VEGETATION PATTERNS IN THE NORTHERN JARRAH FOREST OF WESTERN AUSTRALIA IN RELATION TO DIEBACK HISTORY AND THE CURRENT DISTRIBUTION OF *PHYTOPHTHORA CINNAMOMI*

by

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This thesis is presented for the degree of
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DECLARATION

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

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Keith L. McDougall

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ABSTRACT

Dieback, largely attributed to the fungal plant pathogen *Phytophthora cinnamomi*, is characterized in the northern jarrah forest by multiple deaths of many plant species, including the dominant, *Eucalyptus marginata* (jarrah), a species of great commercial importance. The wide host range of the pathogen has major implications for the biodiversity of the ecosystem. The first records of dieback in the jarrah forest were made in the 1920s.

Despite the magnitude and long history of the impact in the jarrah forest, little is known about the vegetation changes that result from dieback. In this dissertation, I develop a model of vegetation change related to dieback by examining the vegetation of a range of dieback sites and relating the patterns identified to the current distribution of *P. cinnamomi*. The study is the first explicit investigation of floristic and structural patterns on dieback sites in the jarrah forest.

Substantial floristic differences were found between dieback and unaffected vegetation. The patterns are strongly correlated with the age of the original dieback event. There was little difference, however, in the mean number of species / quadrat between dieback and unaffected vegetation. The time since the inception of dieback was estimated using aerial photography. The oldest dieback sites located had been affected prior to 1951. Of the species found less frequently on these old dieback sites, 64% had not previously been associated with *P. cinnamomi* infection. Some of these were assessed for their susceptibility in glasshouse pathogenicity tests. New records of susceptibility were made at the species, genus and family levels. Several species regarded as being highly susceptible to infection by *P. cinnamomi* were found as frequently on old dieback sites as in unaffected vegetation. Many of the species found more frequently on dieback sites were probably present at the time of the initial dieback event. Others, mostly annuals, may have been introduced from nearby vegetation types with open canopies, such as granite outcrops. If plant invasions have occurred following dieback, the small

differences in species richness between dieback and unaffected vegetation may hide a great reduction in species richness due to dieback.

Structural changes following dieback may have a profound effect on some species regardless of their susceptibility to infection. A spatial association with trees on dieback sites was demonstrated for a range of species. The apparent reliance of some understorey species on tree cover is discussed in relation to current theories of patch dynamics.

Two methods were used to isolate *P. cinnamomi* from dieback sites. *In situ Banksia grandis* baits were more effective at detecting *P. cinnamomi* than *ex situ* baited soils, especially when *P. cinnamomi* was apparently rare.

P. cinnamomi was frequently isolated from creek edges with a long history of dieback and from active dieback fronts but was rarely found on sloping dieback sites affected prior to 1980. It is not clear if the *P. cinnamomi* present on pre-1951 dieback sites has persisted there since the initial dieback event or been re-introduced from active dieback fronts upslope.

Very few highly susceptible species appear to be totally eliminated by the pathogen at the time of the initial dieback event. The mass deaths at that time are followed by a period of recolonization of susceptible species with highly germinable seed. The survival of the new cohort of these species is a function of the time taken to produce another crop of seed.

Susceptible species may persist on the pre-1951 dieback sites because of highly germinable seed, young reproductive age, copious seed production and animal dispersal. The rarity of *P. cinnamomi* on these sites must greatly contribute to their persistence.

Pathogenicity testing in excised stems indicated that resistance to the movement of *P. cinnamomi* in plant tissue develops in jarrah populations on many dieback sites, although

it is unlikely to be integral to regeneration. Evidence of resistance in other species investigated could not be found.

The key elements in the model of vegetation change developed in the thesis are (i) the on-going occurrence of *P. cinnamomi* on dieback sites, (ii) the susceptibility of plant species to infection by *P. cinnamomi*, (iii) the sensitivity of plant species to structural changes, (iv) the proportion of a plant population killed, (v) the capacity of plant species for rapid recruitment after dieback, (vi) the time taken for plant species from germination to reproduction, and (vii) the capacity of plant species to invade. Stochastic factors such as fire, logging, climatic perturbations, and diseases caused by other pathogens, cannot be quantified and easily incorporated into the model.

Predictions are made about the future vegetation of dieback sites, contingent on intervention by forest managers. An epidemic - recovery cycle, involving concomitant fluctuations in pathogen and host populations, has been hypothesized by some authors for sites affected by *P. cinnamomi*. There is evidence of such a cycle on a small scale. On a larger scale, epidemics on dieback sites in the jarrah forest may be isolated in space and time.

The importance of long-term ecological studies of jarrah forest vegetation to our understanding of natural forest processes and the effects of dieback is stressed.

CONTENTS

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CHAPTER 1: INTRODUCTION

1.1 The Northern Jarrah Forest

The northern jarrah forest occurs in the Darling Range to the east of Perth (Figure 1.1). Its western boundary is sharp, being defined by a steep north-south escarpment. Its other boundaries are diffuse. In the north and east, as rainfall decreases, the northern jarrah forest grades into a woodland dominated by wandoo (*Eucalyptus wandoo*). In the south, as rainfall increases, forest dominated by karri (*Eucalyptus diversicolor*) occurs.

1.1.1 Flora and Vegetation

Jarrah[1] is the sole dominant tree in much of the northern jarrah forest. Despite this, considerable variation has been recognised in the understorey. Havel (1975) attributed understorey differences to variation in soil fertility, soil structure, rainfall and topography. Jarrah is replaced as structural dominant on some water-gaining sites by other eucalypts or tall shrubs (Havel 1975) and on some sites with ironstone-rich surface soils or outcropping granite by low-growing shrubs, herbs and cryptogams.

Jarrah may grow to a height of between 15 m and more than 25 m depending on rainfall (Abbott et al 1989). Its timber is harvested for a wide range of uses. In the sense of Specht (1981), the forest dominated by jarrah may be a woodland, open-forest or closed-forest, depending on the time since logging, the degree of other disturbance and the natural density of trees. Its original structure is likely to have been tall open-forest. A middle storey of *Banksia grandis*, to a height of about 8 m, is usually present. The cover of this small tree often greatly exceeds that of jarrah. The sense of a closed community is then attributable to *Banksia grandis* rather than to jarrah. In places, *Allocasuarina fraseri* dominates the middle storey, often with few accompanying jarrah.

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[1] The vernacular is in common usage for tree species in the jarrah forest and will be used throughout this thesis. Common names used are: blackbutt (*Eucalyptus patens*), bullich (*Eucalyptus megacarpa*), jarrah (*Eucalyptus marginata*) and marri (*Eucalyptus calophylla*).

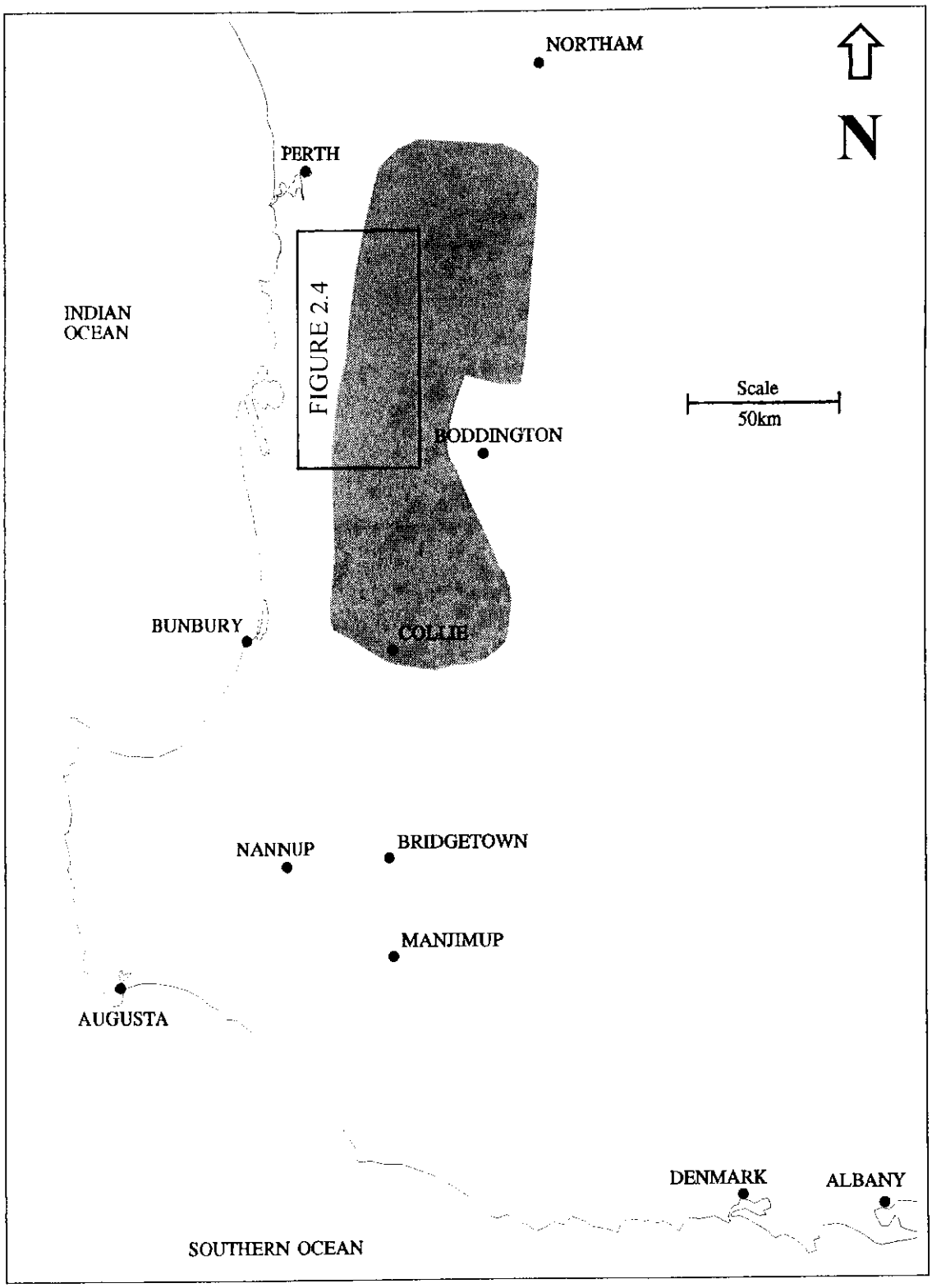


Figure 1.1 Location of the northern jarrah forest in south-western Western Australia (stippled area). The terms "northern" and "southern" have been used in the literature to delimit the geographical extremes of the narrow ecosystem dominated by jarrah. The boundary is arbitrary but usually regarded as being in the vicinity of Collie (eg. Shearer and Tippett 1989). All of the research for this thesis was done in the northern part of the forest. The term "jarrah forest" will be used throughout the thesis unless a distinction is required. The location of Figure 2.4 is also shown.

The northern jarrah forest flora contains a large component of perennials. Six plant families (7% of the families with species in the forest) make up 45% of the flora: Fabaceae (9%), Liliaceae (6%), Mimosaceae (5%), Myrtaceae (8%), Orchidaceae (7%), and Proteaceae (9%) (Bell and Heddle 1989). Grasses (Poaceae), which are an important component of many plant communities in Australia, comprise less than 2% of the forest flora (Bell and Heddle 1989) and a minuscule proportion of the plant cover.

Many jarrah forest species, including the major tree species, are capable of resprouting after fire. Few species are obligate seeders. Many of these are annuals (Bell et al 1993).

1.1.2 Climate

There is a strong summer / winter pattern in both temperature and rainfall in the jarrah forest (Figure 1.2). At Dwellingup, on average, 78% of rain falls between May and September. High temperatures in summer correspond with low rainfall. Months with no rainfall are common in summer. There is a marked east - west trend in rainfall. Annual rainfall on the scarp at the western edge of the forest averages between 900 and 1200 mm. At the eastern edge of the forest, rainfall is around 650 mm annually. The northern jarrah forest climate is described in detail by Gentilli (1989).

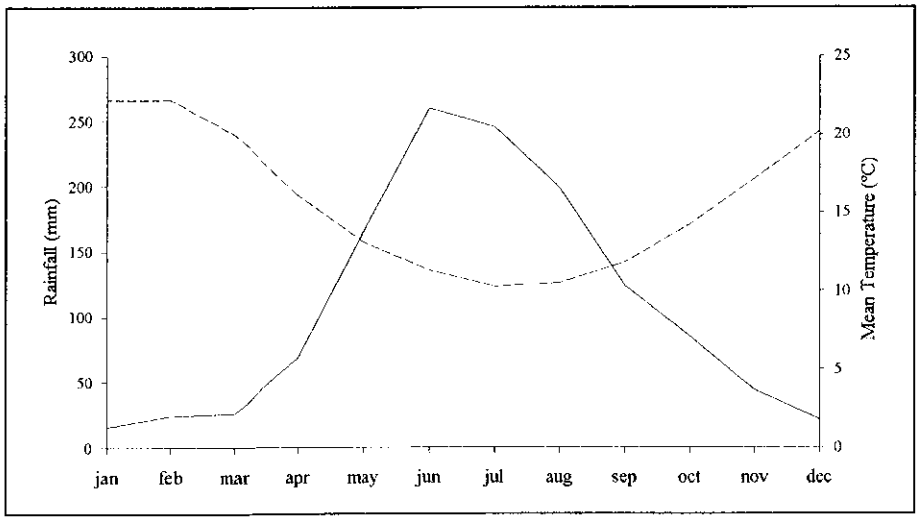


Figure 1.2 Mean monthly rainfall (mm) (———) and mean monthly temperature (°C) (------) for Dwellingup; 53 years of records.

1.1.3 Landforms, Soils and Hydrology

The northern jarrah forest occurs on gently sloping, undulating terrain. Gradients in excess of 10° are rare, being found largely on the western scarp, where the Darling Range adjoins the coastal plain, a few major waterways near the scarp, and some granite outcrops. Valleys tend to be broadest near their headwaters. Relief in the upper parts of valleys is generally less than 100 m. Landforms of the Darling Range have been described in detail by Mulcahy et al (1972) and Churchward and Dimmock (1989).

The Darling Range is dominated by soils of lateritic origin. A typical profile on slopes of shallow valleys towards the western edge of the Range consists of several distinct layers of varying thickness. The surface layer consists of gravel amongst grey-brown sandy loam to a depth of up to 2 m. The gravel content of this layer commonly exceeds 50%. In places, granular ironstone dominates the upper profile and may represent more than 75% of the soil mass. Below the gravelly sandy loam is often a layer of duricrust, a concretion of iron and aluminium materials. The duricrust layer is undulating. In places it may allow the ponding of rainwater that percolates through the soil above. At a small scale the duricrust may not reflect the topography of the land surface above. Pipes and cracks in the duricrust allow the penetration of tree roots into deeper soil layers. Between the duricrust and parent rock is a layer of clay up to 30 m thick. Many of the gently sloping valley floors in the western part of the Range have orange loams beneath a thin layer of leached grey loam with very little gravel (Churchward and Batini 1975, Churchward and Dimmock 1989, Shearer and Tippett 1989).

The gravelly soils are highly permeable when wet. Overland runoff is uncommon because of the high infiltration capacity of lateritic soils (Bettenay et al 1980, Sharma et al 1987), occurring mainly when heavy rain falls on dry soils, which are mildly hydrophobic (McArthur and Clifton 1975, Shearer and Tippett 1989). The lateritic gravels in the upper part of the profile have a great water storage capacity and trap much of the

rainfall. The duricrust layer impedes the throughflow of excess water. Water reaching the duricrust layer may penetrate it, pond or flow laterally over it, depending on the sub-surface topography of the duricrust and the abundance of root channels and cracks. Lateral seepage from upslope may keep sites lower in the landscape moist well into the dry season (Shearer and Tippett 1989). The creeks and wetlands of the jarrah forest have free water only during winter and early spring.

Between 60% and 90% of rainfall in the southern jarrah and karri forests is transpired by vegetation, so little recharge of groundwater occurs in average rainfall years (Borg et al 1987). The removal of trees by logging leads to an increase in soil water storage and a temporary rise in groundwater (Stoneman 1988).

1.1.4 Factors Affecting Plant Species Abundance

Processes intrinsic to a plant community, such as even-agedness, may result in sudden changes in plant abundance. Factors external to plants and plant communities are important vectors of change. Such factors have proliferated in the jarrah forest since European settlement in Western Australia in the first half of the 19th Century.

Fire has probably long been a disturbance factor in the jarrah forest, resulting either from lightning strikes or deliberate burning by aboriginal peoples. The flora is well adapted to such disturbance. Other disturbances, before Europeans began to use the forest's resources 150 years ago, could have included the gathering by aborigines of fleshy tubers, digging and grazing by native herbivores, periodic outbreaks of plant and animal pathogens, and rare or localised climatic events such as tornadoes or prolonged drought. Such disturbances are not quantifiable.

The value of jarrah as a hardwood timber brought more widespread disturbance to the forest following European settlement. The methods used in logging operations have

changed greatly since the early part of this century (Havel 1989). Logs were initially hauled along railways. The increased use of trucks and larger machinery in the middle part of this century necessitated the construction of many roads and tracks. Jarrah are not clear-felled. Some seed trees are left during logging operations. However, disturbance occurs to understorey and middle storey species during cutting, moving and storage of timber on log landings. The effects of logging and subsequent silvicultural techniques of stand thinning on pattern and process in forest sub-strata are unknown.

Prescribed burning is conducted by the Department of Conservation and Land Management (CALM) to reduce fuel and the potential for wildfire. Burning is usually done in spring when the fire is more easily controlled. These fires are generally of low intensity. The frequency of burning varies in space but an interval of 5 - 10 years is desired. Wildfires still occur.

The network of roads in the forest facilitates localized disturbance activities such as apiary, seed collection, wildflower harvesting, firewood collection and adventure driving.

Native fauna such as kangaroos occur in the forest and must have some impact by grazing and soil scratching, although to what extent is unknown. Fauna, especially feral pigs, cause substantial, albeit localised soil disturbance, especially in wet areas.

Exotic flora may initiate changes to indigenous vegetation by competition. The jarrah forest is relatively free of weeds at present. The occurrence of weeds (e.g. *Acacia* spp. from eastern Australia) around old logging settlements, landscaped picnic areas, and farms at the margins of the forest suggests that this may not always be the case.

A major factor in vegetation change in the jarrah forest has been the introduction of the fungal plant pathogen, *Phytophthora cinnamomi*.[2]

[2] *Phytophthora cinnamomi* will hereafter be written as *P. cinnamomi*. The latin names of plants are written in full to avoid confusion.

1.2 Dieback in the Northern Jarrah Forest

1.2.1 History

Death of jarrah in patches was first reported in south-western Western Australia in 1921 in the Darling Range near Perth. Further patches were noted to the south near Myara Hill later in that decade (Podger 1968). The malaise was clearly of concern in the 1940s because a research station was set up at Dwellingup to investigate the deaths (Havel 1989). Over the following decade, the dieback syndrome was described and research was undertaken to link the dying jarrah patches, as they were then called, to soil nutrition and plant pathogens (Wallace and Hatch 1953, Batini and Hopkins 1972). An association between dieback areas and the fungus *P. cinnamomi* was established in the 1960s (Podger 1968).

Although factors other than *P. cinnamomi* have been associated with plant death in the jarrah forest, such as diseases caused by *Armillaria luteobubalina* and canker fungi (Shearer 1994), *P. cinnamomi* is widely regarded as being the primary cause of dieback. There is, however, evidence that waterlogging during extreme weather events or following forest thinning may cause multiple jarrah deaths, either directly or by pre-disposing already stressed plants to infection by *P. cinnamomi* (Davison 1994). An investigation of a possible relationship between weather patterns and major dieback events is presented in Appendix 2 of this thesis. Regardless of the factors associated with jarrah decline, *P. cinnamomi* is clearly a major factor in contemporary forest processes. It has been linked with the infection and death of many species from a wide range of plant families and of varying life forms (Podger 1972, Shearer and Dillon 1995).

1.2.2 The Disease Process

P. cinnamomi is a soil borne fungus. The summary of its life cycle, below, is based on the detailed description of Shearer and Tippett (1989). The species infects its hosts via motile zoospores or less commonly by germinating chlamydospores. Zoospores are produced directly from sporangia. The production of sporangia from mycelium in infected roots occurs when the soil is moist and warm. Sporangial production may occur at temperatures as low as 12°C but is optimal at temperatures between 25 and 30°C. The co-occurrence of warm and moist conditions in surface soils is brief on jarrah forest slopes, normally a month or two in spring and autumn. High temperature and low soil moisture in the gravelly surface soils of the jarrah forest slopes are unfavourable to *P. cinnamomi* reproduction, infection and survival over summer. In such sites, *P. cinnamomi* is rarely recovered from soil in summer using baiting techniques (Schild 1995). In the surface soils of water-gaining valley sites, which receive water seeping from higher in the landscape during summer, *P. cinnamomi* can be recovered throughout the year (Shearer and Tippett 1989). *P. cinnamomi* has been located up to 3 m below the soil surface (Shea et al 1983). At such depth in the soil profile, fluctuation in temperature is less and conditions may favour sporulation of *P. cinnamomi* for longer periods (Kinal 1993), although the density of host roots is also likely to be less (Crombie et al 1988). The period available for sporulation in surface soils of sloping forest sites may be extended slightly during spring and autumn if plant and litter cover is removed, due to increased soil temperature (Kinal 1993). The reproductive capacity of *P. cinnamomi* varies with soil type and the vegetation present. Sandy gravel soils from forest slopes favour sporangial production whilst some loam soils from valley bottoms do not favour sporangial production or are even antagonistic to it (Sochacki 1982, Murray 1983). Greater production of sporangia has been reported in soil under *Banksia grandis*, a species that is highly susceptible to infection, than in soil under *Acacia pulchella*, a field-resistant species (Cary 1982). Sporangial production is affected by pH. It has been recorded between pH 3.3 and 8.5 (Blaker and MacDonald 1983). For this

reason, the neutral gravelly surface soils of the jarrah forest slopes are optimal for sporangial production whereas the acidic sub-surface clays are not (Shearer and Tippett 1989).

Dispersal of *P. cinnamomi* zoospores may occur through host root tissue or in free-flowing water. Water regularly ponds or moves over the duricrust layer following winter rain, if there are few cracks and roots canals. Water may also collect between the duricrust and clay layer below. Soil temperature at these depths is adequate for sporulation and root infection by motile zoospores (Shea et al 1983, Kinal 1986, 1993). Rare, large summer rainfall events are thought to favour *P. cinnamomi* growth within hosts rather than its dispersal or reproduction (Shearer and Tippett 1989). Coarse-textured soils, such as the gravelly sands found in much of the forest, are more favourable to zoospore dispersal than fine textured valley loams (Newhook et al 1981). Propagules of *P. cinnamomi* may also be dispersed in soil containing infected root material by humans, on cars and equipment, and by animals such as feral pigs (Shearer and Tippett 1989).

P. cinnamomi has been recovered after summer from dead *Banksia grandis* (Shea 1979, Schild 1995), dead *Xanthorrhoea preissii* (Schild 1995) and dead *Dryandra sessilis* (Rockel et al 1982), and so host tissue may be important for pathogen survival near the soil surface at times when reproduction is not possible. The pathogen may also survive in the roots of species that are not killed by it (Phillips and Weste 1984, Shearer and Dillon 1995).

The longevity of *P. cinnamomi* on dieback sites in the jarrah forest has received little attention, perhaps because of the difficulty of differentiating longevity and re-infection. Monitoring of *P. cinnamomi* populations in eastern Australia suggests that the pathogen may be locally transient. Duncan (1994) and Duncan and Keane (1996) found that populations of *P. cinnamomi* declined rapidly beneath infected dead plants of

Xanthorrhoea australis in a Victorian dieback site. A prolonged decline in *P. cinnamomi* activity and detection has been reported by Weste and Ashton (1994) for dieback sites in the Brisbane Ranges of Victoria.

1.2.3 Impact

Dieback sites in the jarrah forest may vary in the degree of death, the rate of death and in the sequence of species that die. *Banksia grandis* is generally regarded as extremely susceptible to infection and is rapidly killed. Since it is large and widespread in the jarrah forest, the first indication of dieback is usually the sudden death of one or more plants of this species. Deaths may occur slowly along dieback fronts (boundaries between unaffected forest and dieback forest), in small patches within unaffected forest, or suddenly in large patches. The differential impact of *P. cinnamomi* is evident at the time of the first deaths. Plants of some species die whilst plants of other species do not. Plants of families such as Proteaceae, Epacridaceae, Dilleniaceae and Fabaceae are especially prone to infection and are often found dead on recently affected dieback sites (Batini and Hopkins 1972, Shearer and Tippett 1989, Weste 1994). Jarrah may or may not die at the same time as the *Banksia grandis*. Jarrah commonly take some years to die, do not die at all, or die back in the crown before resprouting from the base or trunk.

The death of the upper strata and resultant changes in habitat may affect species not regarded as susceptible to infection. For instance, Wills (1993) reports the disappearance of *Stylidium scandens*, an apparently field-resistant perennial forb, from dieback sites in Stirling Range National Park, near the south coast of Western Australia.

1.2.4 Host Susceptibility

Whilst *P. cinnamomi* is commonly recovered from dead plants of species such as *Banksia grandis*, it has also been recovered from live species not normally associated

with infection and not presumed to be killed by the pathogen (Phillips and Weste 1984, Shearer and Dillon 1995). This suggests that susceptibility alone is not a good indicator of a plant's response to infection in the field. In their study of plant susceptibility in the northern jarrah forest, Shearer and Dillon (1995) noted that previous studies had failed to associate plant death with the recovery of *P. cinnamomi*. For this reason, it has been impossible to rank species on their degree of susceptibility. In addition, the possibility that some species die because of structural changes following dieback (Wills 1993) means that unless plants of a species were tested for an association with *P. cinnamomi*, their susceptibility would remain unknown, even if there were multiple deaths in an infested area.

Shearer and Dillon (1995) developed a ranking system for susceptibility based on the frequency of deaths on dieback sites and the frequency of *P. cinnamomi* isolation. Their five susceptibility groups, which will be referred to later in the thesis, are described in Table 1.1. Groups 3 and 5 contain species most likely to be highly susceptible.

Table 1.1 Susceptibility groups of Shearer and Dillon (1995) for species in the northern jarrah forest.

Group	% of active disease centres in which species dies	*P. cinnamomi* isolation from dead plants	Examples
1	0	-	*Acacia barbinervis* marri
2	≤ 33.3	0	*Hibbertia hypericoides* *Lechenaultia biloba*
3	≤ 33.3	frequent	*Hibbertia quadricolor* *Lomandra sonderi*
4	≥ 33.3	infrequent	jarrah *Macrozamia riedlei*
5	> 50	frequent	*Adenanthos barbiger* *Banksia grandis* *Xanthorrhoea preissii*

1.2.5 Interpretation of Dieback

Dieback sites in the jarrah forest are commonly identified by the presence of dead plants, especially those known to be susceptible to infection by *P. cinnamomi*. *Banksia grandis* is an especially good indicator of dieback. If there are good indicator species present, dieback sites are easy to locate in the field, immediately after death. With time, however, small plants shed their leaves and rot. Larger plants may be destroyed by fire. If jarrah is not killed or there were few susceptible species present, the dieback status of vegetation may be difficult to interpret. Salvage logging operations in the 1950s and 1960s removed most dead and dying jarrah on many dieback sites. Although these sites clearly look different to unaffected vegetation now, there is no evidence left to link their appearance to infection by *P. cinnamomi* or even to be sure that large numbers of plant deaths occurred.

Aerial photography is currently used to evaluate dieback in the jarrah forest (Shearer and Tippett 1989). With large-scale, shadowless images, interpreters can identify deaths of some of the smaller arborescent plants. Such resolution is not possible with earlier black and white photography. However, with good stereoscopic equipment it is possible, with some of the photography available for the forest, to observe individuals of jarrah with negligible crowns. It is not possible to tell if they are dead. However, in this way, sites may be identified that displayed symptoms consistent with those attributed to *Phytophthora*-induced dieback.

Since the old dieback sites studied in this work were identified using aerial photography, dieback will be used in subsequent chapters to describe the decline of the tree layer and its associated symptoms. This is likely to be related, at least in part, to infection by *P. cinnamomi* but cannot be presumed to be so.

1.3 Vegetation Change Associated with Disease and Loss of Tree Cover

1.3.1 General Causative Factors

Much of the literature on vegetation change in forests involves studies of the patterns and processes of commercial trees in relation to disturbance. Oliver and Larson (1990) have reviewed this subject. Changes in understorey species following forest disturbances appear to have received less attention (e.g. Metzger and Schultz 1984, Moore and Vankat 1986, Collins and Pickett 1988, Hughes et al 1988). Disturbances on a small scale (e.g. a tree fall) or large scale (e.g. a wildfire) are seen as integral to forest development. The canopy gaps created by disturbance may cause changes in light quality and quantity, temperature, soil moisture and litter deposition. In some forests, these physical changes allow the germination, reproduction or invasion of species that favour forest openings. Forests undergoing such processes can be described as mosaics of vegetation and disturbance. These changes tend to be cyclic. The subject is reviewed in Pickett and White (1985).

The introduction of foreign plants or animals may alter the frequency and duration of cycles, or break the cycles altogether. Vegetation change following the decimation of American Chestnut (*Castanea dentata*) by the fungus *Cryphonectria parasitica* has been studied in some detail (e.g. Keever 1953, Woods and Shanks 1959, McCormick and Platt 1980, Stephenson 1986). American Chestnut was once the dominant or co-dominant of many deciduous forests in the eastern United States. Plant deaths were first recorded early this century. Forty years later, the American Chestnut had been eliminated as a forest dominant (Krebs 1985). Most of the studies of vegetation change have recorded the contemporary canopy composition and contrasted it with that expected in a model chestnut forest. Stephenson (1986) was able to revisit a site first measured in 1932. Chestnut in the upper stratum was replaced by species originally

present in the upper stratum (especially an oak, *Quercus rubra*), species originally present only in the understorey, and species that invaded from outside the site. Chestnut survived as a small tree. Predictions of future forest composition based on host-pathogen interactions and the dynamics of associated tree species do not appear to have been considered in studies of American Chestnut forests.

Changes in vegetation in *Metrosideros* forest in Hawaii following crown dieback have been investigated by Jacobi (1983). Although pathogens, including *P. cinnamomi,* may be associated with *Metrosideros* forest dieback (Papp et al 1979), Mueller-Dombois (1987) proposes a largely natural process for the decline. Under the cyclic "cohort senescence model" of Mueller-Dombois (1987), death occurs to a large proportion of mature *Metrosideros* trees. This is followed by recruitment of *Metrosideros* seedlings. Eventually, the canopy closes again. Biotic agents, such as *Phytophthora cinnamomi*, if present, are seen in this model as hastening the decline of forests already pre-disposed to dieback due to old age. Part of the evidence for this is that *Metrosideros* recruits and understorey species are not adversely affected. In the time that the canopy is open, invasion by light-loving species, including weeds, occurs. Some of these alien species may affect the cycle by suppressing regeneration of canopy species (Jacobi 1993).

1.3.2 *P. cinnamomi*-related Vegetation Changes

Worldwide, *Phytophthora cinnamomi* has a profound effect on a wide range of agricultural crop species, such as pineapple, avocado, apple, and citrus. In Australia, it has received most attention in native plant communities because of its impact on commercial forestry species and rare plants. The pathogen has been recorded in all States, in a wide range of plant communities (Weste 1994). Despite this, vegetation changes have been studied in relatively few affected communities.

Podger and Brown (1989) recorded a decline in species richness in temperate rainforest of Tasmania following a loss of canopy species affected by *P. cinnamomi*. They suggest that, although regeneration would be slow, some would occur because of the effective dispersal mechanisms of susceptible species from higher altitudes where the pathogen was inactive. Species extinction was thought to be unlikely because of high altitude refugia.

The most comprehensive studies of change have been made in Victorian plant communities: Brisbane Ranges (Dawson et al 1985, Weste 1986, Weste and Ashton 1994); Wilsons Promontory (Weste 1981); Grampians (Kennedy and Weste 1986). Species abundance and cover in some of these communities have been monitored for up to 30 years. Changes recorded following dieback have included the rapid death of many plants of many species, reduction in tree abundance, the disappearance of many susceptible understorey species, a reduction in plant abundance, species richness and plant biomass, an increase in the abundance of resistant sedges, and an increase in bare ground. Structural changes have been from woodlands with a heathy understorey to open woodlands with a sedge-dominated understorey. Recovery and regeneration of some susceptible species have recently been reported for Victorian dieback sites (Dawson et al 1985, Weste 1994, Weste and Ashton 1994).

There has been much less work done on vegetation change relating to dieback in Western Australia. The following vegetation changes associated with infestation by *P. cinnamomi* have been reported.

- *The density of species susceptible to infection by* P. cinnamomi *decreases.*

P. cinnamomi infects a large number of species, causing many plant deaths (Podger 1972). Some species, such as *Banksia grandis*, succumb quickly and totally and others slowly or not at all. Jarrah may be killed or may persist with reduced crown cover.

