly (low) and 3 repetitions per week at intervals of two days (high).

**Watering frequencies:** weekly, fortnightly and three-weekly.

All combinations of the above treatments were tested. The overall results were expressed as a percentage emergence of viable seeds so that emergence from differing batches of seeds in the field and glasshouse could be compared. Viability was determined by germinating samples from the same batches of seeds used in the experiment, in the laboratory. The data were intended to be analyzed using a three-factor anova with seasons included. In the Winter following the initial run of the experiment, two further treatments were performed using an extra low amount of water, applied once in a given week at either weekly or fortnightly intervals.

The experiments were carried out in an unheated glasshouse, though an air-conditioning system was present to limit ambient temperatures to a maximum of 40°C.
(b) **Laboratory studies**

Laboratory studies on the effects of temperature on germination were performed. For these, environmental cabinets were used. This limited the range of temperature regimes due to the number of available cabinets. The selection of regimes for testing cover the range of combinations of daylength and night/day temperatures that were found to be registered in the study area over different seasons. Unusual or rarely registered temperature and daylength combinations or constant temperature regimes were not investigated. Though the use of thermo-gradient bars, Thompson (1970), Grime and Thompson (1976) has become widespread, achievement of some temperature daylength combinations particularly at low or high temperatures appears to be difficult in some of the apparatus described in the literature. The cabinets provided realistic combinations in a reasonably reliable manner.

(c) **Field studies**

Components of the general model (Figure 7.1) were examined in the field in the aftermath of an array of differing burns. The principal aim was to relate observed variations in emergence to variations in soil moisture. Secondary aims were to relate emergence to effects of season of burn (separate from soil moisture), and time after burning.
This was done using multiple regression techniques, relating the dependent variable, \% emergence of viable, available released seeds to dependent variables, soil moisture, time since burn (in days) and season of burn (a weekly value for each burn on a yearly scale of 1 to 52 was actually used). Seed release in the sample stands of each species were measured as were the viability of samples of seeds taken from the burns so that emergence could be related to estimates of actual seed densities available.

An empirical model of soil-moisture changes in the surface layer was derived from a set of observations taken in the burns, of soil moisture content. The model related soil moisture potential to rainfall in differing months of the year, thus incorporating evapotranspiration effects.

The null hypothesis was that the above factors had no effect on seedling emergence.

In addition to the observations taken from the aftermath of fires in the study area, the data for emergence from the heating/substrate experiment and pilot experiment were analyzed in a similar way. These represented known inputs of seeds in closely spaced sites, close to the rainfall station from which rainfall data used in the soil moisture potential model were taken.

Multiple regression analyses using values of the soil-moisture-potential model were compared with analyses
using rainfall as a substitute thus providing some evaluation of the effectiveness of the soil model.

These analyses were performed to compare the type of relationship between soil moisture and emergence, derived in the glasshouse, with other indices of moisture such as rainfall. This was done to verify in general, the suitability of the soil moisture-emergence relationships in field situations. Detailed verification of the specific relationships derived in glasshouse was performed in a subsequent exercise. In this case, the predictions of emergence in the heating/substrates experiment were made using the glasshouse-derived relationships and estimated patterns of soil moisture. These predictions were then compared to the observed amounts of emergence.

7.3 Glasshouse experiments.

Methods

Soil was placed to a depth of approximately 10 cm in circular (20-cm diameter) pots. The soil was taken from a site in the field where the relevant species are found, and was sieved and sorted to remove stones and large pieces of wood, or charcoal. Fifty seeds were placed in each pot with only one species in any given pot. The experiment was arranged in six blocks on glasshouse benches in a conventional randomized block design. The first run was commenced at the beginning of April 1982 and was terminated in late August 1982. The second run was begun in
mid-December 1982 and readings were finished at the end of March 1983. However, watering treatments were carried through in 2 blocks until August, and results for the March-August 1983 period were recorded separately. As well, two replicates each of two additional watering treatments were run during the Winter of 1983.

Each watering consisted of two applications of 100 ml per pot performed in the early morning and late afternoon respectively. The additional treatments in Winter 1983 consisted of single waterings of 100 ml of water per day.

Seed viability was tested using three replicates of fifty seeds each, per species. These were germinated on a laboratory bench in petri-dishes.

Blank soil pots were arranged in four of the blocks for soil-surface-moisture measurements. Five pots per block were used, and from each a replicate was taken from the top 3 cm of soil, weighing about 20 grams. These were each wrapped in aluminium foil and the moisture content was determined gravimetrically. Drying was done in a forced-draught oven at 105°C for 48 hours (Reynolds 1970), and the results calculated as the percentage by weight of oven dry soil.

The moisture potential of the soil was estimated using the filter-paper method (Fawcett and Collis-George 1967). Briefly this involved measuring the moisture
content of filter papers inserted into soil samples of varying moisture content. After the samples and paper were allowed to equilibrate the moisture contents of the papers were measured and the soil moisture characteristic was derived from the calibration table given in Fawcett and Collis-George (1967) for the paper. Detailed methodology was similar to that given by Fawcett and Collis-George (1967).

Results

(a) Winter and Summer emergence in the glasshouse.

Total emergences in all species and the lengths of observations, are given in Table 7.1. In the Winter treatment, (Table 7.1 (a)) significant block effects were found in Petrophile in 2 blocks in the 3 week-low water treatment. This was due to rain-water leakage causing high emergence. The other blocks in this treatment had no emergences. Therefore, for the purposes of analysis the deviant readings were each substituted with values of 1%. In B. serrata (Winter), significant heterogeneity of variances amongst the treatments (angular-transformed values) were found by Cochrans testing. This was due to the high variation in emergence in the 3 week-high treatment (Table 7.1 (a)). To retain a balanced design both three-week treatments were omitted. The 3-week-low treatment had few emergences in any species (Table 7.1 (a)).
A comparison between Winter and Summer emergence was not performed due to the low overall emergence in the Summer treatment. However values for the 1-week-high treatments in *B. ericifolia* were compared, this being the only treatment to approach the magnitude of its Winter counterpart (Table 7.1). The results ($t = 1.252 \ p \geq 0.20$, d.f. = 10) showed that % emergence of viable seed was not significantly different between Summer and Winter in this treatment.

Analysis of variance of the overall Winter results (angular-transformed % emergence of viable seeds) were performed with the adjustments to the data given above. The results varied with species. In *B. ericifolia* only watering frequencies had a significant effect (Table 7.2) and S.N.K. testing showed that means of all three levels were different. In *B. serrata*, heterogeneity existed amongst treatments (significant interaction, Table 7.3), with the highest mean occurring in the 2 week-high and lowest in the 2 week-low. The untested 3 week-high mean fell between the two lowest means in the analysis (Table 7.1 (a)). In *Petrophile*, a significant interaction occurred (Table 7.4) and S.N.K. testing revealed that the lowest and highest means (3 week-low and 1 week-low) were significantly different from the other group. In *Isopogon*, both main factors were significant (Table 7.5). The means of the one- and two-week frequencies were not significantly different but both differed from the 3-week mean.
In Summer, no emergence occurred in *Isopogon* and emergences were restricted to the weekly-high and 2-week-high treatments in other species except for *B. serrata* where some seedlings emerged in the one week-low treatment (Table 7.1 (a)). Except for the comparison already discussed in *B. ericifolia*, these levels of emergence were low in relation to the Winter treatment, though a reasonable amount occurred in the *Petrophile* 1-week-high-water treatment. The most obvious feature of the comparison was the tendency of all species in Summer (except *Isopogon*) to have emergences in the 1-week-high treatment. In both Winter and Summer, this treatment kept the soil surface at a constant level of saturation and whilst this had a possible depressing effect in Winter, this was not the case in Summer.

The continuation of the Summer treatment into the Winter of 1983 gave totals which when added to the Summer data were in some instances substantially less than those in the corresponding treatments in Winter 1982 (Table 7.1 (a), (b)). Comparisons of angular-transformed means for individual treatments in all species (Tables 7.5) were carried out between means for all six replicates in Winter 1982 and means for totals of the two replicates maintained through Summer and Winter 1983.

These comparisons were non-significant in *B. ericifolia*, whilst some significance was found at high watering levels in all the other species (Table 7.5). The extra Winter
treatments (Table 7.1 (a)) gave results that differed slightly from the trends in the previous Winter in that the one-week-extra low treatment yielded totals either equal to or greater than the one-week-low treatments of the previous year. The 2-week-extra-low values were generally lower in *Isopogon* and *Petrophile* than the previous 2-week-low treatments (Table 7.1 (a)).

Differences in rates of emergence in the Winter treatments (Figures 7.2 - 7.5) occurred mostly between the 2 week-low and 3 week-high and the other wetter treatments in all species. The order in which these differences appeared varied amongst the species (Figures 7.2 - 7.5). Rates for Summer are not illustrated but were generally retarded by comparison.

Soil-moisture-content data were converted to water potential and the various samples were compared within Summer and Winter treatments to give an overall view of changes of water potential under the two differing watering intensities (Figures 7.6 and 7.7). The contrasts between Summer and Winter were great (Figures 7.6 and 7.7).

**Discussion**

As outlined in the introduction one of the aims of this work was to summarize the results in a way that related the proportions of emergence to averaged trends in
soil moisture as a way of comparing differing cycles of wetting and drying. This aim is explored here. Before discussing this, the effects of treatments can be summarized. Several points are worthy of mention. Firstly, the saturated (1-week-high) treatment in Winter yielded lesser levels of emergence than others. A depressing effect of saturation on emergence was noted. Secondly, in those treatments in Summer and Winter where emergence was low, considerable germination was observed. In many cases radicles and hypocotyls had deeply penetrated the soil but the cotyledons failed to emerge.

The comparisons of emergence between Winter 1982 and combined Summer-Winter 1983 indicated that in Petrophile, Isopogon and B. serrata under some high-moisture cycles, seeds which apparently were prevented from emerging by high temperatures for some months, may lose their ability to respond with the onset of cooler conditions. In other treatments and in B. ericifolia, non-significant but consistent, similar trends were present. It was concluded that as many of the seeds in these treatments were observed to germinate but not emerge in Summer, that prolonged inhibition of moistened and responsive seeds by external controls other than moisture may cause pre-emergence seed mortality. Generally, in all species, the trends were for the treatments which sustained a high number of days with the soil at or close to field capacity (Table 7.1 (a), Figure 7.6) to produce the highest levels of emergence. It is this theme that is explored below.
Rates of emergence in relation to average soil moisture levels.

This analysis provided a means of generalizing the complex set of trends generated in the experiment.

The rates of emergence of different proportions of viable seed were related to soil moisture. This was done by plotting the relationship between time to emergence and the proportion of time soil moisture was at or below field capacity (-0.3 bars W.P.) for each treatment. Plots for 10%, 25% and 50% emergence of seedbank are given for each species (Figures 7.8 - 7.11), based on the Winter treatments. Regression data are summarized (Table 7.6). Such plots related the different cycles of wetting and drying and their effect on emergence. The times of emergence were logarithmically transformed (log$_{10}$).

In Petrophile, Isopogon and B. ericifolia the data (log-transformed) suggested that a straight line would fit. However, in B. serrata this was not the case, and two straight lines were fitted by eye to the 25% and 50% emergence data. No formal regression was used in these levels. Generally, in the first three species, the lines were a reasonable fit, though consistently in all species the weekly treatments deviated the most, indicating the characteristics of this treatment hastened emergence beyond the time expected from the simple proportion of days at field capacity.
Relationships between species varied considerably as suggested by the differing slopes of the lines with *Isopogon* showing the narrowest range of response times and *B. ericifolia* showing the widest. Within species, slopes of lines for differing emergence levels varied. In all species, the higher proportions of emergence were restricted as moisture proportions decreased. In *Isopogon* and *Petrophile*, 25% emergence was possible over the same moisture range as 10% emergence. The moisture range at which 50% emergence was achieved was truncated below 0.50 in *Petrophile* and 0.60 in *Isopogon*. In both *Banksia* species, greater sensitivity was shown with the cut-off being below 0.60 for the 25% and 50% levels of emergence. For the higher emergence levels, the bottom of the plotted lines represented the approximate boundary between moisture proportions able and unable to stimulate those amounts of emergence. For *B. serrata*, failure to show 50% emergence under constant saturation meant that an area of exclusion existed for this level of emergence at very high moisture proportions. This may be due to fungal infection of the species under these very high moisture contents.

Because of the limited results obtained for the Summer treatment a similar analysis was not attempted.
Conclusions.

The glasshouse results showed that emergence may be limited in Summer months, except under very high soil-moisture conditions. This implied some temperature control over emergence.

The relationships between soil moisture proportions and time to emergence show that the effects of moisture are cumulative with repeated pulses of high soil moisture stimulating activity in seeds. This accords generally with the hypothesis outlined by Watt (1974) regarding seeds stored on the soil surface and their cumulative response to successive rainfall events. It appeared reasonable to describe thresholds in times for different moisture proportions (proportions of time spent at field capacity) that produced given levels of emergence. Such a model implied that seed response in any given batch of seed is variable in that some seed will emerge under a particular moisture regime whilst some will fail to respond indefinitely if that moisture regime is maintained.

The design of the experiment was limited to using constant applications of given watering intensities. Variations in intensity within treatments may have been of further use in relating the results to real situations in the field.
Despite this limitation the results formed a basis for extrapolation into the field particularly as they were based on behaviour of seeds on soil. They gave a basis for possible predictions of emergence under known or simulated soil moisture conditions. The central aim of the field study was to verify the type of relationship explored here, under real field conditions.

7.4 Laboratory studies.

Methods

The possible inhibition of germination and emergence was indicated in the Summer glasshouse experiment. This was studied in an experiment performed in growth or environmental cabinets, which were used to vary the temperature regimes on a diurnal cycle.

A simple temperature experiment was initially carried out to test the effects of four temperature ranges representing the likely ambient extremes measured in the field and seasonal intermediates. The temperature regimes used were 30/15, 25/15, 20/12 and 15/5 degrees celsius, (hot, warm, cool, low, respectively) on the following day/night (light/dark) cycles: 13/11, 12/12, 11/13 and 10/14 hours respectively. For this experiment germination was carried out in perspex boxes designed to stabilize humidity between temperature treatments and chiefly to provide a large reservoir of water that would prevent the germination substrate from
drying out, particularly in the warmer treatments. This was done by drilling holes in the top of the box through which wicks of paper were suspended into the water below. Filter papers (Whatman 42) were used as the substrate for seeds and these were placed over the wicks. The level in the reservoir was maintained constantly. A lid was placed over the top of the box, each box containing four filter paper circles on which were each placed 50 seeds. A circle in each box was allocated to a species, hence all boxes contained a single replicate of all four species. Four boxes per cabinet were used, the whole experiment being subsequently repeated once.

Germination was scored as radicle emergence greater than 1 millimetre. Germinated seeds were removed on scoring. The experiment was run for ninety days on each occasion.

Results

Checks of filter paper moisture over the diurnal cycle between treatments showed that no difference occurred in the degree of saturation of the papers. Results for the two runs of the experiment differed little and were pooled in all species.

High temperatures inhibited germination in all species (Table 7.7). Inhibition was complete in Isopogon and Petrophile and partial but substantial in the Banksia species.
Maximum germination in all species occurred in the coolest treatment (Table 7.7), with other treatments varying according to species (Table 7.7, Tables 7.8 - 7.10). Rates of germination varied between species (Figures 7.12 - 7.15) according to treatments. In the Banksia species, there was little overall difference between treatments, though times of initiation of germination differed with both the cooler treatments giving the longest delays (Figures 7.12 - 7.15). In Petrophile and Isopogon, greater disparity was found between rates for differing treatments (Figures 7.14 and 7.15). The coolest treatment produced the most rapid germination in Petrophile but not in Isopogon (Figures 7.14 and 7.15).

Discussion

The temperature responses threw into relief, results from the glasshouse. Clearly germination and emergence are suppressed under high temperatures, falling well within the range recorded at the soil surface in Summer (see Figure 7.16). The patterns found in the Summer glasshouse treatment are in agreement with the laboratory results in terms of between-species responses. The degree to which high moisture availability facilitated emergence in Summer declined in the order: B. ericifolia > B. serrata > Petrophile. When both laboratory and glasshouse results were considered it appeared that Isopogon was effectively prohibited from emerging in Summer.
In comparison to the results for P. serrata given by Sonia and Heslehurst (1978), these results conflict in the indicated optimum and response to low temperatures, but are in agreement with response at high temperatures. As well, the peak germination (uncorrected for viability) was here somewhat higher (89% vs 60%). The minimum temperature combinations used by Sonia and Heslehurst were 10/10, and 14/14 degrees celsius which yielded overall germination of between 5 and 30 percent. Their optimum (defined as 90% potential germination) occurred for combinations between 18 and 24 degrees for both day and night. As no similar treatment in this range were used no direct comparison can be made except to emphasize again that the lower temperatures used in the treatments were obviously optimum. Sonia and Heslehurst found dormancy induced above 30 degrees, and their conclusions with regard to the restriction of germination during Summer are endorsed here. Their prediction of the likelihood of germination flushes at different east coast localities was not borne out in my results. They concluded that germination would be prevented in January, February and July at Sydney, based on mean recorded monthly maxima and minima. Whilst the results here indicated that germination in P. serrata is unlikely but possible under Summer conditions, a mid-Winter optimum is strongly indicated and emergence was observed in July in the field.