Susceptible species are not necessarily eliminated at the time of the initial invasion but, with continued exposure to the pathogen, may eventually disappear (Wills 1993). The disappearance of highly susceptible species (almost entirely woody perennials) is believed to be inevitable (Wills and Keighery 1994).

- *Species diversity declines*

Shearer and Hill (1989) and Keighery et al (1994) have reported decreases in species numbers following dieback.

- *The cover of species that are apparently not adversely affected by* P. cinnamomi *increases.*

Species that are not obviously adversely affected by *P. cinnamomi* in the field (mostly herbaceous perennials) increase following dieback (Wills 1993). Hence, marri has been observed to replace jarrah as the dominant tree and field resistant species of the families Cyperaceae and Restionaceae are regarded as major colonizers of dieback sites (Wallace and Hatch 1953, Davison and Shearer 1989, Shearer and Tippett 1989). Species that normally grow in valley bottoms (e.g. the trees bullich and blackbutt) have been reported to colonize upslope after dieback (Havel 1979). Invasion by field-resistant weeds occurs on some dieback sites (Keighery et al 1994).

- *Recolonization by species susceptible to infection by* P. cinnamomi *may occur after dieback.*

There is evidence of regeneration by susceptible hosts on infested sites of the Swan Coastal Plain (Shearer and Dillon 1996b). *Dryandra sessilis,* a highly susceptible shrub, is regarded as an aggressive colonizer of dieback sites that fluctuates in density with the inoculum level of *P. cinnamomi* (Rockel et al 1982).

- *Changes in structure may affect understorey species composition.*

Wills (1993) has suggested that the perennial herb, *Stylidium scandens*, which is apparently field resistant to *P. cinnamomi*, disappears from dieback sites in Stirling Ranges National Park because of the loss of canopy following dieback.

Many of the vegetation changes listed above are based on observation or inference. This is not a criticism of the observers. The focus of their studies was simply not vegetation change. There has been little work done specifically on vegetation change associated with dieback. Before / after comparisons of Western Australian plant communities affected by *P. cinnamomi* are rare. Wills (1993) remeasured a site, for which a species list had been made in 1976 in newly infested vegetation, at the Stirling Range National Park. A few plots set up by Dr. Frank Podger in the 1960s in a range of healthy plant communities, subsequently infested with *P. cinnamomi*, have recently been re-measured (Neil Gibson, CALM, pers. comm.). There have been no dedicated floristic surveys of dieback sites in the jarrah forest area.

Because of the paucity of information available, it is not surprising that a comprehensive model of vegetation change due to *P. cinnamomi* associated dieback in the northern jarrah forest has not been explicitly proffered in the literature.

Predictions of future dieback patterns have been made, however. Weste (1981) suggested that cycles of epidemic and recovery may occur for some Victorian forests infested with *P. cinnamomi* once inoculum levels fall and regeneration of susceptible hosts occurs. Evidence of regeneration by susceptible hosts has been recorded there by Dawson et al (1985) and Weste and Ashton (1994) but concomitant increases in *P. cinnamomi* inoculum level have yet to be observed. Wills (1993) has suggested that epidemic - recovery cycles could occur in Western Australian plant communities, driven by falls in inoculum levels after the inception of dieback followed by regeneration of

susceptible hosts. There is recent evidence of regeneration by susceptible hosts on infested sites of the Swan Coastal Plain of Western Australia (Shearer and Dillon 1996b). The only reported evidence of an epidemic - recovery cycle in the jarrah forest is associated with the tall proteaceous shrub *Dryandra sessilis*. Rockel et al (1982) observed that the shrub, which they regarded as an aggressive colonizer of dieback sites, was sometimes found dead on dieback sites, individually or *en masse*. They isolated *P. cinnamomi* from dead *Dryandra sessilis* on six dieback sites.

1.4 Aims and Scope of the Study

The primary aim of this dissertation was the development of a model of vegetation change associated with dieback in the northern jarrah forest. This was to be achieved through extensive floristic surveys of dieback sites and unaffected sites of comparable habitat. The surveys would be the first in the jarrah forest to deal specifically with dieback. It was hoped that the model and hypotheses arising from it will foster the establishment of long-term monitoring projects into vegetation changes following dieback, which are desperately needed in the jarrah forest if the plant-pathogen processes are to be properly understood.

The thesis is arranged sequentially, the latter chapters relying on information gathered in the early chapters.

In Chapter 2, surveys of dieback and unaffected vegetation from a wide range of sites are described. The findings are discussed in relation to published observations and measurements of dieback impact. A relationship between dieback history and vegetation is explored. Species differences between dieback and unaffected vegetation are used in subsequent chapters.

In Chapter 3, seven sites with a range of dieback ages are investigated in detail. Characteristics of the vegetation are compared with the current distribution of *P. cinnamomi* to assess the likely role of the pathogen with increasing time. Evidence of regeneration and survival of highly susceptible species are sought. The role of landscape position in the apparent long-term effect of the disease is discussed.

In Chapter 4, a range of species found in Chapter 2 to occur less frequently on dieback sites than on unaffected sites but not known to be susceptible to infection by *P. cinnamomi* are assessed for their susceptibility to infection. An alternative hypothesis that the species are less frequent on dieback sites because of the loss of tree canopy is investigated.

In Chapter 5, the origin of some species found more frequently on dieback sites than on unaffected vegetation is examined.

In Chapter 6, mechanisms that would enable susceptible species found on old dieback sites to persist, notably resistance or fecundity, are investigated.

The findings of the study are summarised in Chapter 7, and developed into a model of vegetation change in the northern jarrah forest.

The portion of the northern jarrah forest available for study was limited by the prescribed burning program of the Department of Conservation and Land Management, bauxite mining operations and the availability of aerial photography. Suitable study sites were found mainly in the high rainfall part of the forest. The lack of comparable unaffected vegetation limited the choice of plant communities.

CHAPTER 2: DIFFERENCES BETWEEN UNAFFECTED AND DIEBACK VEGETATION

2.1 Introduction

Despite more than 70 years of dieback in the jarrah forest, there is little information available on the vegetation of dieback sites. Most assessments of vegetation change following dieback have been derived from observation rather than measurement. There can be no criticism of these assessments. As hypotheses based on the personal experience of the observer, they are an integral part of the scientific process of investigation. However, it is difficult for an observer to be dispassionate about dieback. The disease is clearly catastrophic. Could preconceptions about the magnitude of the catastrophe interfere with assessments of impact? As indicated in Chapter 1, the interpretation of dieback sites becomes more difficult with increasing time since the initial dieback event. With time, additional factors such as salvage logging, differential fire patterns and other disturbances might influence the character of the site as much as dieback. And, if regeneration of susceptible species does occur, would the oldest dieback sites still be identified as dieback sites?

There is also little information available on the floristic composition of unaffected jarrah forest vegetation. Assessments of the impact of disease on vegetation must be based largely on perceptions of what unaffected vegetation should look like. In the only large-scale classification of jarrah forest vegetation, Havel (1975) identified indicator species of the major vegetation types. Whilst the classification of Havel (1975) has enabled the identification of vegetation types based on a few character species, it provides little information on which species commonly comprise each type.

In this Chapter, I present the results of a survey of dieback vegetation and unaffected vegetation in comparable habitat. The survey was done at two levels. The first is a comparison of plant densities across dieback boundaries (referred to below as the Dieback Boundary Survey). In this case, the space between samples is small. The

likelihood of differences being attributable to factors other than dieback is accordingly small (see Methodology Rationale below). The second level involved a survey of dieback and unaffected vegetation across a large portion of the northern jarrah forest (referred to below as the Broad Quadrat Survey of Unaffected and Dieback Vegetation). This was done to assess the importance of time since dieback in shaping the patterns found. Some degree of objectivity was obtained in interpreting the results by the use of aerial photography to determine the approximate age of the dieback impact and other obvious disturbance factors.

The results of the survey are compared with previous measurements and observations of dieback vegetation, and used to identify species and processes for further investigation, which are reported in subsequent Chapters. The rationale for the methodology used in this Chapter will first be described.

2.2 Methodology Rationale

2.2.1 Measurement of Vegetation Change

Changes in vegetation are ideally measured by long-term monitoring. Replicated field experiments can be set up with temporal measurements (i.e. before and after an impact) and spatial measurements (i.e. control and impact). Such before / after - control / impact designs can account for natural spatial and temporal patterns in vegetation (Green 1979, 1993) if adequately replicated in space and time (Underwood 1993).

Vegetation changes resulting from dieback in the jarrah forest are not easily studied with such designs. Before and Control quadrats are likely to be difficult to choose because the movement of infection is confounded by sub-surface terrain and lateral water-movement. Impact quadrats might not be affected for decades, despite being close to dieback boundaries. Control quadrats would be difficult to protect from infection for the time required to identify cycling in populations of species such as jarrah, marri and

Xanthorrhoea preissii, which live for several hundred years. Increasing the distance between control and impact quadrats is likely to introduce additional variables such as soil fertility, soil depth, fire management, and logging history, which would in turn increase the demand for replication. The approach of Dr. Gretna Weste and colleagues in Victoria, to measure change in control and impact sites over time (e.g. Weste 1981, 1986), is a reasonable compromise and at least allows for some evaluation of natural change in vegetation.

Long-term monitoring of recent dieback sites alone would be valuable for quantifying processes of survival, recruitment, infection, invasion and recovery.

The effect of an environmental impact is commonly investigated by space for time substitution (SFT). In SFT studies, sites are chosen in space to represent differences in an environmental variable in time. SFT studies are based on the assumption that variation in space can equal variation in time. The assumption is likely to be less limiting when recently affected dieback boundaries are involved. In these cases, the time interval is short so that other differential disturbance factors will be less important, the space interval is short so that natural variation in vegetation will be minimised, and the presence of dead plants is a check on vegetation homogeneity.

2.2.2 Limitations of Space for Time Substitution

Researchers wishing to study dieback effects in the jarrah forest using SFT must be cognizant of the limitations of the approach and the complexity of the system being studied. The assumptions of space for time substitution may be invalid because:

- *Factors involved in vegetation change other than dieback occur*

There are many disturbances in the forest. The distribution of most is unknown or unquantifiable in space and time. Fires of varying frequency and intensity, logging and

activities associated with logging, other diseases, and localised extreme weather events create a mosaic of disturbance in the forest, which undoubtedly interacts with the mosaic created by dieback. Even within the disturbance recognized as dieback there are varying degrees and rates of plant death.

- *Disturbance factors are not uniformly distributed in space*

The density of harvestable jarrah generally increases with distance from drainage lines (Abbott and Loneragen 1986). Much of the loading and haulage of cut timber traditionally occurred in the lower parts of valleys (based on the position of logging tracks). The degree of salvage logging of jarrah following dieback varies in time and space, ranging from negligible in some recently-affected conservation reserves to clear-felling in dieback sites affected prior to the 1960s, when the extinction of jarrah was presumed to be inevitable because of dieback. Prescribed burning in spring produces a patchy mosaic of burnt and unburnt vegetation. The openness and abundant bare ground of dieback sites are likely to lead to differences in fire intensity and even, perhaps, frequency across dieback boundaries. With increasing time since the initial dieback event, differences in burning patterns could become as important in determining differences in vegetation as the presence or absence of *P. cinnamomi*. Temporal studies might not be able to differentiate such factors either but at least the factors could be quantified and assessed by experimentation.

- *Comparable unaffected vegetation may not be found*

Aerial photographs can give some indication of tree density on dieback sites prior to dieback. However, although unaffected vegetation of similar tree density might be sought in similar situations to dieback sites, there is no guarantee that the sites selected would have supported vegetation similar to the dieback sites. The only occasion when this assumption might be reasonable is when a very recent dieback site is being compared with an adjoining unaffected site and the dead individuals can still be counted on the dieback site. SFT studies of dieback would fail completely if examples of pre-dieback

vegetation do not exist. In this case, the sampling of unaffected vegetation will simply define a different vegetation.

- *There are boundaries in the forest other than dieback boundaries*

P. cinnamomi is thought to have been largely introduced to unaffected vegetation in the jarrah forest by movement of vehicles and soil along logging tracks (Batini 1977). Infestations have then spread beyond the tracks, mainly downhill towards drainage features. The same logging tracks and major roads are now often used as fire management boundaries. Researchers that used SFT studies by sampling across a track would need to be confident that the fire history of the two sides was similar. In the jarrah forest, tracks are routinely used for establishing fire breaks, prior to prescribed burning procedures. These tracks do not necessarily correspond with the boundaries of fire management compartments.

Management boundaries are not always obvious. One of apparent dieback boundaries I initially chose to study proved to have been formed by processes other than infestation of *P. cinnamomi*. Some months after I first visited the site I inspected an aerial photo to assess the age of dieback beyond the boundary. The apparent dieback boundary was an old grazing boundary. It may or may not have also been a dieback boundary. A fenceline was clearly visible on 1951 aerial photos but only a few traces of fencing wire could be found on the ground. In 1951, the differences in vegetation across the fence boundary were enough to show up on aerial photos. The fence was presumably destroyed by fire. Fences are not common in the middle of the forest. The enclosure may have been used to hold horses or bullocks for pulling timber carts.

2.2.3 Optimal Experimental Designs for Space for Time Substitution

Despite its many limitations, SFT has a legitimate place in ecological research. It has value for the generation of hypotheses about impacts (Pickett 1989), it produces results

quickly, and in some cases may be the only technique available. Impacts cannot always be predicted. Once an unexpected and perhaps rare impact had occurred, the only information obtainable about its effects might involve measurements of the impact site and a range of apparently comparable sites without the impact.

The probability of constructing the wrong model from an SFT study of dieback because of the limitations outlined above can be reduced but not eliminated. The existence and variability of disturbance factors other than dieback can be accounted for by replication of impact (i.e. the sampling of many dieback sites) and the measurement of correlation between vegetation and a range of disturbance and environmental factors including dieback. The latter is likely to be difficult because the history of disturbance is not well documented in the jarrah forest.

The cost of constructing the wrong model from an SFT study may not be great if the hypotheses arising from the model can be tested and proven wrong. The greatest danger comes in confusing hypothesis with irrefutable conclusion and difference with change (Underwood 1990).

Replication of impact is essential because of inherent and unknown variability in species distribution. Replication within an impact may give a better estimation of the example studied but, in isolation, will provide no information on the variance of the parameters measured that may be attributable to the impact of interest. Within-impact replication in isolation has been termed pseudoreplication by Hurlbert (1984). Some flaws in pseudoreplication are illustrated below. In Figure 2.1, 200 individuals of a single species were arranged randomly, 100 on each side of a perceived boundary, shown as a heavy line in the centre of the plot. The distribution was generated using random numbers for x and y co-ordinates. A grid of 21 quadrats is superimposed over each side of the boundary. A typical method for determining whether there is a difference in the number of individuals on each side of the boundary would involve comparing the means of, say, five square root transformed density measures using a t-test. The null hypothesis

tested in this case would be that there was no difference in density on the two sides of the boundary. In the example shown, the mean densities of 100 permutations of five sets of quadrats were compared. Six of the 100 comparisons were significantly different ($P < 0.05$). This is close to the limit of $P < 0.05$ commonly set for tests of significance of difference between means.

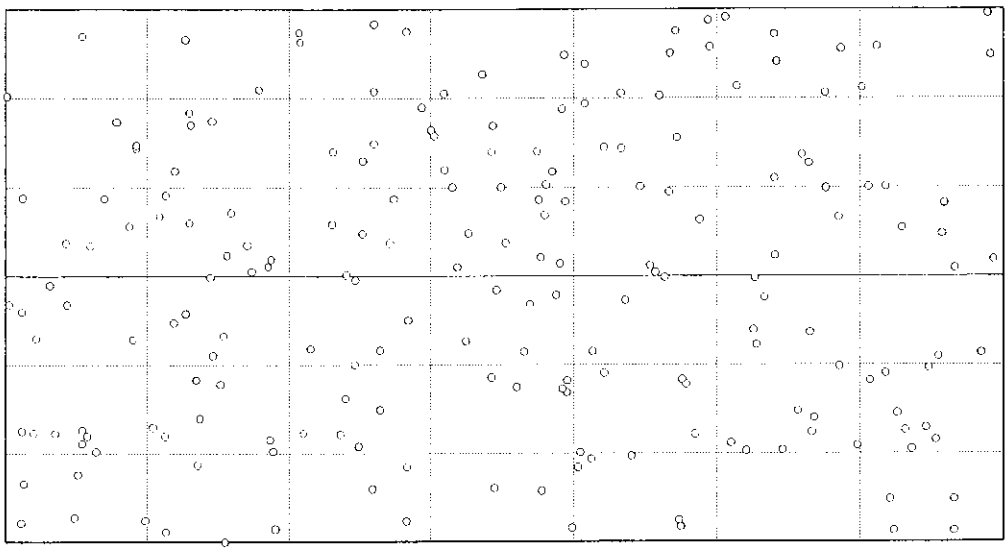


Figure 2.1 Random arrangement of 200 individuals, 100 on each side of a boundary, with a grid of 21 quadrats superimposed.

Species, however, are not necessarily randomly distributed. Figure 2.2 shows the distribution of a species that is naturally aggregated. This distribution was generated randomly with five random seeds to limit the x and y co-ordinates. There are 100 individuals on each side of the boundary. When 100 permutations of the means of five pairs of randomly chosen quadrats were compared for square root transformed density using a t-test, four pairs were significantly different ($P < 0.05$). That is, the probability of wrongly rejecting the null hypothesis is 0.04, which would generally be acceptable. However, when the nine permutations of five horizontally connecting quadrats on each side of the boundary are compared, 21 of the possible 81 combinations were significantly different ($P = 0.26$). That is, the null hypothesis might be wrongly rejected in 26% of paired samples containing five quadrats in a row. However, without a knowledge of the distribution of the species across the entire site, which would entail sampling the entire site, there would be no way of judging an appropriate selection of quadrats. Differences

in frequency measures of species with patchy distributions may be especially prone to mis-interpretation unless the quadrat size is large enough to have a high probability of containing the species when present. In Figure 2.2, the frequencies obtained from 100 subquadrats in the adjacent pairs of quadrats across the boundary would be significantly different as determined by chi square tests of independence for three of the seven pairs. A quadrat size approaching the minimal area of the community, in the sense of Poore (1955), would negate the problem but make frequency an inappropriate measure of difference in Figure 2.2. The use of many sites to obtain frequency measures would be an optimal strategy.

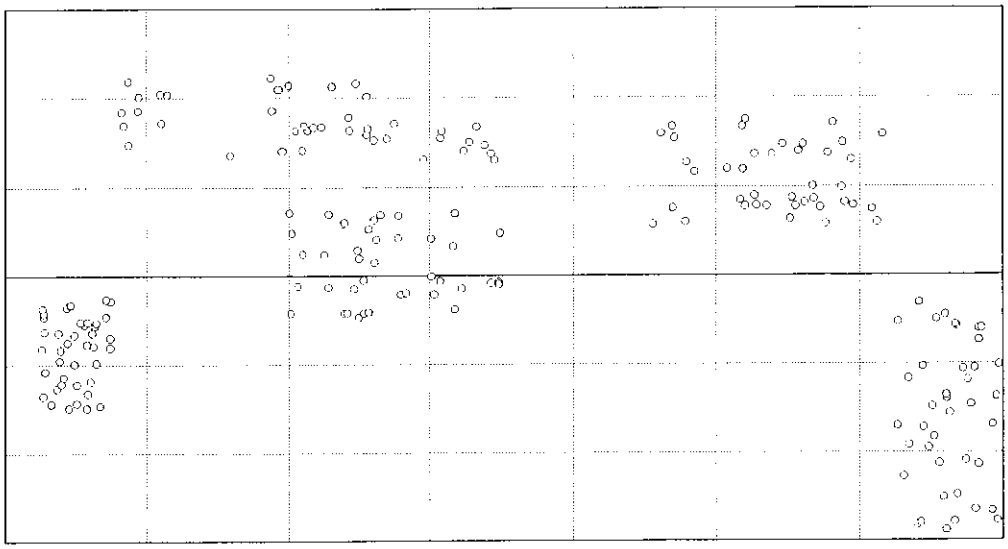


Figure 2.2 Aggregated arrangement of 200 individuals.

The worst case in a SFT study using pseudoreplication is shown in Figure 2.3, where a species distribution is governed by some environmental gradient other than the impact of interest. The individuals were arranged randomly such that the density in the top sixth was twice the density in the second sixth, which was twice the density in the third sixth, etc. In 100 permutations of five sets of quadrats on each side of the boundary, 99 were significantly different as determined by a t-test of square root transformed density. A high probability of rejecting the null hypothesis that there is no difference in density across the boundary is to be expected given the large difference in density that does

exist. However, without a knowledge of the environmental gradient operating on the system, the difference could easily be attributed to the impact being studied.

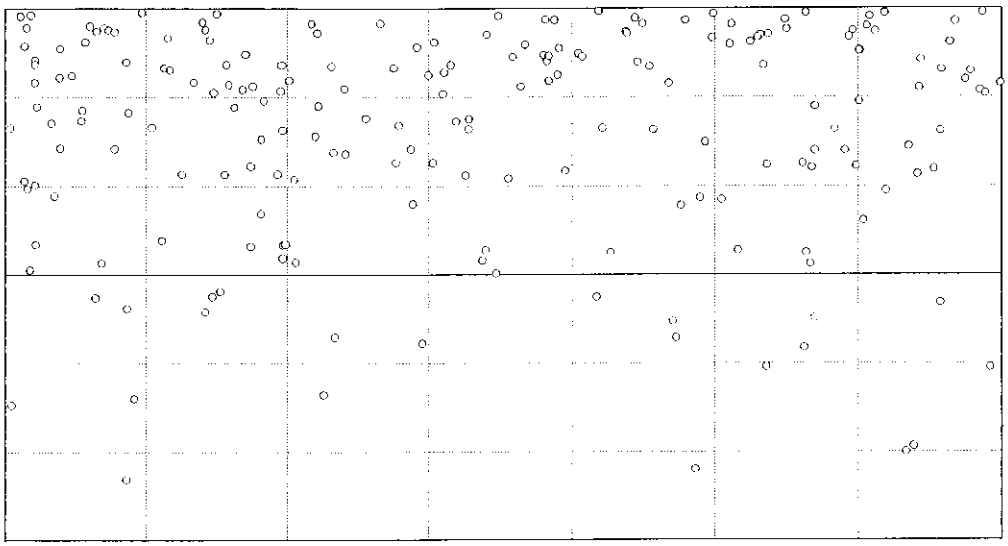


Figure 2.3 An arrangement of 200 individuals governed by an environmental gradient.

The assumptions and limitations cannot be removed from a SFT study. However, their effects can be minimised. Species aggregation and environmental gradients may be impossible to assess once the impact has occurred if the impact interacts with the gradient. The probability of incorrectly accepting or rejecting null hypotheses will therefore be least when there is repeated sampling of the impact. That is, effort is best directed at replication of sites rather than replication within sites. Randomization of quadrats is important. The replication of control sites, regardless of the number of impact sites, may allow some estimation of environmental gradients. Consideration should be given to optimising quadrat size to minimize the risk of making incorrect decisions about null hypotheses when frequency measures are used. Features that could be management boundaries (e.g. roads and rivers) should not be used as impact boundaries unless a thorough history of management is available.

In the current study, I use SFT in the construction of a model of vegetation change associated with dieback. As many sites as possible are used to minimize the possibility of mis-interpreting intra-site variation in vegetation and maximise the possibility of

averaging environmental gradients and disturbance patterns. I also attempt to account for some environmental gradients by measuring them and determining their significance as factors affecting the vegetation of dieback sites.

2.2.4 Taxonomy

The nomenclature of species referred to in the text follows Marchant et al (1987), except where revisions have recently been published. Departures in nomenclature are referenced in Appendix 1, where all species located in the study are listed with their authorship. Exotic species are prefixed with an asterisk (*) throughout the thesis.

In some cases, fertile material was not available to allow identification. In such cases, species were included as an aggregate of a genus or family. Some plants did not seem to fit published descriptions. These and other taxonomic matters are described below.

Burchardia umbellata

At two sites, there were plants with flowers apparently indistinguishable from the typical *Burchardia umbellata* but with only a single flower, borne on a very short stem. At one of these sites this was the only form present, at the other, the typical tall-stemmed plant with umbellate inflorescences was more common. Both forms were included in *B. umbellata*.

Danthonia spp.

Most specimens collected fitted the description of *Danthonia setacea*, although some were close in floret length to *Danthonia caespitosa*. *Danthonia acerosa* was observed near a granite outcrop but was not found in a quadrat. Because plants of this genus were abundant on many dieback sites and their diagnostic characters are largely microscopic features of the floret, it is possible that other species were present.

Drosera macrantha / Drosera pallida

Drosera macrantha was common at many sites studied. *Drosera pallida* is superficially similar to *Drosera macrantha* and occurs in the jarrah forest, although it was not collected. It may have been present in some quadrats. To minimize time spent on plant identification in the field, all climbing *Drosera* species were recorded as *Drosera macrantha*.

Dryandra lindleyana

This taxon was recently separated from the group previously known as *Dryandra nivea* (George 1996). More than one subspecies occurs in the jarrah forest. The revision was not available at the time of the survey so no distinction could be made at a sub-specific level.

Haemodorum spp.

Haemodorum discolor was collected in the survey but, judging from the range of leaf width and number observed, more than one species occurred in the study area. Flowering of many species occurs in summer and was often missed. All taxa collected were referred to as *Haemodorum* spp.

Hibbertia acerosa / Hibbertia rhadinopoda

When not in flower, these species are separable on their leaf apices (Marchant et al 1987). The leaf apices of shrubs found in the survey ranged from blunt to somewhat pungent and both species may have been present. However, the leaves never seemed as pungent as a specimen of *Hibbertia acerosa* observed at the Perth Herbarium. I believe that most, if not all, of the material in the study area is referable to *Hibbertia rhadinopoda*.

Hibbertia amplexicaulis / Hibbertia perfoliata

These species differ in their size of flower and shape of floral bracts. When not in flower they are difficult to tell apart. All *Hibbertia* spp. with stem clasping leaves were recorded as *Hibbertia amplexicaulis*, which seemed to be the more common of the two species.

were placed in either of two groups. Within the *caespitosa* group, *Lomandra brittanii, Lomandra caespitosa, Lomandra integra, Lomandra micrantha* and *Lomandra nigricans* were positively identified. *Lomandra odora* may have also been present. Within the *purpurea* group, *Lomandra preissii* and *Lomandra purpurea* were positively identified and *Lomandra drummondii* may also have been present.

Opercularia vaginata / Opercularia apiciflora

Flowering material was rarely present for identification of these taxa. Only *Opercularia vaginata* was confidently found. It is possible that the vegetatively similar *Opercularia apiciflora* was present at some sites.

Pterostylis spp.

This aggregate included *Pterostylis barbata* and *Pterostylis recurva*. The latter was the more common and the former tended to occur on damper sites.

Schoenus spp.

Schoenus grammatophyllus and *Schoenus nanus* were recorded. Other taxa may have been present at some sites.

Stipa spp.

Three taxa were identified: *Stipa campylachne, Stipa hemipogon* and *Stipa mollis*. Plants were often collected with immature florets, making identification uncertain.

Thelymitra spp.

Plants of this genus could not always be identified because flowers were too young or too old at the time of sampling. *Thelymitra crinita* was certainly present.

Trachymene spp.

Trachymene sp. A and *Trachymene pilosa* were recorded. *Trachymene* sp. A was never found as tall as it is described in Marchant et al (1987) but it was always much taller than *Trachymene pilosa*. When not in fruit and especially in the early stages of growth, the two

taxa could not be confidently differentiated. *Trachymene pilosa* seemed to occur only in dieback vegetation, whilst *Trachymene* sp. A occurred also in unaffected vegetation.

2.3 Methods

2.3.1 Dieback Boundary Survey

Potential sites for study were chosen by inspecting a range of dieback boundaries identified on 1994 aerial photographs. 1980 aerial photographs of the same areas were inspected to ensure that dieback near the boundary had occurred between 1980 and 1994. Limits were set for the area and nature of dieback vegetation before site inspections were made so that there would be some degree of objectivity in choosing sites. One quadrat was to be placed on each side of the boundary. The dieback quadrat had to fit within a uniform area of standing dead *Banksia grandis* (the jarrah overstorey could be in any condition). At least one of the dead mature *Banksia grandis* had to have leaves still attached or still on the ground. This would mean that at least some of the impact had occurred in the last few years. Once I had determined that the dieback area was suitable, I checked the adjoining unaffected vegetation. The unaffected quadrat had to be within 50 m of the dieback quadrat and as near to it as the other criteria would permit, had to have a similar pre-dieback density of *Banksia grandis* and jarrah, a similar amount of outcropping rock, and had to be on the same slope and preferably beside the dieback quadrat rather than upslope from it. Although some sites had been logged within the last couple of decades, there was no indication of recent salvage logging. Given these limits, a maximum quadrat size of 200 m^2 was possible at all sites. Because *Banksia grandis* was abundant at all sites, the boundary between dieback and unaffected was very sharp.

Ten sites were sampled (Figure 2.4). Seventeen of the 20 quadrats were rectangular (20 x 10 m). Other dimensions giving the same area were required for three quadrats which would not fit into dead *Banksia grandis* patches. Quadrats were marked out with compass and tape measure with checks made of diagonal distances. The vegetation of sites was Havel

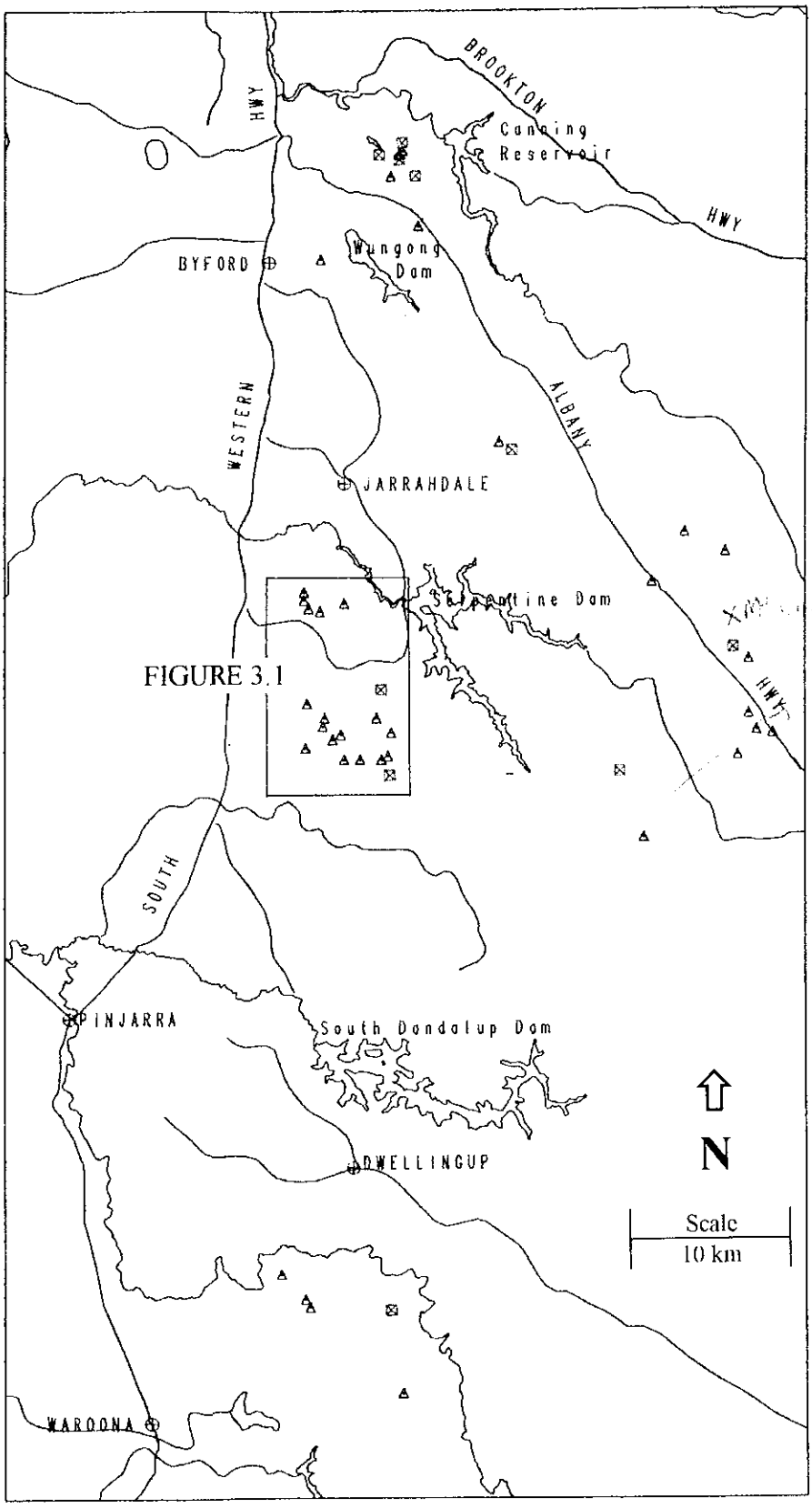


Figure 2.4 General location of quadrats. ☒ indicates the location of a quadrat used in the dieback boundary survey (section 2.3.1) - these were also used in the Canonical Correlation Analysis and 2 x 2 G Test of independence (section 2.3.2); △ indicates the location of a quadrat used only in the Canonical Correlation Analysis and 2 x 2 G Test of independence. In some cases, a single symbol may represent many quadrats located in close proximity.

Type P or S, although one site had a few plants of *Pteridium esculentum*, an element of Type T (Havel 1975). All sites were on slopes with orange gravels in loamy sand soils, above drainage features. Recently affected sites of other vegetation types (e.g. drainage communities) with boundaries that met the criteria described in the methods could not be located. The unaffected quadrat was beside the dieback quadrat on six sites and upslope from it in four sites. None were separated by roads or other features that may have also been fire management or logging boundaries. Some mature jarrah had recently died in three dieback quadrats. At most other sites there were isolated recent jarrah deaths near the quadrat. The dieback sites would have been classified as intermediate to high impact, according to ratings applied to dieback vegetation by dieback interpreters from the Department of Conservation and Land Management (Shearer and Tippett 1989). There was evidence of salvage logging nearby on some sites.

The density of species in a quadrat was determined in the following way. A list of all species occurring within the quadrat was made. Conspicuous species were then counted across the entire quadrat. Less conspicuous species were counted in six 2.5 x 2.5 m sub-quadrats, four in the corners of the main quadrat and two midway along the long sides of the main quadrat. In a few cases it was necessary to move a sub-quadrat slightly if it occurred over a large tree trunk, stump hole or other abnormality. It was difficult to define an individual for some species. For resprouting shrubs such as *Adenanthos barbiger* and *Leucopogon capitellatus*, I arbitrarily separated individuals if I could place my foot lengthwise between shoots (i.e. about 30 cm). For clump-forming species such as *Stylidium amoenum* and *S. hispidum*, a clump of plants that was clearly connected at the soil surface was recorded as a single plant. It was not possible or practical to count some species. Consequently, *Dryandra lindleyana*, some tufted monocots (such as *Tetraria capillaris*), some *Lomandra* spp. (especially if they were not in flower), and terete-stemmed *Lepidosperma* spp.), and species of Restionaceae were given a cover estimate in each of the sub-quadrats in which they occurred. *Tetraria capillaris* and terete-stemmed *Lepidosperma* spp. were aggregated as Cyperaceae spp., and narrow-leaved Lomandras as *Lomandra* spp. because most were not in flower at the time. Once the sub-quadrat sampling was complete, I checked that all species in the initial list had been given a

cover or density measure, and that the estimate seemed reasonable based on what I had seen in the entire quadrat. If species had been missed, I searched the whole quadrat for them. *Allocasuarina fraseriana, Banksia grandis,* jarrah and marri were divided into plants less than 3 m tall and plants greater than or equal to 3 m for the purpose of counting. The cover of each tree species was estimated for the entire site by summing the cover of individual trees or clumps of trees. Total tree cover (≥ 3 m), including *Banksia grandis*, was determined as accurately as possible by adding the cover of the component species and subtracting any overlap. The cover of litter, bare ground and plants less than 3 m tall was estimated in each sub-quadrat. Dead individuals of species were noted but not counted.

2.3.2 Broad Quadrat Survey of Unaffected and Dieback Vegetation

Site Selection

Dieback sites were chosen from aerial photography, field searches and information supplied by research staff of CALM and Alcoa. Unaffected vegetation was sampled as close as possible to dieback sites. When there was no unaffected vegetation on the same slope or in the same catchment as a dieback site, recent aerial photography was inspected to find examples of unaffected vegetation in comparable topographic positions nearby. Although a variety of aerial photography was used, the principal ones are listed in Table 2.1.

Table 2.1 Principal aerial photography used to estimate age of dieback on survey sites. 1940s photography was obtained from the Australian Surveying & Land Information Group (AUSLIG), post 1950s photography was obtained from the Department of Land Administration (WA). North and south refer to photo coverage relative to the town of Dwellingup.

Date of Photography	Reference	Scale (approx.)	Area covered
1941 October	MAP 1829 etc.	1 : 14 000	north
1943 November	MAP 1054 etc.	1 : 23 000	south
1951 April	WA 88 etc.	1 : 16 000	north
1958 November	WA 487 etc.	1 : 15 000	south
1960 November	WA 692Z etc.	1 : 16 000	north
1968 December	Proj. J 20	1 : 9 000	north
1980 February	790085	1 : 26 000	all
1994 January	930400	1 : 19 000	all

The age of dieback on the sites chosen could not be determined accurately. Aerial photography was used to place sites into one of three dieback age categories: pre-1951, 1968 - 1980 and post-1980. Sites where all *Banksia grandis* plants were alive were judged to be unaffected.

Pre-1951 Dieback Sites

The majority of sites with the earliest evidence of dieback were affected prior to 1951. A few sites were affected prior to 1941. Aerial photography for 1951 was not available for six sites with ironstone-dominated surface soils. These were interpreted from 1958 aerial photographs. Dieback would have occurred between 1943 and 1958 on these sites. To avoid confusion, all of the oldest dieback sites are referred to as pre-1951 throughout the thesis. The six ironstone sites are used in a single analysis (canonical correspondence analysis), and so the use of pre-1951 to group dieback sites by age is true in the majority of cases.

Sites were judged to be suitable only if there were patches of trees on the photos with minimal foliage visible and other causes of their decline (such as fire and logging) could not be found. The actual death of trees was not possible to determine on aerial photos. Almost all trees with open crowns on 1951 photography were removed by salvage logging between 1951 and 1960 and so their survival cannot be assessed. Burning and logging records were checked for pre-1960 dieback areas. None of the thin-crowned jarrah patches on 1950s photography could be adequately explained by burning or logging. Burning records held at CALM began in the summer of 1937 / 38. It seems unlikely that small apparently dead or dying jarrah patches observed on 1941 photography would not have partially recovered from a localised fire prior to 1937, had that been the cause.

1968 - 1980 Dieback Sites

Many quadrats were in areas severely burnt by a bushfire in January 1961. Patches of apparently recent dieback on 1968 photos may have been attributable to the lasting

effects of the fire, although there was apparently widespread dieback in the mid to late 1960s following the exceptionally wet winters of 1963 and 1964 (Podger 1968, McKinnell 1981). The dieback category of intermediate age used in this study was determined by comparison of 1968 and 1980 aerial photographs to avoid the possibility of mis-interpreting the effects of the 1961 bushfire.

Post-1980 Dieback Sites

The most recent dieback sites generally had standing dead jarrah stags or dead *Banksia grandis* as evidence of dieback. Parts of these sites had probably been affected within the last five years.

Survey Procedure

Prior to sampling, the precise quadrat location within most sites was determined on aerial photographs using random numbers for distances and directions from prominent features such as track intersections. The approximate location of quadrats is shown in Figure 2.4.

A species-area curve (Poore 1955) was obtained by nested quadrat sampling of a dieback-free forest stand in Jarrahdale Road, east of Jarrahdale: 90% of species were found in an area of 240 m^2 and 95% of species in an area of 360 m^2 (Figure 2.5). A quadrat of 400 m^2 was adopted because it has been used by other researchers in the forest (e.g. Vlahos and Bell 1986) and it allowed for some variation in quadrat size. Quadrats were laid out by pacing three sides and checking the fourth side and a diagonal. Prior to the survey, I determined the average length of my pace uphill and downhill using a tape measure. A tape measure and compass were initially used for laying out quadrats but problems with thick understorey and magnetic interference from subsurface rock made this technique extremely difficult and frustrating. Small variations in quadrat size are unlikely to influence the analysis of quadrat data or the interpretation of results when the quadrat size

is at or above the optimal size. If they did, it would be necessary to determine a species - area relationship for each sample and vary the quadrat size accordingly.

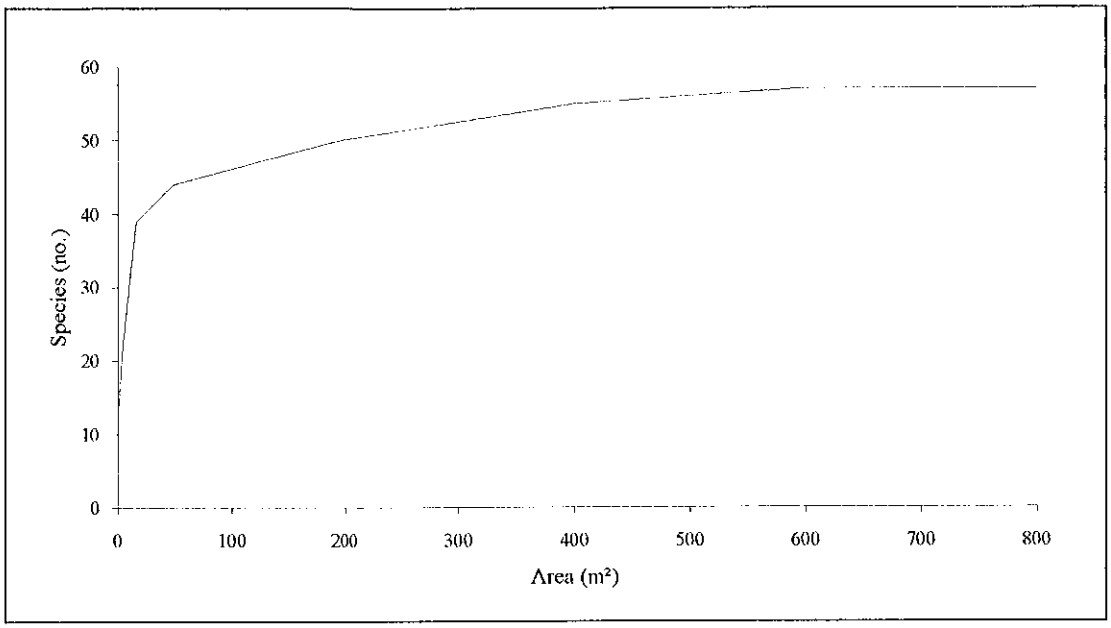


Figure 2.5 Species-area curve for unaffected jarrah forest, Jarrahdale Road, east of Jarrahdale.

Within each quadrat, a list was made of all species present with an estimate of their projective foliage cover on a four point scale, where 1 was equivalent to a cover less than 6.25% (or 25 m^2), 2 to a cover of greater than or equal to 6.25% and less than 25%, 3 to a cover of between 25% and less than 50%, and 4 to a cover of 50% or more. Bare ground, litter cover and outcropping rock cover were estimated. Aspect and slope were measured. Three trowels of soil were taken to a depth of about 10 cm from inter-plant spaces near the centre of each quadrat to determine the proportion of gravel in surface soil. The samples were bulked for each site, dried at 105°C for 48 hours and passed through a 2 mm sieve to separate the soil and gravel portions. The portions were then weighed.

All sites were visited at least once in early spring (September), mid to late spring (October - December) and summer (January - February) between 1993 and 1996 to detect the range of species present.

A total of 217 quadrats were sampled, 143 of these in dieback vegetation.

2.3.3 Litter Biomass and Surface Soil Characteristics in Unaffected and Pre-1951 Dieback Vegetation

After visiting a few dieback sites it was clear that litter cover and quantity was greater in unaffected vegetation. However, the distribution of litter is extremely uneven, especially on dieback sites, so quantification of differences would have been very difficult without a large number of samples. In addition, the patchiness of fire, which was evident on some recently burnt sites, would make comparisons questionable unless the fire distribution and intensity were known.

The sparseness of ground cover on dieback sites means that litter is not held where it falls. It clearly blows around and collects around the few plants and large fallen branches and trunks that occur on dieback sites. To obtain some measure of litter quantity and the contribution of various species (as opposed to litter production), a site was chosen, which had recently been burnt and had examples of dieback vegetation and unaffected vegetation on the same slope. Litter, excepting pieces of stem greater than about 2.5 cm in diameter, was collected in four 1 m^2 quadrats in dieback and unaffected vegetation in February 1996. The area (Site 11, Chapter 3) had been burnt in October 1993. Leaves of *Xanthorrhoea preissii* had been burnt back to the stem on both dieback and unaffected parts of the site so the fire intensity was probably great and similar on both parts. In many other areas burnt in the same fire, leaves of *Xanthorrhoea preissii* were either singed at the tips or unburnt altogether suggesting a great range of fire intensities within the same conflagration.

Samples were taken every 10 m along a transect across the slope from a randomly chosen starting point. To make samples more comparable, no large plants (e.g. tree trunks, *Xanthorrhoea preissii* trunks), rocks or large branches were included in the quadrat, which would have diminished the area available for litter accumulation. In the dieback area there were no problems in obtaining a sample of this nature. In the unaffected area, it took

several misses before four samples could be taken. In the unaffected area there was a layer of decomposing litter at the soil surface, which was difficult to collect without taking the top few mm of organic soil as well. Samples in the unaffected area are probably under-estimates of litter quantity. Litter was placed in hessian bags. It was then dried in ovens at 70°C for 48 hours, separated into categories (*Banksia grandis* leaves, eucalypt leaves, marri fruit, jarrah fruit, twigs < 2.5 mm in diameter, and other material) and weighed.

The soil surface and upper 15 cm of the soil profile of one of the pre-1951 dieback and unaffected litter quadrats were described and photographed.

2.4 Data Analysis

2.4.1 Dieback Boundary Survey

Density data were square root transformed and cover data were angular transformed prior to analysis. The transformed data were tested for homogeneity of variances between dieback and unaffected vegetation with an F-test. For species with equal variances, the significance of differences in density or cover between dieback and unaffected vegetation was determined by t-test for paired comparisons on the transformed data. Five species had variances for the two samples that were significantly different ($P < 0.05$): *Eucalyptus marginata* ≥ 3 m, *Goodenia caerulea, Tetratheca hirsuta, Trachymene* spp. and *Xanthosia candida*. The assumption of equality of variance was not met so the t-test for paired comparisons could not be legitimately used. Wilcoxon's signed-ranks test for two groups, arranged as paired observations (Sokal and Rohlf 1981) was used instead for these species.

2.4.2 Broad Quadrat Survey of Unaffected and Dieback Vegetation

To determine if the age of dieback is significantly correlated with species composition, the data were analysed using canonical correspondence analysis (CCA) in the ordination

package CANOCO version 3.10 (ter Braak 1987 - 1992). Factors included in the analysis were the plant species present and their cover value, the time since dieback, rock cover (%), slope, aspect, % gravel, minutes south of latitude 32°, minutes east of longitude 116°, and dominance of ironstone on the soil surface (0 = ironstone absent and 1 = ironstone 100% cover on surface). Since aspect is a circular measure, where the smallest number (0) is equivalent to the largest (360), a two part binary system was used (1 = south facing, 0 = north facing; 1 = east facing, 0 = west facing). Geographic location was included to identify variation across the north - south and east - west range of quadrats.

Factors that could have been artifacts of dieback (e.g. depth to watertable, cover of trees, bare ground and litter) were not included in the analysis. Also excluded from the analysis were time to last burn and time since last logging. Time to last burn was excluded because of the patchiness of burning in the cool, prescribed fires conducted by CALM. Myara forest block, where many quadrats were sampled (see Chapter 3), was burnt in a prescribed fire in October 1993. When I first inspected the area in July 1994, it was clear that many small patches escaped the fire altogether. After two years, although severely burnt areas were still obvious, it was difficult to distinguish areas that had not been burnt from those burnt lightly. Using information about prescribed burning for forest blocks that had not been burnt for a decade or more would clearly have been questionable. Time since logging was not used because detailed records were not kept until 1968. Even after this date the logging information appears to be general and it would not be possible to accurately assess the logging history of the area surrounding quadrats. For instance, one quadrat in Myara block probably escaped logging altogether, despite widespread logging in the vicinity in the mid-1960s. The jarrah within and around the quadrat are much larger than elsewhere in the block. They are also mis-shapen and were probably avoided during the last logging operations. Some of the sites sampled were also salvage logged, especially in the 1950s according to aerial photography, although there are few records of these operations held by CALM.

Dieback sites in wet areas, where no unaffected vegetation in comparable sites could be found, were omitted from the analysis.

CCA was performed without down-weighting rare species. No species or samples were made passive and no transformations were done. The significance of the eigenvalue of the first axis was assessed using 999 permutations in an unrestricted Monte Carlo permutation test.

The significance of differences in the frequencies of each species between unaffected vegetation and dieback vegetation was determined by a 2 x 2 G-test of independence (Sokal and Rohlf 1981). Dieback vegetation with few or no quadrats in similar unaffected vegetation, namely those occurring on ironstone dominated soils and shallow valleys, were excluded from these analyses. All quadrats sampled for Chapter 3 were included to increase the sample size and the likelihood of detecting differences. Because more very old dieback quadrats were sampled from the western side of the study area and more of the younger dieback quadrats were from the eastern side of the study area, unaffected quadrats were randomly chosen for comparison such that the proportion of quadrats from east and west was similar in each group compared. Consequently, the set of unaffected quadrats is different in each 2 x 2 comparison.

To test if the species found to be significantly different in dieback vegetation are represented by the range of unaffected vegetation sampled, detrended correspondence analysis (DCA) was performed on unaffected quadrats, excluding the two quadrats sampled with ironstone soils. The likelihood that the significant differences detected in the 2 x 2 G-test are representative of change may be greatest for species found in a wide range of unaffected vegetation. Species that occur only in floristically similar unaffected quadrats may be found to be less frequent in dieback vegetation simply because dieback vegetation that had once been comparable was not sampled. DCA was chosen because correspondence analysis (CA) had produced a strongly arched ordination.

2.5 Results

2.5.1 Dieback Boundary Survey

Twelve species had a significantly different density in dieback vegetation compared with unaffected vegetation (Table 2.2). Only two of these (*Thysanotus thyrsoideus* and *Trachymene* spp.) had a greater density on the dieback side of the boundary. There were great differences in density for some species at a few sites but a non-significant difference overall. This suggests that either (i) more sites were required to detect differences satisfactorily, (ii) there were great natural differences in vegetation between unaffected and dieback quadrats, or (iii) there was too great a range of dieback ages represented in the dieback quadrats. The first and third of these propositions seem plausible because most of the differences in means were in the same direction as the quadrat study (described below) even if they were not significant.

Table 2.2 Density (plants per 100 m^2) of species occurring in six or more sites with 95% confidence limits. Values are back (square root) transformed except for species labelled **c**, which are back (arcsine) transformed cover estimates. Significance of differences was determined by t-test for paired comparisons for species other than those marked **w**. For these species, the significance of differences between means was determined using Wilcoxon's signed-ranks test for two groups, arranged as paired observations. Probability (P) > 0.05 unless otherwise specified.

	UNAFFECTED				DIEBACK			
	n	mean	- 95%	+ 95%	mean	- 95%	+ 95%	P
Acacia barbinervis	8	4	0	20	6	0	27	
Adenanthos barbiger	10	13	9	17	4	2	7	<0.001
Agrostocrinum scabrum	8	1	0	3	1	0	2	
Amphipogon amphipogonoides	10	23	12	38	24	12	41	
Astroloma pallidum	8	1	0	4	2	1	3	
Banksia grandis < 3 m	10	26	15	39	4	0	11	<0.001
Banksia grandis ≥ 3 m	10	10	8	13	0	0	0	<0.001
Boronia fastigiata	10	9	2	21	4	0	12	
Bossiaea ornata	7	70	7	195	49	4	142	
Caladenia flava	7	3	0	12	2	0	7	
Chamaescilla corymbosa	8	10	0	38	14	2	35	
Comesperma virgatum	8	3	1	8	1	0	2	
Conostylis setosa	10	27	2	82	41	4	117	
Cyperaceae (other) **c**	10	0.2	0.0	0.7	0.2	0.0	0.6	
Drosera erythrorhiza	6	16	2	46	7	1	17	
Dryandra lindleyana **c**	7	0.4	0.0	1.0	0.8	0.0	2.7	

Table 2.2 (cont.) Density (plants per 100 m^2) of species occurring in six or more sites with 95% confidence limits.

	UNAFFECTED				DIEBACK			
	n	mean	- 95%	+ 95%	mean	- 95%	+ 95%	P
Gompholobium preissii	6	39	2	125	41	3	123	
Hemigenia ramosissima	6	3	3	28	5	0	24	
Hibbertia amplexicaulis	9	26	5	63	6	0	22	<0.01
Hibbertia commutata	9	18	6	37	2	0	6	<0.001
Hovea chorizemifolia	10	16	6	33	17	4	38	
Jarrah < 3m	10	6	3	9	9	4	17	
Jarrah ≥ 3m **w**	10	3	3	4	2	1	3	
Jarrah total	10	9	6	13	12	6	19	
Kennedia coccinea	7	2	0	5	0	0	1	
Lasiopetalum floribundum	6	2	0	12	2	0	7	
Lechenaultia biloba	9	20	5	44	36	17	63	
Lepidosperma angustatum **c**	7	0.0	0.00	0.0	0.0	0.00	0.0	
Leptomeria cunninghamii	6	1	0	6	2	0	6	
Leucopogon capitellatus	6	9	1	26	4	0	11	
Leucopogon nutans	9	4	1	8	2	0	6	
Logania serpyllifolia	6	1	0	5	1	0	5	
Lomandra hermaphrodita	7	30	14	52	34	11	69	
Lomandra caespitosa group **c**	10	0.3	0.0	0.7	0.2	0.0	0.8	
Lomandra purpurea group	7	4	1	7	1	0	5	
Lomandra sonderi	6	6	1	15	3	0	11	
Lomandra spartea	8	9	2	22	17	3	42	
Macrozamia riedlei	7	4	0	11	2	0	8	
Marri < 3 m	10	3	1	6	5	1	10	
Marri ≥ 3 m	9	1	0	1	0	0	1	
Marri total	10	4	2	7	5	2	11	
Opercularia echinocephala	6	22	2	64	10	0	40	
Opercularia vaginata	6	5	0	18	6	1	13	
Patersonia babianoides	8	1	0	5	3	0	8	
Pentapeltis peltigera	9	9	3	20	16	3	37	
Persoonia longifolia	8	4	2	5	0	0	1	<0.001
Pterochaeta paniculata	8	0	0	0	20	0	90	
Scaevola calliptera	10	8	1	21	6	0	20	
Stylidium amoenum	10	54	28	88	28	5	69	
Stylidium hispidum	10	36	6	94	47	18	89	
Stylidium junceum	9	9	3	20	3	0	10	<0.05
Stylidium schoenoides	10	1	0	3	0	0	1	
Styphelia tenuiflora	10	4	2	6	0	0	1	<0.001
Tetrarrhena laevis	10	7	0	23	4	0	15	
Tetratheca hirsuta **w**	9	13	3	32	0	0	1	<0.001
Thelymitra crinita	10	1	0	2	3	0	7	
Thysanotus multiflorus	6	5	1	12	1	0	7	
Thysanotus thyrsoideus	9	8	2	19	20	9	36	<0.05
Trachymene spp. **w**	8	0	0	3	47	3	143	<0.01
Trichocline spathulata	10	12	4	25	13	4	29	
Trymalium ledifolium	9	17	0	68	28	0	106	
Xanthorrhoea gracilis	10	3	2	6	2	0	5	
Xanthorrhoea preissii	10	9	5	13	9	4	15	
Xanthosia candida **w**	10	23	7	49	9	4	16	<0.05

With the exception of live *Banksia grandis* (≥ 3 m), which by definition was absent on the dieback side of boundaries, species for which *P. cinnamomi* has been recovered from dead individuals (Shearer and Dillon 1995) were rarely absent in recently affected dieback vegetation when they were present in adjacent unaffected vegetation, although they may have been less dense. There was very little difference in frequency for these species between dieback and unaffected quadrats (Table 2.3).

Table 2.3. No. of dieback and unaffected quadrats containing species for which *P. cinnamomi* was recovered from dead individuals by Shearer and Dillon (1995).

	UNAFFECTED	DIEBACK
Adenanthos barbiger	10	10
Banksia grandis < 3 m	10	8
Banksia grandis ≥ 3 m	10	0
Bossiaea ornata	6	6
Hibbertia amplexicaulis	9	6
Hibbertia commutata	8	6
Jarrah < 3 m	10	10
Jarrah ≥ 3 m	10	9
Lasiopetalum floribundum	4	6
Leucopogon capitellatus	6	6
Leucopogon nutans	9	7
Lomandra sonderi	6	5
Macrozamia riedlei	6	7
Persoonia longifolia	8	5
Styphelia tenuiflora	9	6
Trymalium ledifolium	7	7
Xanthorrhoea gracilis	10	8
Xanthorrhoea preissii	10	10

The mean number of species in unaffected vegetation (61.3 ± 3.1) was not significantly different from the mean number of species in dieback quadrats (61.6 ± 2.7) as determined by a t-test for paired comparisons. The covers of trees, litter, and understorey plants were significantly less in dieback vegetation and the cover of bare ground significantly more on the dieback side of the boundary (Table 2.4).

Table 2.4 Mean % cover of litter, understorey plants, bare ground and trees (including *Banksia grandis*) with 95% confidence limits at the ten sites. Values are back (arcsine) transformed. Significance of differences determined by t-test for paired comparisons.

	UNAFFECTED			DIEBACK			
	mean	- 95%	+ 95%	mean	- 95%	+ 95%	P
Litter	80	76	83	59	50	68	<0.001
Understorey Plants	38	33	43	26	21	31	<0.001
Bare Ground	5	3	8	28	22	34	<0.001
Trees	53	45	60	16	9	25	<0.001

2.5.2 Broad Quadrat Survey of Unaffected and Dieback Vegetation

Quadrat data for dieback and unaffected vegetation are summarized in Table 2.5.

The pre-1951 dieback vegetation sampled had on average five fewer species per quadrat than the unaffected vegetation or 1968 - 1980 dieback quadrats sampled. Despite this, pre-1951 dieback sites on slopes contained 251 of the 321 species or species groups recorded in the survey compared with 222 species for unaffected sites.

The unaffected vegetation had more shrub species and more shrub cover than dieback vegetation on sloping sites. Unaffected vegetation had more perennial herb species than pre-1951 dieback vegetation but slightly less cover. The cover of perennial herbs is only substantial in wet pre-1951 dieback sites (30.1 ± 7.1%), which is largely attributable to the great cover of some species of the family Restionaceae in several quadrats. Species of the families Cyperaceae and Restionaceae were dominants or co-dominants of the understorey more often in dieback sites but only greatly so in wet sites. On sloping dieback sites, species of Cyperaceae or Restionaceae were dominant or co-dominant on only a quarter of sites. The shrub *Hibbertia hypericoides* was dominant or co-dominant on as many sites.

Table 2.5 Summary of quadrat data for dieback and unaffected vegetation. Means and standard errors are given. The dieback groups are those used by Shearer and Dillon (1995): Groups 3 and 5 included species from which *P. cinnamomi* was most frequently isolated from dead individuals; group 5 species died more frequently in active dieback centres than group 3 species. See Table 1.1 for complete description of groups.

	Unaffected vegetation on slopes (n = 74)	1968 - 80 dieback on slopes (n = 66)	Pre -1951 dieback on slopes (n = 67)	Pre -1951 dieback on wet sites (n = 10)
Species Richness (No. of Species)				
Total	59.8 ± 1.0	59.9 ± 1.0	54.4 ± 1.0	54.8 ± 2.6
Shrubs	25.1 ± 0.6	21.9 ± 0.7	17.8 ± 0.6	19.0 ± 1.1
Perennial herbs	26.3 ± 0.7	27.2 ± 0.8	23.8 ± 0.6	25.3 ± 1.6
Annual herbs	0.8 ± 0.2	3.6 ± 0.3	6.0 ± 0.3	4.7 ± 0.7
Total species	222	262	251	160
Cover (Overlapping %)				
Shrubs	24.2 ± 1.7	14.1 ± 1.7	16.6 ± 1.8	32.9 ± 5.6
Perennial herbs	5.5 ± 0.7	10.2 ± 1.1	8.3 ± 0.9	30.1 ± 7.1
Annual herbs	0.1 ± 0.0	1.2 ± 0.2	2.7 ± 0.3	1.9 ± 1.0
Cover (Total %)				
Trees	41.4 ± 2.7	15.9 ± 1.5	13.1 ± 1.3	10.9 ± 2.0
Litter	74.5 ± 2.2	40.2 ± 2.2	27.1 ± 1.6	39.7 ± 6.2
Bare ground	6.3 ± 1.4	29.9 ± 2.8	48.6 ± 2.3	22.4 ± 3.6
Overstorey (% quadrats with ≥ 10% cover)				
Banksia grandis	86	3	0	0
Jarrah	58	40	4	0
Marri	7	19	33	40
Understorey (% quadrats dominant or co-dominant)				
Cyperaceae / Restionaceae	16	27	27	50
Hibbertia hypericoides	20	25	31	20
Dieback Group				
3 (Species / quadrat)	4.3 ± 0.2	2.6 ± 0.2	1.4 ± 0.2	0.7 ± 0.3
(Total species)	9	9	9	3
5 (Species / quadrat)	6.3 ± 0.2	5.0 ± 0.2	4.0 ± 0.2	4.1 ± 0.5
(Total species)	11	11	9	8

The unaffected vegetation sampled had more tree cover, more litter cover and less bare ground than dieback vegetation sampled. Bare ground was greatest on the oldest sloping dieback sites. The frequency of marri with ≥ 10% cover was greater in dieback quadrats and the frequency of jarrah with ≥ 10% cover was less on dieback sites. *Banksia grandis* had a cover of 10% or greater on a few 1968 - 80 dieback sites but was absent from all pre-1951 dieback sites.

The dieback sites sampled had fewer species regarded as being highly susceptible to infection by *P. cinnamomi* (i.e. in Shearer and Dillon (1995) susceptibility groups 3 and 5). However, of the 20 highly susceptible species found in unaffected vegetation, only two (*Banksia grandis* and *Leucopogon verticillatus*) were absent from pre-1951 dieback vegetation.

In the 2x2 G-test of independence, of the 299 species and species groups compared, 50 species had a significantly higher frequency in pre-1951 dieback vegetation than in unaffected vegetation ($P < 0.05$) (Table 2.6) and 53 species had a significantly lower frequency in pre-1951 dieback vegetation than in unaffected vegetation (Table 2.7). There were fewer species with significant differences in frequency between unaffected vegetation and 1968 - 80 dieback vegetation (26 species more frequent in 1968 - 80 dieback vegetation and 29 species less frequent in 1968 - 80 dieback vegetation). With only two exceptions, these species also had significantly different frequencies in the comparison of pre-1951 and unaffected vegetation. *Stylidium hispidum* and *Xanthosia huegelii* had a significantly greater frequency in 1968 - 80 dieback vegetation compared with unaffected vegetation but did not have a significantly different frequency when pre-1951 dieback quadrats were compared with quadrats from unaffected vegetation (Table 2.6). Of the remaining 186 species, which did not have significantly different frequencies, 51 occurred in at least 10% of quadrats in either unaffected or dieback vegetation (Table 2.8). This is the smallest % frequency that could produce a significant difference.

Only one of the nine species found to be less dense in dieback vegetation in the dieback boundary survey (*Xanthosia candida*, Table 2.2), was not also less frequent in pre-1951 dieback quadrats. Of the two species which were more dense in dieback vegetation in the dieback boundary survey, one (*Trachymene* spp.) was also significantly more frequent in dieback quadrats in the broad quadrat survey (Table 2.6), whilst the other (*Thysanotus thyrsoideus*) was significantly less frequent in dieback quadrats in the broad quadrat survey (Table 2.7).

Table 2.6 Percentage frequency of species with a significantly higher frequency in dieback quadrats compared with unaffected quadrats as determined by a 2 x 2 G-test of independence. $P < 0.05$ is indicated by *. *P. cinnamomi* susceptibility: the numbers 1 to 5 are the susceptibility groups of Shearer and Dillon (1995) - (species in groups 1 and 2 are regarded as field resistant, species in groups 3 and 5 as highly susceptible, and species in group 4 as displaying a range of susceptibilities); D indicates a species that Shearer and Dillon (1995) obtained *P. cinnamomi* from dead individuals; S indicates a species from which *P. cinnamomi* has been obtained from live plants or plants of unrecorded health by [a] Podger (1968), [b] Gardner and Rokich (1987), [c] Shearer and Dillon (1995).