This discrepancy came about principally by extrapolating data obtained for seeds collected from Stradbroke
Island in Queensland. Variation between populations of seeds used here and those from the above location may account for the observed differences. Whilst they conceded the possibility of population effects, they did not examine them. Similarly, it would then be unwise to extrapolate the results for the species studied here further than the regional and perhaps habitat boundaries of the study. The results of both studies indicate that the control of germination in *B. serrata* at high temperatures may be constant between seed populations but that the optimum and lower limits may be flexible.

7.5 Field studies

Methods

Seedling emergence after burns.

Sites were selected in the aftermath of various unplanned fires and these are referred to in chronological order as burns I (December 1980), II (April 1981), III (July 1981), IV and V (May 1982).

In the obligate seeding species, *B. ericifolia* and *Petrophile pulchella*, sampling was carried out specifically in dense stands using randomly located quadrats. In *B. serrata*, areas were deliberately located under mature trees carrying significant numbers of cones. A similar method was tried in *I. anemonifolius* though with less success.
The sampling pattern for the latter species was done because their usual pattern of distribution is one of scattered mature individuals in most sites.

In *B. ericifolia* and *P. pulchella*, the quadrats were arranged along transects, which in turn were positioned deliberately in dense areas of the chosen stands. Each transect contained twenty circular quadrats, with quadrat size being standardized at 0.1 m² in area. Quadrats were constructed of wire and fixed with metal pegs to the ground, providing stable permanent areas for recording of emergence and establishment.

In *B. serrata*, areas of varying size were used for sampling, according to the size, morphology and density of trees located within or around them. Because these areas were large and emergents were fairly sparse, mapping of seedlings at each visit, as carried out in the quadrats for *B. ericifolia* and *Petrophile*, was not done. Instead, individual seedlings were marked with small flags and numbered. A similar method was used for *Isopogon* in Burn I, though with small quadrats of fixed size clustered in groups of four around large burnt bushes. Emergence, however, was found to have occurred outside the quadrats in all cases and observations were abandoned. Difficulty was encountered with finding adequate numbers of bushes in some other burns and hence analysis of emergence in this species in the field was not done. Methods for the construction
of the heating/substrate experiment near Warrah are given in the previous chapter. In this experiment all seeds were laid out at the beginning of each treatment in the experimental quadrats. At sites of all the burns and at the experimental site, observations were carried out as frequently as possible, though the interval between observations was not constant and was large in all cases after the initial twelve months at each site had elapsed. At each visit, newly emerged seedlings were recorded and mapped or tagged, survival of previously scored seedlings was recorded and samples of soil (for determination of moisture) and, soil surface and ambient temperature, rainfall and seed release were taken according to the methods given below.

**Seed-Release Estimation.**

Two methods were used. In burns I and II, cones of each species were collected at regular intervals and removed to the laboratory where the proportion of empty follicles was determined. At the *B. serrata* site in Burn I, the seedbank was located high in the canopy of old large trees and no collections were made but estimations based on casual observation and extrapolation of results in other burns were made. At the sites where cone collections were made two samples were drawn on each occasion from two heights (approximately 1 metre and 2 metres) in the canopy in *B. ericifolia* and *P. pulchella* stands. Samples were drawn from stands adjacent to but away from
The transects or marked areas, but care was taken to ensure that the burn and scorch heights in both stands were as similar as possible.

The alternative sampling method involved labelling of sets of individual cones, which were left in situ, and marking of the follicle/bracts which had shed their seeds. Marking was done initially within a fortnight of each burn and was continued as regularly as possible afterward. Marking of empty follicle/bracts was done using white typing correction fluid which proved resilient over 12 + months. This method gave a more detailed view of seed release, excluding error induced by sampling batches of cones through time. Ten cones were selected at each site, at two different heights (approximately 1 metre and 2 metres, respectively) in B. ericifolia and P. pulchella on bushes directly adjacent to the quadrats.

**Seed-viability estimation**

A mean value for each species was taken from viability trials of mixed batches of seed drawn from several populations for each species. The mean values were from varying numbers of replicates for each species. Each replicate was of fifty seeds. For the heating/substrate experiments, viability was directly estimated for the batch of seeds used with four replicates each of fifty for each species. In all cases, seeds were germinated on Whatman 42 filter
paper circles in glass petri dishes on laboratory benches. The seeds were kept saturated until germination had ceased.

**Seedbank estimation.**

For *B. ericifolia* and *P. pulchella*, the number of cones in a one-metre wide strip along each transect were counted. The mean number of follicles per cone was estimated from a random sample of ten to forty cones. A correction was made for open follicles at the time of burning, based on measurements made elsewhere on unburnt cones. After correction, for viability, the seedbank per square metre (or per area in *B. serrata*) was estimated.

**Soil-moisture estimation.**

The percentage moisture content was estimated gravimetrically. Collection was made using a teaspoon, followed by wrapping in aluminium foil (Reynolds 1970). Samples of around 20-50 grams were taken (after Reynolds 1970) from the top 2 cm of soil, the 3 - 6 cm level and from the ash layer at each site. Five replicates of each sample were removed on each occasion and dried in a forced draught oven at 105°C, for 48 hours. Weighing was done before and after drying and the results were expressed as percentage moisture of oven-dry soil weight.
Samples of soil and ash were separately removed from each site for the determination of their moisture characteristics (water potential versus soil-moisture content) using the filter-paper method.

Measurements of rainfall, soil and ambient temperatures.

Over the duration of the study daily rainfall and temperature maxima and minima were recorded at the Crommelin Field Station at Pearl Beach, a location central to all sites (see Appendix 2). As well, rain gauges were placed at each site for varying lengths of time. This was done principally to check the correspondence between the rainfall totals at the sites and those totalled at Pearl Beach. Rainfall patterns at the sites generally corresponded to those experienced at Pearl Beach, though intensity of rainfall varied.

'Mechanical thermohydrographs were similarly placed at each site for varying periods to ascertain daily seasonal ambient temperature profiles close to the soil surface. These were deliberately placed in open unshaded positions, typical of each site. Some difficulty was encountered with directly measuring daily profiles of temperature on the soil surface. No adequate reliable equipment was available for this purpose and therefore some measurements were carried out using a hand held mercury thermometer. These were done in the Winter of 1983 at differing times
on differing days. Similarly, measurements were done in pots of soil in the glasshouse in the Summer of 1982/83. These instantaneous readings were all done on bare soil surfaces in unshaded positions. In the glasshouse, readings on wet and dry soils were taken.

Some of these results are summarized in Figure 7.16 a, b, c. In Summer (Figure 7.16 a) under direct sunlight, dry soil surface temperatures reached over 50°C. In most cases dry soil surface temperatures exceeded the ambient measure. By contrast wet soil temperatures were often below the ambient. Winter measures in the field gave a similar pattern, though the soil-ambient temperature difference was less marked (Figure 7.16 b). In Figure 7.16 c, the seasonal ranges of durations of daily temperatures are illustrated, for 3 days characteristic of Winter, Spring and Summer, as experienced under burnt conditions (Burn I). These data were used as a basis for the treatments in the growth cabinets, described above.

Soil-moisture-potential model.

As seed of the species under study germinated on or near the soil surface (0 - 3 cm) a model of water availability was derived for the soil surface layer. This was done empirically using the soil moisture content data taken at each sampling date. Moisture histories for each site
were drawn up and conversion to surface soil water potentials were performed using the moisture characteristic curves derived for each site. Drying curves of soils were then formulated after rainfall events of differing intensity by pooling moisture-potential data across sites and differing sample times. Any suspect data at sites influenced by falls not recorded at the rainfall station were rejected. These curves defined water potential at varying days after the cessation of each rainfall event. The rainfall events were based on daily figures measured at the Crommelin Research Station (Warrah) at Pearl Beach. Drying curves for three different classes of soil surface condition were derived. These were burnt bare soil, burnt soil with a cover of ash and litter and for ash and litter alone. The data used in the first class came from Burns I, IV and V sites and from measurements made in special heated plots in the heating/substrate experiments. Some sites in Burns II and III had considerable coverage of litter and partially burnt litter due to the generally lower intensity of the fires in them. These data were used to derive the second of the above classes.

Rainfall events were divided into two categories defined as high intensity and low intensity. These categories were respectively defined as where:

(i) rainfall exceeded 10 mm on any single day regardless of registrations on any adjacent days;
(ii) rainfall was less than 10 mm on any day and
where rain on any adjacent day was of a similar magnitude.

The drying curves derived from the soil data were assembled for various pairs of months with similar evaporation characteristics as measured at the Sydney Bureau of Meteorology station. These were December-January, February-November, March-October, April-September, May-August and June-July. From these plots of raw data a relationship was derived between the number of days the soil remained at field capacity (water potential = -0.3 bars) from the onset of the rainfall event and after the cessation of rainfall for each type of rainfall event, in each pair of months. The number of days in any month-pair, for either rainfall class, spent at field capacity was termed for convenience the number of "moist soil days" or M.S.D.

Results

Overall emergence after burns.

In *B. ericifolia* and *B. serrata*, most emergences occurred in the first 12 months after the various fires (Tables 7.11 - 7.15). Seedbank data for all species are given in Table 7.16. In *Petrophile*, subsequent emergences were high relative to the amounts in the first year (Tables 7.11 - 7.15). In all species, differences in intensities between burns at the sample sites can be gauged
by the comparative trends in seed release (Tables 7.11 - 7.15). In all species considerable differences in overall % emergence of viable seeds were apparent at various intervals after burning. Within-site variability between replicate transects was high in B. ericifolia and Petrophile (Tables 7.11 - 7.16).

Soil-moisture Potential.

Considerable variation was found in bare-soil drying curves based on raw data (Figures 7.17 - 7.22), especially in the low-intensity rainfall category. Data for soils covered with litter and ash were more variable and are not presented here nor were they used for further analysis. Due to variability and lack of data points in some months in bare soil the M.S.D. model was fitted by eye using the data and personal impressions from the field as an extra guide. (Figure 7.23). Extra criteria were added to cope with very low-rainfall events (Figure 7.23). These were based on personal observations.

Data for the years 1981-1983 inclusive (Appendix 2) for rainfall at Pearl Beach were then examined and the numbers of M.S.D. per week and calendar month were calculated (Appendix 3).
Discussion

Soil-moisture potential

Despite the limitations inherent in the relationships assembled above they represent an improvement in the ad-hoc approach used by most authors who have noted the duration of moist conditions after rainfall events. Mott (1974) noted that after 25 mm of rainfall (intensity unstated) the soil surface was likely to remain at field capacity for approximately 48 hours whilst a Winter fall of 15 mm (intensity unstated) would give an equivalent water potential for a subsequent period of 4 to 5 days. These observations were for the arid Murchison Region of Western Australia in sandy loams. Mott et al. (1976) provided drying data for soils of varying texture which showed that a sandy soil dried to wilting point after rainfall of 72 mm (over 2 days) in 48 hours, in Summer. These data were for burnt and covered pasture near Katherine in the Northern Territory. Allowing for the differences in latitude and solar radiation as well as likely humidity and their influence on evaporation, these data accord reasonably with those presented here for similar sandy soils.

The model of M.S.D. (-0.3 bar potential) was derived principally for use as a reasonable index to which to relate emergence. It can be seen from Figures 7.17 - 7.22, that during drying following a given type of rainfall, lower water potentials existed for widely differing times between seasons.
Comparisons between the model developed for the field (Figure 7.23) and the duration of soils at field capacity in the glass-house (Figures 7.7 and 7.6) showed good congruence between the differing rainfall levels and watering levels in the relevant months in which measures were taken.

Overall trends in emergence, rainfall and soil moisture

*B. ericifolia* and *Petrophile*.

Comparisons of emergence data with soil moisture and rainfall data (Tables 7.11 - 7.15) calculated on a monthly basis after each burn suggested that emergence occurred when rainfall exceeded 400 mm in any 3 month period or when more than 200 mm occurred in any month. The same responses corresponded to values of 40 and 20 M.S.D. respectively. In all sites, these trends held to varied degrees in the first twelve months after each fire with some exceptions:

(i) In Burn I, for both species, little or no response was found to high-moisture levels (rain and soil) in the tenth and eleventh months;

(ii) In Burn II, little response in both species was found to high-moisture levels in the 2nd month;

(iii) In Burns IV and V, little response occurred
to high moisture encountered in the third month whilst emergence seemed to be more greatly stimulated by high moisture in the fifth month.

Generally, emergence did not occur in the months of January and December when these months fell in the first 12-month post-fire period, and though estimated M.S.D. values for these months were low, rainfall was high, indicating it was of high intensity. (see month 2 of values in Burn I, January 1981, and month 9 and 6 values for Burns II and III, January 1982). Very low rainfall occurred in December-February 1982/83 and M.S.D. values were low.

Differing rates of emergence after initial imbibition between Banksia and Petrophile possibly accounted for differing temporal patterns in the pulses of emergence following the moisture events described above.

Generally Petrophile was slower to respond. This was confirmed in the glasshouse/laboratory studies.

As noted above, emergence after 12 months varied between the species with no emergence occurring in all but one site for B. ericifolia but with considerable emergence occurring in Petrophile (Tables 7.11 - 7.15). Where emergence after 12 months occurred in both species the relationship between moisture (rain and soil) suggested above, seemed similar. Generally Petrophile showed a slower
rate of seed release hence more fresh seeds were being released in the second post-fire year. This may account for the greater response in this species in the second year.

*B. serrata*

Though the relationship with moisture given above seemed to hold with this species, one site was somewhat anomalous in the synchrony of initial emergence and high rainfall/M.S.D. (Table 7.12). In Burn II, initial emergence came after 2 months of low rain and estimated M.S.D. values. In Burn I, emergence occurred initially during a month of very high rainfall and M.S.D., after a preceding month of high rainfall and low M.S.D. (January 1981), but during a month of very high rainfall and M.S.D. A similar pattern occurred after Burns IV and V, though emergence was delayed the longest in these burns. Emergence was generally restricted to the first 12 months after the post-burn; in each case there was a strong initial pulse followed by only small amounts. The results indicate a lesser requirement in terms of moisture than the other species and/or a rapid rate of emergence in response to high moisture levels in the first 12 months. The overall difference in emergence between Burns I and II and Burns IV and V may have something to do with the delayed start to emergence experienced in the latter sites and the very dry conditions experienced in months 7 to 10. The contrasting wet conditions in months 11 and 12 did not greatly stimulate emergence as in the other species, indicating that seeds of *B. serrata* may lose their ability to respond after a length of time on the ashbed.
General Discussion and Summary

It was concluded that an initial explanation of the results could be made using rainfall and the M.S.D. estimates, though the results were somewhat variable especially between species. Emergence was shown to be possible in all months other than January and mid-late December. This conformed with results of temperature experiments in the laboratory and the Summer glasshouse experiment. In the field also, these results indicate that germination and emergence was restricted by high Summer temperatures.

A number of hypotheses can be put forward to explain the high within-site variability (and between-site variability especially in *B. ericifolia* found in Burns IV and V). Firstly, considerable shifting of seeds on the soil surface may have occurred. The movement of ash and litter suggest this is likely, but the positioning of quadrats was made so that, in *B. ericifolia* and *Petrophile*, density of the stand surrounding them was uniform. This was not possible in stands of *B. serrata*, and losses in seeds from the quadrats would have most likely exceeded any inputs from the surrounds. At best the seedbank assessment in the transects and areas was an index of approximate seed availability. Whether this held in reality is unknown. Alternatively or in addition to this explanation, extreme variability in seed viability may have been responsible. This heterogeneity would have had to occur on an area or bush basis. Such variability was shown to be unlikely in other stands (see Chapter 4).
Overall, in *B. serrata* and *Petrophile*, where differences in emergence between burns after 12 months existed, emergences were lower in Burns IV and V (May 1982 burn date). Overall these burns experienced the lowest rainfall and estimated M.S.D. values, especially in the first 9 months after fire (Tables 7.14 and 7.15). Later periods of high moisture at the end of the 12-month period and beyond did not stimulate either of these species at this site. In *Petrophile*, some response occurred but the overall figures are lower than in other burns.

It would seem that an hypothesis that related high moisture levels to an optimum time for post-fire emergence may be framed. At least following fires of moderate intensity, high available moisture at around six months after burning may be optimal. This figure may be less in *B. serrata*. The next step was to test the variables outlined in the introduction using multiple regression. The trends given above were thought to be suited to modelling, using linear regression.
Further analysis was attempted using multiple regression techniques. This was done to investigate the degree of control between emergence and moisture (both rain and soil) on a fine scale and as a basis for establishing the usefulness of these variables as predictors of emergence. In addition, date of burn within the calendar year, and time after burn were included as variables. The independent variables were related to individual observations of emergence (dependent variable) in each species, in each burn. Emergence of seedlings was expressed as a percentage of available seedbank. A set of 22 different equations were generated for each species, each equation differing in the type of moisture variable used but having a constant set of values for the dependent variable and the other two independent variables. The independent moisture variables consisted of two sets of differing rainfall or soil moisture data. Rainfall values for each of six weekly periods prior to each emergence observation were used separately along with the progressive weekly sums of rainfalls: that is, weeks 1 and 2, weeks 1, 2 and 3, weeks 1, 2, 3, 4, weeks 1, 2, 3, 4, 5 and weeks 1, 2, 3, 4, 5, 6. Each differing rainfall term was used so that a set of eleven equations were developed. Similarly M.S.D. values were calculated for each week prior to each observation over six weeks. The M.S.D. values for each week were progressively averaged in the manner described for the sum of rainfall and each of these variables were used. For each
equation developed, the week in the calendar year in which each of the five burns occurred was scored. For convenience, the year was begun at the beginning of December (Summer), Week 1 being the first week in December and Week 52 being the last in November. The time of each observation after the relevant burn was scored in days with the burn day being Day 0. Available seedbank was estimated from the relevant seed-release data for site/species, however it was decided to express percentage emergence at each site as the amount of viable seedbank. Seeds already emerged were subtracted from the estimates of released viable seedbank at any given sample time, 14 days before the sample date. This was done to allow for a minimum period of adequate exposure of all seeds to moisture, especially in the two weeks prior to each sample observation.