SPECIES	Unaffected (n=50)	Dieback 1968 - 80 (n=47)		Unaffected (n=54)	Dieback pre-1951 (n=60)		*P. cinnamomi* susceptibility
Acacia barbinervis	56	66		50	70	*	1
Acacia nervosa	6	4		6	25	*	1
Acacia obovata	0	4		0	12	*	
**Aira cupaniana*	0	9		2	40	*	
Astroloma pallidum	56	62		50	73	*	2
Baeckea camphorosmae	18	32		7	58	*	2
Burchardia umbellata	20	36		26	52	*	
Centrolepis aristata	0	13	*	0	30	*	
Chamaescilla corymbosa	24	40		35	68	*	
Comesperma calymega	2	21	*	2	35	*	
Danthonia spp.	10	55	*	11	45	*	
Drosera erythrorhiza	48	53		44	77	*	
Dryandra lindleyana	74	98	*	69	97	*	4 D S bc
Gompholobium knightianum	58	74		50	72	*	4 D
Gompholobium marginatum	0	9		2	30	*	
Gompholobium preissii	32	60	*	22	42	*	
Goodenia caerulea	4	23	*	6	37	*	
Haemodorum spp.	26	55	*	30	58	*	
Hakea lissocarpha	6	19		2	48	*	2 Sb
Hyalosperma cotula	0	11	*	4	27	*	
Hypocalymma angustifolium	20	62	*	15	65	*	2 Sab
**Hypochoeris glabra*	4	23	*	4	23	*	
Hypolaena exsulca	6	13		4	17	*	
Isotoma hypocrateriformis	0	43	*	0	73	*	
Jacksonia alata	0	4		0	15	*	
Laxmannia squarrosa	2	17	*	0	33	*	
Lechenaultia biloba	78	89		78	95	*	2 Sc
Lepidosperma angustatum	42	64		35	80	*	2
Levenhookia spp.	6	60	*	6	82	*	
Levenhookia stipitata	0	4		0	10	*	
Lobelia spp.	2	30	*	0	17	*	
Loxocarya fasciculata	14	13		2	20	*	1
Mesomelaena tetragona	0	13	*	0	32	*	1
Millotia tenuifolia	8	45	*	6	28	*	
Neurachne alopecuroidea	6	34	*	2	50	*	
Olearia paucidentata	0	2		0	15	*	
Patersonia pygmaea	22	30		20	42	*	1 Sb
Phyllanthus calycinus	10	17		20	57	*	2

Table 2.6 (cont.) Percentage frequency of species with a significantly higher frequency in dieback quadrats compared with unaffected quadrats as determined by a 2 x 2 G-test of independence. $P < 0.05$ is indicated by *. *P. cinnamomi* susceptibility: the numbers 1 to 5 are the susceptibility groups of Shearer and Dillon (1995) - (species in groups 1 and 2 are regarded as field resistant, species in groups 3 and 5 as highly susceptible, and species in group 4 as displaying a range of susceptibilities); D indicates a species that Shearer and Dillon (1995) obtained *P. cinnamomi* from dead individuals; S indicates a species from which *P. cinnamomi* has been obtained from live plants or plants of unrecorded health by [a] Podger (1968), [b] Gardner and Rokich (1987), [c] Shearer and Dillon (1995).

SPECIES	Unaffected (n=50)	Dieback 1968 - 80 (n=47)		Unaffected (n=54)	Dieback pre-1951 (n=60)		*P. cinnamomi* susceptibility
Podolepis gracilis	0	4		0	20	*	
Podotheca angustifolia	0	11	*	0	20	*	
Prasophyllum parvifolium	0	0		0	23	*	
Pterochaeta paniculata	2	79	*	7	95	*	
Schoenus spp.	0	11	*	0	27	*	
Stipa spp.	10	21		0	25	*	
Stylidium hispidum	68	89	*	72	82		
Stylidium repens	0	6		0	23	*	
Tetraria octandra	12	38	*	11	53	*	
Trachymene spp.	26	49	*	31	83	*	
Tripterococcus brunonis	28	60	*	26	47	*	
**Vulpia bromoides*	0	0		0	12	*	
Waitzia nitida	0	15	*	0	32	*	
Xanthosia huegelii	0	11	*	0	7		

Table 2.7 Percentage frequency of species with a significantly lower frequency in dieback quadrats compared with unaffected quadrats as determined by a 2 x 2 G-test of independence. $P < 0.05$ is indicated by *. *P. cinnamomi* susceptibility: the numbers 1 to 5 are the susceptibility groups of Shearer and Dillon (1995) - (species in groups 1 and 2 are regarded as field resistant, species in groups 3 and 5 as highly susceptible, and species in group 4 as displaying a range of susceptibilities); D indicates a species that Shearer and Dillon (1995) obtained *P. cinnamomi* from dead individuals; S indicates a species from which *P. cinnamomi* has been obtained from live plants or plants of unrecorded health by [a] Podger (1968), [b] Gardner and Rokich (1987), [c] Shearer and Dillon (1995).

SPECIES	Unaffected (n=50)	Dieback 1968 - 80 (n=47)		Unaffected (n=54)	Dieback pre-1951 (n=60)		*P. cinnamomi* susceptibility
Acacia lateriticola	42	36		46	25	*	2
Acacia urophylla	24	4	*	22	0	*	2
Adenanthos barbiger	88	74		98	55	*	5 D Sb
Agrostocrinum scabrum	88	43	*	85	22	*	
Amphipogon amphipogonoides	64	60		67	37	*	
Banksia grandis	98	26	*	100	0	*	5 D S ab
Boronia fastigiata	86	57	*	93	27	*	2
Chorizema rhombeum	12	9		13	2	*	
Clematis pubescens	20	0	*	22	0	*	1
Comesperma virgatum	58	32	*	67	10	*	1
Daviesia preissii	42	15	*	35	0	*	
Dianella revoluta	36	13	*	33	8	*	3 D
Drosera stolonifera	44	38		39	18	*	
Hibbertia amplexicaulis	80	47	*	96	15	*	3 D Sb
Hibbertia commutata	54	19	*	56	25	*	3 D Sab
Hibbertia glomerata	0	0		13	2	*	
Hibbertia huegelii	38	36		48	17	*	
Hibbertia quadricolor	52	40		52	23	*	3 D
Hovea chorizemifolia	94	85		91	57	*	2
Hybanthus floribundus	16	2	*	17	0	*	
Jarrah	100	89	*	100	80	*	4 D Sa
Kennedia coccinea	50	21	*	48	2	*	1 Sc
Labichea punctata	56	23	*	44	3	*	
Lasiopetalum floribundum	38	26		33	7	*	3 D Sab
Leptomeria cunninghamii	28	17		33	2	*	2
Leucopogon capitellatus	62	23	*	65	38	*	3 D Sb
Leucopogon verticillatus	38	2	*	46	0	*	3 D Sab
Logania serpyllifolia	22	9		19	3	*	
Lomandra caespitosa "group"	72	45	*	80	40	*	
Lomandra purpurea "group"	48	32		52	22	*	
Lomandra sonderi	86	57	*	76	23	*	3 D Sb
Loxocarya cinerea	34	13	*	35	15	*	4 D
Mesomelaena graciliceps	32	19		24	3	*	
Monotaxis occidentalis	6	6		9	0	*	
Olax benthamiana	14	0	*	11	0	*	
Opercularia echinocephala	50	57		50	30	*	1 Sb
Opercularia vaginata	36	23		37	17	*	
Patersonia babianoides	66	45		59	15	*	
Pentapeltis peltigera	84	77		81	50	*	1

Table 2.7 (cont.) Percentage frequency of species with a significantly lower frequency in dieback quadrats compared with unaffected quadrats as determined by a 2 x 2 G-test of independence. $P < 0.05$ is indicated by *. *P. cinnamomi* susceptibility: the numbers 1 to 5 are the susceptibility groups of Shearer and Dillon (1995) - (species in groups 1 and 2 are regarded as field resistant, species in groups 3 and 5 as highly susceptible, and species in group 4 as displaying a range of susceptibilities); D indicates a species that Shearer and Dillon (1995) obtained *P. cinnamomi* from dead individuals; S indicates a species from which *P. cinnamomi* has been obtained from live plants or plants of unrecorded health by [a] Podger (1968), [b] Gardner and Rokich (1987), [c] Shearer and Dillon (1995).

SPECIES	Unaffected (n=50)	Dieback 1968 - 80 (n=47)		Unaffected (n=54)	Dieback pre-1951 (n=60)		*P. cinnamomi* susceptibility
Persoonia longifolia	90	13	*	89	2	*	4 D Sab
Platysace compressa	66	43	*	61	17	*	4 Sac
Pteridium esculentum	16	0	*	15	0	*	4
Pterostylis spp.	58	28	*	54	32	*	
Scaevola calliptera	64	55		59	20	*	2
Stylidium amoenum	76	64		83	27	*	
Stylidium junceum	78	74		80	25	*	
Stylidium schoenoides	56	32	*	59	17	*	
Styphelia tenuiflora	86	43	*	85	18	*	5 D
Tetrarrhena laevis	66	32	*	74	8	*	1
Tetratheca hirsuta	96	40	*	96	3	*	1 Sa
Thysanotus multiflorus	14	2		24	3	*	
Thysanotus thyrsoideus	62	30	*	69	33	*	
Trichocline spathulata	74	62		72	42	*	1

Table 2.8 Percentage frequency of species with no significant difference in frequency between dieback quadrats and unaffected quadrats as determined by a 2 x 2 G-test of independence. Species with % f ≥ 10 in at least one type included. *P. cinnamomi* susceptibility: the numbers 1 to 5 are the susceptibility groups of Shearer and Dillon (1995) - (species in groups 1 and 2 are regarded as field resistant, species in groups 3 and 5 as highly susceptible, and species in group 4 as displaying a range of susceptibilities); D indicates a species that Shearer and Dillon (1995) obtained *P. cinnamomi* from dead individuals; S indicates a species from which *P. cinnamomi* has been obtained from live plants or plants of unrecorded health by [a] Podger (1968), [b] Gardner and Rokich (1987), [c] Shearer and Dillon (1995), [d] Giles Hardy (Murdoch University, pers. comm.). ? = isolated from *Hibbertia acerosa*, which may be the same species as that referred to as *Hibbertia rhadinopoda* in this thesis (see section 2.2.4 Taxonomy).

SPECIES	Unaffected (n=50)	Dieback 1968 - 80 (n=47)	Unaffected (n=54)	Dieback pre-1951 (n=60)	*P. cinnamomi* susceptibility
Allocasuarina fraseriana	22	19	19	23	4 D Sabc
Bossiaea aquifolium	26	19	22	8	4 D
Bossiaea ornata	78	70	63	43	4 D Sb
Burnettia nigricans	16	11	19	10	
Caladenia flava	42	38	56	60	
Conostylis serrulata	38	43	26	27	2
Conostylis setigera	16	19	6	10	Sa
Conostylis setosa	72	87	80	93	2
Cyathochaeta avenacea	40	47	43	28	
Dampiera linearis	78	89	63	62	1 Sa
Daviesia decurrens	60	53	43	38	5 D Sc
Dillwynia sp. A	8	17	4	13	
Drosera macrantha	90	74	87	73	
Drosera platystigma	16	19	9	22	
Dryandra sessilis	14	13	19	20	5 D Sb
Elythranthera brunonis	22	17	24	27	
Eriostemon spicatus	18	32	30	38	1
Gompholobium polymorphum	26	13	19	7	
Grevillea pilulifera	8	15	7	13	
Grevillea wilsonii	14	17	4	3	4
Hakea ruscifolia	16	15	13	7	4 D
Hakea stenocarpa	14	17	15	22	
Hemigenia ramosissima	14	17	15	27	
Hibbertia hypericoides	38	47	43	48	2 Sc
Hibbertia rhadinopoda	68	79	80	67	? Sab
Lagenifera huegelii	16	11	24	13	
Lepidosperma sp. F "group"	30	32	28	45	
Leucopogon nutans	74	57	81	73	5 D Sc
Leucopogon oxycedrus	16	13	13	10	
Lomandra hermaphrodita	58	70	59	62	
Lomandra spartea	66	72	65	80	
Loxocarya flexuosa	50	62	50	37	
Macrozamia riedlei	60	47	63	65	4 D
Marri	88	89	89	93	1 Sd
Patersonia rudis	38	45	28	32	4 D

Table 2.8 Percentage frequency of species with no significant difference in frequency between dieback quadrats and unaffected quadrats as determined by a 2 x 2 G-test of independence. Species with % f ≥ 10 in at least one type included.

SPECIES	Unaffected (n=50)	Dieback 1968 - 80 (n=47)	Unaffected (n=54)	Dieback pre-1951 (n=60)	*P. cinnamomi* susceptibility
Petrophile striata	30	30	19	23	4 D
Pimelea suaveolens	16	17	17	17	5 D
Pronaya fraseri	18	21	19	23	
Ptilotus declinatus	10	11	7	12	
**Senecio vulgaris*	6	19	7	10	
Sphaerolobium medium	26	28	13	25	4
Stachystemon vermicularis	22	17	22	12	
Stylidium calcaratum	18	23	26	42	
Tetraria capillaris	78	79	67	83	
Thelymitra crinita	50	47	46	58	
Tricoryne elatior	18	28	19	18	
Trymalium ledifolium	50	60	54	72	4 D Sb
Xanthorrhoea gracilis	94	94	96	87	5 D Sb
Xanthorrhoea preissii	74	83	76	87	5 D Sb
Xanthosia atkinsoniana	44	34	31	23	2
Xanthosia candida	30	26	39	23	1

Almost one-third of species more frequent on dieback sites are annuals. There are only two annual species (**Senecio vulgaris* and *Stylidium calcaratum*) in the list of species equally frequent on dieback sites and none in the list of species less frequent on dieback sites (Table 2.9). Allowing for species that have a life form not easily categorized as herbaceous or woody, there appears to be little difference in the representation of perennial herbs. However, when annuals are removed from % calculations, the proportion of perennial herbs is greater for species more frequent in dieback sites (62%).

Table 2.9 Percentage of species listed in Tables 2.6, 2.7 and 2.8 with annual, perennial herb and perennial woody life forms.

Species in dieback sites	Annuals (%)	Perennial herbs (%)	Perennial woody (%)
More frequent (Table 2.6)	32	42	26
Less frequent (Table 2.7)	0	47	53
Equally frequent (Table 2.8)	4	49	47

P. cinnamomi has been isolated from species that were found more frequently (Table 2.6), less frequently (Table 2.7) and equally frequently (Table 2.8) on dieback sites. Of the five dieback groups of Shearer and Dillon (1995) (see Table 1.1, page 11), groups 1 and 2 are likely to contain mainly species resistant to *P. cinnamomi* infection, and groups 3 and 5 contain species most susceptible to infection. Group 4 contains species of a range of susceptibility. As might be expected, none of the species that were more frequent in pre-1951 dieback vegetation and many species which were less frequent in pre-1951 dieback vegetation were from the most susceptible dieback groups (Groups 3 and 5) (Table 2.10). However, 14 species less frequent in pre-1951 dieback vegetation were from the *P. cinnamomi* resistant groups 1 and 2, and six of the species which did not have a significantly different frequency in pre-1951 dieback vegetation were from the most susceptible group 5.

Table 2.10 Number of species listed in Tables 2.6, 2.7 and 2.8 in each of the dieback groups of Shearer and Dillon (1995). Species in groups 1 and 2 are regarded as field resistant, species in groups 3 and 5 as highly susceptible, and species in group 4 as displaying a range of susceptibilities

Dieback Group (Shearer and Dillon 1995)	Less frequent in dieback vegetation (Table 2.7)	Equally frequent in dieback vegetation (Table 2.8)	More frequent in dieback vegetation (Table 2.6)
1	8	4	5
2	6	4	7
3	8	0	0
4	5	10	2
5	3	6	0

The biplot of sites and environmental variables generated by CCA is shown in Figure 2.6. Of the environmental variables used, the time since dieback and the minutes east of 116° longitude explained most of the variation in sites. The eigenvalue of the first axis, which is strongly correlated with age since dieback, is significant ($P < 0.001$). The quadrats can be arranged into groups according to their dieback age with very little overlap. The dominance of ironstone in the upper soil profile also appears to be important in separating sites.

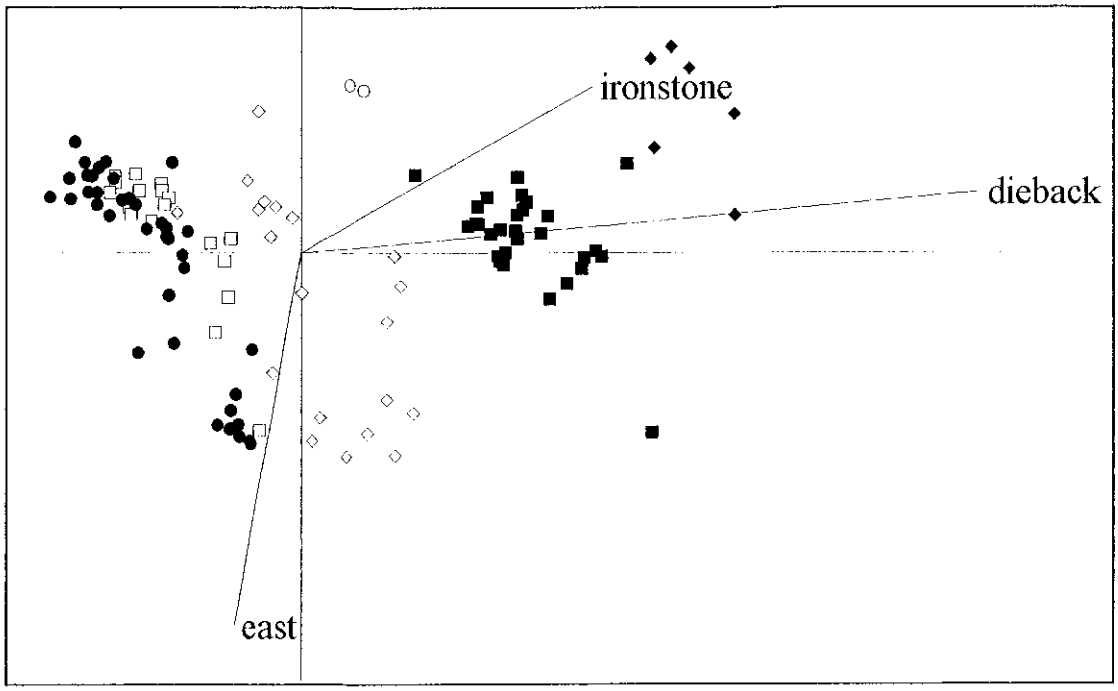


Figure 2.6 Biplot of sites and environmental variables from canonical correspondence analysis (CCA). The sites are classified by their dieback history and amount of ironstone as non-ironstone vegetation: ● unaffected; □ dieback post-1980; ◊ dieback 1968-80; ■ dieback pre-1951. Ironstone vegetation: ○ unaffected; ◆ dieback pre-1951. Differences in species composition are displayed according to the environmental variables of importance. The environmental variables are represented by solid lines: age of dieback (*dieback*); minutes east of 116°E (*east*); % ironstone in surface soil (*ironstone*). Their length and direction are an indication of their importance on the two axes. Only the three most significant variables are plotted.

When the range of species standard deviations are plotted for the first two axes of the detrended correspondence analysis (DCA) of unaffected quadrats, five of the 53 species with a significantly lower frequency in pre-1951 dieback (*Acacia urophylla, Clematis pubescens, Hybanthus floribundus, Olax benthamiana* and *Pteridium esculentum)* are found to be very restricted in their distribution (< 25% of the standard deviation represented by the first axis) (Figure 2.7). That is, they occur only in floristically similar quadrats. The probability of sampling dieback vegetation that once contained these species may be low. Three species (*Acacia urophylla, Clematis pubescens* and *Pteridium esculentum*) are characteristic of the T type vegetation of Havel (1975).

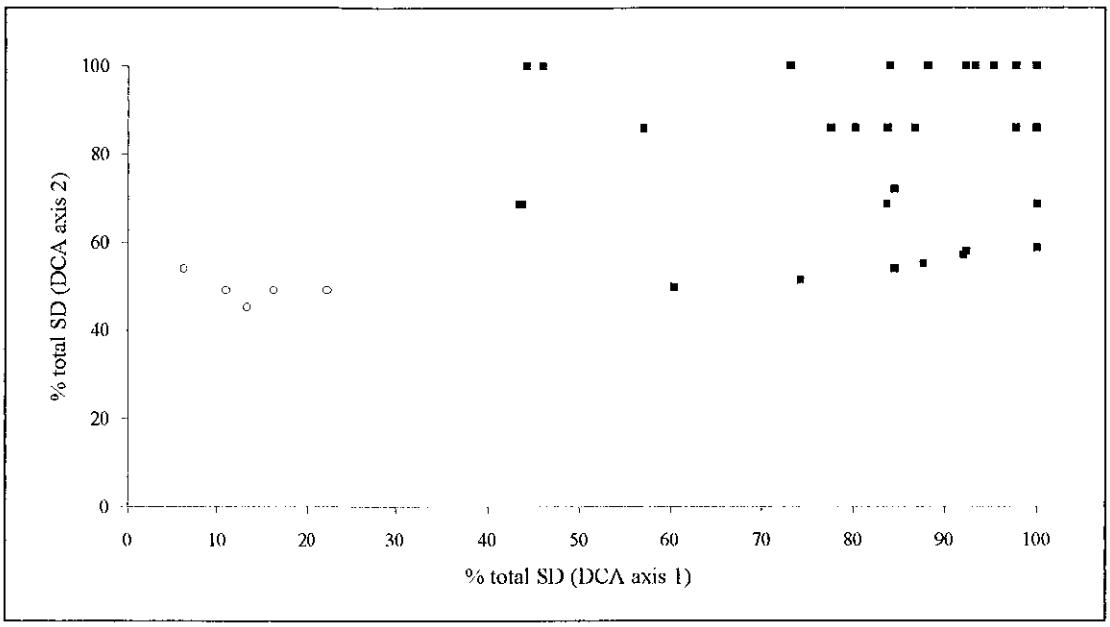


Figure 2.7 Percentage of total standard deviation (SD) explained on axis 1 and 2 by each species in the detrended correspondence analysis (DCA) of unaffected quadrats. Total standard deviation equals the largest standard deviation of any species on each axis. The five species referred to in the text are represented by an open circle.

2.5.3 Litter Biomass and Surface Soil Characteristics in Unaffected and Pre-1951 Dieback Vegetation

Litter biomass was 5.9 tonne ha^{-1} in unaffected vegetation, just over two years after the site was burnt compared with 2.2 tonne ha^{-1} in pre-1951 dieback vegetation (Table 2.11). Tree species (jarrah, marri and *Banksia grandis*) made up more than 80% of the litter biomass in unaffected vegetation. The true figure is probably somewhere over 90% because the other material category contained small leaf fragments and bark. *Banksia grandis* leaves, which were not present on the dieback site, accounted for 12% of litter in unaffected vegetation. Litter biomass in pre-1951 dieback vegetation was almost 40% of that in the unaffected vegetation. The major differences in composition were in *Banksia grandis* leaves, eucalypt leaves, jarrah fruit and other material, which was composed largely of leaf fragments, small twigs and bark.

The soil profile to a depth of 15 cm in an unaffected quadrat and a pre-1951 dieback quadrat are shown in Figure 2.8 and 2.9 respectively. A thick cover of litter protects the soil surface in the unaffected forest (Figure 2.8a). The soil surface and top 5 cm of soil is highly organic sandy loam. Gravel is not prominent on the soil surface (Figure 2.8b, 2.8c). At 15 cm depth, gravel is obvious in the soil matrix and the amount of organic material has clearly decreased (Figure 2.8d). Litter was sparse in the pre-1951 dieback site (Figure 2.9a). It is dispersed by wind, collecting around surviving plants. Gravel dominates the soil surface (Figure 2.9b). There is little organic material mixed with it. Small patches of organic loams can be found on pre-1951 dieback sites, especially in low lying spots and under plants of *Xanthorrhoea preissii*. This suggests that water and perhaps wind remove the fines from the gravel after dieback. The profile below the surface gravels on the pre-1951 dieback site appears similar to that of the unaffected site (Figure 2.9c, 2.9d).

Table 2.11 Litter characteristics of an unaffected and pre-1951 dieback site. Means and standard errors are given.

	Unaffected vegetation n = 4	Pre-1951 dieback vegetation n = 4
Composition		
Banksia leaves (g m^{-2})	69 ± 24	0 ± 0
Eucalyptus leaves (g m^{-2})	148 ± 18	64 ± 15
Marri fruit (g m^{-2})	31 ± 13	24 ± 22
Jarrah fruit (g m^{-2})	35 ± 9	3 ± 1
Twigs <2.5 mm (g m^{-2})	196 ± 41	101 ± 49
Other material (g m^{-2})	115 ± 28	31 ± 5
Other material includes:	*Acacia* fruit *Acacia urophylla* leaves *Bossiaea ornata* leaves *Dryandra lindleyana* leaves *Dryandra sessilis* leaves eucalypt bark eucalypt leaf fragments *Leucopogon nutans* leaves *Lomandra* sp. leaves *Persoonia longifolia* leaves *Platysace compressa* stems small twigs *Xanthorrhoea gracilis* leaves *X. preissii* leaves	*Dryandra lindleyana* leaves eucalypt bark eucalypt leaf fragments eucalypt seed *Hakea stenocarpa* leaves *Loxocarya flexuosa* stems *Patersonia pygmaea* leaves *P. rudis* leaves small twigs *Xanthorrhoea gracilis* leaves *X. preissii* leaves
Biomass		
Tonne / ha	5.9 ± 0.6	2.2 ± 0.6

(a)

(b)

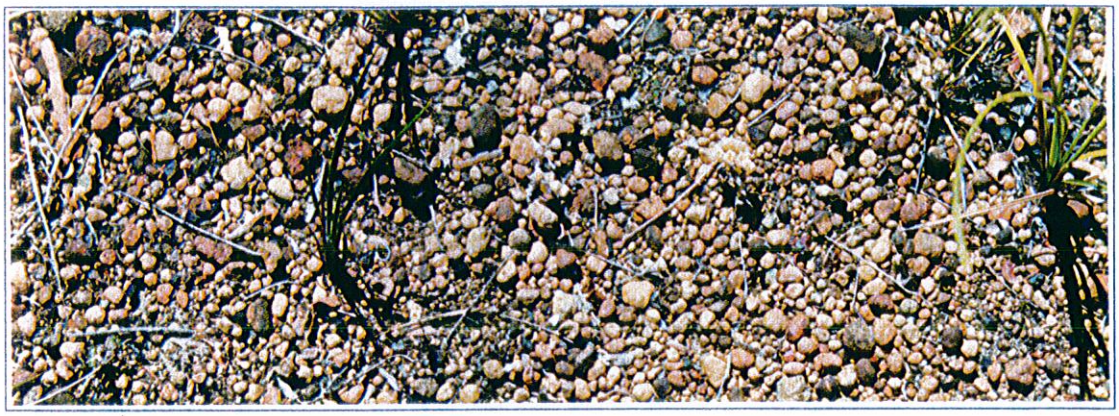
(c)

(d)

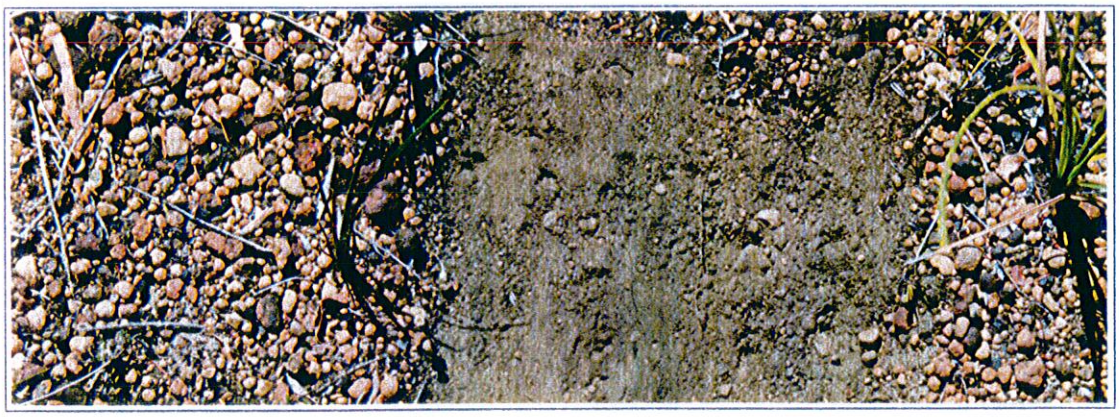
Figure 2.8 Litter layer (a), soil surface (b), 5 cm depth (c) and 15 cm depth (d) of an unaffected quadrat.

(a)

(b)



(c)



(d)

Figure 2.9 Litter layer (a), soil surface (b), 5 cm depth (c) and 15 cm depth (d) of a pre-1951 dieback quadrat.

2.6 Discussion

Dieback and unaffected vegetation of similar habitat are different. There are differences in species composition, life-form composition, structure, bare ground, litter cover and litter biomass. The differences increase with age of dieback, which is strongly correlated with the vegetation patterns identified.

Many of the findings from this survey of dieback sites are consistent with previous observations of the effects of dieback. Species richness, measured as number of species / quadrat, is lowest in the oldest dieback sites, although the total number of species recorded in pre-1951 dieback vegetation was greater than in unaffected vegetation. Bare ground cover is greater on dieback sites. Some highly susceptible species are absent or extremely uncommon on the oldest dieback sites. Marri, a field resistant species, is the dominant tree of many dieback sites, although, on average, its projective foliage cover on pre-1951 dieback sites is only 10%. This is partly because the crowns of the tallest marri are usually very sparse. Many appear to have been wind damaged, a possible consequence of the removal of adjoining trees of similar height. If the vegetation of the pre-1951 dieback sites sampled is indicative of change, marri has not obtained the structural position once held by jarrah. The number and cover of annual species was greater on dieback sites. *Scaevola calliptera*, a species not thought to be directly affected by *P. cinnamomi,* was found to be less common on dieback sites in this study and in *Banksia* woodlands on the Swan Coastal by Shearer and Dillon (1996a).

Some findings from the present survey are less consistent with previous observations. The proportion of pre-1951 dieback quadrats dominated by field-resistant species of Cyperaceae or Restionaceae (perennial herbs) was greater than in unaffected vegetation. However, the shrub, *Hibbertia hypericoides*, was the dominant or co-dominant in as many pre-1951 dieback sites as perennial herbs in these families. Perennial herbs were a commonly dominant feature only in wet dieback sites. Since no sampling was possible in unaffected wet vegetation, there is no way of even speculating on whether this is a

change from normal. The replacement of shrubs (woody perennials) with herbaceous perennials recorded in Victoria by Dawson et al (1985) and Weste (1981, 1986), and proposed for Western Australian vegetation by Wills (1993) and Wills and Keighery (1994) does not seem to be general in the jarrah forest.

P. cinnamomi has not been reported as being recovered from plant tissue of 64% of the species significantly less frequent on pre-1951 dieback sites. Many of these species are herbaceous perennials. Wills and Keighery (1994) suggest that almost all of the species highly susceptible to infection by *P. cinnamomi* are woody perennials. If the differences in frequency recorded in the present study for species not known to be susceptible to infection by *P. cinnamomi* represent real declines, the differences might be attributed to the effects of habitat change following dieback, as reported by Wills (1993) for the herbaceous perennial *Stylidium scandens*, or to insufficient testing for susceptibility to infection by *P. cinnamomi*. Studies of the effect of habitat changes and pathogenicity tests of species not known to be susceptible to infection are described in Chapter 4.

Assuming that every part of each dieback quadrat sampled in the boundary study had been affected by *P. cinnamomi*, susceptible species are not immediately eliminated by the pathogen. Such immediate survival was reported by Wills (1993) for dieback sites in the Stirling Range National Park. Dawson et al (1985) found that disease escapes were common in dieback sites in the Brisbane Ranges and that total elimination of species was rare. Even though all mature *Banksia grandis* plants had been killed in the present study, younger plants of *B. grandis* were present on eight out of the ten quadrats. This suggests either that further recruitment is possible in this species or that the pathogen is more likely to kill adult plants. Although the latter proposition has not been tested, the former proposition is certainly true. Seedlings were commonly observed on the dieback sides of boundaries, at times in great abundance. Since the age of young *Banksia grandis* can be determined with some certainty from annual growth marks on stems, it is clear that most *Banksia grandis* plants at the dieback boundary were less than 10 years old and had probably appeared since the initial dieback event. Based on what is known about *Banksia*

grandis ecology, a new cohort would be expected to appear once the canopy was opened following dieback. There is evidence to suggest that *Banksia grandis* is a gap species. Its seed is highly germinable (Abbott 1984a), has no special pre-treatment requirement (Bell et al 1993) and germinates better in the light than in the dark (Bell 1994). Abbott (1984b) found that *Banksia grandis* plants were more likely to grow near other *Banksia grandis* plants than next to jarrah. This is consistent with the suggestion of Bell (1994) that *Banksia grandis* has increased greatly in abundance since logging.

If the majority of species commonly killed by *P. cinnamomi* are not eliminated soon after dieback, the questions arise: (i) are they eliminated at all?; (ii) are the plants found on the oldest dieback sites survivors or recolonizers?; and (iii) are surviving populations resistant to being killed by *P. cinnamomi*? An attempt is made to address the first two of these questions in Chapter 3. The third question is addressed in Chapter 6.

Some species are more frequent in pre-1951 dieback vegetation than in unaffected vegetation. Many of these species are apparently absent in unaffected vegetation. This contrasts with species less frequent on dieback sites, almost all of which were present in at least one dieback quadrat. If the differences recorded in species frequency between pre-1951 dieback vegetation and unaffected vegetation are indicative of change, the species found more frequently on dieback sites may have (i) been rare in unaffected vegetation and increased in abundance in response to the more open conditions that appear to develop on dieback sites or (ii) invaded from elsewhere. If invasion has occurred, the small difference recorded in mean species richness between dieback and unaffected vegetation (59.8 ± 1.0 species / quadrat in unaffected vegetation and 54.4 ± 1.0 species / quadrat in pre-1951 dieback vegetation) may obscure a large decrease in species richness following dieback. An investigation into the possible origin of some species more frequent in dieback sites is presented in Chapter 5.

Differences in the amount of litter and bare ground between dieback sites and unaffected sites will cause differences in physical characteristics such as temperature and moisture

near the soil surface, which could potentially have a profound effect on species recruitment (see Chapter 4), and differences in biological characteristics such as microbial populations. The lack of ground plant cover and litter cover on dieback sites clearly results in the repositioning of resources. Litter is moved by the wind, collecting around the bases of surviving plants, and the top few mm of highly organic soil is eroded, leaving a gravelly surface and small patches of organic soil in dips in the landscape. Although overland water flow is supposed to be rare in the jarrah forest (Bettenay et al 1980, it clearly occurs, especially in dieback sites. The lateritic forest soils are mildly hydrophobic when dry (McArthur and Clifton 1975). It is possible that the abundant litter cover of unaffected sites lessens this effect, whilst on dieback sites, the first rains of autumn wash much of the upper organic layer away. The loss of organic soils in dieback sites could be extremely important because these hold some of the nutrients and much of the seed that could contribute to regeneration.

The importance of taxonomy in ecological studies is well illustrated in the *Hibbertia commutata* group. Marchant et al (1987) recognise the variability of the taxon, which was evident in the present study. Variants were commonly found with entire or slightly toothed leaves. The common forms have hairy stems. The young leaves are also hairy but with age the hairs become restricted to leaf edges and midribs. Hairs are of two lengths, short and very long, the long hairs being much less common than the short hairs. Although most plants of *H. commutata* found on the oldest dieback sites keyed out to this taxon based on floral characteristics, they appeared distinct in the field and were clearly so on closer examination. Most plants of old dieback sites have a silvery appearance. This is due to the abundant, uniformly long hairs on stems and both surfaces of young and old leaves. The leaves are shorter than typical plants in unaffected forest and have one or two teeth towards the leaf apex. This form was seen in unaffected and dieback forest in Churchman forest block but only in dieback forest elsewhere. It may prove to be a resistant form of *H. commutata,* which displays a phenotypic shift in the more open dieback sites, or a separate taxon. If it is a distinct taxon and it had been more

common than it was in dieback vegetation, *H. commutata* may have been falsely assessed as unaffected by dieback. Further taxonomic investigation is warranted.

Taxonomic research may also be of importance in assessing susceptibility and field response to infection by *P. cinnamomi.* Differences have been reported in the frequency of death and isolation of *P. cinnamomi* in apparently identical species on infested sites in separate geographic locations (Shearer and Dillon 1996b). For instance, *P. cinnamomi* was frequently isolated from dead plants of *Hibbertia hypericoides* by Shearer and Dillon (1996b) on the Swan Coastal Plain but was not isolated from dead plants of the species by Shearer and Dillon (1995) in the jarrah forest. Shrubs of this species were also found dead more frequently on active dieback sites of the Swan Coastal Plain than on active dieback sites in the jarrah forest. Shearer and Dillon (1996b) suggest that genetic differences in the plants examined or environmental influences on the infection process and disease expression may be important in the differences observed. In the case of *Hibbertia hypericoides*, different taxa may have been examined. Marchant et al (1987) note three variants of this species in the Perth area alone. Genetic differences in *P. cinnamomi* hosts are worth investigation for the possible development of *P. cinnamomi* resistant races.

CHAPTER 3. VEGETATION PATTERNS IN RELATION TO DIEBACK HISTORY AND THE CURRENT DISTRIBUTION OF *P. CINNAMOMI*

3.1 Introduction

For epidemic - recovery cycles to occur on dieback sites in the jarrah forest as hypothesized by Wills (1993), *P. cinnamomi* must persist on dieback sites despite the disappearance of most susceptible host plants. *P. cinnamomi* has become difficult to isolate from soils and dead plants on old dieback sites in Victoria concurrently with the re-colonization of highly susceptible species (Weste and Ashton 1994). Long-term monitoring of jarrah forest soils for the presence of *P. cinnamomi* has not been reported, although the pathogen is thought to survive in the roots of field-resistant hosts (Shearer and Tippett 1989). The persistence of *P. cinnamomi* is perhaps more likely in jarrah forest soils than in the soils of Victorian forests because of the potential sub-surface flow of water containing inoculum from active dieback fronts upslope from older dieback sites.

In this Chapter, I present the results of a study into the distribution of *P. cinnamomi* on seven dieback sites. I relate the frequency of *P. cinnamomi* detection to the distribution of species found to be less frequent, more frequent, and susceptible but equally frequent on dieback sites in Chapter 2. Evidence for re-colonization and survival of hosts after the initial impact is also presented.

3.2 Methods

3.2.1 Study Sites

The availability of sites suitable for long-term study was limited by the imminence of prescribed burning and quarantine restrictions on access to dieback sites during winter. After much field searching, Myara forest block, which was burnt in a prescribed fire in

October 1993 and not planned for further burning during field work, was chosen. Myara block was the second forest area of dying jarrah reported in Western Australia, in the late 1920s. It was last logged in the mid 1960s. Within Myara Block I examined aerial photos for sites with a progression of dieback in time and in a small space. Three ages of dieback-affected vegetation (pre-1951, 1968 - 1980, and post - 1980) and unaffected vegetation were sought for each site. As previously indicated, dieback during the period between 1951 and 1968 was difficult to interpret because of extensive salvage logging in the 1950s and a severe bushfire in 1961.

The 25 sites that appeared suitable on aerial photos were then inspected on the ground. Sites were rejected if they did not have all dieback ages (zones) or if the areas containing the dieback ages were too small to sample. Within the post - 1980 dieback zones, I looked for recent deaths of *Banksia grandis*, which indicated that *P. cinnamomi* may have been active in at least part of the zone. Several sites were found to have no active dieback front and many had a patchy unaffected zone. A few sites had excessive disturbance - one site had been planted with exotic eucalypts and several were riddled with tracks. Six sites had all dieback ages and were suitable for sampling. One further site was added that had a small unaffected zone and active dieback zone but had a large unaffected and active dieback zone nearby on the opposite side of the small valley.

The dieback time transects invariably ran from the valley bottoms (pre-1951) to the higher parts of slopes (unaffected). Within the very old zone (pre-1951 dieback), there was a flat section of creek edge. The soils of the creek edge were more loamy than on the slopes and had much less gravel in the profile. Most had no surface covering of gravel. Some valley soils were distinctly orange coloured below the grey surface, unlike the gravelly soils upslope, which were uniformly greyish brown below the light coloured gravel surface. The creek edges were treated separately making five zones on each transect. The separate treatment of the creek edges was determined partly after site inspections and partly from the initial aerial photograph study. Apart from the soil differences, the creek edges were structurally distinct from the adjoining slopes. The greater cover of trees on the creek

edges was also obvious on the aerial photographs. It would have been impossible to sample objectively from the pre-1951 dieback zone without either separating the creek edges from the slopes or ignoring the creek edges altogether. In their dieback interpretation, the creek edges were also different from the adjoining slopes. In the earliest aerial photographs it is difficult to see many apparently dead trees in the creeks. This may be because the background tones in the creeks are darker and there were fewer jarrah to have been affected. However, the differences between the creek edges and adjoining slopes warranted their separation in the study. Unaffected creek edge vegetation was not present at any of the sites and only a few small examples, floristically similar to the sites studied, have been seen by the author in the vicinity. This is not surprising because logging tracks, thought to have been one of the major vectors for *P. cinnamomi* spread, are positioned near most of the creek edges. *P. cinnamomi* activity is also supposed to be greater in such water gaining sites (Shearer and Tippett 1989).

The locations of the seven sites studied in Myara forest block are shown in Figure 3.1. The upper parts of all sites were on gravelly sandy loam. The dominant of the unaffected zone was jarrah and from an inspection of the stumps in the pre-1951 dieback zone, jarrah had once extended to the edge of the valley bottom. Under the system of Havel (1975), the vegetation of the unaffected portions of the sites would have been classified as Type S with elements of Type T at two sites. Four of the creek edges would have been classified as Type C. Some characteristics of the sites are listed in Table 3.1.

Table 3.1. Differentiating characteristics of the seven study sites. [1] Approximate distance from creek edge vegetation to unaffected vegetation

Site	Slope (°)	Aspect (°)	Creek edge dominants	Creek edge soils	Transect length (m) [1]
1	2 - 10	70	Bullich	Loam	200
4	1 - 5	210	Bullich / Blackbutt	Loam	350
5	2 - 10	40	Bullich	Loam	200
9	1 - 3	350	Jarrah / Blackbutt	Loam	200
10	2 - 6.5	45, 180	Marri	Sandy loam	250
11	3 - 7.5	100	Jarrah	Loam	250
23	1 - 7	340	Bullich / Blackbutt	Loam	300

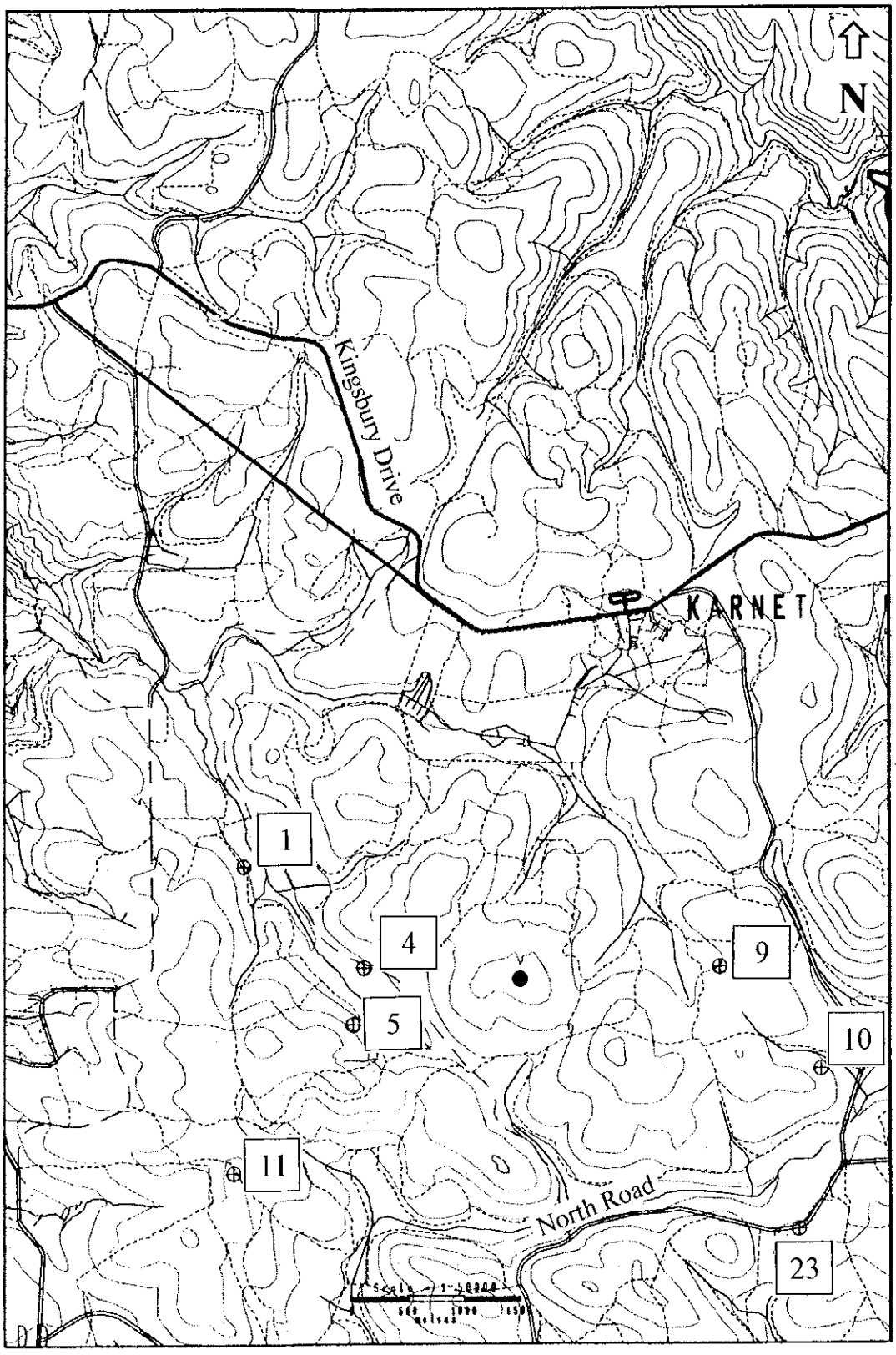


Figure 3.1 Location of the seven sites described in this Chapter. The numbers indicate the position of sites and are the same as those used in the text. ● indicates the position of the granite outcrop referred to in Chapter 5. Contour interval is 20 m.

Five quadrats (20 x 20 m) were established along transects across slope in four of the zones at each site: pre-1951 dieback vegetation on creek edges, pre-1951 dieback vegetation on slopes, 1968-80 dieback vegetation on slopes and unaffected vegetation on slopes. The post-1980 zone at each site, which was much smaller than other zones, could only accommodate one quadrat. This was positioned where recent deaths of *Banksia grandis* had occurred so at least some of the quadrat was in post-1990 dieback.

The zones were given a letter (Figure 3.2) and the quadrats numbered. At the first site sampled, two additional transects were placed in the pre-1951 dieback slope zone with the intention of mapping the trees growing on the site. This time consuming work was abandoned on future sites. However, the labelling system for the transects and quadrats was maintained. For ease of reference to data sheets, it is repeated here. Examples of zones F, G, C and A are shown in Figure 3.3.

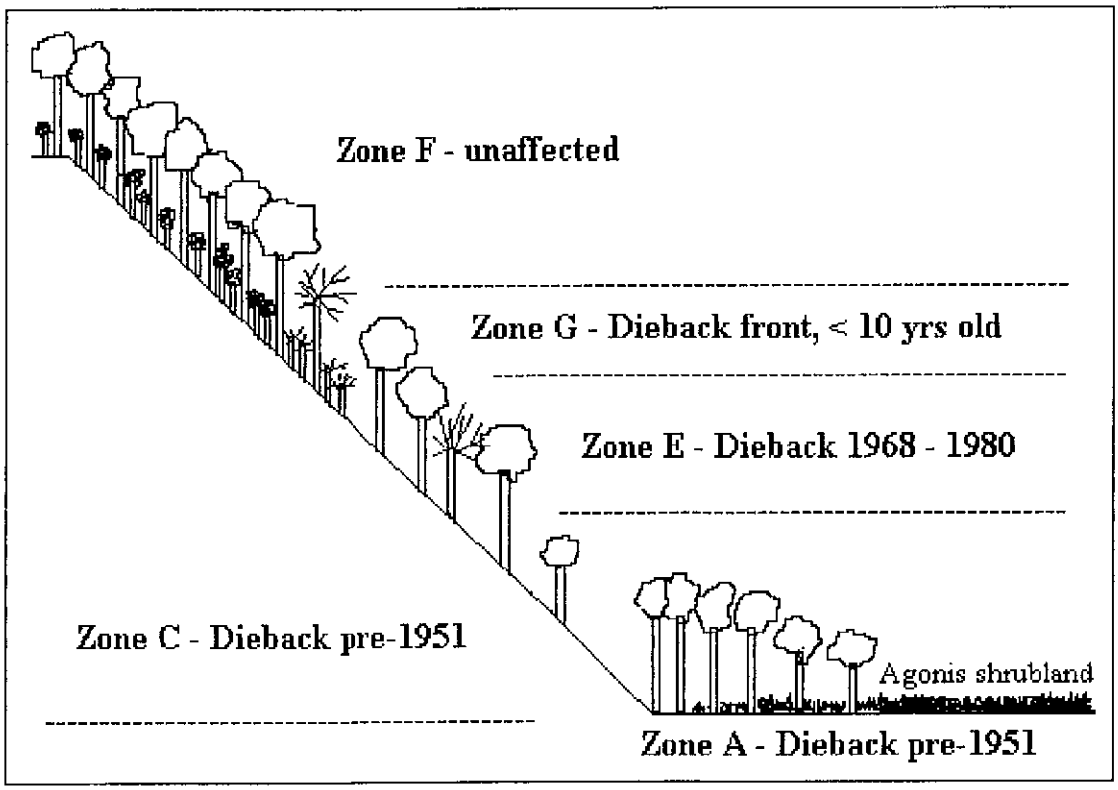


Figure 3.2 Schematic illustration of zones described in text. The vertical scale has been exaggerated.

Figure 3.3a Unaffected vegetation (zone F) showing the thick middle storey of *Banksia grandis*. Site 23.

Figure 3.3b Active dieback front (zone G), Nanga Rd, south of Dwellingup, showing dead *Banksia grandis* and a tall dead *Xanthorrhoea preissii*.

Figure 3.3c Zone C vegetation looking towards zone E in background, site 11. Note abundant *Xanthorrhoea preissii*, bare ground and patchiness of litter.

Figure 3.3d Zone A vegetation, site 1. The gum barked eucalypts are bullich (*Eucalyptus megacarpa*). The palm-like plants in the foreground are *Macrozamia riedlei*.

3.2.2 The Distribution of *P. cinnamomi*

The distribution of *P. cinnamomi* at the seven sites was investigated by two methods: *in situ Banksia grandis* baiting and soil baiting.

In situ Banksia grandis *baiting*

Thirty 12 week old *Banksia grandis* seedlings were planted into each of the dieback zones of the seven sites on the 19th and 22nd of June 1995 (Figure 3.4). The seedlings were placed in small holes, three paces apart. The holes were dug using a mattock. The bottom of the jiffy pot was removed at the time of planting to facilitate root extension. Soil was packed around the plants. A small handful of slow release fertiliser (four month Osmocote™) was added to the area around each seedling to accelerate root growth. The mattock was drenched in 70% alcohol after each zone was planted to minimize the risk of moving the pathogen between zones and sites. The mattock was not sterilized between each hole within a zone because of the excessive time it would have taken. The overall risk of spread appeared to be low at the time of planting because of the unseasonally dry soils. Soil did not remain on the mattock after each hole was dug. Although the possibility of soil contamination within zones cannot be ruled out, it was felt that the probability of contamination was related to the abundance of *P. cinnamomi* in the zone. Therefore, zones with abundant *P. cinnamomi* might be over-estimated but zones where *P. cinnamomi* was rare were unlikely to be affected. When averaged over seven sites, the lack of hygiene within zones seemed reasonable.

Seedlings were not placed in zone F (unaffected vegetation). This zone was the control for the study. If *P. cinnamomi* had been detected it could have meant either that the pathogen had recently invaded but had not yet produced symptoms or that *P. cinnamomi* occurred naturally in symptom-less vegetation. Since it would not have been possible to determine which was true, there seemed little point baiting in zone F. The latter proposition is unlikely because *P. cinnamomi* has not been isolated from soils in

unaffected vegetation despite extensive surveys for it (e.g. Podger 1968). Not baiting in zone F also reduced the possibility of importing contaminated soil to the unaffected vegetation. For the purposes of the study the amount of *P. cinnamomi* in zone F was defined as zero.

The *Banksia grandis* seedlings had been grown from seed in jiffy pots at the Alcoa of Australia Ltd nursery at Marrinup, which practices stringent hygiene to prevent infection of its stock by *P. cinnamomi*. It is extremely unlikely that the pots already contained *P. cinnamomi* at the time of planting. There were no dead individuals amongst the 900 seedlings, from which the planted seedlings were chosen. Almost two trays of seedlings were left over and used in other experiments. None of the almost 60 seedlings in these two trays died during the next two months in a temperature-controlled glasshouse.

Figure 3.4 A *Banksia grandis* seedling planted in zone E of site 23. The photo was taken in summer about eight months after planting.

Over 40 mm of rain fell between the 23rd and 25th of June, soon after the planting, and the rainfall for July was above average.

Plants were inspected regularly. Dead individuals were harvested on seven occasions during the following year: October 6, November 15, December 5, February 13 (&19), April 1, May 13, and June 17.

Dead plants were dug up with a trowel and placed in plastic bags. As much of the soil and jiffy pot as possible was removed from around the roots in the field. The trowel was sprayed with 70% alcohol after each plant was dug up. A different trowel was used for each zone to further minimize the risk of cross-infection. The following day, the dead plants were washed to remove excess soil. Roots and collars were surface sterilised in 100% alcohol for about 20 seconds and then rinsed in de-ionized water. The principal plant axis (main root to main stem) was cut into horizontal then vertical sections and plated onto *Phytophthora*-selective agar and incubated in the dark at 23°C. Agar plates were inspected daily for *P. cinnamomi* during the following week.

The selective medium used for isolations of *P. cinnamomi* described in this thesis contained cornmeal agar (17 g l^{-1} of de-ionized water autoclaved at 121°C for 20 minutes), ampicillin (0.1 g l^{-1}), pentachloronitrobenzene (0.1 g l^{-1}), rifampicin (0.5 ml l^{-1}), hymexazol (0.05 g l^{-1}), and nystatin (1 ml l^{-1}). This medium is routinely used by the Department of Conservation and Land Management in Western Australia for the detection of *P. cinnamomi*. In its composition, it is similar to the medium developed by Masago et al (1977) for the selective isolation of *Phytophthora* species from *Pythium* species, except that cornmeal agar is used instead of potato-dextrose agar, as suggested by Erwin and Ribeiro (1996), and benomyl is not included.

Soil Baiting

Twenty soil samples were collected near the planted *Banksia grandis* seedlings from each of zones A, C, E and G at five sites in late September 1995, giving a total of 400 soil samples. Four identical trowels were used to collect soils. The trowel was pushed into the soil and twisted to mix it. The point of the trowel reached to about 10 cm below the soil surface. Each soil sample was removed, placed in a sealable plastic bag and labelled. The trowel was then sprayed thoroughly with 70% alcohol. Another trowel was used for the following sample to allow the alcohol to dry on the first.

The following day, 200 g of soil from each sample in zone C, E and G was weighed and placed into numbered 750 ml open plastic containers (11 x 15.5 x 4.5 cm). Tsao (1983) reported that a water:soil ratio of at least 4:1 (v/v) was required for maximal *Phytophthora* detection, especially if inoculum levels were low. The exact ratio for the soils I collected was difficult to determine in these zones because of their high but variable gravel content. As part of the volume, the gravels would contribute little or none of the inoculum in the sample. Sieving the soils prior to baiting would have necessitated lengthy sterilization procedures for the sieve and increased the risk of cross-contamination of samples. The average gravel content of the soils in zones C, E and G of the sites sampled was 70% (determined gravimetrically in the Broad Quadrat Survey of Chapter 2). This would have meant that, on average, 60 g of soil was baited from each sample on sloping gravelly sites (zone C, E and G). To each container, 300 ml of de-ionized water was added, giving a water:soil ratio of 5:1. Whilst the soils from zones C, E and G were similar in texture and gravel content and should have been similar in the extractability of *P. cinnamomi*, it was difficult to determine a comparable amount of soil for samples from zone A. The soils were clearly different. They had much less gravel than adjoining sloping sites and much more organic material, much more loam and much less sand. I placed 150 g of soil and 400 ml of de-ionized water into each container for zone A samples. A subsequent baiting test was conducted to check if the differences in soil properties had grossly affected the results (see below).

About 15 *Eucalyptus sieberi* cotyledons and 15 *Pimelea ferruginea* leaves were floated upside down on the water of each plastic baiting tray. These baits have been used previously for detection of *P. cinnamomi* by Marks and Kassaby (1974) and Greenhalgh (1978) (*Eucalyptus sieberi*), and Hardy (Murdoch University, pers. comm.) (*Pimelea ferruginea*). The trays were incubated at 22°C in darkness at night and with little light during the day, and checked daily. Evaporation occurred from the trays so additional water was added from time to time. Additional cotyledons and leaves were added if the existing ones sank when the water was poured in. They were very difficult to find in the organic valley soils, once they had sunk. After 5 days, apparently infected cotyledons and leaves were plated onto *Phytophthora*-selective agar and incubated at 23°C in darkness. Plates were checked for *P. cinnamomi* under a compound light microscope daily for the next seven days. Soils in the trays were stirred at day seven. This is believed to increase the chance of detection (Carla Wilkinson, Murdoch University, pers. comm.). Apparently infected leaves and cotyledons were plated out again at day nine and incubated at 23°C in darkness. Plates were checked daily. Mycelial growths on the agar that resembled *P. cinnamomi* but could not be positively identified were sub-cultured.

To check if the differences in soil between zone A and other zones had affected the extractability of *P. cinnamomi*, an additional baiting was attempted using the same soils. Twenty days from the start of the baiting, when the soils had more or less dried out, they were emptied into 20 cm free-draining pots and placed into an air-conditioned glasshouse with an automatic watering system. Air temperature was measured hourly with four probes of a data logger for another experiment in the same glasshouse during much of the trial. 99% of hourly temperature readings were between 14.8°C and 35.8°C. The glasshouse was covered with 70% shade cloth in summer and autumn to reduce the diurnal fluctuation in temperature. Each pot was placed on a plastic stand, which was not in contact with other pot stands so that contamination would not occur from water draining from pots. The soil level was at least 5 cm below the top of each pot to prevent splash of soil during watering. Watering was done from above with a fine 360° spray nozzle, also to minimize splash contamination. A 12 week old *Banksia grandis* seedling

was planted into each pot the following day. The plants were inspected regularly. *Banksia grandis* seedlings were removed when dead and plated out onto *Phytophthora*-selective agar. The trial was stopped after 207 days.

3.2.3 The Persistence of *P. cinnamomi* in Dead Plants over Summer

In March 1996, plants that had died recently but still had some leaves attached were harvested from zones C and E. As much root material as possible was collected and plated onto *Phytophthora*-selective agar, and incubated at 23°C.

To test whether *P. cinnamomi* was present but dormant in the dead plants that tested negative, all plant material that had been plated out was removed from plates after the week of incubation and put into plastic trays (11 x 15.5 x 4.5 cm) with a 2 cm covering of de-ionized water. The material from plants that tested positive was included as a test of the method. Plant material of species with more than one sample from the same site was combined and put in a single tray. The plant pieces were then tested for *P. cinnamomi* presence using *Pimelea ferruginea* leaves as bait. Apparently infected leaves were plated out onto *Phytophthora*-selective agar and the plates monitored over the following week. The trays were allowed to dry out. The baiting trial with *Pimelea ferruginea* leaves was then repeated. Agar plates were inspected for the presence of *P. cinnamomi* daily for one week.

In October 1995, one *Banksia grandis* shrub on site 1E died. The base of the stem was sampled at the time of death and plated onto *Phytophthora*-selective agar. *P. cinnamomi* was not detected. Using the method of age determination in proteaceous shrubs described by Lamont (1985), the shrub was found to be seven years old. In March 1996, the plant was excavated to a depth of about 0.5 m. The primary root and one secondary root were found to be lesioned (blackened throughout) about 10 cm below the soil surface. The lesioned portion was about 75 mm long. A small part of the lesion and the tissue on either side were plated onto *Phytophthora*-selective agar and the remainder cut

into small pieces and placed in a 20 cm pot about 50 mm below the top of the pot. A *Banksia grandis* seedling was placed in the pot with its roots touching the cut pieces. The pot was filled with potting mix and placed in a heated glasshouse with an automatic watering system. After three months, four more *Banksia grandis* seedlings were added to the pot because the pathogenicity experiment described in Chapter 4 had shown that a small proportion of *Banksia grandis* seedlings could survive for long periods in the presence of *P. cinnamomi*.

3.2.4 *P. cinnamomi* Hosts on Pre-1951 Dieback Sites

All plants and as much of their root system as possible, which were growing within 0.5 m of three *in situ Banksia grandis*, from which *P. cinnamomi* had been recovered, were removed with a trowel 20 days after the recovery to identify possible hosts of *P. cinnamomi* on pre-1951 dieback sites. The following species were sampled:

Site 1 *Dampiera linearis, Dryandra lindleyana, Gompholobium knightianum, Hibbertia hypericoides, Lechenaultia biloba, Lepidosperma angustatum, Patersonia pygmaea, Petrophile striata,* and *Sphaerolobium medium.*

Site 9 *Hibbertia rhadinopoda, Isotoma hypocrateriformis, Leucopogon nutans,* and a *Lomandra* species.

Site 10 *Conostylis setosa, Hibbertia rhadinopoda, Hypocalymma angustifolium, Hypolaena exsulca, Lomandra sonderi* (dead), and *Tetraria capillaris.*

Plant material was plated onto *Phytophthora*-selective agar and incubated in the dark at 23°C. The plates were inspected over the following week for the presence of *P. cinnamomi*.

3.2.5 Flora and Structure in Relation to *P. cinnamomi* Distribution

On the seven sites studied, the following floristic and structural data were collected in each zone for comparison with the findings for the distribution of *P. cinnamomi*. Data were collected in five quadrats / zone for zones A, C, E and F, and one quadrat / zone for zone G. There was insufficient area in zone G at most sites for more than one quadrat.

- the presence or absence of species less frequent on pre-1951 dieback sites than in unaffected vegetation (see Table 2.7, page 52), species more frequent on pre-1951 dieback sites than in unaffected vegetation (Table 2.6, page 50) and species from which *P. cinnamomi* has been recovered from dead individuals (Shearer and Dillon 1995) yet were found equally frequently in pre-1951 dieback and unaffected vegetation (species marked with a D in Table 2.8, page 54);
- the diameter over bark at breast height (DOB) of every tree;
- plant deaths;
- an estimate of litter cover, tree cover and bare ground;
- the densities of species from three Shearer and Dillon (1995) dieback groups: four highly susceptible species (Group 5) (*Adenanthos barbiger, Leucopogon nutans, Xanthorrhoea gracilis, Xanthorrhoea preissii*), two species of intermediate susceptibility (Group 4) (jarrah, *Macrozamia riedlei*), and one field resistant species (Group 1) (marri);
- the cover of jarrah and marri - done by estimating and summing the dimensions of individual trees, allowing for overlapping cover.
- the stem height of all *Xanthorrhoea preissii*;
- the basal diameter of *Macrozamia riedlei* (at sites 1, 5, 23, and part of 4);
- the number of species in each quadrat (except in zone A).

3.3 Data Analysis

3.3.1 Plant Density and *P. cinnamomi* Distribution

The relationship between the recovery of *P. cinnamomi* and the density of species measured was investigated by stepwise multiple regression. Two additional variables were analysed to help explain variation in density: time in years since the dieback event in each zone (zone F was given the value zero); the % gravel content of the surface soil (determined gravimetrically, as described in Chapter 2). The latter variable was added because of the clear differences in density for some species between zone A and C. Since the gravel content of zone A soils was much lower than for soils in other zones, this variable effectively separates zone A from the other zones.

Correlations were determined between each variable and density. Where one of these was significant, as determined by a t-test of the null hypothesis that the correlation is zero, partial regression coefficients were calculated for two and three variables. The significance of adding one or two variables in the proportion of variance explained was determined using an F-test.

Multiple regression of estimates of % recruitment since the time of the first dieback on the sites (i.e. since about 1951) for marri (DOB < 20 cm), jarrah (DOB < 20 cm) and *Xanthorrhoea preissii* (stem height < 50 cm) was also performed on the three variables.

In cases where the variables could not explain a significant amount of the variation, stepwise multiple regression was attempted omitting zone G. Data for this zone may have confounded the analysis. The rate of change in density and recruitment in zone G is likely to be much greater than in other zones. The absolute values of density and recruitment will therefore be more sensitive to time. That is, a difference of one or two years in the time since dieback in this zone could amount to large differences in density and recruitment. This is unlikely to be the case in other zones.

Prediction equations were determined for each dependant variable as described in Sokal and Rohlf (1981).

The applicability of tests of significance of differences between sample means of species numbers, cover and plant numbers (density) was determined by an F-test of sample variances. Density data were square root transformed and cover data were arcsine transformed for this analysis. Variances of species numbers were homoscedastic. A t-test for paired comparisons was used for comparison of these means. Variances of density and cover data were often heteroscedastic, despite the transformations. A non-parametric test of significance was used with these data (Wilcoxon's signed-ranks test for two groups, arranged as paired observations (Sokal and Rohlf 1981). Since this test requires at least six sample pairs for detection of significant differences in a two-tailed test, its use in the analysis of data from the seven sites sampled is unlikely to be powerful. That is, a difference will only be significant if all values from one zone are greater or lesser than values from another zone or, if there is a single aberrant pair, the difference in its values must be less than that of at least five other pairs. The minimum significance level possible with this test and number of samples is 1.56%. Therefore, for all differences found to be significant, the probability of a Type I error will be $P < 0.05$.

3.4 Results

3.4.1 The Distribution of *P. cinnamomi*

In situ Banksia grandis *baiting*

Rainfall for the period of baiting was above average by 20 mm or more only in July and October 1995 (Figure 3.5). There was below average rainfall from January until the end of the trial.