All observations up to around 500 days post-fire, were used in each species, later observations being omitted because the interval between samples was too large to realistically expect that any observed emergence would have been attributable to the events six weeks prior to sampling. Analyses were performed using the SPSS package (Nie et al. 1974). Percentage emergences were angular-transformed for the analysis. Values for individual transects in each burn were entered as replicates at each date of sampling. Proportional M.S.D. values were also angular-transformed for analysis.
Results

The relevant equations for each species are summarized in Tables 7.17 - 7.19. None of the equations explained a major proportion of the variation in emergence. Overall, estimated M.S.D. values accounted for little more of the variation than did rainfall (Tables 7.17 - 7.19). Time and burn date, where their entry was significant, accounted for little of the explained variance, except for time in *B. serrata*. A breakdown of species results is given below.

**Banksia ericifolia**

Rainfall in individual weeks accounted for more variance than any of the cumulative totals with rainfall in week 5 the best predictor of emergence. Neither burn nor sample time was significant when entered into any equation.

Soil moisture gave a higher $r^2$ for the average M.S.D. for all six weeks than any other soil moisture variable. When soil moisture was a variable, burn time was consistently significant, the negative slope indicating that emergence for any given moisture and sample time combination was slightly higher in the earlier burns, most likely Burn I. Overall average M.S.D. was a better predictor than cumulative or individual weekly rainfall.
**Petrophile pulchella**

A larger amount of variance was accounted for in the Petrophile equations, generally by the moisture variable and to a lesser degree, burn time. Sample time was consistently non-significant. As with *B. ericifolia*, rainfall in week 5 was the best predictor, with cumulative data offering inferior $r^2$ values. Again average M.S.D. for all six weeks gave the best soil moisture prediction though this was slightly below the week-5 rainfall $r^2$. Burn time was again negatively correlated with emergence as in *B. ericifolia*, though the amount of variance accounted for was very small.

**B. serrata**

In this species most variance was consistently accounted for by sample time, irrespective of moisture variables. The negative slope, though shallow, indicated that emergence was stronger sooner rather than later after each burn. The pattern of highest moisture $r^2$ for the other species was reversed in *B. serrata* with cumulative rainfall in all six weeks giving best prediction and M.S.D. in week 6 giving best soil prediction. Moisture $r^2$ values were low. Burn time was non-significant.
Discussion

The maximum values of $r^2$ for each category of moisture variable were listed above, but, in all species for the individual weekly entry of the variables, the optimum values were preceded with values only slightly less, indicating that inputs of moisture in differing weeks have some effect. This could imply differing rates of response at different times (possible seasonal influences on emergence rate) and/or polymorphism amongst a given batch of seeds in their rate of emergence.

The similar overall responses of *B. ericifolia* and *Petrophile* to the two moisture variables indicate possible like overall rates of emergence and thresholds of stimulation. The lesser predictive power of cumulative data (for rainfall) over that of individual weeks suggested that as a stimulus to emergence individual weekly rainfall may be a useful predictor. In contrast the best mean soil predictor (average M.S.D. for all weeks) may be interpreted as showing that maintenance of some average threshold level of moisture in the soil through the period of emergence may be necessary for the successful completion of the process. The significance of burn time, despite the very low level of variance accounted for, may be interpreted conservatively as indicating more favourable site conditions for emergence, namely in Burn I.

For *B. serrata*, the less clear-cut relationship between moisture and overall emergence after burning, that
was noted above, was reflected in these results. This may be the result of considerable variability amongst batches of seeds to given levels of available moisture. The response was greater soon after burning, perhaps as a result of changes in site conditions due to regenerating cover in the various strata and/or a possible decline in response of seeds that had lain on the soil for a considerable time. This trend was significant in the other species (though with low $r^2$ values). The results from the previous chapter showed that losses in viability and predation in the Banksia species may be small or absent, therefore the hypothesis that seeds may lose their response or die from some other cause due to habitat changes may be valid. This result conformed with trends in the glasshouse.

The following limitations of this study may account for the low overall amount of explained variance in emergence:

(i) Rainfall and hence M.S.D. estimates were based on data remote (up to 10 km) from some sites. The moisture regimes used may have been in error compared to those which actually occurred at the sites;

(ii) The moisture model used was developed for bare loamy sand soils. Some sites such as in Burns II and Burn III developed considerable litter layers due to scorch induced leaf fall not present in the aftermath of the other burns. Litter effects
on emergence in *Petrophile* and *B. serrata* were noted in the previous chapter (though overall levels of emergence may not have been affected in *B. ericifolia* rates of emergence and may have been altered in this and other species).

(iii) Site-soil hydrologies may not have been alike due to profile and textural differences. Though care was taken in ensuring homogeneity of site slope and stands, differences in soil types occurred and, in some sites in Burns II and III, water-logging occurred to a degree not found in other sites and burns. This was not apparent at the time of site selection. Combined with possible extraneous rainfall influences (falls not recorded at Warrah or of differing intensity), the model of M.S.D. for loamy sands may have departed greatly from reality in these sites on some occasions.

A possible change in either the type of multi-variate analysis or the use of other climatic data may have given better results, though the use of extra climatic data which may have been related to rainfall would have violated the assumptions of independence between independent variables.

A further limitation may be that seeds responded to moisture tensions less than field capacity (-0.3 bars), though the use of this index proved sound in the glasshouse.
Ultimately the factors which caused the high levels of within-site variations between transect replicates may have been responsible for a large part of the variation. These may have been related to the methods of seed-release and seedbank assessment and also within-site variations in soil textures.

In an effort to constrain some of the above sources of error, a further similar analysis was carried out on emergence data for both the pilot (commenced May 1982) and main (commenced November 1982) heating/substrate experiment. As well, these data allowed some assessment of *Isopogon* emergence in the field.

**Analyses of emergence in the heating/substrates experiment.**

**Methods**

The emergences through time in this experiment (Tables 7.20 and 7.21) were treated in a similar manner to the above sites. Greater congruence existed between the rainfall and this experimental site in terms of distance and periodic checks of rainfall registrations, the site being 2.5 km from the field station. As well, the experimental layout gave greater control over variations in seed movements and within-site soil-type heterogeneity. Problems with seed release calculations were overcome by the single sowing of seeds.
Data for treatments with heated and unheated soils, either bare or with ash (see previous chapter) were used as these treatments had no effect on overall emergence (see previous chapter), though effects on rates of emergence were possibly present. This was one source of error in the analysis that was accepted. The treatments yielded four and twelve replicate readings of emergence respectively for sampling date.

Results

An increase in overall variance \( r^2 \) accounted for by the equations occurred in all species and though variable in magnitude (Tables 7.22 - 7.25), it was greatest in *B. ericifolia* and slight in *Petrophile* and *B. serrata*. Maximum values of \( r^2 \) for emergence of *Isopogon* in relation to rainfall and soil moisture were comparatively high though in no equation was the majority of variance accounted for. Trends in the various rainfall and soil moisture equations which gave peak \( r^2 \) values (Tables 7.22 - 7.25) were overall similar to those derived from the burns (Tables 7.17 - 7.19).

Greater variability was found in the significance of burn time and sampling time between species, with interaction occurring between these and each of the moisture variables. For the pair of equations with highest values of \( r^2 \) in each species, considerable contrasts were found. In *B. ericifolia* for rainfall, burn and sample time were non-significant whilst for soil moisture both were signi-
ificant (Table 7.22). Burn time was positively correlated indicating slightly greater response in conjunction with moisture in the November treatment, whilst sample time was negatively correlated indicating diminishing seed response over time. In Petrophile, the same pattern occurred, except that burn time was non-significant when entered with soil (Table 7.24).

For B. serrata, the result was identical to Petrophile (Table 7.23). Isopogon gave opposite results with both variables significant in conjunction with rain but only time of burn significant with soil moisture. Unlike the other species, sample time was positively correlated with emergence indicating that seed response was enhanced with time. In addition, higher $r^2$ values of 5 and 9% for burn and sample times were registered (Table 7.25). It was apparent again that within species, high variation between quadrats must have played a part in restricting the predictive power of the variables. For the moisture variables themselves, the $r^2$ values were considerably higher than the corresponding maxima in the field burns in the two Banksia species, though not in Petrophile. In all cases soil moisture offered little if any overall improvement over rainfall in accounting for emergence.

Discussion

This exercise was most useful in highlighting the timing of emergence in relation to moisture within and
between species and emphasizing the importance of average soil moisture conditions over periods greater than a week. The experiment showed that seeds were responsive to moisture for up to 12 months, as was indicated in the other field observations, though the response may wane after the initial pulses of emergence have passed in these species. As heavy predation and inviability were discounted earlier (see previous chapter) what is the reason for this? As indicated by infrequent low watering in the glasshouse, seeds may be brought to the point of germination or near germination but never emerge. Such conditions in the field may if prolonged cause seed mortality. That is, seeds thus exposed may fail to respond to subsequent heavy wetting. Preece (1971) reported emergence in mulga (Acacia aneura) seeds failed, if after radicle extension, the seeds dried out. It was demonstrated in the previous chapter and here in the emergence experiment (November treatment) that largely unwetted seeds could survive exposure on the soil over an extremely hot Summer without severe losses of viability. It can be concluded that the response of seeds on the soil in open conditions subject to wetting may decline in the long term.

The inability of both moisture and rainfall to account for large amounts of variations in emergence may be due in both burn sites and experiments to the relatively large and variable times between sampling compared to the daily measurements taken in the glasshouse. A considerable amount of error was inherent in the estimation
of emergence dates in the field and this lack of resolution may be a major source of the disparity between the amounts of emergence and the values of moisture (rain and soil) advanced to explain them.

The coarseness of sampling may have contributed also to the lack of any improvement in the amount of variance explained by the soil model over rainfall, though as rainfall averages were not used this may be speculation.

The use of field capacity as essentially a soil moisture index, though quite successful in the glasshouse, may, in the more variable conditions encountered in the field, be partially responsible for this result.

In summary, it was concluded overall that, in all species:

(i) average modelled soil moisture measures offered a logical explanation of variations in emergence as did rainfall;
(ii) burn times may be important (under the limited range offered in the experiment), though where these were significant some interaction with various moisture measures may be present;
(iii) seed response in B. ericifolia, B. serrata and Petrophile may decline after seeds have lain on the soil for 12 months. As well, some decline within that period may be evident, though the opposite occurred in Isopogon.
The results for the soil moisture model (M.S.D. as a function of calendar months) in the field in combination with the effectiveness of the averages at field capacity in the glasshouse encouraged their further use in attempting to predict average emergence patterns from seasonal climatic data. There was a nearly equal justification for using rainfall as a predictor of emergence, based on the field results. However, the combination of field and glasshouse data for average soil moisture as developed as a predictor of emergence were persisted with. It was considered that the field results verified the general thrust of the relationships demonstrated in the glasshouse. Therefore a detailed, quantitative test of these relationships was justified, and was performed using the soil-moisture data relevant to the heating/substrate experiment.

7.7 Predictions of emergence in the field.

Aims

The glasshouse relationships were tested by comparing predicted amounts of emergence with actual observed amounts. This was necessary to verify their utility and applicability in the field and justify their further use in modelling the effects of post-fire emergence.

Methods

Emergence - soil moisture relationships were applied to M.S.D. estimates derived for the heating/substrates
experiments (see Tables 7.20 - 7.21). Seeds in those experiments could be regarded as analagous to a single pulse of seed-release and therefore, week by week averages of M.S.D. were compiled for each experiment (May and November runs) and were input progressively into the equations given in Figures 7.8 - 7.11 and Table 7.6 for each species. Several crucial assumptions were used to predict emergence from these equations.

Seeds were assumed not to decline in responsiveness in the 12-month period following release. Secondly, the relationship between soil moisture and time to emergence was, as noted in the discussion above, developed by examining cycles of uniform watering and their effect. The situation in the field differed in that wet and dry spells of varied length occurred. The average moisture durations at field capacity caused by differing length wet and dry spells were assumed to be approximated by the glasshouse relationships. The soil moisture emergence relationship was also used here in a wider range of months (March - November) than over which it was derived (April - September).

The final criterion used was related to temperature control of emergence. As shown above, temperature was assumed to restrict emergence in Summer and hence it was assumed in the average year that no emergence would take place in December, January and February, unless the average moisture data showed very high proportions in any of these
months. Further, any moisture in these months (if not regarded as stimulatory) was assumed to have no further effect.

The moisture averages experienced by seeds were considered progressively for each month after the seeds had been placed in the field. The appropriate amount of seedbank that could have emerged within the available time at the prevailing average moistures was computed from the glasshouse-equations for each species. If, in successive months, there was no change in the amount that could have emerged (usually where the average moisture level remained constant or declined) no further emergence was scored. Only where the addition of successive months increased the average moisture was further emergence scored, provided the total time period was non-limiting (Table 7.6, Figures 7.8 - 7.11). This was in accord with the model of emergence proposed in the discussion of the glasshouse studies.

Results and Discussion

Comparison of real and simulated results for the Warrah experiment.

The checking of the model against the Warrah experiment showed the accuracy of the predictions varied between species (Table 7.26). The results for the first (May) treatment were for all species in the right predicted range
of percentage emergences. However though the real timing of the bulk of emergences followed quite close to those predicted, a quantity of seedlings did emerge after the predicted peaks.

A reasonable agreement between actual and predicted timing of emergence was found in the second treatment (November) though with the exception of *Isopogon*, the predictions overestimated real emergence especially in *B. serrata*. It appeared that the response of seeds exposed to months of low soil moisture followed by several months of very high moisture lagged behind the expected response of seeds exposed to the overall average.

Generally, the predictions gave satisfactory approximations of emergence and were considered to verify the extrapolation of the glasshouse results, in detail, to the field. As a result, simulations of burns in differing seasons were performed to test for possible differences in emergence based on average rainfall data. These are described in the next section.

### 7.8 Predictions of fire-seasonality effects.

**Introduction**

It was concluded that the components of the model (Figure 7.1) given in the introduction were sufficiently
known to allow the effects of varying seasons of fire to be integrated in a general manner. As stated, the use of a soil-moisture model as one component of this general model was accepted for this purpose.

Individual circumstances surrounding any particular burn, shape the response of seeds. Whilst these cannot be known in advance, predictions based on events immediately past may be reasonably extrapolated. In this section, varied times of burning were assessed using average data on moisture derived from rainfall data collected over 50 years for Sydney, by the Bureau of Meteorology. The effects of differing burn times were modelled in the "average" year, and, as well, the frequency of events defined as stimulating given levels of emergence were examined so that the yearly chance of particular levels of proportional emergence could be calculated.

Reliance was placed on detailed extrapolation of glasshouse and laboratory results. Though such a method is fraught with difficulty (Mott and Groves, 1981), attempts to explain and predict germination and emergence patterns in the field are continually reported in the literature. As it was concluded that the field studies verified the trends found in the laboratory and glasshouse, here these extrapolations were made with some confidence.
Methods

The 50-year rainfall data were assembled and from these the soil surface moisture was estimated using the M.S.D. model developed above. Monthly estimates of M.S.D. were made for each year (Appendix 4,a) and the proportions of M.S.D. per calendar month were averaged over all years. The response of seeds to hypothetical fires in differing seasons was assessed against the moisture patterns in the average year. The glasshouse relationships between time to emergence and proportional duration of soil at field capacity were used to estimate likely proportions of emergence.

Burns were simulated at the beginning of the months of February, April, September and December, and, for each, the average moisture data were related to the pattern of seed release over the following 12 months. Emergence was estimated at 3, 6 and 12 months after each burn by tracing the response of each monthly block of seeds released over that period.

Seeds were assumed to have been released at a rate, in each species, found after moderate intensity fires (Chapter 5). The amount of seed released during any month was for the sake of simplicity assumed to have been released in a block at the end of each month after the fires, though in reality seed-release was a more continuous phenomenon (see Chapter 5). Such a method of modelling seed
release simplified estimations of emergence from each monthly batch of seeds assumed to have become available on the soil surface.

Calculations of emergences were based on the methods and assumptions outlined in the previous section. The moisture average experienced by each block of seeds was considered progressively for each month in relation to the time since release. The appropriate amount of seed that could have emerged as seedlings in the time available was calculated in an identical way to that outlined in the previous section. Therefore at 3, 6 and 12 months after each hypothetical fire in each species, the sum of emergences was made up of contributions from blocks of seed release which had been exposed to the calculated moisture conditions for differing amounts of time and from differing starting dates such that at the end of n months after any fire:

\[ s_1 + s_2 + s_3 \ldots \ldots \ldots + s_n \]

seeds had been released, where \( s_n \) was the amount of seeds (% of total seedbank) released during month \( n \) after the fire. Emergence was given by:

\[ E_1 + E_2 + E_3 \ldots \ldots \ldots + E_n, \]

where \( E_n \) was equal to the proportion of the amount of seedbank released in month \( n \) that had emerged. Therefore, at the end of 12 months, seeds released in the first month after fire had
been exposed to moisture for 11 months, whilst those released in the eleventh post-fire month had one month's exposure. In this way the effects of timing of seed-release could be seen, and contributions of seeds released at differing times could be compared.

Results.

Rainfall averages are given along with the estimates of mean monthly moist soil days (Table 7.27). It was decided that the values for January and December were low enough to unequivocally reject the possibility of emergence occurring in those months. This was also done for February, though with less certainty as the moisture data are of comparable magnitude for some other months included in the analyses (Table 7.27).

The patterns of seed release calculated for each species are illustrated in Figures 7.24 - 7.27. A tally of progressive monthly M.S.D. averages was calculated for each burn for each block or cohort of released seeds (Appendix 4, b) for the 12 months following the burns. From these, the responses of each block of released seeds was calculated (Tables 7.28 - 7.31). Results were calculated for the 3-, 6- and 12-month periods after each simulated burn (Tables 7.28 - 7.31). In Isopogon and the two Banksia species, little difference was found between burns after 12 months, though the results were
achieved at differing rates (Tables 7.28, 7.29 and 7.31). Similar rates amongst treatments occurred in all species. Greater disparity between burns was found in Petrophile at 12 months (Table 7.30). In Petrophile, greater amounts of emergence occurred after the burns in the latter half of the year (Table 7.30).

Discussion

The results in Petrophile and their relationship with the seed release patterns and predicted emergence must be considered. This species had the widest spread of response times (in relation to proportional moisture) and slowest rate of seed release, hence the effects of varying periods of moisture within 12 months produced the most variation in predicted emergence. Hence greater emphasis is placed on events after 12 months, particularly in the 12-18 month period, than for the other species which released more seed closer to the burn. Consideration of seed viability, moisture and site conditions must be made although beyond the scope of this simple predictive exercise, if this period was to be modelled. However, the predictions reflect on the situation found in the real burns where substantial emergence occurred mostly in Petrophile after 12 months. The predictions indicate the probable importance of late released seeds in contributing to this.
In the simulations, seeds released in the first 6–8 months of the average year were able to achieve the maximum level of emergence concurrent with the most moist period of the average year (Winter). Variations in predicted responses were mostly caused by late released seeds and the moisture regimes they faced. This was particularly evident in Petrophile compared to the other species and was responsible for the differences in total emergence between burns. Due to the comparatively slower rates of seed release in Petrophile at most levels of heating (Chapter 5), burns early in Summer or Spring in the average year, produced patterns of simulated seed release that deposited the bulk of the seedbank either before or during the onset of the most favourable moisture period (Winter). In the other species, this pattern was achieved with either burns in late Summer or Autumn. Due to the lower rate of seed release in Petrophile, burns needed to occur earlier than in other species so that the timing of seed release would be optimal with the most favourable moisture conditions.

Variations in predicted response were mostly caused by late released seeds and the moisture regime they faced. Hence changes to the 12-month figure in the second year would be largely dependent on these seeds, which in all cases, but especially the Banksia species and Isopogon, were a minor proportion of the seedbank. Slower rates of seed release, as would occur after very cool fires, would yield lesser amounts of emergence and place more importance
on potential emergence in the second year. The effects of site modifications in the second year after burning and their effect on emergence and survival are not directly known, though the development of a transpiring canopy after 12 months may have a detrimental effect on moisture availability, as for example, discussed by Parsons (1968), Withers (1978), Orme and Leege (1974). As well as shading, other competitive effects may directly or indirectly change emergent response.

Another consideration that would influence the pattern of results was that of seed mortality, especially in that proportion of the seed population which failed to emerge at low moisture levels. Though seeds were generally shown to survive periods of low moisture and high temperatures in the field or glasshouse, possible mortality of germinated or ungerminated seeds was indicated. If the survival of unemerged seeds declines within 12 months of release, depending on moisture and/or seasonal conditions, then the patterns of predicted emergence may be changed. If such a decline were uniform (unaffected by seasonal conditions for example) through time, then those burn times in the average year giving the most rapid emergence would be favoured. These were late Summer and Autumn (Tables 7.28 - 7.31) in the Banksia species and Isopogon and Spring - early Summer in Petrophile.

The effects of variations in fire intensity, through altered seed-release patterns need to be considered. In
all species, higher rates of initial seed release, than those simulated, can occur under high-severity fires (see Chapter 5). For optimal, rapid emergence in the average year, in all species, increased rates of seed release caused by hotter fires would allow optimum burn times to be delayed further into Autumn in the Banksia species and Isopogon and later in Summer in Petrophile, compared to the times of burns simulated in Tables 7.28 - 7.31.

On the other hand, fires cooler than those simulated, giving slower rates of seed release, would spread emergence substantially in all species to varying degrees into the second year post-fire. One consequence of this would be to possibly advantage the initial seedlings to emerge, in terms of long-term survival and reproduction. In Chapter 3, it was shown that smaller suppressed plants particularly in B. ericifolia and Petrophile tended to suffer higher mortality, and were less likely to set cones. One of the main effects of fire-intensity in the obligate seeders may be therefore to influence the size-structure in post-fire populations. Solbrig (1981), in a study of the significance of plant size in the perennial herb Viola sororia, concluded that as a size hierarchy was present in populations, that favoured the survival of a few large dominant individuals at the expense of smaller plants, the factors which determine the size distribution are quite crucial. Solbrig's (1981) study indicated that growth rates were not inherited but that circumstances surrounding emergence and the characteristics of seeds produced in differing situations of disturb-
ance and density interacted to determine growth rates in individuals and plant size. In this study, it can be seen how aspects of fire-intensity variations and seed release in interaction with circumstances governing germination and emergence may spread emergences differently through time. The results in Chapter 3 showed that mortality may be concentrated in *B. ericifolia* and *Petrophile* stands in small plants, and that growth rates were unrelated to size. Hence those plants that emerge first may become the dominants in stands. Under slow rates of seed release, a wide spread of emergence times is likely, and later released seeds may produce seedlings with an inherent disadvantage. Emergence times may be more closely spaced and resultant seedling and established plant competition may be more intense after high-intensity fires which cause rapid seed-release. The full ramifications of these effects on stand structure and reproduction output may be worthy of further study.

In summary, it can be concluded from the responses in the average year that:

(i) In the *Banksia* species and *Isopogon*, there was no effect of fire seasons;

(ii) In *Petrophile*, Spring–early Summer burns produced greatest emergence one year after fire;

(iii) The above results are sensitive to: changes in seed-survival, possibly induced by long exposure to low water levels; changes in fire intensity and concomitant rates of seed release,
in ways that are likely to maximise emergence following burns which will release seeds to coincide with the season of highest moisture levels; — Winter.

**Generalizations and Conclusions**

(i) **Generalizations in time.**

The results predicted from the average year do not enable prediction of what will occur in any real year. This will depend on actual rainfall and soil-moisture patterns. Rather, they confirm the null hypothesis that, on average, the burn time in any given year will not affect the amount of emergence that occurs afterward, in three species: *B. ericifolia*, *B. serrata* and *Isopogon*. In *Petrophile*, the hypothesis was rejected, though overall results were shown to be strongly dependent on events in the second year post-fire.

For those species unaffected by burn-time, under the conditions of the stimulation, the practical consequences of these results may be considered. In particular the situation where fires recur repeatedly in a particular season (through planning or otherwise) may be considered. The result from the average year would indicate that the averaged abundances of seedlings produced in the aftermath of a large run of fires would not differ from a similar sample occurring in another season in the Banksias and *Isopogon*. A definitive test of this conclusion would be to examine the frequency distributions of percentage
emergences after simulated fires over a large sample of years. Time prevented the inclusion of such an analysis in this thesis, though it will be incorporated in a forthcoming paper, based on the 50 year data set.

Deviations from the assumptions of the simulation may cause this conclusion to be rejected in these species, and particular seasons of burns may differentially affect emergence in the manner discussed above. Such deviations may come about through mortality of seeds and fire-intensity variations.

(ii) Generalizations in space.

The predictions relate specifically to the Sydney rainfall station and the populations of seeds studied. The potential for within-species variation was highlighted in the laboratory work. The predictions also pertain to the model of surface moisture in bare, loamy sand soils derived and tested in the laboratory and field. The degree to which they relate to other substrates and soil types is unknown.

The average rainfall data of other stations closer to the study area were compared with Sydney averages (Table 7.32). The results show some deviation in the Summer months. Though calculations of average soil moisture were not performed for these stations, it was considered
that the deviations would not greatly affect the predicted outcomes.

A consequence of the predictions in any large area with a run of burns in differing localities would be that emergences, when averaged over a larger sample of times, would tend toward the levels of those predicted from the average year. Sites distributed in space would vary in emergence, according to the frequency distribution of the differing yearly moisture regimes or "moisture events". As indicated, these will be examined in a future paper.

(iii) **Probability of particular levels of emergence.**

The frequency distributions of years or sequences of months (moisture events) yielding certain levels of emergence are not presented in detail here. However, the chance of moisture events which would yield a certain level of emergence occurring in any one year could be calculated from the 50-year averages. The data used suggested that if seedling emergence of greater than 50% of seedbank was to occur in each species an average M.S.D. proportion of 0.70 + would have to be sustained for at least 3 successive months (≈ 90 days). In any year, this would have to occur within six months of a fire if this overall level of emergence (for the total seedbank) was to be achieved within 12 months of the fire. Yearly data from the soil averages (Table 7.33) are presented for the 9 out of 50
individual years (taken from Appendix 4,a) where these criteria were fulfilled. It was concluded that in the region of around 15-20% of years, burns would yield these very high emergences of seedlings from the seedbank. The data in Tables 7.33 indicated that in those years the necessary runs of very moist months tended to occur in either the first half or middle (Winter) part of the year.

On the other hand, it would seem (see Appendix 4,a) that emergence of 10% of seedbank in all species was possible in virtually every year out of the sample of 50.

In conclusion, overall, in all species, if abundances of seedlings are to be maximised, and it is accepted that some mortality of seeds will occur if they remain unemerged for long periods, then burns must be timed to produce bulk seed-release in late-Summer-Autumn, at high fire-intensity levels. The actual time of the burn will be dependent on fire-intensity-dependent patterns of seed release particular to each species.
CHAPTER EIGHT: POST-FIRE SURVIVAL IN SEEDLINGS -
THE EFFECTS OF MOISTURE AND FIRE SEASONS.

8.1 General Introduction

This chapter is divided into two sections. The first and main section examines seedling survival after a series of burns (those described in Chapter 7) in the field over a number of years in each. The chief aim of this section was to describe the overall patterns of survival in seedlings and to detect ages of seedlings where the risk of death may be highest. In the second section, the influences of available soil moisture on survival were examined in the field and in a glasshouse experiment. This was done to provide an evaluation of the consequences of burns in differing seasons for seedling survival in a manner broadly similar to that used in the previous chapter. That is the control of moisture on survival was evaluated against patterns of seasonal soil moisture. The effects of factors other than moisture on seedling survival were discussed in Chapter 6. Rightly or wrongly these were considered to be largely independent of seasons in their operation. A full examination of factors such as predation was not attempted here in interaction with the effects of moisture; rather, moisture is examined largely in isolation.

Various studies and reviews have indicated that periods of low moisture or "droughts" may cause mortality
in plants (eg: Sharitz and McCormick 1975, Mack 1977, Cook 1979, Hodgkinson 1979, Solbrig 1980). Evidence from some studies of post-fire seedling survival suggest that Summer is often a hazardous period for seedlings due to droughting. Whelan and Main (1979) correlated peaks of mortality in seedlings of a wide range of species, after fires in Western Australia, with Summer droughts in 2 successive years. Similar effects were presented by Orme and Leege (1974) for seedlings of Ceanothus and for the mallee Eucalyptus incrassata by Parsons (1968) and Wellington (1981). Specht et al. (1958) related mortality in Banksia ornata and other South Australian heath species to periods of drought in both Summer and Winter. As well considerable deaths in B. ornata seedlings were found to occur with frosts. Specht et al. (1958) noted that the period of greatest risk in B. ornata seedlings was within a year of emergence. Purdie (1976) concluded in relation to the effects of fire season in leguminous shrubs that seedling regeneration will vary according to the conditions experienced after a burn. Drought along with frosts, predation and fungal attacks were given by Purdie (1976) as sources of mortality which may vary both in intensity and in some cases timing. Her conclusion was that post-burn conditions were essentially unpredictable, and that as a consequence trends in seedling regeneration may be difficult to predict.

An attempt was made here to take up the challenge implicit in this conclusion, as was done for emergence in
8.2 Post-fire Survival - Field studies.

Introduction

Studies on the survival of seedlings were conducted in the quadrats in Burns I-V described in Chapter 7. Survival and growth of emerged seedlings in all species was monitored. Though emergence in *Isopogon* in some of these burns was not described in Chapter 7, some observations on survival in seedlings of this species are presented here.

A chief aim of this work was to relate the survival of seedlings to soil moisture in a way similar to that attempted in the previous chapter with seedling emergence. This was done using an index of soil moisture derived from simple climatic data. Early observations of seedlings in Burn I (further details given later) indicated that mortality may be heavily concentrated in the first few months after emergence. As well, periods of high soil moisture, following heavy or prolonged rain appeared to be correlated with high mortality or high levels of damage to seedlings. Whether these effects were caused by rain-drop damage or waterlogging was unknown. An index of soil moisture was sought which could be related to mortality in times of both low and high moisture with some sensitivity. Whilst measurements of subsoil moisture were taken in each
site down to 6 cm, depth, the observed rooting depths of newly emerged seedlings (in both field and laboratory samples) often exceeded this, and therefore no attempt was made to model subsoil moisture in the empirical way done in Chapter 7. Instead estimates of moisture storage were derived using the WATBAL program (Keig and McAlpine, 1974). These provided a weekly measure of the percentage of maximum possible soil water storage. Briefly this is calculated by the following relationship (Keig and McAlpine, 1974):

\[ NSTR_N = (NSTR_{N-1} + NRAIN_N) - NDMD_N \]  

(Equation 8.1)

where \( NSTR_N \) = water storage in week \( N \)

\( NRAIN_N \) = rainfall in week \( N \)

\( NDMD_N \) = water demand in week \( N \)

and where \( NDMD_N = AETCF_N \times PETCF_N \times EVAP_N \)  

(Equation 8.2)

where \( EVAP_N \) = evaporation in week \( N \)

\( AETCF_N \) = actual evapotranspiration co-efficient

\( PETCF_N \) = potential evapotranspiration co-efficient

The main inputs into the model therefore are weekly rainfall and evaporation data, whilst the maximum storage (MAXST) term is defined by a value for soil field capacity (by volume). The actual evapotranspiration co-efficient is a function of the percentage:
The PETCF<sub>N</sub> term can be set according to site and vegetation characteristics as well as seasonal variations. Values of this term were discussed by Specht and Jones (1971) and Specht (1972). Specht and Jones (1972) reported a function defining this term for burnt South Australian heathland. Further discussion of the WATBAL model can be found in Keig and McAlpine (1974).

**Emergence and mortality patterns**

The patterns in emergence in each site were such that cohorts of seedlings could be identified which arose on certain dates of sampling (see Tables 7.11 - 7.15 in Chapter 7). The fates of these seedlings could be distinctly traced through time. Seedlings were spread through the sample quadrats in a way that placed individuals of differing cohorts together in the same quadrat. Wide variations in density of seedling quadrats occurred in Petrophile and *B. ericifolia*, whilst in *B. serrata* and *Isopogon* variations in the density of quadrats also occurred but overall densities were low. As a result, the effects of density on survival in *B. ericifolia* and Petrophile were examined.

The patterns of mortality were related, in the *Banksia* species and Petrophile, to soil moisture within individual cohorts. This was done after preliminary analysis showed

\[
\frac{NSTR_{N-1} + NRAIN_N}{MAXST} \times 100
\]

(Equation 8.3)
that significant differences in the overall amounts of deaths occurred between burns and between some cohorts within burns. As well, the deaths observed over several years in each species' cohorts were concentrated in the first 100 days after emergence. Therefore emphasis was placed on relating trends in seedling survival, in the initial period after emergence, to moisture. As the intervals between sampling were shortest in all species in most cohorts during this time, it was considered that errors in relating the estimated time of death to moisture at that time would be minimized compared to later times after emergence, where sampling intervals were far larger. As no useful data on the initial emergence period in *Isopogon* were available this species was excluded from this part of the study.

In summary, the following data and analyses are presented in sequence, as follows:

(i) Survival rates for species cohorts within burns are quantified and regressions of numbers of survivors versus age are fitted for data from larger cohorts.

Survival was described using life-tables, which summarize the following data (Hett and Loucks, 1968, Caughley 1977):

(a) the age-class or age-interval \( (x) \);
(b) population numbers or density \( (l_{x}) \);
(c) mortality or numbers or proportion dying in between age-intervals \( (d_{x}) \);
(d) mortality rate \( (q_x) \) between age intervals;
(e) rate of survival between age intervals \( (p_x) \).

To these data two basic models of survival representing Deevey Type II and III (see Chapter 3) survival were fitted using regression techniques derived from equations used by Hett (1971) and Hett & Loucks (1971) in their analyses of survival in *Acer* saccharum seedlings. These models were negative exponential and power functions respectively.

(ii) Sources of mortality were briefly contrasted within species cohorts;
(iii) The numbers of deaths in cohorts and burns were compared within species;
(iv) The effect of quadrat density on mortality in Petrophile and *B. ericifolia* was tested. These analyses are discussed initially below and work on moisture and mortality is presented subsequently.