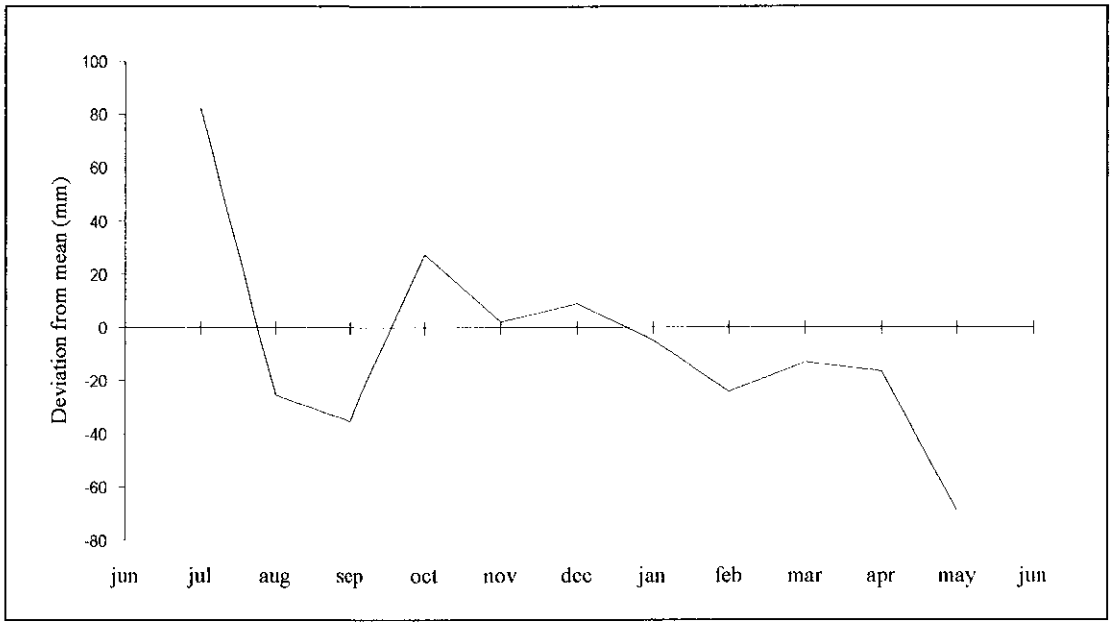


Figure 3.5 Deviation (mm) from average monthly rainfall for Dwellingup between July 1995 and May 1996

P. cinnamomi was most frequently isolated from *Banksia grandis* planted in zone A (pre-1951 dieback at creek edges) and zone G (dieback fronts) (Table 3.2). Although it was rarely isolated from older dieback sites on slopes, three of the seven pre-1951 dieback sites and four of the seven 1968 - 1980 dieback sites on slopes contained the pathogen.

Table 3.2. % of positive *P. cinnamomi* recoveries from *in situ Banksia grandis* baiting. Thirty plants were placed in each zone at each site.

	Site							
Zone	1	4	5	9	10	11	23	% of total planted
A	10	27	0	47	17	17	33	21
C	3	0	0	3	7	0	0	2
E	0	0	0	7	7	3	3	3
G	30	13	53	53	53	23	23	36

Most of the plants from which *P. cinnamomi* was isolated were harvested between early October and early December. The rate of isolations was greatest between the first and second harvests in October / November (Figure 3.6). At the harvest of 15 November, 93% of the 96 dead *Banksia grandis* seedlings tested positive. All of these had clearly visible lesions of the upper root, collar and lower stem. The rate of *P. cinnamomi* positive deaths

declined rapidly after the December harvest. There was one *P. cinnamomi* positive death in the February harvest, which occurred in zone A. There were two *P. cinnamomi* positive deaths in the harvest in the April harvest, both in zone G and one *P. cinnamomi* positive death in zone G in the May harvest. The numbers of *Banksia grandis* testing positive and negative varied greatly from site to site (Figure 3.7).

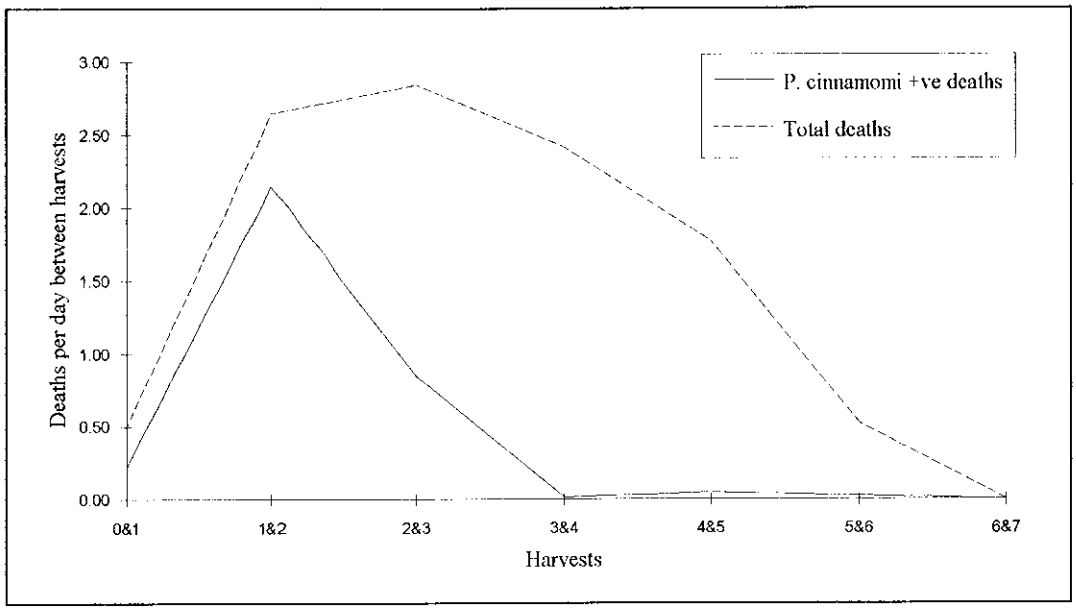


Figure 3.6 Rate of *P. cinnamomi* positive and total deaths of in situ *Banksia grandis* baits. Harvests: 1 = 6 Oct 1995; 2 = Nov 15 1995; 3 = Dec 5 1995; 4 = Feb 13 (&19) 1996; 5 = Apr 1 1996; 6 = May 13 1996; 7 = Jun 17 1996.

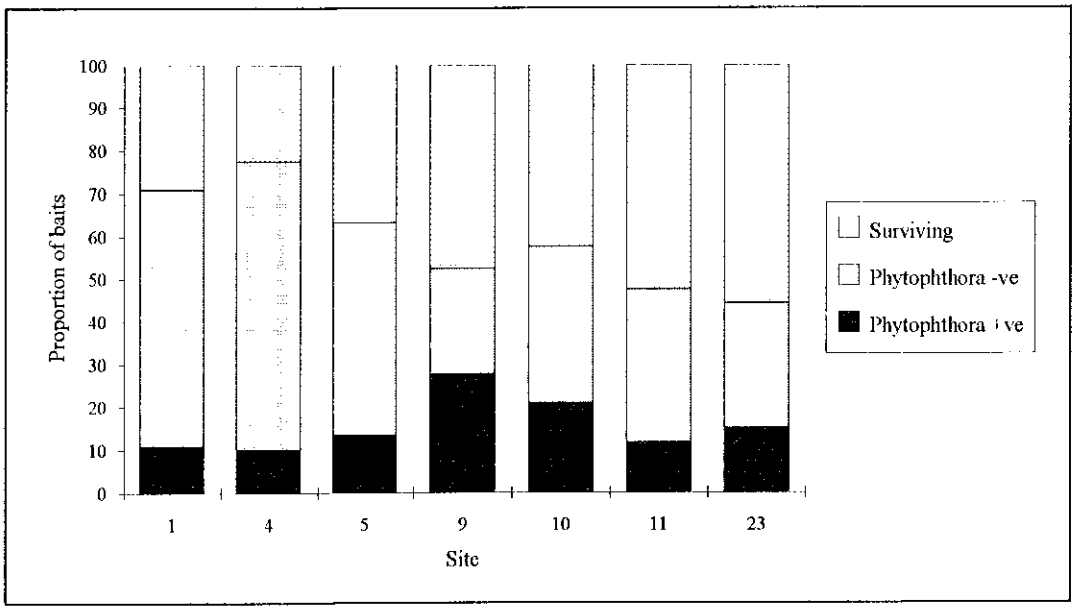


Figure 3.7 Proportions of *Banksia grandis* baits surviving and dying (and testing negative or positive for *P. cinnamomi*) at the seven sites.

The number of deaths of in situ *Banksia grandis* remained relatively high between October and April. This included periods when there were few positive recoveries of *P. cinnamomi*. The majority of deaths without a positive *P. cinnamomi* isolation did not occur at the same time as the majority of deaths with a positive *P. cinnamomi* isolation (Figure 3.8).

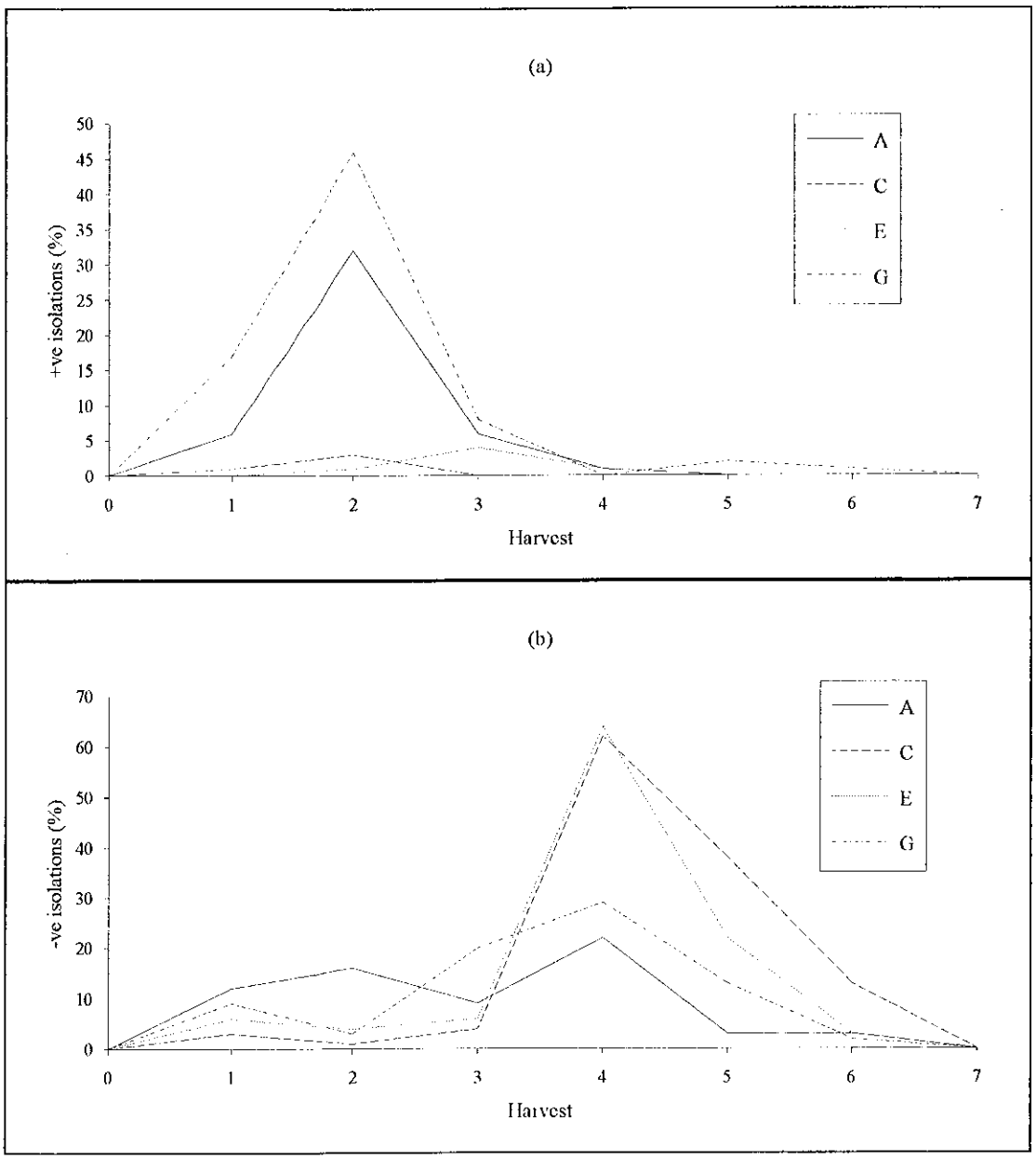


Figure 3.8 % of positive (a) and negative (b) isolations from dead *Banksia grandis* baits at each harvest. Harvests: 1 = 6 Oct 1995; 2 = Nov 15 1995; 3 = Dec 5 1995; 4 = Feb 13 (&19) 1996; 5 = Apr 1 1996; 6 = May 13 1996; 7 = Jun 17 1996.

Most deaths where *P. cinnamomi* could not be recovered were recorded at the February and April harvests (Figure 3.8). There were more deaths at these times in zones C and E than in zones A and G, although this may have been partly because there were fewer survivors in zones A and G. Deaths also tended to be site-specific at these harvests. For instance, there were 49 dead plants collected from zone C and E at site 1 in February but only two dead plants from the same zones at site 10. There were no deaths between the May and June harvests. Most of the dead plants after the December harvest were not lesioned. However, it was clear for the February harvest that some dead *Banksia grandis* were lesioned yet did not yield *P. cinnamomi*. At the April harvest, lesions were recorded and compared with the fungi that grew on the *Phytophthora*-selective agar on which they were placed. *Fusarium* spp. commonly grew on plates with lesioned material. In a Fischer's exact test of independence, the null hypothesis that the presence of *Fusarium* spp. and lesions on dead *Banksia grandis* were independent was rejected (P = 0.01).

Fusarium spp. are ubiquitous in the soil and species within the genus are extremely difficult to differentiate (Domsch et al 1993). This makes an association between *Banksia grandis* death and a particular *Fusarium* sp. difficult to demonstrate. As a preliminary test of such an association, pieces of agar from a plate from one site (1C) were removed and placed in four pots containing 18 month old *Banksia grandis* plants to see if deaths would occur with similar symptoms to those observed in the field. The *Fusarium* growth on the plate used appeared to be pure. The pots and four plants in similar pots not infected with the *Fusarium* were placed in an air-conditioned glasshouse with an automatic watering system on the 9th of April. For the first month, plants were watered three times daily for five minutes. This was reduced to twice daily for four minutes as the temperature in the glasshouse dropped towards winter. One plant from an infected pot died suddenly after 55 days. The stem was slightly lesioned but not as obviously as the plants that had been collected from the field in April. A *Fusarium* sp. was recovered from the stem using *Phytophthora*-selective agar. The other *Banksia grandis* plants survived for another six months when the trial was stopped.

Some of the dead *in situ Banksia grandis* that tested negative for *P. cinnamomi* showed signs of insect damage. These could be lesioned or non-lesioned. Insect damage, presumably termites, was especially prominent in zone A at some sites.

Soil baiting

P. cinnamomi was recovered from 11 of the 400 soil samples (Table 3.3). Most recoveries were from the creek edge in pre-1951 dieback zones (zone A) and active dieback fronts (zone G). However, even in these zones soils from only two of the five sites tested positive. There were no recoveries from pre-1951 dieback zones (zone C) on slopes.

Table 3.3. % of positive *P. cinnamomi* recoveries from soil baiting. Twenty samples were taken from each zone at each site. The % recovery of *P. cinnamomi* using *in situ Banksia grandis* baits is included for the same sites in parentheses (from Table 3.2) to aid in comparison.

	Site					
Zone	1	4	5	11	23	% of total samples in zone
A	0 (10)	15 (27)	0 (0)	0 (17)	10 (33)	5 (17)
C	0 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (1)
E	0 (0)	0 (0)	0 (0)	5 (3)	0 (3)	1 (1)
G	0 (30)	5 (13)	20 (53)	0 (23)	0 (23)	5 (28)

Soil baiting failed to detect *P. cinnamomi* in seven of the zones / sites where it was detected using *in situ Banksia grandis* baits (Table 3.3). None of the zones / sites that tested *P. cinnamomi* positive with soil baiting were not also detected using *in situ Banksia grandis* baits.

Eucalyptus sieberi cotyledons and *Pimelea ferruginea* leaves were plated out from 78 % of the soil samples. No detections of *P. cinnamomi* were made on *Phytophthora*-selective agar plates after three days. Six detections were made from the platings on day 5 of the incubation and five detections from the day 9 platings. Only one detection was made solely from *Pimelea ferruginea* leaves. This does not necessarily mean that

Pimelea ferruginea leaves were ineffective baits. The *Eucalyptus sieberi* cotyledons changed colour quicker and more definitely and tended to be plated first, although they also sank more readily when additional water was added.

The subsequent baiting of the soils with live *Banksia grandis* seedlings, which was done as a check on the different soil : water ratio used for zone A soils, was consistent with the results obtained using *Eucalyptus sieberi* cotyledons and *Pimelea ferruginea* leaves. All of the *Banksia grandis* seedlings planted into pots containing soils that had tested positive for *P. cinnamomi* died: 23A and 5G after 43 days, 4A after 48 days, 11E after 57 days, and 4G after 75 days. All of these *Banksia grandis* seedlings tested positive for *P. cinnamomi* when plated onto *Phytophthora*-selective agar. None of the *Banksia grandis* seedlings grown in soils that had tested negative for *P. cinnamomi* died during the 207 days of the trial.

3.4.2 The Persistence of *P. cinnamomi* in Dead Plants over Summer

P. cinnamomi was isolated from recently dead *Xanthorrhoea preissii* and *Leucopogon nutans* in late summer but not from a range of other species (Table 3.4). Of the two *Xanthorrhoea preissii* plants sampled, the plant from which *P. cinnamomi* was recovered was only beginning to show signs of leaf chlorosis. The other plant had died in early spring and its leaf crown had recently been shed. The *Leucopogon nutans* shrub from which *P. cinnamomi* was recovered was not obviously different from other *Leucopogon nutans* collected. All were mature plants with large stems. The time of death is not known for any of these plants but was probably some months before they were excavated. The majority of leaves had already fallen by that time. None had obvious lesions. *P. cinnamomi* was not recovered from the roots of the seven year old *Banksia grandis* plant excavated. The baiting using live *Banksia grandis* seedlings was stopped after six months when none of the five seedlings had died.

Table 3.4. Isolation of *P. cinnamomi* from recently dead plants collected in summer. + indicates a positive recovery of *P. cinnamomi*.

Species	Site	Obvious lesion	Selective agar	Pimelea baiting 1	Pimelea baiting 2	Banksia baiting
Banksia grandis	1E	YES	-	-	-	-
Dryandra sessilis (four plants)	1C	NO	-	-	-	
Jarrah (seedling)	4C	NO	-	-	-	
Hibbertia rhadinopoda (five plants)	10C	NO	-	-	-	
Hibbertia *rhadinopoda* (three plants)	23C	NO	-	-	-	
Leucopogon nutans (two plants)	4E	NO	-	-	-	
Leucopogon nutans	10C	NO	+	-	-	
Leucopogon nutans (five plants)	10C	NO	-	-	-	
Xanthorrhoea preissii	4E	YES	+	+	+	
Xanthorrhoea preissii	5C	YES	-	-	-	

Of the two plants found to contain *P. cinnamomi* in this trial, only the roots of the *Xanthorrhoea preissii* plant repeatedly yielded *P. cinnamomi* with additional baiting procedures.

3.4.3 *P. cinnamomi* Hosts on Pre-1951 Dieback Sites

Roots and stems of all plants sampled adjacent to a dead in situ *Banksia grandis* seedling from which *P. cinnamomi* was recovered tested negative for *P. cinnamomi*. The *in situ Banksia grandis* hole at site 9 was in the middle of a large bare patch. There were very few plants growing within 1 m of the hole. Most of the plants were annuals.

Banksia grandis plants that were less than 3 m from *Banksia grandis* plants that had tested positive for *P. cinnamomi* remained healthy and apparently unaffected throughout the trial at sites 9C, 9E, 10C and 23E.

3.4.4 Flora and Structure in Relation to *P. cinnamomi* Distribution

Species Richness

There was no significant difference in species richness (number of species per quadrat) between any of the zones measured as determined by a t-test for paired comparisons (Figure 3.9). No attempt was made to assess species richness in zone A. The vegetation of zone A was inherently different from that of the other zones. Although many species of the zones upslope occurred in zone A, many zone A species did not occur beyond the zone A boundary (e.g. several species of the Family Cyperaceae, *Banksia littoralis, Conospermum capitatum, Kunzea* sp., and *Mirbelia dilatata*).

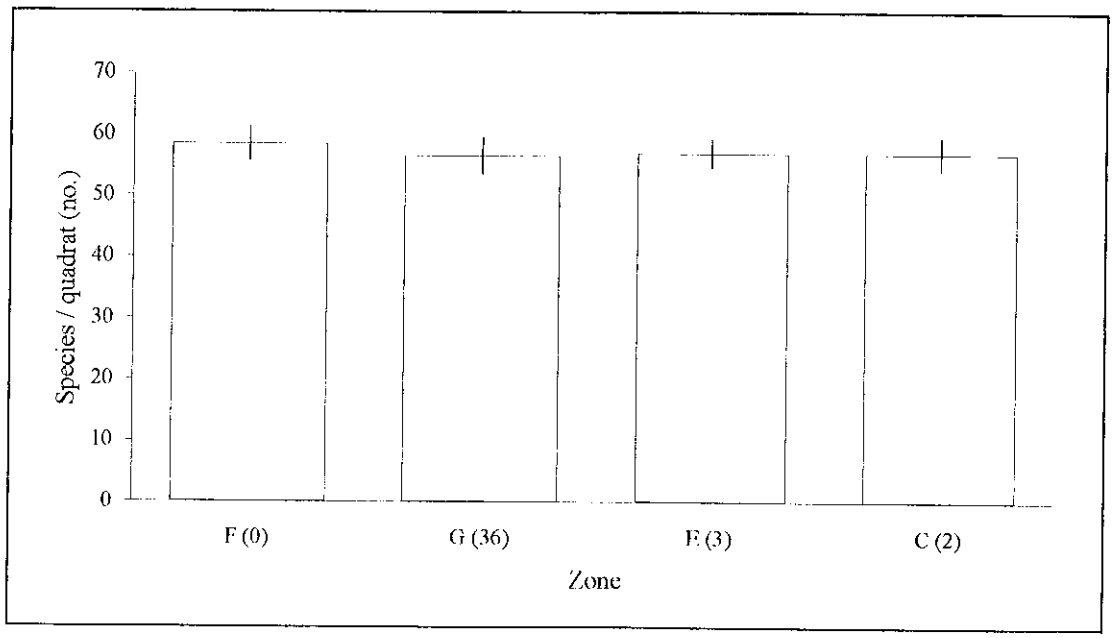


Figure 3.9 Mean species / quadrat in zones C, E, F and G with standard error bars (n = 7). The % of *P. cinnamomi* positive *Banksia grandis* baits obtained in each zone is shown in parentheses (Zone F was defined as zero for the purposes of the study).

Tree cover, Litter Cover and Bare Ground

Zone F had significantly greater tree cover and litter cover and less bare ground than other zones ($P < 0.05$) as determined by a Wilcoxon's signed-ranks test for two groups, arranged as paired observations on arcsine transformed data (Figure 3.10). Zone C had lesser tree cover than zones A and E. The presence of two additional tree species, bullich (*Eucalyptus megacarpa*) and blackbutt (*Eucalyptus patens*), in six of the sites in zone A contributes to the difference in tree cover and litter cover between zone A and zone C. Zone C had significantly less litter cover and more bare ground cover than any of the other zones. The substantial litter cover in zone G, compared with other dieback zones on slopes, is largely attributable to the recent death and leaf shedding of *Banksia grandis* and jarrah plants.

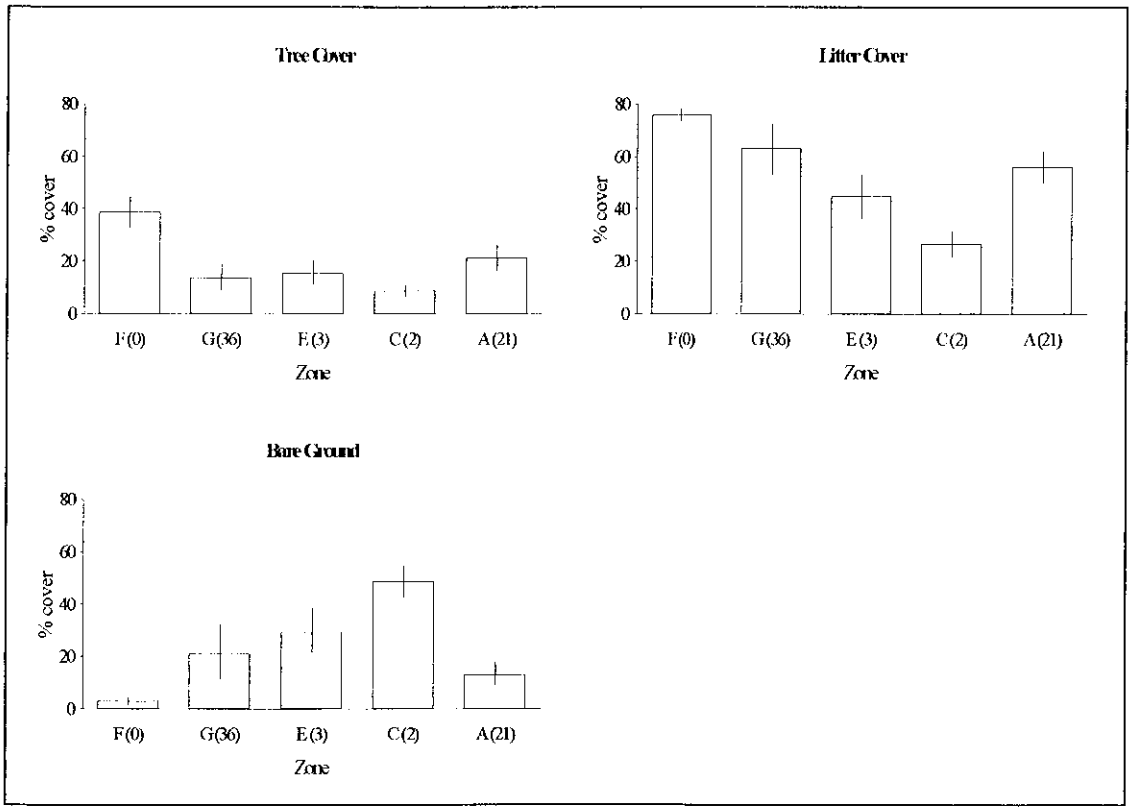


Figure 3.10 % cover of trees, litter and bare ground with 95% confidence limits. The % of *P. cinnamomi* positive *Banksia grandis* baits obtained in each zone is shown in parentheses (Zone F was defined as zero for the purposes of the study).

Jarrah and Marri Cover

Mean jarrah cover was significantly greater in zone F than in any of the other zones as determined by a Wilcoxon's signed-ranks test for two groups, arranged as paired observations ($P < 0.05$) (Figure 3.11). Mean jarrah cover in zone C was significantly less ($P < 0.05$) than in all zones except zone A, and even in this case there was only one site where mean jarrah cover in zone C was greater than in zone A.

There was no significant difference between the mean cover of marri in any pair of zones. On average, marri cover was less than 10% in all zones. The small cover of marri in zone C may have been partly attributable to wind damage. Many of the tallest marri trees provided little cover despite having trunks 1 m in diameter and 25 m in height. A few tall marri in zone C sites lost large branches during the period of study and one marri tree at site 4C, which was about 20 m tall, broke in two during a storm in May 1995.

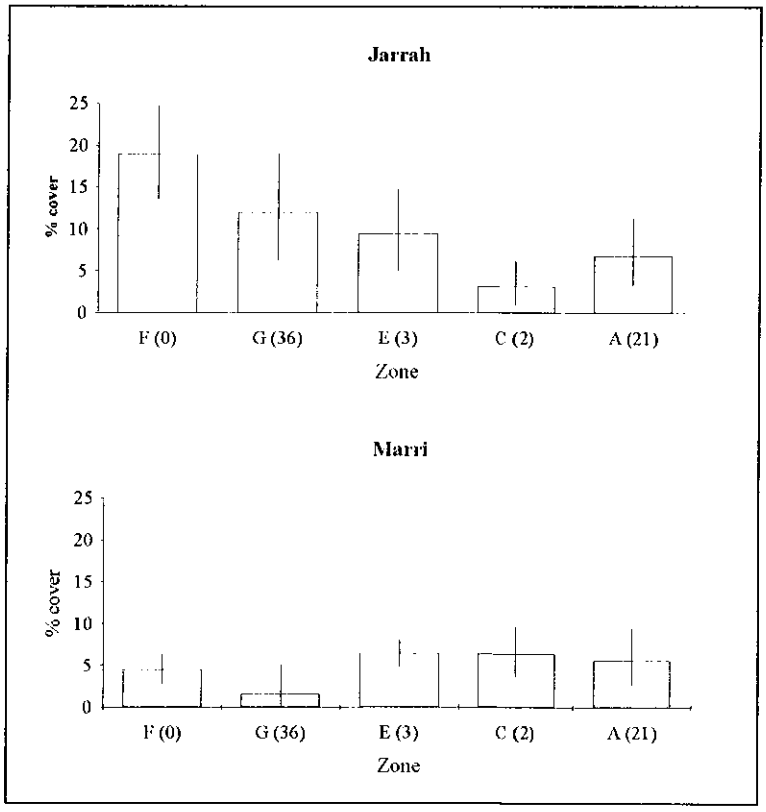


Figure 3.11 % cover of marri and jarrah with 95% confidence limits. The % of *P. cinnamomi* positive *Banksia grandis* baits obtained in each zone is shown in parentheses (Zone F was defined as zero for the purposes of the study).

Species Found Less Frequently in Pre-1951 Dieback Vegetation

The number of species / quadrat less frequent in pre-1951 dieback vegetation (Table 2.7, page 52) is less with increasing time since dieback (i.e. from zone F to A) (Figure 3.12). All pairs of means except A - C and A - E are significantly different as determined by a t-test for paired comparisons ($P < 0.05$). This is to be expected for zones F, G, E and C because data from quadrats in these zones were used in the analysis that generated Table 2.7. Zone A quadrats, which were not used in the analysis, had a similar mean number of species less frequent in dieback vegetation / quadrat to zone C, which is of comparable dieback age.

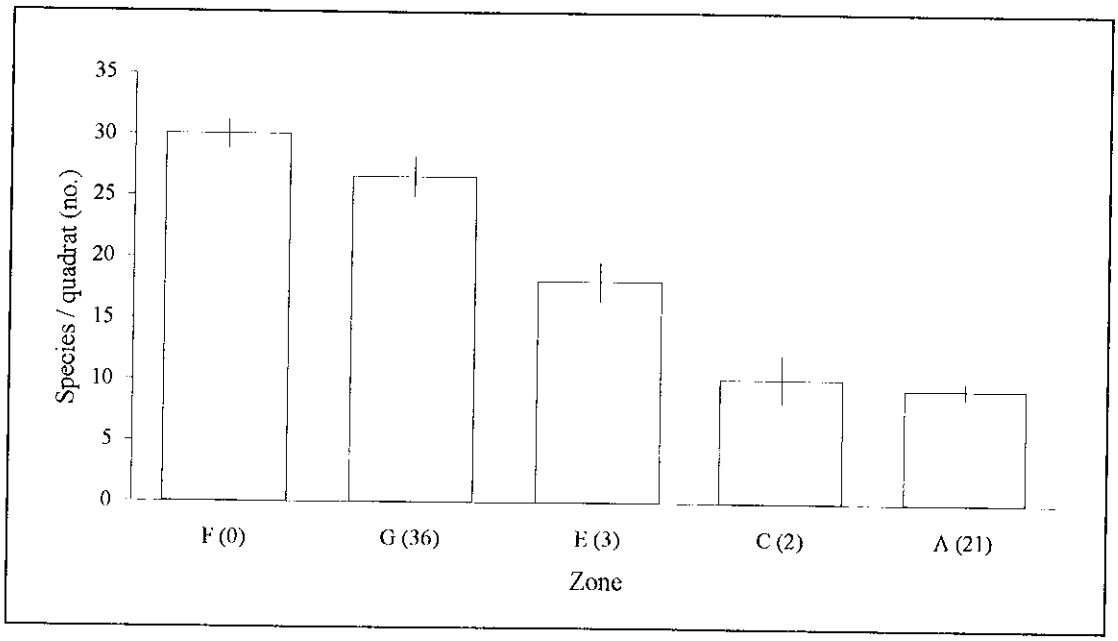


Figure 3.12 Mean species / quadrat that were found less frequently in dieback vegetation, with standard error bars (n = 7). The % of *P. cinnamomi* positive *Banksia grandis* baits obtained in each zone is shown in parentheses (Zone F was defined as zero for the purposes of the study).

Species Found More Frequently in Pre-1951 Dieback Vegetation

The number of species / quadrat found to be more frequent in pre-1951 dieback vegetation (Table 2.6, page 50), was more with increasing time since dieback (i.e from zone F to zone C), as expected. (Figure 3.13). There were however, significantly fewer of these species / quadrat in zone A than in zone C, despite the two zones being of similar dieback age. All pairs of means except A - E and A - G are significantly different as determined by a t-test for paired comparisons ($P < 0.05$).