8.3 Survival and density effects

Methods

The quadrats presented in Chapter 7 were monitored until mid-1983 in all species. Sample areas, similar to those used in *B. serrata* of varied size, were set up for *Isopogon* around mature burnt bushes in Burns I and II and,
though attempts to document emergence and early survival proved elusive, established seedlings in and around the sample areas were found in August 1981 (Burn I) and May 1982 (Burn II). These were monitored and measured as for the other species.

On each visit to each quadrat (full details of sampling dates are given in Chapter 7, Tables 7.11 - 7.15), seedlings were mapped and measured and notes on their physical condition were made. Dead seedlings which were still present were described and allotted to four categories of deaths: disappeared without trace, damaged and disappeared, damaged and dead but dead plant present, and undamaged, dead and plant present. Cohorts were identified by the sampling dates on which seedlings first appeared.

In *B. serrata*, *B. ericifolia* and *Petrophile*, survivorship was described in each quadrat and a model was fitted using regression techniques. As discussed above alternative survivorship models were tried in each instance these being: (after Hett, 1971 and Hett and Loucks, 1971.

\[
\ln N_x = \ln N_0 - bx \\
\text{or } \ln N_x = \ln N_0 - b \ln x
\]

where \( N_x \) = numbers at time \( x \)

\( b \) = survival rate = regression slope

The exponential model in equation 8.4 corresponds to Deevey Type II survival whilst the power-function (equation 8.5)
models Deevey Type III survival (see Figure 3 in Chapter 3).

Within-species tests of the frequency of deaths between major cohorts and burns were performed to determine if levels of mortality were similar. The tests of density effects on survival were done for data from a selected period of the study in each burn within *Petrophile* and *B. ericifolia*. As seedlings with widely differing "birthdays" occurred in individual quadrats within each burn, it was felt that the best basis for comparisons of density effects would be to pool all quadrat and transect data for each burn into arbitrarily defined density classes. Three classes were chosen representing: low density (1 or 2 plants per quadrat); medium density (3 or 4 plants per quadrat); high density (5 or more plants per quadrat). The effects of density were tested over a period of a year in each burn when emergence had largely ceased. In all cases this period commenced in the second year after burning. As a consequence no analysis was performed in Burns IV and V, as the study ended during the second post-fire year in these cases. In each burn for each species, the numbers in each density class at the commencement of the designated period were summed and the numbers of deaths in each class over the subsequent year were tallied. Comparisons of the frequency of mortality between density classes were performed using the 2-way G test (Zar, 1974). The ages of seedlings at the commencement of the density analysis period varied widely in all classes. Comparisons within ages could not be carried out, however, and the analysis was therefore performed on the multiple-aged sample.
Results

Due to limitations on space a presentation of full life tables for all species is not made here. Rather, estimates of $d_x$ at age $x$ are given in abbreviated tables. Abbreviated life-tables for each major cohort of seedlings within burns and species are presented in Tables 8.1 - 8.4. Sample dates presented in these life-tables were a sub-sample of those actually done, in order to condense the data and to even up differences in sampling intensity between young and old seedlings. A full list of sampling dates is given in Chapter 7, Tables 7.11 - 7.15. Major cohorts were defined as those in which 5 or more seedlings emerged on the same sample date. Inspections of the life-table data (Tables 8.1 - 8.3) in all species other than Isopogon showed that in many cases the bulk of mortality was often heavily concentrated in the first 100 days after emergence. Emergences in Petrophile for Burns IV and V were too few to be regarded as cohorts.

Comparisons of mortality between cohorts (up to 100 days after emergence) and burns within species (Tables 8.5 - 8.7) revealed several significant trends. In B. ericifolia comparisons of cohorts within Burns I and II could not be carried out, due to the large number of low contingency table frequencies ($\leq 5$) (Zar, 1974) (Table 8.5). However a between Burns comparison showed that significant heterogeneity existed. A further breakdown of this analysis (Table 8.5) showed that Burns I and II displayed similar frequencies of mortality, but that the other burns were all dissimilar.
The overall levels of mortality in Burns I, II and III were substantially less than those in Burns IV and V (Table 8.5). This corresponded with the severe drought conditions that prevailed in the October-emerged cohorts in Burns IV and V. (see next section for further details).

In Petrophile, testing between cohorts in Burns I and III was carried out (Table 8.6) and this showed that significant differences in mortality occurred in Burn I between cohorts. In particular, high mortality occurred in cohorts (d) and (e) in Burn I. These corresponded with times of very high rainfall or soil moisture after emergence (see next section). In Burn III, some heterogeneity was apparent but was non-significant (Table 8.6). Mortality in Burn II proved to be significantly lower than in Burns I and III. (Table 8.6).

In B. serrata, differences between burns were non-significant but some heterogeneity was apparent (Table 8.7). Mortality was proportionally higher in Burn II.

Overall calculations of proportional survivorship were performed for each burn within species by lumping together proportional cohort survival data over the full time spans over which observations were carried out. Only cohorts with more than 10 individuals were used to avoid bias in the proportional values. This exercise gave an overall survivorship curve for each burn within species (Figures 8.1 - 8.4). As discussed above, alternative regression models were tested
and the results (Figures 8.1 - 8.4, Tables 8.8 - 8.11) indicated that survivorship patterns varied within species. Survivorship curves presented in (Figures 8.1 - 8.4) were those models which gave highest co-efficients of determination ($r^2$) for equations with significant F ratios for the slopes (Tables 8.8 - 8.11). Half-lives for seedlings in each burn were calculated and are presented in Tables 8.8 - 8.11.

In all species there was a strong trend toward high rates of mortality at young ages, reflected in the number of burns which were more suitably modelled by the power function. Rates of survival varied widely as reflected in the half-life values. In *B. ericifolia*, half-lives of seedlings were short in Burn V, whilst in Burns I and III they exceeded 1000 days and in Burn II they approached infinity (Table 8.8). In *Petrophile*, moderate half-lives were found in Burns I and II whilst they approached infinity in Burn III (Table 8.9). In *B. serrata*, estimated half-lives (Table 8.10) in all burns approached infinity. In *Isopogon* also, half-lives (Table 8.11) were long in both burns.

Fates of seedlings in the first 100 days differed with species and in some cases between burns within species. In *B. serrata* and also *Isopogon*, fewer seedlings disappeared without trace than those which died either intact or after being damaged (Table 8.14). In *Petrophile*, the bulk of seedlings disappeared without trace usually at very early ages, in all burns (Table 8.13). In *B. ericifolia*, a
similar pattern was found in Burns I-III, however, in Burns IV and V many seedlings were observed to die intact or after being damaged (Table 8.12).

This correlated with the extreme drought conditions that followed the emergence of these cohorts. At later ages ($\geq 100$ days) in these 3 species and in *Isopogon*, disappearances were fewer and deaths during the 1982/83 Summer in many cohorts appeared to be almost exclusively due to drought. In some cohorts, a few deaths in the *Banksia* species and *Petrophile* were caused by burnt, dead limbs and stems collapsing on established seedlings. Many seedlings survived in a bent or even broken state. Bradstock (1977) found this to be a prominent source of mortality in seedlings of *B. ericifolia*.

Analysis of density effects on survival in older established seedlings of *Petrophile* and *B. ericifolia* revealed no significant effects (Tables 8.15 - 8.16).

Discussion

*B. ericifolia*

The burns with both the highest initial and overall mortality (IV and V) (Tables 8.1 and 8.5) experienced a severe post-emergence summer. The dead seedlings found in these were observed over a number of visits to visibly wilt from the top leaves downward from December 1982 - February 1983.
Many survivors suffered heavy wilting damage but held on. This drought took toll of older seedlings in an apparently similar manner in the other burns. Whilst the power function modelled survival most successfully, the initial rates and proportions of mortality differed amongst all burns. As the bulk of emergence was effectively concurrent in Burns II and III (Table 8.1) differences in mortality between them may be attributed to individual site characteristics. The nature of these is unknown. The overall patterns of mortality in all burns indicated that early mortality may be heavy (first 100 days) and hence seedlings are most vulnerable in this period.

The large number of disappearances amongst seedlings in Burns I - III appeared to be related to the incidence of heavy rain in many cases. Cases of seedlings which were broken or uprooted and washed away were directly observed and these were usually very young seedlings with cotyledons or first juvenile leaves only. It is possible that rain-drop damage and/or flooding may be responsible for this.

Petrophile

As emergence was low in Burns IV and V survival in these burns were not discussed here. In Burns I-III the power-function proved to offer a better model of survival indicating that initial mortality after emergence was most severe. As with B. ericifolia, differences between Burns II and III in the relative frequencies of mortality indicated
site effects, as emergences were concurrent in both burns.

A similar interpretation to B. ericifolia was placed on the data for fates of dead seedlings from Burns I - III.

B. serrata

By comparison to B. ericifolia and Petrophile, B. serrata seedlings were less prone to disappearance and either died intact or after suffering visible damage. In Burns IV and V, the few seedlings that died appeared to have succumbed to wilting. Though not specifically illustrated here, most older seedlings which died appeared to succumb to drought in 1982/83.

Isopogon

Though immediate post-emergence mortality was not directly observed, subsequent mortality in seedlings from an age of around 50 days onward took place in Burn I at an initially higher rate than at later ages. Deaths in Isopogon, were observed in largely intact seedlings.

In all species, mortality in seedlings, whether best modelled by a power function or exponential function (Tables 8.8 - 8.11), was initially much higher than in established plants (see Chapter 3). In some burns, however, later rates of deaths fell to levels similar to those in
older established stands. The factors which affect seedling numbers operate most potently when seedlings of all the species studied have just emerged.

In Petrophile and B. ericifolia, density effects up to the levels observed had little impact. It is unlikely that density would have much effect at very young ages though this was not tested.

8.4 Effects of moisture.

Introduction

Ideally a multi-factorial experiment examining the combined actions of soil moisture, density and predation was desired. With regard to moisture especially, some pilot trials were commenced in early 1981 in the field but difficulty was had in applying multiple levels of watering in an effective way to quadrats. Also, natural rainfall interfered with the treatments in a way that may have invalidated them. Further experimental field studies were not pursued, principally because of the problem of applying multiple levels of water (not just a simple presence or absence of water) and relating or calibrating these waterings to real rainfall events, and because the lack of control over extraneous natural rainfall could not be overcome in the time available. Though a simpler watered versus unwatered
comparison was possible, this would not have given any insight into effects of the range of soil moisture conditions found normally in the field and shown to control emergence. Rather an exercise in soil-water modelling and correlation with observed survivorship patterns after real burns was performed. As well a glass-house droughting experiment was done to test the effects of lengths of varied drought periods on seedling survival.

The results from the previous section indicated that mortality was strongly influenced by site effects. As well, the causes of deaths of seedlings seemed to vary in a way that may have been related to extremes of rainfall and/or soil moisture levels in the first 100 days after emergence. As mortality was strongly concentrated in this initial period after emergence, the attempts to correlate an index of soil moisture and survival were made in this period for individual cohorts within burns. Because of differences between burns and cohorts in the amounts of mortality, survival data could not be bulked within species, nor could a model relating % mortality to a single universal moisture index be used.

Ideally a model was sought which would relate seedling size, lifespan and survival to variations in the soil moisture index in a way that would account for variations in seedling survival. Such a model, however, proved difficult to fit to the type of data available, especially to test the hypothesis that a correlation may exist between both low
and high levels of soil moisture and high levels of seedling mortality. Rather, a simpler exercise was performed on the data from the main cohorts (those with 5 or more seedlings).

The life-spans of seedlings which died in the first 100 days were estimated, as was the soil moisture index at the time of death in a two-week period. The null hypothesis that the moisture index at the times when deaths occurred was not significantly different from that when deaths did not occur was tested by comparing the frequencies of soil moisture index classes in both categories, over all cohorts, in all burns, in each species. A non-significant result could have 2 meanings. Either moisture had no effect on seedling survival, or that differing extreme levels of moisture, such as high or low moisture, may have similar effects. The method was incapable of distinguishing between the alternative explanations if a non-significant comparison occurred. However, some insight was gained by examining this hypothesis in differing size classes of seedlings.

A glasshouse experiment was performed to examine the effects of periods of low soil moisture on the survival of freshly emerged seedlings. The experiment was designed to test the effects of several repeated cycles of droughting of differing length. Concurrent measurements of soil moisture at the rooting zone were performed to determine trends in soil moisture potential under the differing treatments and to relate these to the results.
Field studies.

Methods

The index of soil moisture used was percentage soil water storage given by equation 8.1 (see Introduction) calculated by WATBAL (Keig and McAlpine, 1974). This calculation is performed on a weekly basis and for the study area weekly water storages were calculated using the rainfall data for Pearl Beach for the years 1981 - 1983. (Appendix 2). Calculated water storages are given in Appendix 5. Weekly evaporation estimates were derived from mean monthly estimates of daily evaporation from the Sydney weather station. (Appendix 6).

The WATBAL package offered 2 methods of calculation of the actual evapotranspiration co-efficient (AETCFN, equations 8.2 and 8.3). These were either a step function or continuous function relating to water storage (Keig and McAlpine 1974). Calculations were carried out using both options. These gave nearly identical results and only the results produced by the continuous function are discussed here. The potential evapotranspiration co-efficient used was the value suggested by Keig and McAlpine (1974) of 0.80. Values given by Specht and Jones (1971) were considered, however considerations of simplicity and the nature of the measure as an index favoured using the suggested value. A value of 94 mm by volume for field capacity was used to define maximum water storage, this
being the value employed in the previous chapter for the loamy sands typical at many of the sites. The program produced 52 consecutive weekly values for each year starting from the 1st of January. These values were a percentage of maximum possible water storage.

The mortality data were assembled by scoring the lifespans of dead seedlings and the sizes at death. Sizes of all emergents were recorded on each visit to the quadrats by mapping the seedling positions. Size was measured to the tip of the highest leaf. Lifespans were calculated by scoring the date of death as the mean day between sampling dates (dates of emergence were similarly estimated). Size at death was assumed to be that recorded in the sample immediately prior to death.

For each cohort, a moisture index history was prepared commencing, from the week in which emergence was scored (Appendix 7). Moisture storages for the 14 successive weekly periods after emergence were tabulated and averaged into 7 fortnightly values (Appendix 7). This was done so that the level of resolution of moisture history generally matched the sampling resolution.

The lifespans of dead seedlings were tabulated against size and average moisture storage in the period in which death occurred. The data were aggregated into a few size classes within species. These were chosen to represent different phases of growth.
For each species the frequencies of classes of all water storage periods encountered by cohorts in the 14 week period were calculated as were the frequencies of all periods in which seedlings died. Within species, the pooled data for sites and cohorts were tested using the G-test of independence.

Results

Data were initially analyzed according to sizes of individuals in each species. The size classes chosen represented different phases within species. In *B. ericifolia* seedlings with cotyledons only or at heights up to 3 cm were lumped into the smallest size class. Seedlings from 4–8 cm comprised the next class and those of 9–10 cm high, the following one. Larger sizes did not occur in the period after emergence. In *B. serrata*, the same three classes were also used, though only a few individuals died in the two larger classes, whilst in *Petrophile* only the first two classes were used, as these covered the range of sizes of dead plants. In all species, the smallest class covered seedlings with cotyledons only or juvenile leaves. The larger classes covered seedlings with progressively more adult leaves.

The results in *B. ericifolia* for the smallest size class showed a wide distribution of water storages at which deaths occurred (Table 8.17). These were aggre-
gated into 3 classes for testing: 0 - 39%, 40 - 69%, 70 - 100% of the moisture stored at field capacity. The results of a G-test of independence of frequencies were non-significant (Table 8.17).

Results for the two larger size classes (Table 8.17) were pooled and the frequencies for the 0 - 39% and 40 - 69% pooled classes were found not to be significantly different (Table 8.17). No deaths occurred at higher water storages. A similar method with similar results was carried out in Petrophile and B. serrata. (Tables 8.18 and 8.19).

In B. serrata and Petrophile, frequencies of deaths were too low in larger seedlings for analyses to be performed. (Tables 8.18 and 8.19). However, no deaths occurred at high water storages (> 50%) (Tables 8.18 and 8.19) in both species.

Discussion

In all species the null hypothesis of deaths being unrelated to the level of water storage was accepted, in the smallest size class. Deaths occurred across a wide range of water storages and this may be interpreted as showing: that deaths were independent of water storage or that the relationship between mortality and the moisture index was complex.
By comparison in the larger size-class, though deaths were fewer there was an indication that deaths were concentrated in the lower half of the water storage range. This conclusion along with the field observations on the survival of seedlings under either drought or after high rainfall led to the conclusion that there was a complex relationship between moisture and death specific to small, newly emerged seedlings. The contrast between size classes lends weight to the hypothesis that small seedlings with few leaves and a more tenous root system may be susceptible to disturbance under heavy rainfall. Larger more firmly anchored seedlings would appear to be more resilient. Another possibility was that some fungal problems or other disease or predator may be promoted at high moisture levels and small seedlings may be more vulnerable. That many small seedlings disappeared in B. ericifolia and Petrophile may lend some credence to this hypothesis.

It was concluded that the results of the analysis of water storage and field observations indicated that drought may have some common effect on survival across all seedling sizes (up to 100 days). In small seedlings an additional effect on survival was incurred at higher levels of the moisture index. In older seedlings (> 100 days), field observations in all species indicated that drought was a major source of death.

Whilst some pin-pointing of the relationships between
moisture and death were provided by the above analyses and observations in *B. ericifolia*, *B. serrata* and *Petrophile*, more specific relationships between moisture and proportions of deaths could not be formulated. Hence in small seedlings a definitive judgement of the relative effects of high water versus low water on survival could not be made though each is an important cause of death.