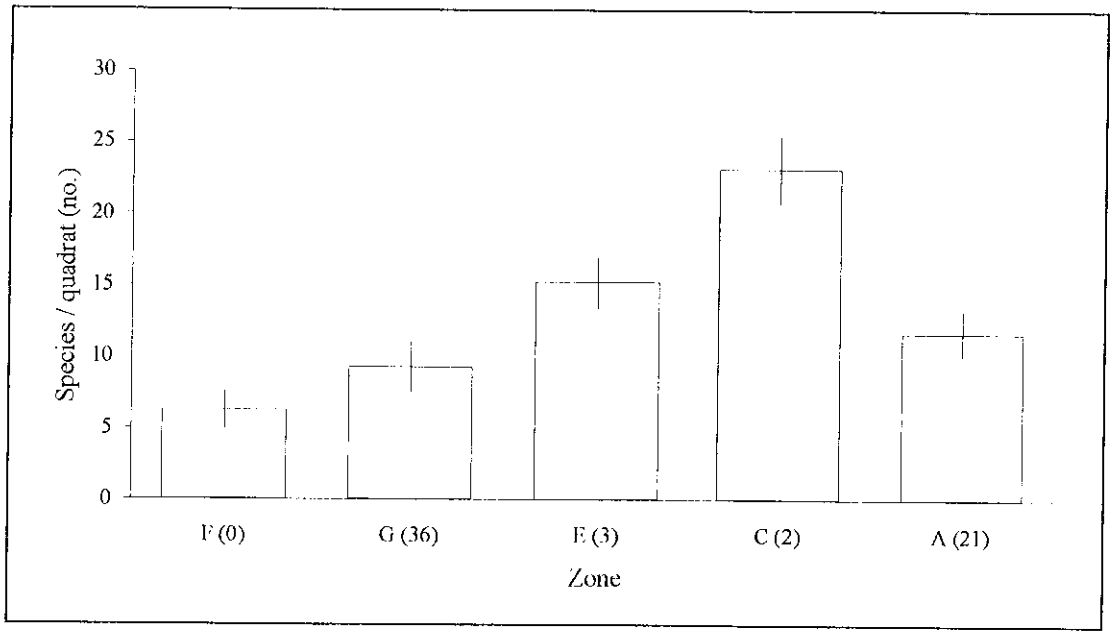


Figure 3.13 Species / quadrat that were found more frequently in dieback vegetation, with standard error bars (n = 7). The % of *P. cinnamomi* positive *Banksia grandis* baits obtained in each zone is shown in parentheses (Zone F was defined as zero for the purposes of the study).

P. cinnamomi *Susceptible Species*

With increasing time since dieback, there are fewer species per quadrat that are both highly susceptible to *P. cinnamomi* infection (Shearer and Dillon (1995) groups 3 and 5) and less frequently found on pre-1951 dieback sites (Figure 3.14). Zone A had fewer of these species than zone C. All pairs of mean number of species per quadrat, except those for the pair C and E, are significantly different as determined by a t-test for paired comparisons ($P < 0.05$).

For highly susceptible species that were found equally frequently in dieback and unaffected vegetation, the only significant differences in number of species per quadrat were between zone A and zones C, E and G ($P < 0.05$).

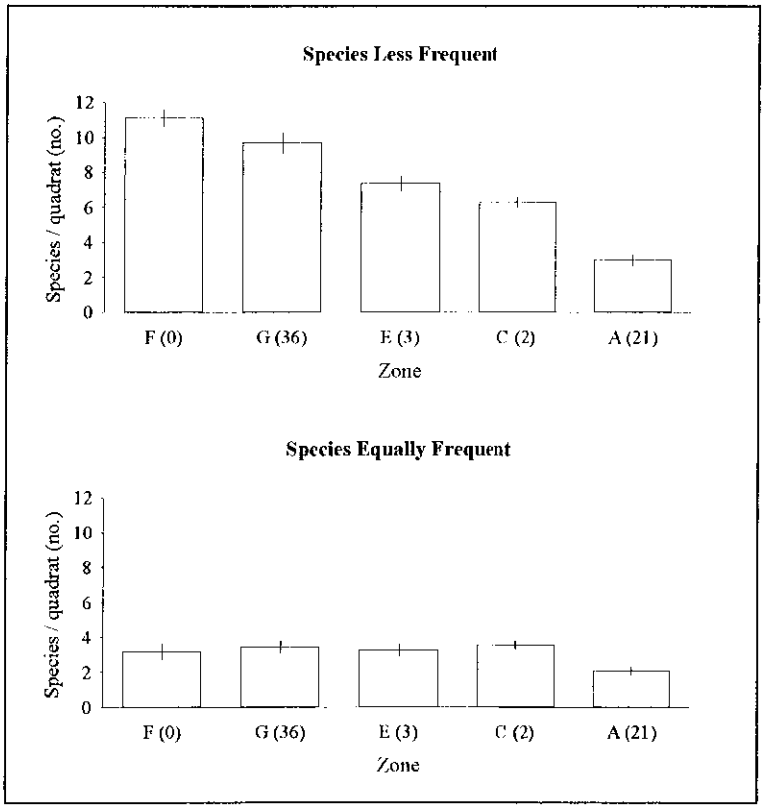


Figure 3.14 Mean number of highly susceptible species / quadrat (from Shearer and Dillon (1995) groups 3 and 5) found less frequently and equally frequently in dieback vegetation by zone with standard error bars (n = 7). The % of *P. cinnamomi* positive *Banksia grandis* baits obtained in each zone is shown in parentheses (Zone F was defined as zero for the purposes of the study).

Multiple Regression of Species Density and Recruitment

The density of most species measured was best explained by the % gravel content of soils (i.e. the abundance or rarity of the species in zone A). Only the density of *Adenanthos barbiger*, *Xanthorrhoea gracilis* and *Xanthorrhoea preissii* (excluding data from zone G) could be explained by the recovery of *P. cinnamomi* alone or in part (Table 3.5). By far the most significant single correlation was between *Adenanthos barbiger* density and time since dieback ($r^2 = 0.64$). The % gravel content of soils was the only significant variable that explained the estimated recruitment in jarrah, marri and *Xanthorrhoea preissii*.

Table 3.5. Significant prediction variables of density and estimated post-1951 % recruitment, and prediction equations. Significance was determined by an F-test. Variables (var.): x_1 = % of positive *Banksia grandis* baits; x_2 = time in years since dieback; x_3 = % gravel in surface soil. D = density (plants / 400 m^2). R = estimated % recruitment since 1951 (% individuals ≤ 20 cm DOB for jarrah and marri and ≤ 50 cm stem height for *Xanthorrhoea preissii*). Significance level of the largest single correlation (Pc) and increment (Pi): * < 0.05; ** < 0.01; *** < 0.001. [a] zone G was left out of the analysis.

Species	Largest single correlation			Significant Increment			Prediction Equation
	var.	r^2	Pc	var.	R^2	Pi	
Density							
Adenanthos barbiger	x_2	0.64	***	x_1	0.73	**	$D = 29 - 0.2(x_1) - 0.5(x_2)$
Jarrah	x_3	0.13	*	x_2	0.36	**	$D = 56 - 0.6(x_2) - 0.6(x_3)$
Leucopogon nutans	x_3	0.13	*				$D = 0.1(x_3)$
Macrozamia riedlei	x_3	0.22	**				$D = 35 - 0.4(x_3)$
Marri	x_3	0.33	***				$D = 50 - 0.5(x_3)$
Xanthorrhoea gracilis	x_1	0.14	*				$D = 53 - 0.4(x_1)$
Xanthorrhoea preissii [a]	x_1	0.18	*	x_3	0.36	*	$D = 3 - 0.2(x_1) + 0.1(x_3)$
Recruitment							
Marri [a]	x_3	0.48	***				$R = 101 - 0.2(x_3)$
Jarrah	x_3	0.14	*				$R = 99 - 0.2(x_3)$
Xanthorrhoea preissii	x_3	0.44	***				$R = 12 + 0.7(x_3)$

Adenanthos barbiger *Density*

The density of *Adenanthos barbiger*, a species less frequent on pre-1951 dieback sites and highly susceptible to infection by *P. cinnamomi*, is inversely correlated with the time since dieback ($P < 0.001$) (Table 3.5). The addition of positive recovery of *P. cinnamomi* from *Banksia grandis* baits to the regression is also significant ($P < 0.01$). Therefore, the density of *Adenanthos barbiger* is less with increasing time since dieback but where *P. cinnamomi* is present, density is further lowered. *Adenanthos barbiger* density was highest in zone F and lowest in zone A at all sites (Figure 3.15).

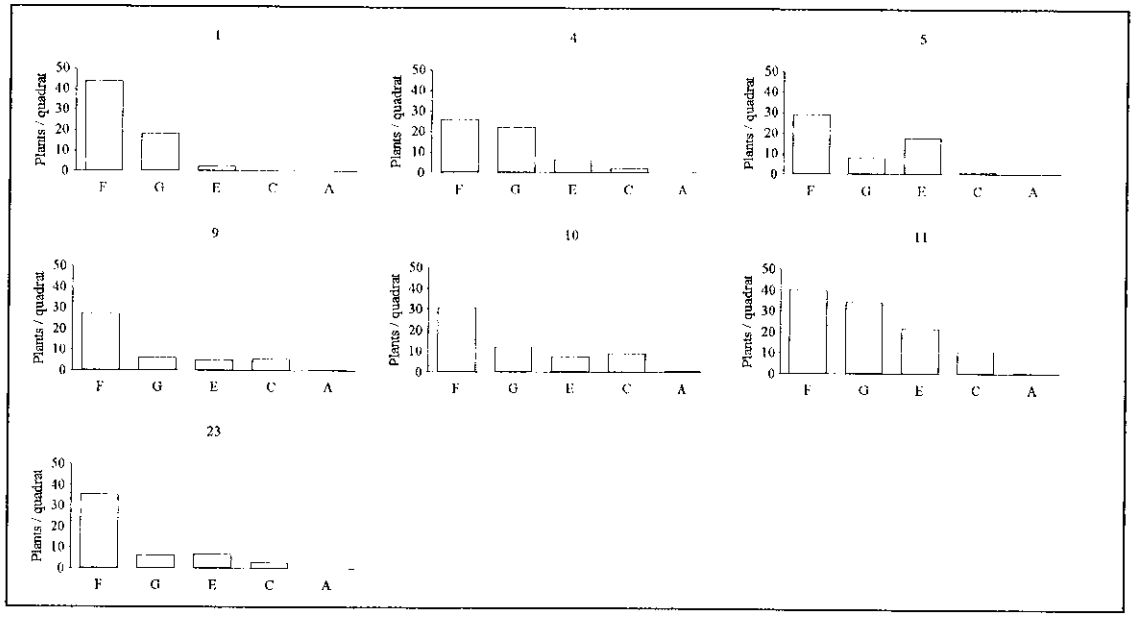


Figure 3.15 Density (plants / quadrat) of *Adenanthos barbiger* at the seven sites sampled.

Leucopogon nutans *Density*

Leucopogon nutans was uncommon in zone A at all sites (Figure 3.16). Despite it being regarded as amongst the most sensitive to infection by *P. cinnamomi* by Shearer and Dillon (1995), it was more common in zone C (pre-1951 dieback vegetation) than in zone F (unaffected vegetation) at six sites. The significant correlation of *Leucopogon nutans* density with % gravel in surface soils reflects the lower mean density in zone A (Table 3.5). It is possible that the species simply does not normally grow in that zone.

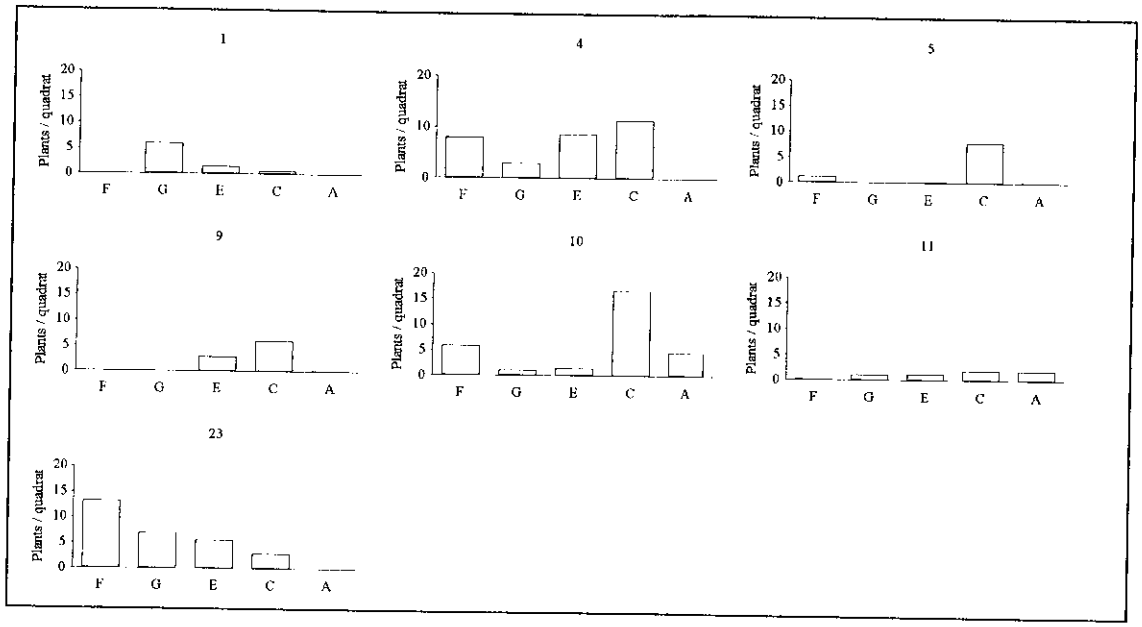


Figure 3.16 Density (plants / quadrat) of *Leucopogon nutans* at the seven sites sampled.

Xanthorrhoea gracilis *Density*

Xanthorrhoea gracilis density was greater in zone F than zone G and zone A at five sites (Figure 3.17). Density was inversely correlated with the frequency of *P. cinnamomi* recovery using *in situ Banksia grandis* baits (Table 3.5). Despite this *Xanthorrhoea gracilis* was present in all zones at all sites.

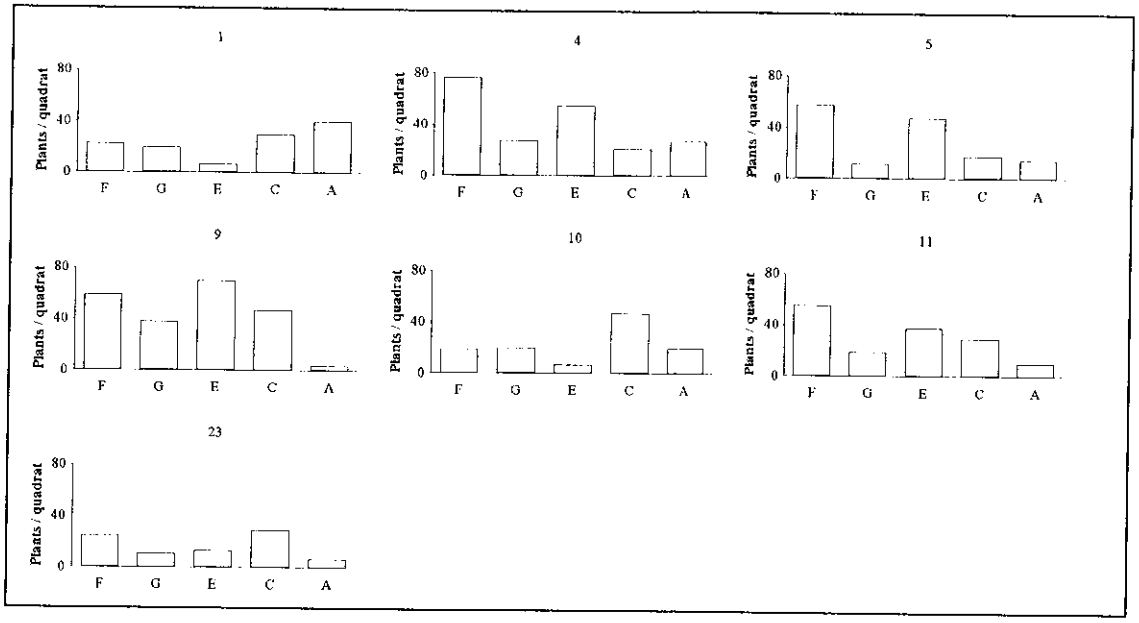


Figure 3.17 Density (plants / quadrat) of *Xanthorrhoea gracilis* at the seven sites sampled.

Xanthorrhoea preissii *Density*

Xanthorrhoea preissii plants were most abundant in zone F or zone G at six of the seven sites (Figure 3.18). *Xanthorrhoea preissii* density was inversely correlated with the frequency of recovery of *P. cinnamomi* (Table 3.5). The amount of gravel in the soil surface also explained a significant amount of variation in *Xanthorrhoea preissii* density.

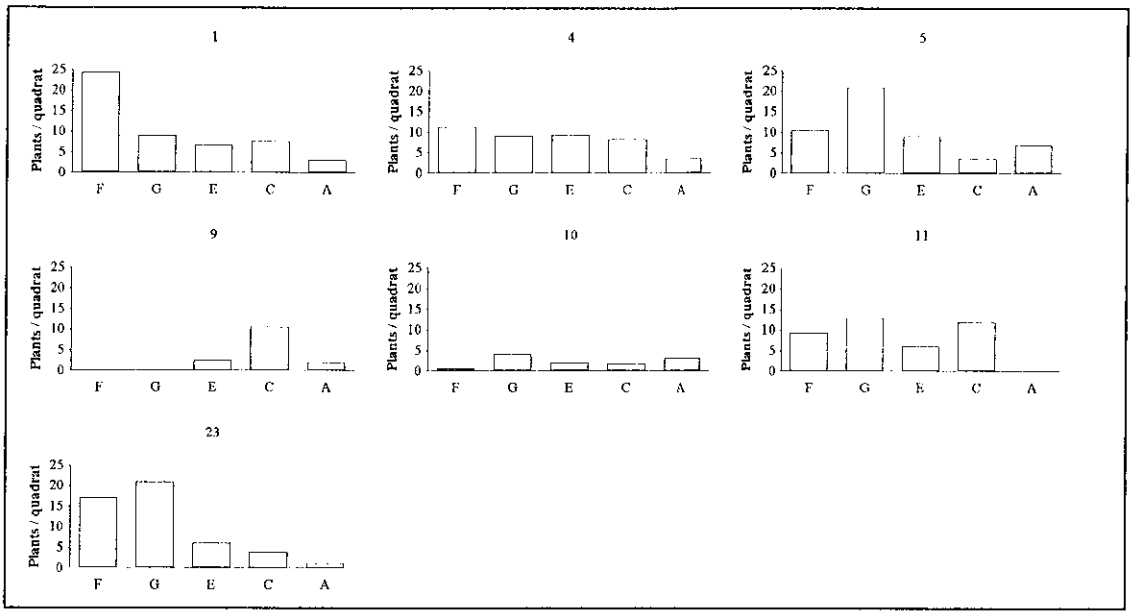


Figure 3.18 Density (plants / quadrat) of *Xanthorrhoea preissii* at the seven sites sampled.

Xanthorrhoea preissii *Stem Height Distribution*

The population structure of *Xanthorrhoea preissii* is a reverse J curve in sites C, E and F, indicating continuously recruiting populations (Figure 3.19). The fewer plants in the first height class in zone G is perhaps attributable to the small sample size. The populations in zone A have relatively fewer individuals in the small height classes, when compared with populations in the other zones, and more in the tallest classes. The only plants located that had stems > 275 cm in height were in zone A. In zone A, 22% of plants were > 200 cm tall, whilst in zone F only 3% of plants were > 200 cm tall.

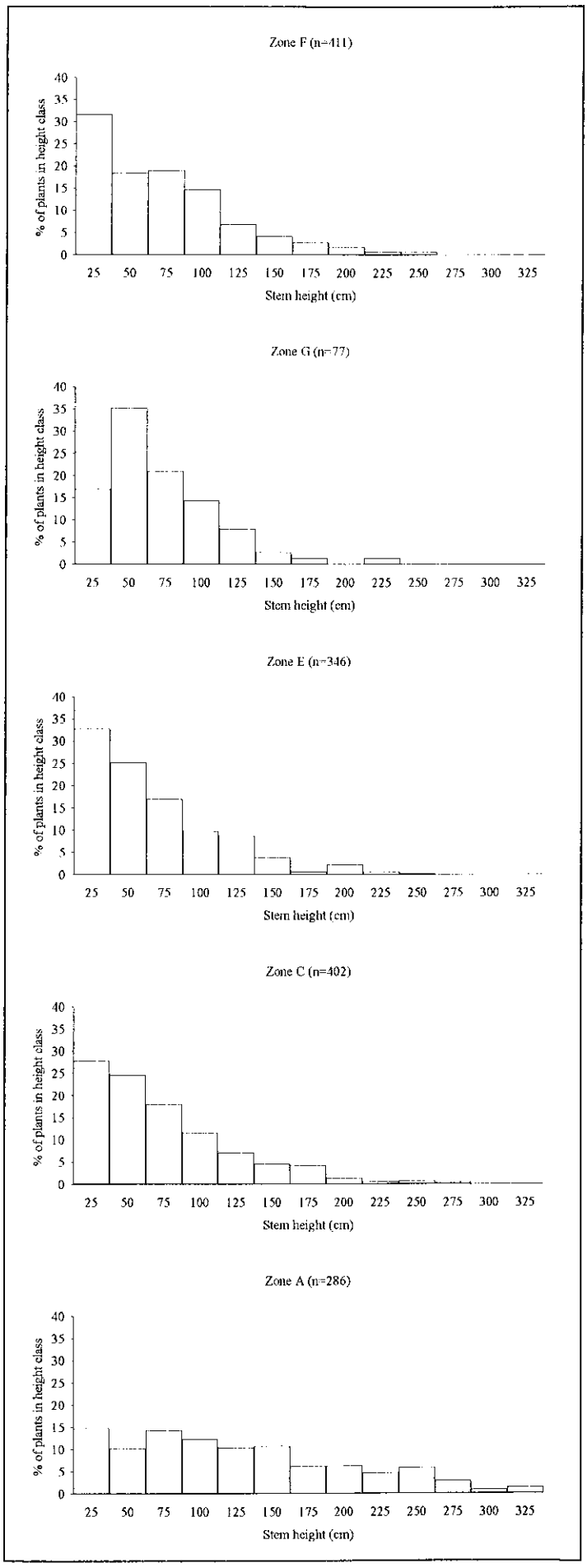


Figure 3.19 Stem height (cm) distribution of *Xanthorrhoea preissii* in each zone. Data were pooled for each class interval at the seven sites.

Xanthorrhoea preissii *recruitment*

An obvious explanation for the absence of tall *Xanthorrhoea preissii* in zones on slopes would be that *Xanthorrhoea preissii* in zone A grow faster than *Xanthorrhoea preissii* in other zones (i.e. the plants in zone A are taller but of similar age to plants upslope). Using the method of Lamont and Downes (1979) for estimating the age of *Xanthorrhoea preissii*, the distance between annual stem waves was measured on recently dead plants to determine if there is a difference in growth rate between dieback zones. Two dead plants were possible to age in zone A and eight in zones C or E. The mean and standard error of annual stem increment for plants sampled in zone A are 1.51 ± 0.24 cm and for zone C and E are 1.43 ± 0.08 cm. The means are not significantly different as determined by a t-test. Evidence for the antiquity of tall zone A plants is provided by their morphology. Most of the tallest plants in zone A were branched. Lamont and Downes (1979) indicated that the stem elongation rate in *Xanthorrhoea preissii* slows following branching, so the tall zone A plants recorded may have effectively been older than indicated by the annual stem waves. Both of the zone A plants measured were unbranched.

The values obtained for age of *Xanthorrhoea preissii* are within the range found by Lamont and Downes (1979). Using the regression equation developed by Lamont and Downes, which relates age and height in *Xanthorrhoea preissii* (Height = -4.61 + 1.42 x age), the proportion of plants surviving and recruited after dieback events can be estimated, assuming that the density of *Xanthorrhoea preissii* was once uniform across the landscape (Table 3.6).

Table 3.6. Estimate of the *Xanthorrhoea preissii* population surviving dieback (as % of original population, assuming that density in zones A, C, and E at the time of dieback was the same as that currently in zone F) and the number and % of plants recruited since dieback (in all quadrats within each zone, i.e. 1.4 ha).

	Zone			
	F	E	C	A
Dieback age (approximate)		20	45	45
Plants surviving dieback (%)		38	29	19
Plants recruited since pre-1951 dieback (no.)	231		130	27
(%)	(63)		(55)	(28)
Plants recruited since post-1968 dieback (no.)	113	68		
(%)	(31)	(33)		

Despite the assumption made, it is clear that the initial impact did not eliminate the entire population in any zone. It is also clear that *Xanthorrhoea preissii* has continued to recruit in dieback zones. Although this appears to be poorer in all dieback zones when numbers of recruits are calculated, when the percentage of the population recruited since dieback is calculated, recruitment in zones C and E is similar to that in unaffected vegetation during the same periods. Recruitment has only been poor in zone A. This was also indicated in the multiple regression (Table 3.5) where there was a significant inverse correlation between the estimated *Xanthorrhoea preissii* recruitment since 1951 and the % of gravel in surface soils (i.e. young plants tend not to occur in zone A). Assuming that the natural size and rate of death of *Xanthorrhoea preissii* populations were once uniform across the landscape, the post-dieback death rate exceeds the recruitment rate only in zone A. That is, *Xanthorrhoea preissii* populations are only likely to become extinct in the lower parts of the landscape.

The abundance of *P. cinnamomi* in some zone A sites may be contributing to the local extinction of *Xanthorrhoea preissii*. There is a negative correlation between the abundance of *P. cinnamomi* in zones A, C and E (as measured by the number of positive *Banksia grandis* baits) and the abundance of *Xanthorrhoea preissii* ($r = -0.58$, $P < 0.05$) (Figure 3.20). This suggests that *Xanthorrhoea preissii* is fairly persistent despite the initial action of *P. cinnamomi*, but when *P. cinnamomi* is also persistent, its population will gradually decline.

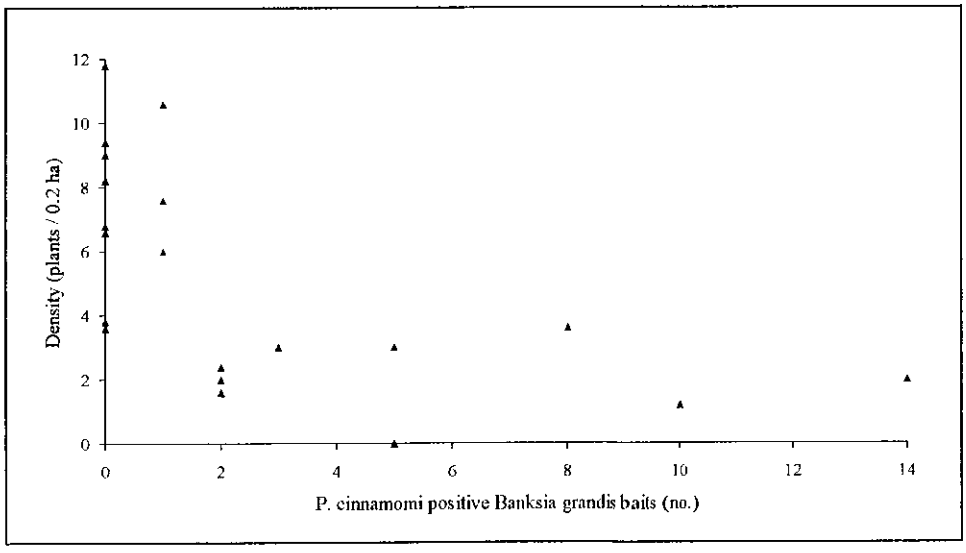


Figure 3.20 Relationship between number of *P. cinnamomi* positive *Banksia grandis* baits and density of *Xanthorrhoea preissii* density; $r = -0.58$.

Macrozamia riedlei *Density*

When present in zone F, *Macrozamia riedlei* was more abundant in Zone F than dieback sites on slopes (zones C and E). It was most abundant in Zone A at four sites (Figure 3.21), which were dominated by bullich. Its prediction equation (Table 3.5) reflects the abundance in zone A, although it is poor in predicting density in some unaffected sites.

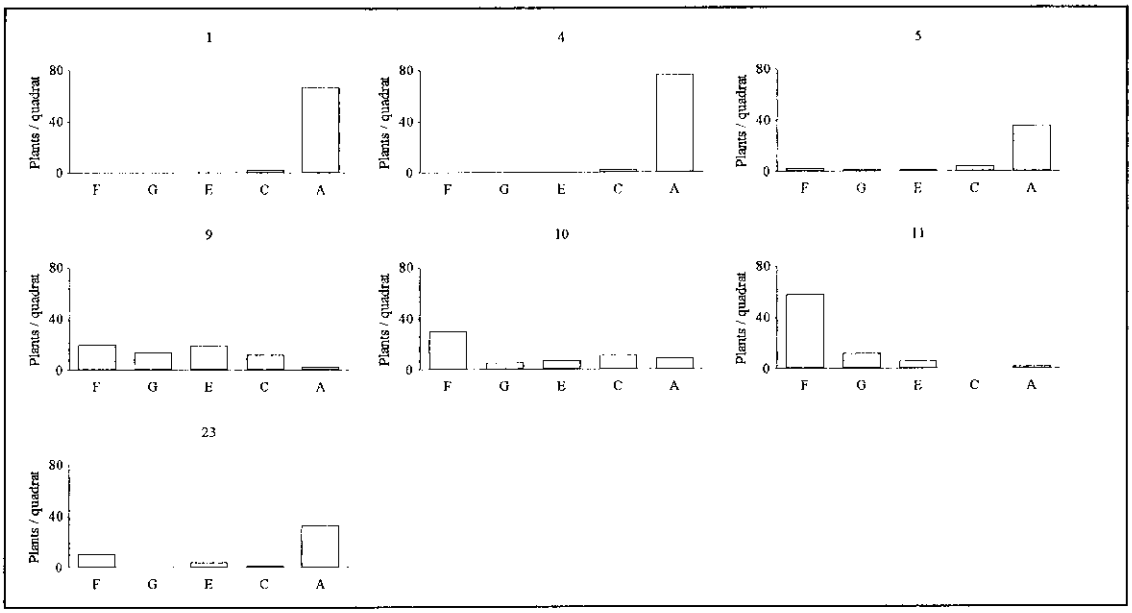


Figure 3.21 Density (plants / quadrat) of *Macrozamia riedlei* at the seven sites sampled.

Macrozamia riedlei *Basal Diameter Distribution*

The *Macrozamia riedlei* population appears to be recruiting in all zones where the density was large enough to show patterns (Figure 3.22). The largest basal diameter classes are missing from dieback sites on slopes (Zone C). There is no correlation between *P. cinnamomi* recovery and *Macrozamia riedlei* density, as there was with *Xanthorrhoea preissii*.

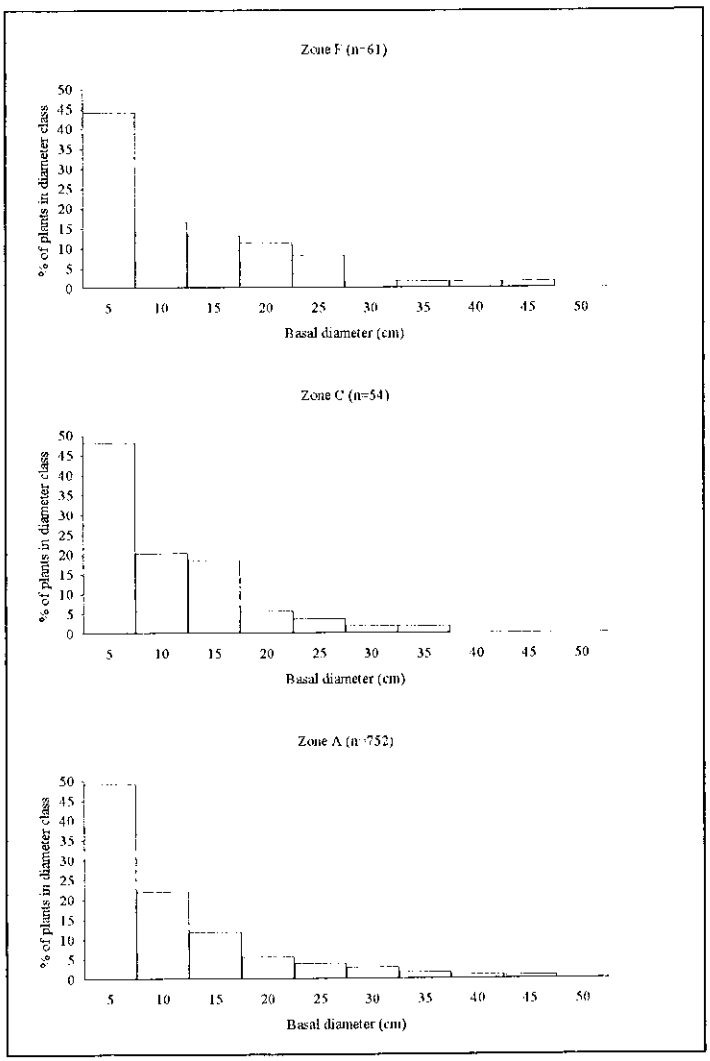


Figure 3.22 Basal diameter distribution of *Macrozamia riedlei* in zones A, C and F. Data were pooled for each class interval at the four sites sampled.