Quantifications of drought effects on survival in young seedlings were explored in a glasshouse experiment.

8.5 Glasshouse experiments.

**Methods**

Five treatments were used in all species. Water was added, weekly, fortnightly, three-weekly and monthly over a two-month period from November 1982 to January 1983. As well, an unwatered treatment was used.

The experiment was carried out in pots filled with soil identical to those used in the experiments described in Chapter 7. Seedlings were raised in each pot from about 30 seeds per species, by watering constantly over about 5 weeks. At the start of the experiment, seedlings were thinned to 10 per pot. Each species was represented in separate pots, there being two replicates per treatment per species. All seedlings were in the cotyledonary stage when thinned. Constant watering ceased at the time
of thinning, and the watering treatments were timed from this date according to their respective frequencies. Separate blank pots were set up containing soil only. These were watered at various occasions during the experiment and readings of soil moisture at the rooting zone were carried out at varied times after watering in order to determine the drying characteristics of the soil at this depth. Treatments were arranged in 2 blocks on a bench and waterings consisted of 100 ml per pot applied at given times. A similar experiment was conducted by Burrows (1973) to examine survival at low water potentials in mulga (Acacia aneura).

Results

Seedlings of all species showed declines under the less frequent watering treatments (Tables 8.20 - 8.23). Rates of decline differed amongst species as did the degree of mortality. B. serrata was the only species to register a large proportion of deaths in the one-week treatment. In terms of overall degrees of mortality, B. ericifolia could be labelled as the most drought-resistant species followed by Isopogon (Tables 8.20 and 8.23). In terms of rates of mortality a similar order was followed. Petrophile suffered heavy mortality after the initial 2 weeks without water had passed (Table 8.21), as did B. serrata (Table 8.22), after 3 weeks. Declines in B. ericifolia and Isopogon were registered after 4 weeks. In the 3-week and 2-week treatments significant declines
occurred in all species in the interval up to the second or third waterings.

Results for soil moisture (Figure 8.5) indicated that moisture contents below permanent wilting point ($\sim 2\%$ O.D. weight) were achieved at the rooting zone (5 - 10 cm soil depth) in 4 days.

Discussion

The results indicate that over several watering cycles the crucial cut-off in terms of survival lay between the 2-week and 3-week treatments in all species. Periods of over 10 days of sub-soil moisture at or below wilting point, repeated several times, inflicted either total or severe mortality. In B. serrata, this threshold may be lower, at around 4 or more days at wilting point after a number of weekly watering cycles.

8.6 General Discussion

The glasshouse experiment demonstrated the potential drought conditions that may cause mortality in newly emerged species. Other glasshouse work, done principally as a pilot trial for the heating/substrates experiment described in Chapter 6, involved the presence of constantly saturated conditions over some months with seedlings present.
Growth of fungi and mosses on the soil surfaces in some trays were noted but virtually no mortality occurred indicating no sensitivity of any of the study species to saturated conditions. Indirectly these observations confirmed that seedling losses at high levels of the moisture index may be due to raindrop disturbance or surface water flow. Experiments are needed to investigate this hypothesis.

The glasshouse work quantified the effects of drought and the field results indicated the role of drought in mortality. How can these results be related to fire seasonality? That is, do fires in differing seasons have some effect through differing risks of drought-related mortality?

Levels of the moisture index likely to result in death could be defined both from the field data and glasshouse work. In the glasshouse, high mortality occurred in all species if soil moisture potential at the rooting zone fell below permanent wilting point (\(-15\) bars) for over a week and if such droughts were repeated several times. Such a level of moisture potential would be equivalent to moisture storages (as calculated by WATBAL) of less than 20%.

Using this definition, the frequency of hazardous weekly drought periods from an average annual set of weekly water storage values could be examined. This set
of storage values were calculated in the same way as were those for the 1981 - 1983 period except that the daily rainfall values used were for Sydney from 1931 - 1982 inclusive. Individual yearly data were computed and then averaged to give values for the 52 weeks of the year (from the 1st January) (Figure 8.6). A further calculation was done to produce frequency distributions in each of the five water storage classes: 0, 1 - 24, 25 - 49, 50 - 74, 75 - 100% water storage.

In the "average" year weekly moisture storage was below 20% in 13, effectively consecutive weeks (1 - 3, and 43 - 52). (Figure 8.6). This corresponds to a period from late Spring to mid-Summer (30th October - 21st January). From this it may be concluded that young seedlings (freshly emerged, \(< 100\) days) would suffer heavy mortality if they had emerged at the onset of this period. By contrast, if emergence was timed for mid-year in the average year the particularly vulnerable pre-100 day period would not coincide with the onset of the long continuous period of low moisture storage. Some mortality in older seedlings would be incurred by this drought, however such mortality in most cases in the study-species was less than in the first 100 days. From the point of view of optimal burn times, this result bolsters the conclusion made in Chapter 7 for the average year. That is, burns timed to produce bulk emergence at the beginning of Winter will suffer least from drought-related mortality and may produce higher levels of emergence. Burns timed to produce emerg-
ence in late Spring will fare worst in terms of amount of emergence and drought-caused mortality.

If the frequencies of low weekly water storages are examined, the chance of mortality induced by drought can be compared at differing times of the year. If the most extreme drought class is examined (zero storage) (Figure 8.7) it can be seen that the frequency dropped rapidly from week 11 (19th March) and stayed low until week 39 (1st October), with a sustained period of zero frequencies from week 21 (28th May) to week 31 (6th August). As a baseline indicator of the yearly chance of drought hazard in any given week, these data indicated that in June-July the risk of death due to drought may be zero whilst in mid-Summer there is an 80% chance (40/52 years) of this level of storage occurring in a single week.

The data do not indicate the frequency of combinations or cycles of weeks which were shown in the glasshouse to be important. However, the contrasts between Summer and Winter are stark enough to warrant the above conclusions based on the data in Figure 8.7.

If the frequencies of moisture storages from 1 - 29% are examined (Figure 8.8) and added on to the values for the zero class, the differential between Summer and Winter is lessened but is still distinct.

It was concluded that deaths may also be caused at
high moisture storages in *B. ericifolia*, *B. serrata* and *Petrophile*, possibly through disturbances caused by heavy rain. This occurred in the smallest seedlings in the first 100-day period after emergence. In the average year (Figure 8.6), the highest weekly water storages occurred in mid-year, though values above 60% were achieved in only 3 weeks in mid-Winter. The risk of death through rainfall damage as indicated by high moisture storage may be inverse in its seasonal occurrence to that caused by drought. An attempt was made to study the frequency of high water storage using values in the storage class of 75 - 100% (Figure 8.9). This showed that very few weeks occurred in Summer in this moisture class whilst there were up to 28 years (week 25, 25th June) in Winter where these storages occurred. The requirement in terms of numbers of weeks at this level of storage to cause a given level of mortality is unknown, therefore the results provide only a general indication of risk.

To obtain an overview of the distribution of periods likely to cause deaths, the weekly frequencies of water storage for the 0, 1 - 25 and 75 - 100% classes were summed (Figure 8.10). The result was that the differences between Summer and Winter based solely on drought were reduced. No periods of risk due to high moisture storage exist during summer. The bulk of the risk is due to drought.

A maximum of 49 years out of 52 were hazardous to seedlings in weeks 50 (17th December), 48 (3rd December)
and 45 (12th November). In contrast from weeks 26 - 32 (2nd July - 13th August) the frequencies were below 30, with other isolated occurrences in weeks 12, 15 and 21. (26th March, 16th April and 28th May). (Figure 8.10).

Any generalizations of overall risk are dependent on the relative amounts of deaths incurred by high and low water storages and variations within these categories. A full assessment of proportional mortality is clearly a complex business. Can generalizations be attempted on the basis of Figure 8.10? It can reasonably be concluded that risks to very young seedlings in the qualitative (but not quantitative) sense may be least in late Winter in all species. The reality in quantitative terms may be different but much further experimentation may be needed to explore this theme. Hence, it may be concluded that burns which produced emergence in Winter may be more favourable in terms of the amounts of emergence produced, and in terms of the general risks of death encountered by young seedlings in the crucial 100 days after emergence, than burns in other seasons.
CHAPTER NINE : CONCLUDING SYNTHESIS -- MODELS OF
ABUNDANCE UNDER VARIED FIRE-REGIMES.

9.1 Introduction

In this concluding chapter I have set out to examine the effect of varied fire-regimes on the species studied by unifying the responses in all life-cycle stages. In this way the whole response of each species is considered.

In the preceding chapters it was shown that fire regimes may substantially affect numbers in all life-cycle stages and the transfers between stages. In each section differences between species have been considered, however, the ramifications of differing responses have deliberately not been highlighted. This was done because, as stated in the introduction, the significance of a given trend must be judged against the whole life-cycle. This is done here so that overall comparisons between species responses to differing fire-regimes can be fully and effectively made.

The nature of these comparisons is quantitative. Changes in abundance in each species are examined and the overall yardstick by which each differing fire-regime is judged is the likely directional change in abundance. The question is asked: under what fire-regimes do species numbers increase, decline or remain stable and over what periods may these occur? This approach also allows a judgement to be made as to whether there is a most important or sensitive part of the life-cycle under each particular set of circumstances.
Initially the changes in numbers within species are examined at high fire-frequencies. Whilst fire-frequency was not the only fire-regime component found to affect numbers, it forms a useful baseline on which changes caused by variations in seasons and intensity may be measured or judged. Fire-frequency has the fundamental effect of determining whether and when a population will produce a new generation of recruits and will determine potentially how many. As the arrival of fire in all the species studied effectively stimulates large-scale recruitment by causing seed-release (Chapter 5) and promoting conditions favourable to the emergence and establishment of seedlings (Chapter 6) it may be helpful to use it as a framework from which to examine overall fire-regime effects.

The first step in this process was modelling changes in abundance at fire-frequencies at the higher end of the scale. The general method taken in each species was to define the fire-regime, in terms of maximum fire-frequency at which population abundances may remain stable (no increase or decrease in numbers). From this basis, fire-regimes likely to cause increases or declines could be identified.

An approach that has been adopted throughout this thesis has been to attempt to identify the range of variation in abundance in differing life-cycle stages or transfers from one stage to the next, both within and between differing levels of controlling factors. In this way "conservative"
and "optimistic" trends can be compared or described and a range of species responses identified. This approach was carried over to the final modelling exercises given here. In particular, the most conservative estimates of trends in numbers have been emphasised. These provided a baseline for each species from which changes that would be certain to cause declines in numbers, could be clearly seen.

9.2 Calculation of overall cohort survivorship.

As a prelude to any modelling, it was necessary to calculate the overall trends in survival from the time of emergence through to the established mature stage in each species. This was done by combining survival data for seedlings, juveniles and mature plants over the relevant time or life-spans encompassed by each stage. Curves of survivorship (or depletion in original cohort numbers) over time are presented in Figures 9.1 - 9.4.

Survival is expressed in terms of the percentage of the original cohort which emerged, which is present at any given time afterward (Figures 9.1 - 9.4). In all species high and low estimates of survival are plotted, based chiefly on the extremes of survivorship found in seedling stage (Figures 9.1 - 9.4). Survival for the first three years (seedling stage) was plotted using the survivorship equations or models (Chapter 8) which described highest and lowest rates of survival in each species. Added to this
were the rates for the juvenile and mature stages. In all species these were identical between these stages, except in *Isopogon* where the rate for young juveniles as opposed to juveniles (lignotuberous) and mature plants, differed (see Chapter 3). In *Isopogon*, the young juvenile stage was therefore assumed to last for 10 years (post-seedling stage). For *B. ericifolia*, estimates of survival given (Figure 9.1) are for deep-soils only.

In *B. ericifolia* and *Petrophile*, estimates of 5 years of age were used to mark the onset of maturity in populations. For *B. ericifolia* and *Petrophile*, the demarcation between juvenile and mature stages (1° juvenile period) was directly observed. For *B. serrata* and *Isopogon*, no direct observations were possible (see Chapter 3), though it is certain that the primary juvenile period greatly exceeds that in the obligate-seeding species. In *B. serrata*, the stem and lignotuber sizes at which maturity was present in a proportion of individuals was identified. It was estimated that it takes approximately 10 years in *B. serrata* to reach a lignotuber size of greater than 4 cm (diameter) in 50% of a young juvenile population (see Chapter 3). Further growth to a potentially mature size may take an additional decade if the results of stem growth analyses of basal resprouters of this size are a reliable indication (see Chapter 3). Hence the 1° juvenile period may be approximately 20 years in this species.
In *Isopogon* the minimum lignotuber size at which maturity occurred lay between 5 and 10 cm (see Chapter 3). As noted in Chapter 8, young juveniles had no discernible lignotuber swelling at the stem base. An illustration of this is given in Figure 9.5, which is a photograph of a young juvenile at eight years of age at the time of writing this thesis. Unless a sudden acceleration in growth occurs at some subsequent age, it would seem that the 1° juvenile period (as a function of lignotuber size and growth) may last a similar or longer time to that in *B. serrata*. It was assumed that the young juvenile (non-lignotuberous phase) ended at age 13 years and the survival calculations were performed accordingly (Table 9.1). As no deaths in juvenile and mature *Isopogon* (lignotuberous only) (see Chapter 3) occurred during the study a nominal death rate of 0.5% p.a. was assumed and used in the survival calculation (Table 9.2). These and further calculations used in the models described below are summarized in Tables 9.1 - 9.2.

### 9.3 Abundance at high fire-frequencies

(i) **Obligate-seeders**

Initially the obligate-seeding species *B. ericifolia* and *Petrophile* were examined. Numerous workers have noted that fires which occur before the end of the primary juvenile period will either severely deplete numbers or cause local extinction of obligate seeders.
This is particularly crucial in species which do not store seeds in the soil and which are not therefore buffered to some degree against such an event. Noble and Slatyer (1980) have accounted for this important feature in their models of species responses.

In *B. ericifolia* (deep-soil only) and *Petrophile*, this critical period lasted 5-6 years (see Chapter 3), though on shallow soils in *B. ericifolia* it may last up to a decade. The deep-soil populations are considered extensively here.

What, then, is the effect of repeated fires soon after the onset of maturity? To answer this question, the seedbank data (numbers of seeds) estimated in Chapter 4, Figures 4.30 and 4.32 were used. These data were assembled as estimates of seedbank produced by stands of 50 plants based on the results for stands of similar size in the field. Seedbank data were used to judge the age at which stand self-replacement would occur if losses at the time of emergence and subsequent survival were taken into account. That is, the numbers of seeds needed to replace a stand of 50 plants at a given age were calculated. These numbers were compared to the estimates of seedbank so that the minimum age of replacement could be determined. This minimum age of replacement, marked the maximum fire-frequency at which, if maintained, numbers of plants would remain constant through time.

Variations in abundance due to differing proportions of emergence and differing rates of survival especially in
very young seedlings (Figures 9.1 - 9.2), which have a strong effect on abundance, may be caused partly by variations in fire-intensity and seasonality as well as other factors. These variations will effectively cause fluctuations in the age value at which replacement occurs. In effect, the extremes defined by these fluctuations will define a range of ages at which replacement may occur depending on the individual circumstances surrounding and/or following each particular fire. Fires at ages below the most conservative estimate (lowest emergence, poorest survival), will cause a decline in abundance. Values above the most optimistic estimate (highest emergence, best survival) will cause a rise in abundance. Such a range of values was determined in *B. ericifolia* and *Petrophile* and these are presented in Figures 9.6 and 9.7.

In both species, the seedbank values which were used were the pair of minimum accumulation rates calculated by using a low estimate of seed cohort growth with age (Figures 4.30 and 4.32, Chapter 4). These were the most conservative estimates of seedbank size that were used. In any case, the results in Figures 9.6 and 9.7 indicated that the most optimistic estimates of emergence and survival required a level of seedbank that was produced upon ripening of seeds in the crop produced from the second year of flowering after the onset of maturity. This corresponded to a value of 7 years of age in both species as the absolute minimum at which repeated firing may result in stable abundance (Figures 9.6 and 9.7). In contrast, the most conservative
estimates of emergence and survival produced age estimates of 12 years for *B. ericifolia* and 18 years for *Petrophile* (Figures 9.6 and 9.7). These ages were the absolute maxima at which repeated firing may result in stable abundance. Firing, repeated at intervals greater than these ages would result in increases in population abundances. Firing at intervals lower than them (but above the given minima) may result in increasing abundances if circumstances determining emergence and survival were more favourable. If emergence and survival conditions remain the same (minimal emergence and survival), fire-cycles of lengths below these maxima will result in decreasing abundance.

In both sets of estimates a primary juvenile period of 5 years is assumed. A delay in the onset of maturity will correspondingly retard the estimates of critical age. In determining these sets of estimates, maximum and minimum emergence percentages of 50 and 10% respectively were used. The maximum and minimum rates of survival were those presented in Figures 9.1 and 9.2.

Percentage emergences (of total seedbank) above and below the respective maximum and minimum values were observed in the field. In Burn V (Chapter 7), calculations of the total proportion of seedbank emerged in both species (using data from Chapter 7) indicated that emergence in some transects fell below 5%. In earlier work in *B. ericifolia*, Bradstock and Myerscough (1981) documented levels of emergence in excess of 50% of total seedbank. Nevertheless the values
used were considered to be good working figures on the basis of data presented in Chapter 7.

Other fire-regime components.

Considerations of variations in fire seasonality and intensity can be made with respect to the models presented for B. ericifolia and Petrophile. As these components exercise considerable control over emergence and initial survival of seedlings (Chapters 4-8) their role in the models (Figures 9.6 - 9.7) will be to set the critical age within the defined range. The conclusions contained in Chapters 7 and 8 indicated that certain fire-regimes may, on average, optimize emergence and seedling survival. It was argued in Chapter 7 that burns which result in bulk seed release in late Autumn - Winter are likely, on average, to produce higher overall levels of emergence in Petrophile and B. ericifolia. This effect is accentuated if seed release is rapid, as results from high-intensity fires, so that seed mortality may be minimized. The times for these high intensity burns which were optimum for subsequent release of seeds and emergence of seedlings varied from late Summer to Autumn for Petrophile and B. ericifolia.

Therefore a fire-regime of repeated burns at high intensity at these times could occur at shorter intervals than in other seasons in order to produce a given level of abundance. When considered against the models in Figures 9.6 and 9.7 such fire-regimes, if optimal for emergence, could
occur at frequencies close to or equal to the minimum values specified. Fire-regimes (combinations of seasons and frequencies) less favourable for emergence would have to occur with longer intervals if numbers were to remain constant.

Fire-regimes which produce Winter emergence were also found on average to favour seedling survival (less qualitative risk of death - see Chapter 8) over those that may cause emergence in differing seasons, particularly Summer.

It was therefore concluded that numbers may remain stable under high-intensity, late-Summer or Autumn burns down to a minimum repeated inter-fire interval of about 7 years. Other combinations of season and intensity may not be able to be sustained at such levels of fire-frequency if numbers are to remain constant in B. ericifolia and Petrophile. The rate of rise in seedbank size with age is such that a slight lengthening in the fire-cycle, of a few years, will, under optimal conditions of establishment, cause a substantial rise in abundance.

In both species, it can be seen that the events that determine the emergence and survival have a large impact on overall rises and falls in abundance at given fire-frequencies. Hence rates of seedbank accumulation with respect to age and controls on seedling numbers, as shaped by the differing fire-regimes components may substantially determine numbers of
individuals through time in B. ericifolia and Petrophile.

(ii) Resprouters

The method used for resprouters was substantially similar. However, rather than using seedbank numbers to define the minimum range of fire-frequencies that could be tolerated without a decline in abundance, varied combinations of fire-frequencies and fire-intensities were modelled and the minimum input of seeds needed to maintain a constant population size was estimated. This amount of seeds was then judged against the likely seedbank size to see if adequate seeds were available. In this way, the likely trend in abundance of each frequency-intensity combination could be assessed in both Isopogon and B. serrata.

These modelling exercises in the resprouters were more complex than in the obligate seeders in that they required the assessment of differential survival in differing life-cycle phases of established plants. As well, some decision had to be made about the initial proportional mix of the differing life-cycle phases, namely mature versus juvenile plants. As with Petrophile and B. ericifolia, the size of Isopogon and B. serrata stands used in the modelling process was 50 individuals; about the same size as was sampled in the studies in the field, and for which trends in seedbank were modelled (see Chapter 4).

Models of response to 3 cycles of differing fire-regime combinations are presented for B. serrata and Isopogon
In Figures 9.8 and 9.9. For each of these exercises, in both species an equal mixture of mature versus juvenile plants was assumed to be present at the outset. In both species but especially *B. serrata* (see Chapter 3) the relative proportions may vary widely. The models used survival data during fires and in the inter-fire intervals supplied in Chapter 2 (Figures 2.4 and 2.6 and Chapter 3 (Figures 3.23 c,d). Three fire-regimes were modelled in each species (Figures 9.8 and 9.9). These were:

(a) a ten-year high-intensity fire-cycle;
(b) a ten-year low-intensity fire-cycle;
(c) a fifteen-year high-intensity fire-cycle.

These were chosen firstly, because the 10-year fire-frequency would seem to be critical in that it marked the borderline in time in *B. serrata*, at least, where recruitment of young juveniles into the pool of fire-resistant and potentially mature individuals occurred. (see Chapter 3). As extreme variations in fire-intensity were found to influence survival strongly in both species at all stages of the life-cycle, it was essential that the estimated effects of the differing severity-levels of burning described in Chapter 2 were modelled here at differing levels of fire frequency. Each species is discussed individually below.

**Banksia serrata.**

In Figure 9.8 (a), it was assumed (see Figure 2.23,c) that no young juveniles could survive high-intensity fires
at an age of 10 years, therefore inputs of recruits after each fire were ignored. Because of this, the population will decline through fire-induced and inter-fire attrition. Juveniles suffer a more rapid decline due to higher death rates (Table 9.1) and an assumed 10% inter-fire transfer to the mature class through normal stem and lignotuber growth. In reality the rate and magnitude of such a transfer will depend on the size structure of the fire-resistant lignotuberous population (see Chapter 3).

Under the fire-regime modelled in Figure 9.8 (a), the number of fire-cycles needed to take the population close to extinction would depend heavily on the relative mix of juveniles and mature individuals at the outset of such a fire-regime. If a population is dominated by juvenile its end will arrive quicker than if dominated by mature plants. Regardless of the initial mix, Figure 9.8 (a) illustrates that juveniles will reach extinction first. This means that a pool of declining mature plants will be present which will continue reproductive activity (accumulation of seedbank) in the inter-fire periods. Such a seedbank will never produce recruits due to fire caused mortality. Should such a fire-regime be broken before extinction occurs the population will have some reproductive capacity through which to accumulate seeds and fire-resistant recruits. It can be seen that many fires in such a cycle would be needed for extinction to occur. However a single interval giving 20 years without a fire, as already discussed in Chapter 3, will allow a measure of recovery.
A reduction in intensity at the 10-year frequency (Figure 9.8 (b)) will have the effect of allowing some recruitment to occur. The model in Fig. 9.8 (b) uses the same starting conditions and inter-fire death rates and transfer rates of juvenile to mature class as those given in Fig. 9.8 (a). Proportions of deaths experienced in burns however differed as given in Figure 2, being less in all life-cycle stages and, most significantly, being set at a level of 50% for young juveniles. This effectively allowed some recruitment into the pool of more fire-resistant juveniles and eventually into the mature pool (see Chapter 3).

In Figure 9.8 (b), the amounts of seeds needed to produce the required number of fire-tolerant juvenile recruits at each subsequent fire are calculated. The required number of juvenile recruits is the number needed to replace those more established individuals lost through attrition: that is the numbers needed to maintain a stable population size. In calculating this quantity of seeds, the most conservative estimates of seedling and juvenile survival (see Figure 9.3) and emergence (10% of seedbank) were used. Therefore the amounts given are the maximum numbers of seeds necessary for replacement or alternatively the most conservative estimate of seedbank required.

A feature of the model in Figure 9.8 (b) is the apparent stability reached in relative proportions of mature and juvenile plants. This is purely a function of the inputs through young recruits being set at replacement level.
However it indicates that no decline in the reproductive pool is likely, provided all other rates of transfers remain the same. Is the level of seedbank that is likely to be present at the completion of each fire-cycle adequate to meet the numbers required for recruitment; that is about 300 seeds?

In the estimations of seedbank presented in Figure 4.31 it can be seen that a level of about 800 seeds is reached seven-eight years after the first crop of cones ripen (this is for the most conservative series of estimates provided in Fig. 4.31). Allowing for a two-year 2° juvenile period, this figure represents the minimum likely seedbank at 10 years post-fire. It comfortably exceeds the required number (300) needed for a stable population size. Therefore within the constraints of both the population and seedbank models it would appear that such a fire-regime will result in an increasing population size.

Several points need elaboration. Firstly the constraints of the models may affect the outcomes. Seedbank was modelled on the basis that the mean numbers of plants setting cones annually would increase from 4 per fifty plants in the first mature season after fire, at a constant rate, to 16 at 25 years. At this rate, 8 mature plants would produce the level of estimated seedbank at 10 years. According to the population model in Figure 9.8 (b), these would come from a pool of 25-26 mature plants. According to the data in Chapter 3 on the proportions of mature plants likely to set cones, this would appear to be easily achieved. If, however, the initial pro-
portion of mature plants was smaller (≤ 10 instead of 25), the amount of seeds present may fall below the levels required for overall population stability should levels of cone production per plant and seeds/cone remain the same.

Another factor that requires serious consideration is the likely level of seed release under low-intensity fires. Data from Chapter 5 indicated that the overall amount of seeds released did not differ between fire-intensity levels, though the rate of release may vary. However, fires of low severity may not affect much of the seedbank in large mature plants. Scorching sufficient to kill branches of small diameter was limited to a maximum height of around 2 metres (see Chapter 2) and as much of the seedbank is carried in crowns which can greatly exceed this height, effective release may be restricted to low and usually old cones. Hence the actual value of seedbank available at low fire-intensities may be a minor proportion of the 800 seeds given above. If so, it is possible that seed numbers may fall below the level needed for replacement.

In summary, it may be concluded that the fire-regime modelled in Figure 9.8 (b) may be marginal in maintaining stability in numbers. It can be seen that the chances of maintaining constant numbers are strongly dependent on the size of the pool of mature plants at the outset of such a fire-regime. This in turn will be influenced by previous fire-regimes. As well, at a low-level of fire-intensity and height of scorch, the adequacy of seed release may be
questionable even if seedbank-size is adequate. Unfortunately, I have not obtained quantitative measures on the responses of cones as a function of height on branches and scorch height in low-severity fires. The conclusions given here assuming adequacy of seed release are based on non-quantitative observations but would appear to be reasonable. A further important conclusion is that the factors which govern the emergence of seedlings and subsequent survival have little significance compared to those which determine juvenile survival in fires and seed availability; namely fire-frequency and intensity. This contrasts with the finding for the obligate-seeders.

The final modelling exercise addressed a slightly longer fire-frequency. A simulation of fires at a level of high-intensity was done on a 15-year cycle (Figure 9.8 (c)). A high intensity was chosen as this imposed the most severe level of attrition on the population. The difference caused by a five-year lengthening in the fire-cycle could then be determined over that modelled in Figures 9.8 (a) and (b). For this exercise it was assumed young 15-year-old juveniles had achieved a level of fire tolerance (to high-intensity fires) commensurate with that given for lignotuberous juveniles in Chapter 2 (Figure 2.4 - 69% survival). Due to the longer inter-fire interval, the proportion of juveniles which progressed to the mature class was increased to 20% (per cycle). As with the previous exercises, inter-fire mortality was set as per Chapter 3, Figure 3.23,(c) at 0.8% per annum.
The results (Figure 9.8 (c)) indicated that the level of seedbank (Table 9.1) would easily exceed the required numbers of seeds. As with the previous exercise, a smaller proportion of mature plants may decrease the available seedbank to levels which jeopardize constancy in numbers. A slower rate of acquisition of fire-tolerance will also accordingly increase the seed numbers required for this constancy. The trade-off between high and low fire-intensities at this fire-frequency may be again the amount of seeds made available. However, if a reasonable number of mature plants are present, the seedbank will be of a size that may render this difference unimportant in terms of constancy in abundance.

In *B. serrata* it may be concluded that the importance of fire-intensity may diminish as fire-frequency increases above the 10-year level modelled in Figures 9.8 (a) and (b). As the seedbank grows and a greater proportion of young juveniles gain fire tolerance with an increase in the inter-fire interval, the circumstances under which a decline may occur may become more tightly confined. These would be important if the pool of mature plants was very small. A full consideration of the models would suggest that if the proportion of mature plants diminishes in a population, the subsequent inter-fire interval needs to be accordingly lengthened. This would be necessary to maintain constancy in numbers or to ensure that declines in abundance are minimized. This would have the effect of maximizing the chance of recruits going through unburnt, from emergence to maturity. In real samples of
plants, where the proportion of mature plants is small (< 20%) compared to established lignotuberous juveniles, fire-cycles approaching a frequency of 10 years should be avoided, especially if they are occurring at high-intensities.

Only where the available seedbank is marginal in relation to the numbers needed to make up for attrition, will the factors which determine emergence and survival of seedlings be of crucial importance. Again this may be likely when the relative size of the mature pool is low.

**Isopogon anemonifolius**

A summary of some of the conditions of the models presented for *Isopogon* is given in Table 9.2. As with the other species, data for survival during and between fires was presented in Chapters 2 and 3 and put to further use here.

The modelling of fire-regime effects in Figures 9.9 (a)-(c) for *Isopogon* was done using the same fire-regimes as were used in *B. serrata*.

As with *B. serrata* repeated cycles of high-intensity fires every 10 years, was assumed to completely kill young juveniles and therefore prevent overall recruitment (Figure 9.9 (a)). The consequent decline in numbers would take place at a faster rate than in *B. serrata* due to the higher mortality found to be sustained in fires by *Isopogon* (see Chapter 2). Otherwise similar conclusions as to the relative declines in
mature versus juvenile plants can be drawn (Figure 9.9 (a)).

Under a ten-year, low-intensity fire-regime (Figure 9.9 (b)), due to the low-growth rate of young juvenile recruits (Figure 9.5) zero fire tolerance was assumed and hence no recruitment was allowed for in the model. The decline in the existing population took place at a slower rate than under high-intensity fires (Figures 9.9 (a) and (b)). Conclusions about the effect of differing initial proportions of mature and juvenile plants in Banksia serrata apply equally to Isopogon.

The third simulation was done using a model which allowed some recruitment of young juveniles into the pool of fire-tolerant lignotuberous juveniles. Mortality during each fire was set at the same level as that determined in Chapter 2 for larger lignotuberous juveniles. Transfers of juveniles to the mature stage were set at 20% per inter-fire period of those juveniles older than 15 years.

The results (Figure 9.9 (a)) indicated firstly, that the amount of seeds needed to maintain population stability at the completion of each fire-cycle approached 3,000. Estimates of seedbank (Figure 4.33) indicated that these requirements were exceeded by an order of magnitude. Isopogon was found to store the most seeds, compared to the other species studied. A further feature contained in Figure 9.9 (c) was the indicated decline in the size of the mature plant pool.
if the numbers of new recruits input were just enough to keep post-fire abundances constant. The magnitude of the seedbank was such however that the potential numbers of real recruits after fire would far exceed those given in Figure 9.9 (c). It is likely that those would filter through into the mature pool in sufficient numbers to reverse such a decline. The seedbank is also of such a size, that if the pool of mature plants declined a substantial seedbank of a size sufficient for replacement would still exist. In Chapter 2 (Fig. 2.6), fire-caused mortality in the "oldest" site (13-years post-fire) was higher than in sites burnt at intervals of 2 and 5 years. If a mortality level similar to that given in (Fig. 2.6) for 13-year plants occurred, then a large input of recruits and seeds would be needed to arrest a large decline in numbers.

The possible differences in *B. serrata* in seed availability due to differences in seed release likely under opposing extremes of fire intensities would not be present in *Isopogon*. Due to the low stature of the plants, most cones would be directly heated and stems killed in low-intensity fires so that overall amounts of seeds released would differ little, though rates of release may vary. Hence fire-intensity in *Isopogon* is of importance purely as a determinant of the amount of mortality sustained in all types of established plants. The modelled proportions of death at differing intensities were higher in *Isopogon*, and in particular mature-plant mortality at all intensities was higher, than in *B. serrata* causing a greater potential decline which was compensated for
by a greater potential to accumulate seeds. As with
B. serrata, the factors which determine emergence and sur­vival would appear to have less primary impact on abundance
than direct fire-frequency and intensity effects on survival
and seedbank size.

In summary, in *Isopogon* it would appear that at the
critical fire-frequencies of around 10-15 years, differences
in fire-intensity may be crucial in determining the nature
of declines in mature plants and numbers of surviving re­cruits. Population stability in the models may be assured at
low-intensities in this range of frequencies, but a fire-cycle
length of 15 years at high intensities may be necessary to
ensure constancy in numbers or an increase in abundance.
(Figures 9.9 (a) - (c)).

9.4 Comparative responses of obligate-seeders and resprouters at
high fire-frequencies.

The range of ages at which population stability may
occur in the obligate-seeders straddles the ranges in fire-
frequencies which mark the thresholds of stability in the
resprouters. Significantly, under the most favourable cir­cumstances surrounding recruitment (post-fire) both obligate­seeders may be able to withstand fire-cycles several years
shorter than the minima outlined for either resprouting
species.

Under the least favourable circumstances, *B. ericifolia*
may withstand cycles of 12 years, being a couple of years
longer than the critical length (at low-intensities) for B. serrata but probably less than or equal to the minimum required in Isopogon (also at low-intensities). For Petrophile under unfavourable conditions the minimum length cycle may equal or exceed that postulated above for Isopogon at high-intensities.

These conclusions pertain to repeated, constant-length long-term fire-cycles. As discussed in Chapter 2, the advantage of the resprouting habit lies in the resilience it offers to a chance pair or trio of closely spaced burns. At high frequencies sustained over long periods the resprouters may decline similarly to the obligate seeders though the rate of decline will be considerably slower. Effectively the resprouters are buffered against periods of unfavourably high fire-frequencies by comparison to obligate seeders. Declines in woody resprouting species at very high fire-frequencies have been documented in Noble (1982) for mallee Eucalyptus and Zedler et al. (1983) for Adenostoma and Xylococculus species of chaparral and by Grano (1970) cited by Gill and Groves (1981). The conclusion that resprouters offer a degree of resilience to occasional very high fire-frequencies in comparison to obligate seeders, was illustrated and discussed by Noble (1981).

These conclusions apply here, though they may be strongly influenced by interactions between sizes and life-cycle stages. This study has identified the critical fire-
regimes, below which abundance may fall. It would appear that in this regard the obligate-seeders in this study may at least match or even be able to tolerate in some circumstances higher fire frequencies than the resprouters. Below these critical fire-frequencies differences between the groups of species lie mainly in the rate at which they fall to extinction. It may be possible, if the models in Figures 9.6 - 9.9 are accurate, that under a sustained 8-12 year fire-cycle, populations of B. ericifolia and Petrophile will be stable in numbers whilst co-habiting populations of B. serrata and Isopogon will be undergoing a continual decline. This will particularly occur if such a fire-regime consisted of high-intensity late-Summer-Autumn burns, thereby maximising the probability of recruitment in the obligate-seeders and inflicting the highest possible mortality on the resprouters. The range of fire-frequencies over which this may happen may be narrow but significant, though in this range Petrophile and B. ericifolia may be susceptible to declines caused by occasional unfavourable recruitment events.

These scenarios are summarized in Figure 9.10.

Several assumptions in B. serrata and Isopogon have been adopted in Figure 9.10. Minimum fire-cycle lengths at low-intensities (not modelled here) in B. serrata were based on observations (see Chapters 2 and 3) that a minor proportion on young juveniles had fire-resistant lignotubers around age 7 years. Whether or not gains through recruitment
of these plants would balance losses and whether seeds were available was not modelled here, though problems with seed release as discussed, are likely. Therefore the estimate of the maximum, low-intensity fire-frequency is an educated guess. The corresponding estimate in *Isopogon* relies also on guesswork; in this case guessing of the minimum age of some fire tolerance in a minor proportion of young-juveniles. As large seedbank sizes in populations at 10 years (post-fire) are assured, as is seed release at low fire-intensities, the small amount of recruitment may be adequate at this length of fire-cycle to replace losses.

9.5 Abundance at low fire-frequencies

Emergence and recruitment and survival of seedlings was shown to be substantially lower in all species under unburnt conditions. Such inputs under high fire-frequencies were not considered as they would have little effect on reproduction or little chance of contributing to the fire-resistant pool of lignotubers under the circumstances modelled in Figures 9.6 - 9.9. At fire-frequencies of the contrasting extreme, such inputs may become important in determining the long-term levels of abundance in each species. The consequences of the most extreme event, that is, the absence of fire are worth exploring. Features of the plants which would be important, are:

(i) Lifespans;

(ii) Numbers of seeds at old ages;
(iii) Rates of emergence and survival in unburnt conditions.

(i) Lifespans

An attempt was made to estimate the life-span of *B. serrata* by radio-carbon dating. Previous attempts in *Eucalyptus* species have been made (Wellington et al. 1979, Lacey 1983) using samples of the lignotuber. Lacey (1983) reported difficulties in choosing the position of sampling from the lignotubers of *Eucalyptus botryoides* due to irregular patterns of wood decay and growth. Wellington et al. (1979) extracted samples from varied positions in lignotubers of *E. incrassata*, both close to the centre and near the periphery and gained estimates of ages of 250 years from the samples at the centre. A similar method was adopted here. Monetary considerations limited the sample size to two and each was taken from a separate plant.

The individuals chosen were the largest and presumably oldest trees found in the general study area (lignotuber diameters over 50 cm). Wood samples were extracted from the centre of the lignotuber at ground level as this appeared to correspond to the geometric centre of the lignotuber. A 30-gram cube from each plant was submitted for analysis, by B. Analytic Inc. of Florida, U.S.A. The results were in each case ages of less than 50 years pre-1950, that is less than about 80 years.
No further analyses were attempted in either this species or Isopogon. The lignotubers in Isopogon bore great similarity to the overall morphology of those in E. botryoides described by Lacey (1983). Due to the difficulties that Lacey (1983) described in selecting wood for sampling no attempt was made at dating in Isopogon.

In B. ericifolia, Bradstock and Myerscough (1981) suggested life-spans of up to 50 years may be achieved largely on the basis of anecdotal fire history information for some senescent stands found in the study area. These and other stands were destroyed in fires in 1977 and 1980 and suitable replacements were not found. Survival data (half-life over 70 years) suggest that this may be an underestimate, though mortality may accelerate in stands older than those sampled here.

In Petrophile a lesser half-life was measured (24.7 years), whilst in B. serrata established plants the value was 86.3 years. These data are inconclusive but suggest that life-spans greater than 50 years may be possible in all species.

(ii) Numbers of seeds and emergence and survival in unburnt conditions.

The results in Chapter 5, suggested that as time since fire increased, substantial amounts of viable seeds would be released annually from unburnt plants in all species. As well, seedbanks in all species continue to grow though at
declining rates, as modelled, with the passage of time since fire (Chapter 4). The potential exists for large-scale recruitment of seedlings from either the annual seed-fall or from seed-falls in senescent vegetation at ages in excess of 20-30 years where plant death triggers seed release from retained cones. Survival and emergence of young seedlings was more restricted in unburnt conditions compared to burnt conditions due to the effects of plant cover and high levels of predation. As was shown in Chapter 6, the emphasis of some of these factors varied, however predation in all species was so intense as to rule out most recruitment. Burning was viewed as having the effect of either removing or saturating seedling predators and therefore allowing the recruitment of seedlings.

Using the data from Chapter 5 on annual seed shed and the likely conclusion (Chapter 6) that a few emergent seedlings will probably escape destruction by predators, some attempt at calculating the rates needed for replacement of dead established plants in unburnt stands can be made. Assuming that a minimum of 10% of seeds (viable) which are released annually, emerge, and of these 10% survive for 3 years to become established in all species, the following annual recruitment levels may be expected in stands of 50 plants over 20 years old:

(i) **B. ericifolia** 4 plants
(ii) **B. serrata** 1 plant
(iii) **Petrophile** 23 "
(iv) **Isopogon** 1 plant

In all species these rates are adequate or in excess of
those required to replace the average number which die each year, found in such stands (Chapter 2). The proposed mortality rate of seedlings is well above that observed in burnt (Chapter 8) and unburnt stands (Chapter 6, for most species). It can be concluded that the levels of recruitment necessary to maintain constancy in numbers is possible in older stands where a seedbank of sufficient size is present. At lesser ages seed release from the seedbank would be insufficient to provide the necessary numbers due to the smaller seedbanks present in all species.

The fates of recruits in all species in unburnt stands after reaching the established phase is open to speculation (Chapter 6). In the dense Petrophile and B. ericifolia stands examined, such recruits may be suppressed and provide little or no reproductive contribution to the stands. However, even if suppressed such recruits may be released if gaps occur due to senescence. The likelihood of this being a significant factor in the maintenance of dense stands in the absence of fire is dependent on the survival rate of established recruits. Anecdotal evidence in Petrophile and B. ericifolia suggests that established recruits suffer high mortality. As well mortality was concentrated in small plants (see Chapter 3). It may therefore be concluded that in these species, in the absence of fire some presence at a site may be maintained by low levels of recruitments and survival, but that high density stands are promoted and maintained under periodic firing. Firing allows massive recruitment and higher levels of survival. Stands in unburnt conditions may persist through
time at low levels of density.

For *B. serrata* and *Isopogon*, suppression of recruits in unburnt stands may also occur. However even if growth is retarded long periods without fire may allow a steady flow of juveniles into the pool of lignotuberous plants at a rate that increases the size of the seedbank and annual seed shed from it. Such an unimpeded flow of individuals into potentially reproductive sizes may result in pools of mature plants in stands of a size in excess of those modelled in Chapter 4. Again, as with *B. ericifolia* and *Petrophile* this will depend on the growth and survival rates of any recruits.

It may be concluded that fire-frequencies up to about 50 years may in all species promote potentially high levels of abundance due to the presence of large seed-storages and, under such fire-frequencies, the potential for increases in population sizes is high. Fire-frequencies of the order of 20-50 years as evidenced by the seedbank and growth data (Chapters 2 and 4) will turn over populations in each species at times which will maximize the potential growth in numbers of established plants. In the resprouters these fire-frequencies will result in juveniles reaching mature sizes without delay (i.e. frequency exceeds $1^0$ juvenile period).

In *B. ericifolia* at these ages, low fire intensities may allow survival of a few large mature trees in stands, thereby buffering them against a one-off very short-fire interval. This effect may be of considerable importance
as a buffer against an occasional extreme event and can only occur at ages in excess of 20 years in *B. ericifolia* stands.

At fire-free intervals longer than 50 years which may begin to exceed the life spans of the species, quantitative estimates of trends may be difficult to predict. However some guesses at qualitative changes in habitats may be used to speculate on the relative fates of the study species.

If stand senescence in *B. ericifolia* and *Petrophile* results in open conditions the emergence and survival of seeds may be enhanced and the species may continue to occupy sites at a level largely influenced by predators. The amounts of seeds available may be adequate for the numbers of plants in the stand to be replaced. In *B. serrata* and *Isopogon*, the fate of stands may be largely determined by progressive inputs of recruits as stands senescence would be less likely to be as concentrated in time and space as in the even-aged obligate-seeding species stands. It is therefore likely, according to the calculated data given above that stands may exist through time in the absence of fire at perhaps reduced levels of abundance. In all species, further work on the survival of plants recruited in unburnt conditions is needed to clarify this point.
This study has concentrated on determining the species responses at high fire-frequencies. The knowledge acquired of the effects of low-frequency fires was less comprehensive due both to the lack of suitable stands which could be accurately aged and limitations on resources. Whilst high-frequency fires are possibly no more important than low-frequency fires from a biological point of view, the prevalence of high-frequency fires in these vegetation types in the Sydney Region makes it imperative to understand their effect in detail.

Unlike the focus of this study, that of Keeley (1977,a) and Keeley and Zedler (1978) was on forming an understanding of the effects of low fire-frequency between groups of resprouting and obligate-seeding shrubs. The authors concluded that the obligate seeding species would be favoured, principally because hotter fires would be favoured by large accumulations of fuel resulting in greater death of sprouting species, causing large gaps to occur in the post-fire cover between the multistemmed resprouting bushes. These gaps would favour seedling re-establishment. The effect of burning old stands as opposed to younger stands would accentuate the size of the gaps already caused by thinning before fires. Hence it was argued that selective pressure would favour reinvestment of internal plant resources to seed production at the expense of the burl-forming habit. Keeley and Zedler (1978) concluded that co-existence of the species would be optimal under a burning frequency somewhat lower than the 20-30 year cycle then
imposed by man on this vegetation. The hypothesis involved some causal interaction with sites of varying aridity, principally that the thinning and death of shrubs during a long interval without fire and in any ensuing conflagration would be enhanced on the most xeric sites (Keeley, 1981). Keeley and Zedler (1978), Keeley (1977) and Zedler (1977) produce further data on other chaparal species besides *Ceanothus* and *Arctostaphylos*, to which the above hypothesis mainly pertains, which, on the basis of relative regeneration proportion of seedlings, formed a continuum of dependence on sprouting. To a large degree these conclusions were dependent on comparative death rates at old ages, > 100 years (post-fire), between the groups of species. Keeley and Zedler (1978) demonstrated that, in obligate-seeding *Ceanothus* and *Arctostaphylos*, rates of survival remain high; that their growth in size is high and outtops cohabiting resprouters, and that seed production is high. Under such circumstances, their conclusions seem to form a reasonable hypothesis that explains the relative co-existence of species under differing fire regimes. Any extension of their hypothesis to differing species and differing circumstances is dependent on these crucial rates of growth, survival and fecundity at old ages. There was no indication in this study of superior survival of obligate-seeders at older ages or possible greater longevity. The circumstances implied that reproductive outputs may increase to maximal levels in resprouting spp. specifically in the long-term absence of fire. *Banksia ericifolia* particularly has the ability to dominate sites and suppress resprouter shrubs such as *Isopogon*, though the
populations, analyzed here, of this species were not taken from such stands. From the data available, it would seem that the hypothesis that resprouters are less favoured by very high frequency of fires cannot be accepted for the study species, particularly as the factors controlling emergence and seedling survival are less dependent on the removal of litter and cover in both *Isopogon* and *B. serrata*.

Under very frequent fires (< 20-year cycles) the key difference between resprouters and obligate seeders may lie in the relative length of the primary juvenile period. Because of the shorter primary juvenile period in obligate seeders a slight but significant advantage is gained at fire-frequencies likely to cause declines in the resprouters. However with this advantage comes a dependence on conditions conducive to optimal seedling emergence and early survival. Such an advantage is likely only where the narrow range of favourable fire frequencies and post-fire conditions are very predictable and consistent. It would appear that the length of juvenile period in resprouters is of lesser importance than the rate of growth of lignotubers to actively fire-resistant sizes, or alternatively the length of the primary juvenile period in the obligate-seeders.

The importance of fire predictability and its influence on species responses in space and time were highlighted by Keeley (1981) and are amply apparent here. Conditions which on average would be most favourable for seedling emergence and survival would be taken advantage of by high-intensity late-Summer and Autumn burns. Frequent, consist-
ent burns of this intensity and season would favour Petrophile and B. ericifolia. Under less frequent firing, all species could increase in abundance and there would be less dependence on the conditions determining seedling numbers in Petrophile and B. ericifolia.

In essence, the method used here, by assessing extremes of emergence (as a % of seedbank) and seedling survival, has allowed quantitative assessment of the effects of high-frequency fires without using any analyses of ratios between seedlings and parent plants as done by Keeley and Zedler (1978). I would contend that this is a better method in that variations in recruitment are directly addressed in relation to causal factors. Ratios of recruitment to established plant numbers vary according to a variety of these factors. Variations in recruitment can effectively be fed into models which will produce ranges of critical fire-frequencies for each species. The models presented in this chapter are essentially an application of the "vital attributes" presented by Noble and Slatyer (1977, 1980, 1981). Whilst Noble and Slatyer's (1980) system was principally presented as a method for modelling the effects of disturbances of differing frequency, as used here, the effects and variations imposed by other components of fire-regimes and other factors may be incorporated quantitatively into the model so that critical ranges of fire-frequencies can be calculated. Noble and Slatyer's (1980) system may be used as a framework for detailed quantitative modelling of fire-regimes effects as the attributes cover all life-cycle stages in an effective manner.
Finally, some brief comments may be made on the "ultimate" consequences (sensu Harper, 1982) of these conclusions. Keeley and Zedler (1978) asked the question, under what circumstances would obligate seeders have arisen, if they can co-exist with resprouters over a wide range of fire-frequencies? On the evidence of Wells (1969), Keeley and Zedler (1978) argued that resprouting is a more primitive mode of persistence and that obligate-seeders may be derived from this basic habit. George (1981) has argued similarly in *Banksia* that the resprouting habit is primitive (though no objective tests of this hypothesis were presented) and that dependence on seeds may be derived. If this hypothesis is accepted, it may be that the obligate-seeding habit in some single-stemmed *Banksia* species, on the basis of contemporary comparisons between *B. ericifolia* and *B. serrata*, arose under circumstances producing frequent, predictable high-intensity late-Summer-Autumn fires. This would effectively require selection for a decrease in the primary juvenile period at the expense of the ability to form a basal stem lignotuber.

Such scenarios are essentially untestable as evolutionary hypotheses, being extensions of "proximal" (sensu Harper 1982) or ecological patterns. We cannot know the real cause of past events and we must assume, in assembling such models, that many factors of the environment and attributes of species are held constant whilst the key factors of interest are assumed to vary in a predictable manner. Nevertheless, such
hypotheses may be useful in drawing attention to the ongoing processes of selection in an ecological context, particularly if they are based on an integrated assessment of responses in all life-cycle stages in plant species.

The results here may be used to reflect on the findings produced by workers interested in the allocation of energy between resprouters and obligate seeders (Carpenter and Recher 1979, Fulton and Carpenter 1979), that obligate seeders may invest more energy in producing seeds than in lignotuberous or burl forming resprouters. Certain fire regimes may promote the expediency of transferring resources from the formation of lignotubers (with high storages of starch, Bamber and Mullette, 1978) in Eucalyptus gummifera and Bamber, pers. comm. in B. serrata) into mechanisms for setting seeds, earlier and in greater quantities than resprouters. Evidence from the study-species may indicate that this has occurred under high-frequency fires.

Auld (1984) concluded that for the soil-stored-seed-regenerator Acacia suaveolens, fire regimes composed of medium-high intensity fires repeated at cycles of 1-30 years will be most favourable in terms of abundance. Auld (1984) also demonstrated that the peak in numbers of viable available seeds in the soil-stored seedbank in A. suaveolens may occur at less than 10 years of age in populations, suggesting that the behaviour of this species may be similar to that of B. ericifolia and Petrophile at fire-cycles less than an
interval of 10 years. As with the obligate-seeders studied here, the emphasis would be placed on predictable, high intensity fires producing Winter emergence (Auld, 1984) if numbers were to be maintained at a constant level at such fire-frequencies. Hence the conclusions given here for obligate seeders may apply in species with differing methods of seedbank storage, in the region. Clearly if the results for co-habiting *A. suaveolens* are taken into consideration, fire-regimes with a fire-cycle length of over a decade may be seen to be conducive to the maintenance of populations of woody shrubs and small trees, regardless of mode of recovery, in the study-area. However the individual characteristics of species may be such that adequate generalizations may need to be based on further data for primary juvenile periods and seedbank accumulation in both sprouters and obligate-seeders. As well studies of the rate of growth of juveniles and their lignotubers in resprouting species and the concomitant acquisition of fire-tolerance may be of great importance.
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