Marri Density

Marri, a field-resistant species, which might be expected to replace jarrah on dieback sites, is more abundant on some dieback sites on slopes than in unaffected vegetation (zone F) (Figure 3.23) but never greatly so. It was most abundant in zone A at five sites. Its abundance in zone A is reflected in the prediction equation determined in the multiple regression of density and recruitment (Table 3.5).

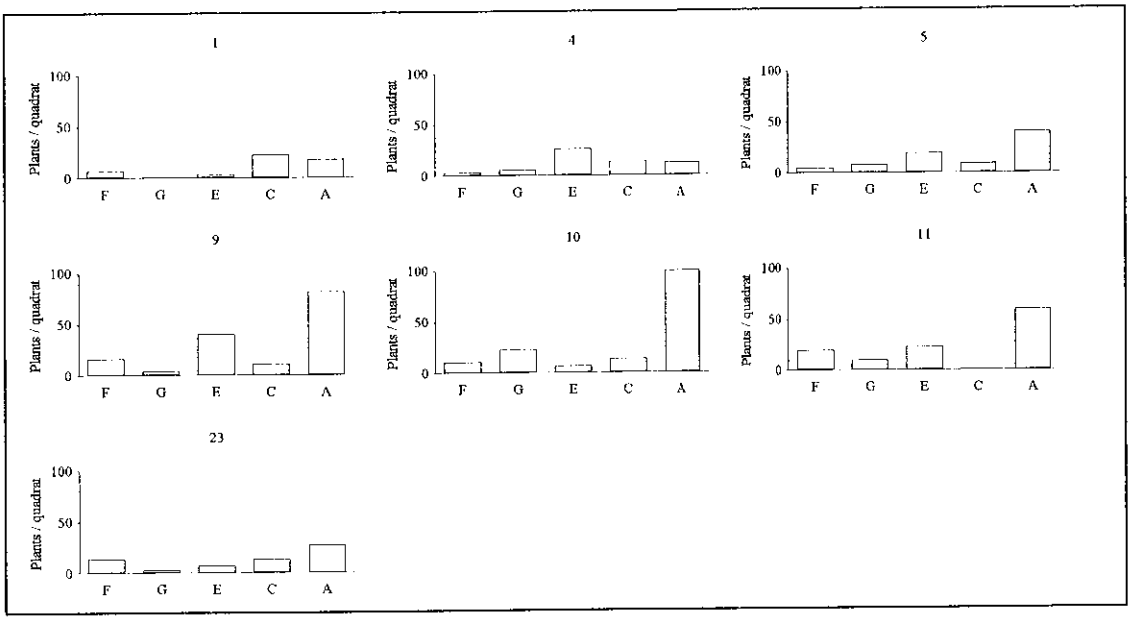


Figure 3.23 Density (plants / quadrat) of marri at the seven sites sampled.

Marri DOB Distribution

The population structure in all zones is a reverse J curve indicative of continuous recruitment. Much of the abundance of marri in zone A is due to seedlings and small trees with DOB < 10 cm (Figure 3.24): 91 % of marri had a DOB < 10 cm in zone A compared with 80% in zone F.

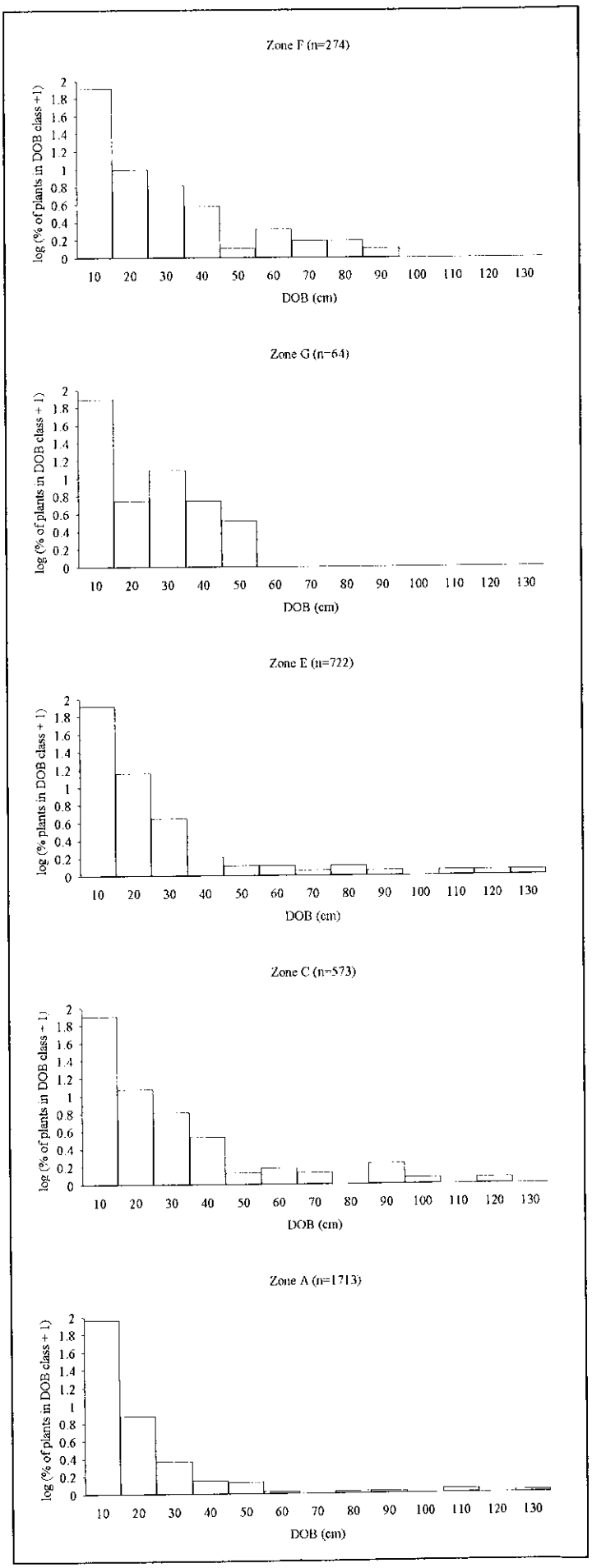


Figure 3.24 DOB (diameter over bark at breast height (cm)) distribution of marri in each zone. Data were pooled for each class interval at the seven sites.

Jarrah Density

Jarrah was less abundant in zone C than in zone F at all sites (Figure 3.25). However, it was more abundant in zone A than in zone F at five of the seven sites. This is reflected in the inverse correlation found between jarrah abundance and the % gravel content of surface soils and the time since dieback (Table 3.5).

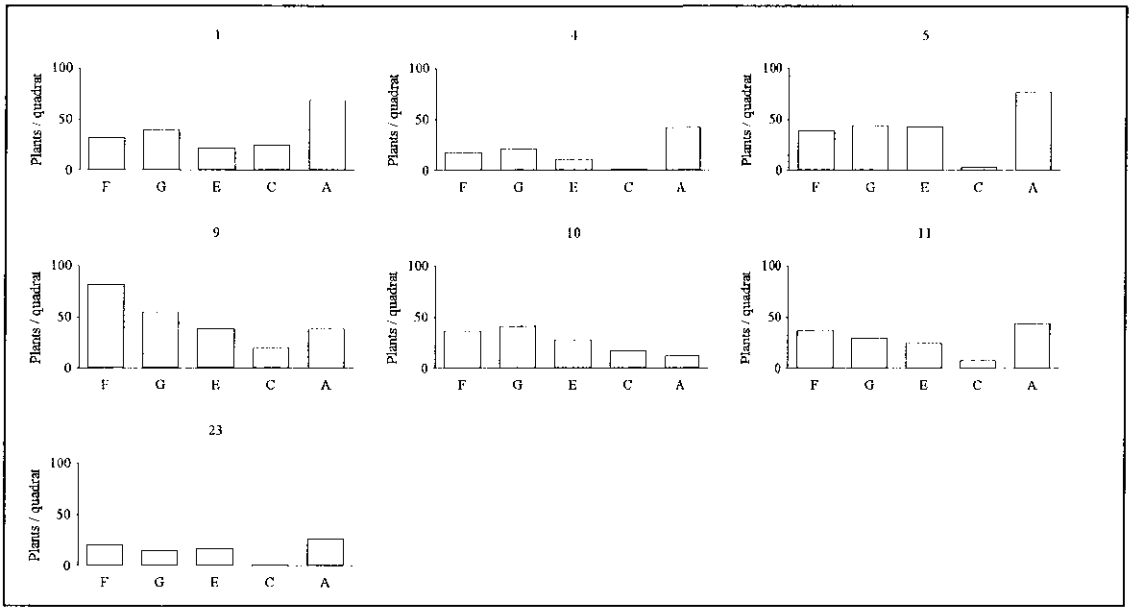


Figure 3.25 Density (plants / quadrat) of jarrah at the seven sites sampled.

Jarrah DOB Distribution

The greater abundance in zone A is attributable to the smaller size classes. There were, on average, 36 jarrah per ha with a DOB ≥ 20 cm in zone A compared with 129 in zone F. This is reinforced by the prediction equation determined by multiple regression of estimated % recruitment since 1951 (Table 3.5) where the % gravel in surface soil is the sole significant variable. The population structure of jarrah is a reverse J curve in all zones, which is indicative of continuous recruitment (Figure 3.26). Zones C and E had few jarrah > 50 cm DOB.

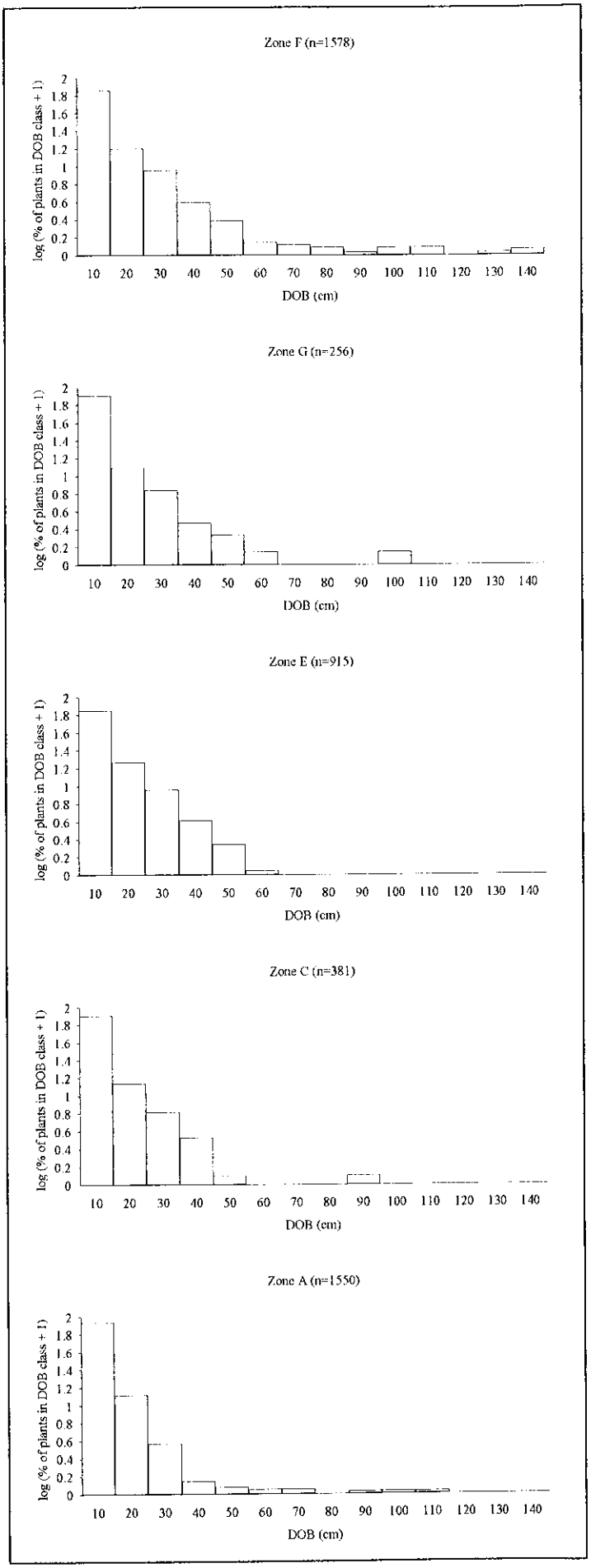


Figure 3.26 DOB (diameter over bark at breast height (cm)) distribution of jarrah in each zone. Data were pooled for each class interval at the seven sites.

Jarrah Recruitment and Survival in pre-1951 Dieback Sites

Abbott and Loneragen (1983) estimate the average diameter growth in jarrah as 0.17 cm per year. This may be greater for growth from coppice and may vary with site and density. Even if jarrah growth on the sites studied was at the upper end of the growth range, and allowing for the width of bark, survivors on the oldest dieback sites (zone A and C) would not be much more than 20 cm DOB. An estimate of the number of trees surviving dieback and recruited since dieback in these zones is shown in Figure 3.27. Some jarrah survive dieback and subsequent salvage logging. The difference between the numbers of jarrah recruits is significant ($P < 0.05$), as determined by Wilcoxon's signed-ranks test for two groups, arranged as paired observations. The difference between the number of jarrah survivors on sites A and C is not significant, although only one site (10) has a greater number of survivors in zone C than zone A. However, because of the massive differences in recruitment, the greater abundance of jarrah in zone A is probably due mainly to recruitment since dieback rather than to survival.

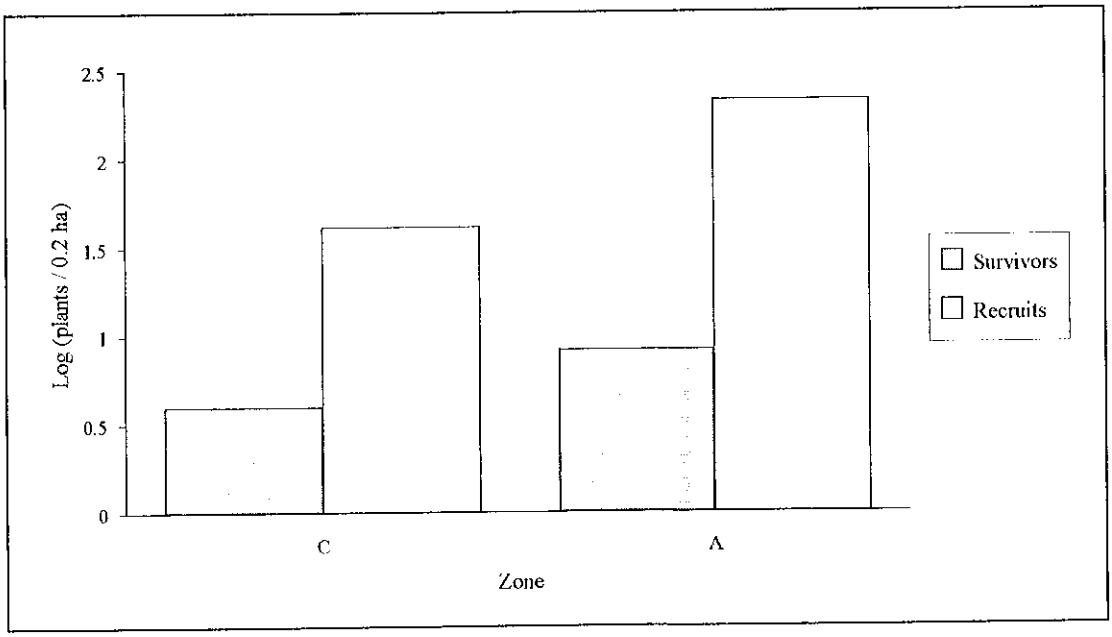


Figure 3.27 Log mean density (plants / 0.2 ha) of jarrah with DOB > 20 cm (putative survivors) and DOB ≤ 20 cm (putative recruits).

Bullich and Blackbutt DOB Distribution

The other tree species present on the sites (bullich and blackbutt) occurred in zone A only. They have populations with a reverse J distribution (Figure 3.28). Whilst this is generally indicative of continuous recruitment, bullich, which was the structural dominant in parts of four of the seven zone A sites, has a interrupted distribution. There are a few individuals in relatively large DOB classes with a gap of three DOB classes containing no members to the small classes containing most individuals.

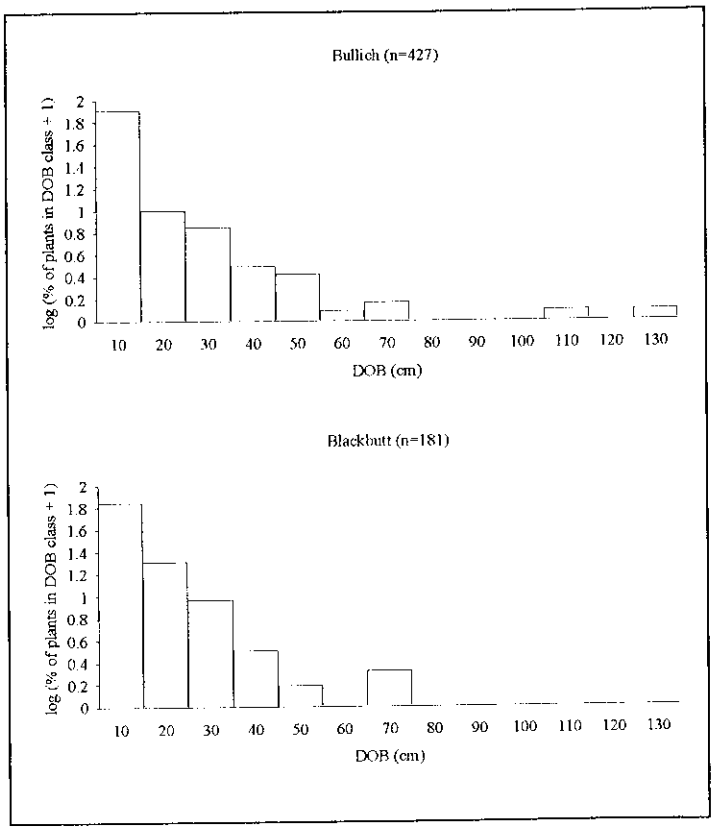


Figure 3.28 DOB (diameter over bark at breast height (cm)) distribution of bullich (*Eucalyptus megacarpa*) and blackbutt (*Eucalyptus patens*) in zone A.

Species Deaths

The number of species with dead individuals per quadrat in a zone appears to be related to the frequency of *P. cinnamomi* detection, except in zone A (Figure 3.29). Zone G had significantly more species with dead individuals / quadrat than all other zones ($P < 0.01$) as determined by a t-test for paired comparisons. Zone F had significantly less species with dead individuals / quadrat than all zones except zone A ($P < 0.05$). On average, 10 of the 60 species in zone G quadrats had dead individuals compared with about one of the 60 species in zone F.

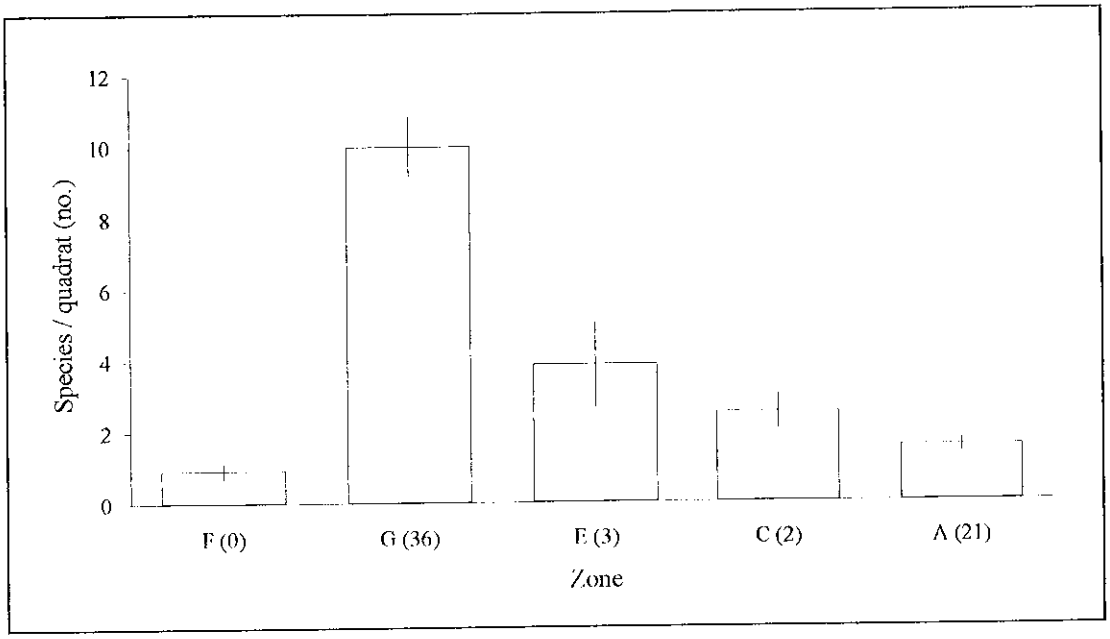


Figure 3.29 Mean number of species with dead plants per quadrat in each zone with standard error bars (n = 7). The % of *P. cinnamomi* positive *Banksia grandis* baits obtained in each zone is shown in parentheses (Zone F was defined as zero for the purposes of the study).

The lower number of species with dead individuals in zone A than expected might logically be explained by the lower number of species susceptible to infection by *P. cinnamomi* in zone A. However, the percentage of susceptible species with dead plants / quadrat is also much greater in zone G than in zone A (Figure 3.30).

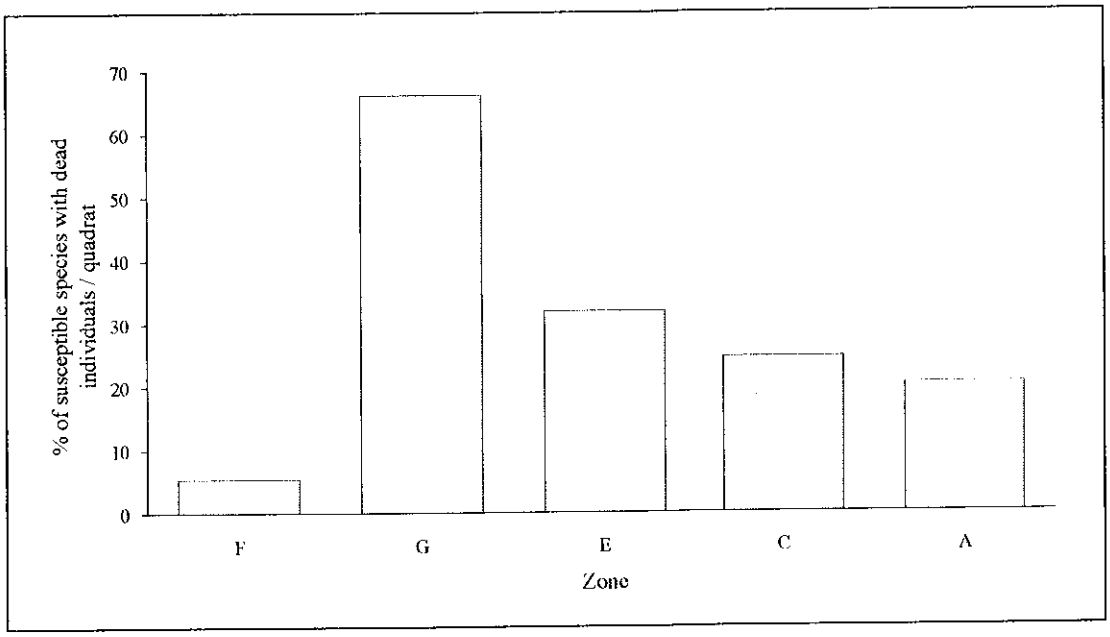


Figure 3.30 The percentage of *P. cinnamomi* susceptible species with dead plants / quadrat for each zone. Susceptible species were those listed in Tables 3, 4 (only species from which *P. cinnamomi* was obtained from dead plants) and 5 of Shearer and Dillon (1995).

Sixty-four species were recorded with dead individuals in the sites studied. 53% of these were species from which *P. cinnamomi* has been recovered. A further 9% were species in genera from which *P. cinnamomi* is recovered from many species. These species might be expected to be susceptible to infection. Some examples of the patterns of death of species that occur frequently in two or more zones are shown in Figure 3.31. Deaths of most of the species that are susceptible to infection by *P. cinnamomi* occur most frequently in zone G. Some susceptible species tend to have less frequent deaths in zone A than in other dieback zones. Some species had deaths in unaffected vegetation. Only a few were widespread. Deaths of *Dryandra lindleyana* may have been mistaken for the shedding of old plant parts, the equivalent of a senescent stage in the sense of Watt (1947). *Dryandra lindleyana* produces abundant shoots from underground stems. The boundaries of plants are often not sharp and shoots commonly die back, even in unaffected forest. *Daviesia decurrens* plants in unaffected forest commonly had dead shoots. In a few cases, all shoots appeared to be dead. The species is a resprouter. Dead plants were not obviously the largest and therefore perhaps not the oldest. *Macrozamia riedlei* died most frequently in zone G quadrats but also died in almost 40 % of zone F (unaffected) quadrats.

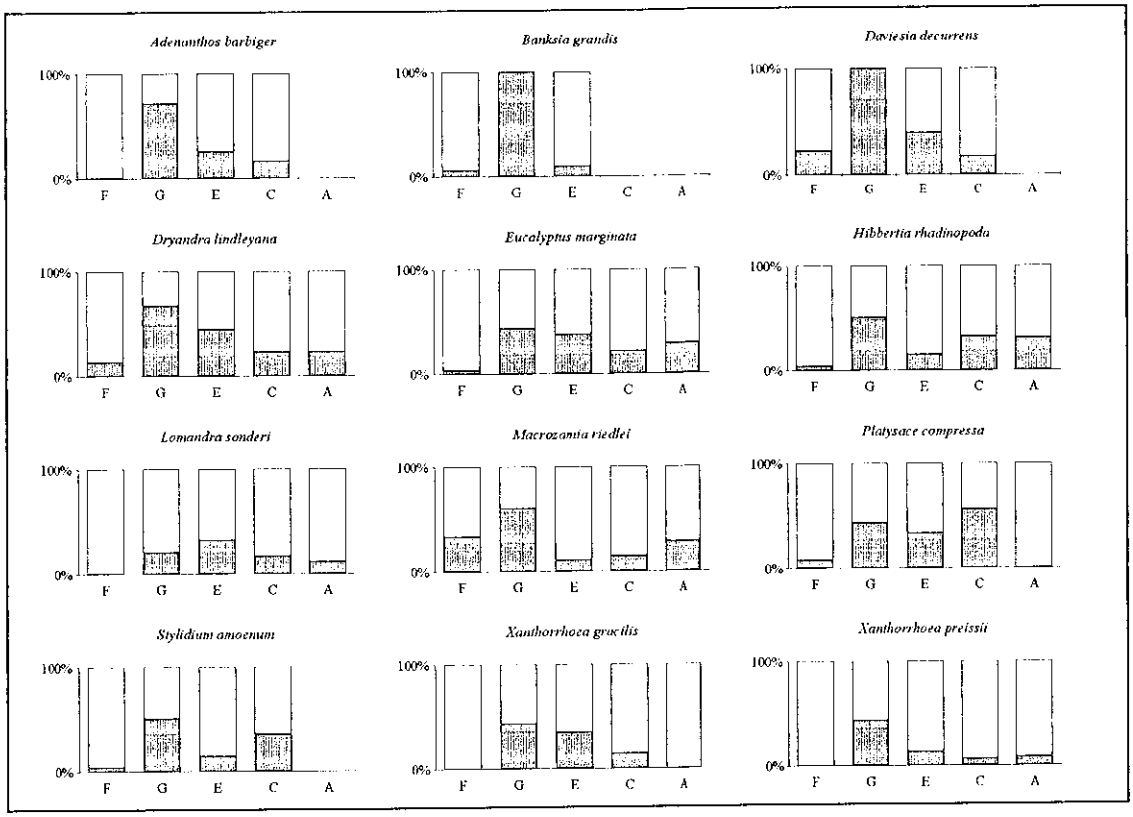


Figure 3.31 % of quadrats in each zone with some dead individuals (shaded) or all live individuals (unshaded) for a selection of species. No data are presented for a zone in which a species had a % frequency of < 25.

Biotic factors other than *P. cinnamomi* are likely to cause plant death in the jarrah forest. In autumn 1995, several *Xanthorrhoea preissii* crowns became yellow at two of the pre-1951 dieback sites studied (Sites 1 and 5) (Figure 3.32). The leaf bases of these yellow crowns were rotten and insect larvae were observed on one. The crowns were subsequently shed. When the plant was unbranched, this resulted in death. However, when the plant was branched, the live branches persisted and plants still appeared healthy more than one year later. Two small affected plants were excavated and roots, stems and leaf bases plated onto selective agar. *P. cinnamomi* was not recovered. The sample was too small to test for any other organism.

Figure 3.32 A dying branch on a *Xanthorrhoea preissii* at site 1, April 1995. The branch was subsequently shed but the remainder of the plant appeared healthy when last inspected in June 1996.

Witches broom, a largely fungal disease that has received little attention in relation to Australian native plants (Jones and Elliot 1986), sometimes develops in *Leucopogon nutans* in both unaffected and dieback vegetation (Figure 3.33). At some sites it is common. Many dead *Leucopogon nutans* at the sites studied had had witches broom.

Figure 3.33 Witches Broom on a *Leucopogon nutans* plant at site 11. The shrub had very few green leaves remaining.

3.5 Discussion

3.5.1 Baiting Techniques

There were marked differences in the ability of the baiting techniques used to detect *P. cinnamomi*. *In situ Banksia grandis* baiting detected *P. cinnamomi* in more than twice as many zones as the baiting of sampled soil. If soil sampling alone had been used to assess *P. cinnamomi* distribution, *P. cinnamomi* might have been regarded as absent from pre-1951 dieback sites. The efficacy of the techniques need not be different, however. The

advantage of *in situ* baits may simply be the temporal component they allow. The majority of recoveries of *P. cinnamomi* from *in situ Banksia grandis* baits were made from the harvest in mid-November. Soil was sampled for baiting in late September. The negative recoveries from soil samples from sites where positive recoveries were later made from *in situ Banksia grandis* may have been due to *P. cinnamomi* inactivity at the time of sampling. Maximal sporulation and zoospore release may have occurred during October, increasing the volume of surface soil containing *P. cinnamomi* propagules and the probability of infecting *Banksia grandis* baits. Soil sampling in mid-November may have been equally effective at detecting *P. cinnamomi*. If baits can be established *in situ* hygienically, there is likely to be a greater chance of finding the optimum time of *P. cinnamomi* activity and a greater chance of detecting *P. cinnamomi* when it is rare. If field sites are not too distant, the amount of work required to detect *P. cinnamomi* confidently is likely to be much less with *in situ* baits because the time of optimal *P. cinnamomi* activity cannot be predicted. Oddly, *in situ* baiting for the detection of *P. cinnamomi* does not appear to have been used before.

Additional baiting was done to soils and some plant material to detect *P. cinnamomi* that might have been missed by the first baiting because of technique (inadequate water:soil ratio in the case of zone A soils) or the possibility of resting structures in *P. cinnamomi*. *Banksia grandis* seedlings were effective baits for checking the presence of *P. cinnamomi* in soils. However, more than one *Banksia grandis* bait per sample might be required for confident recovery of *P. cinnamomi* because of the possibility of resistance to infection (see Chapter 4). The additional baiting techniques used (*Banksia grandis* seedlings, wetting and drying of tissue possibly containing *P. cinnamomi*, repeated baiting with *Pimelea ferruginea* leaves) failed to enhance the detection of *P. cinnamomi*. Since there is no certainty that resting structures were absent, it is not possible to comment on the efficacy of the techniques. The repeated baiting with *Pimelea ferruginea* leaves coupled with the wetting and drying of *Leucopogon nutans* tissue failed to detect *P. cinnamomi* previously recovered by direct plating onto selective agar. This may suggest that *P. cinnamomi* can be killed if baiting procedures are lengthy.

3.5.2 Vegetation Patterns, Dieback Age and *P. cinnamomi* Distribution

Although it was impossible to know whether the vegetation sampled in pre-1951 dieback sites had once been similar to vegetation sampled in unaffected sites (Chapter 2), there is evidence to suggest that at least the structural dominants were similar. Jarrah wood is enduring, and so jarrah stumps are easily identified by their red timber. Jarrah once extended from the edges of creeks to the tops of ridges, and in most places, still does. The density of jarrah may be variable along this transect but a rough estimate of former density can be gained, even on the oldest dieback sites, from inspecting stumps. *Banksia grandis* timber decays rapidly and burns thoroughly. There is no evidence of it now on the dieback sites studied that were more than 20 years old. However, except for creek bottoms, the species can still be found throughout the topographic profile in unaffected vegetation. More importantly, dieback fronts with dead and dying *Banksia grandis* can be found throughout the topographic profile. This suggests that the current distribution of the species is a reflection of the spread of *P. cinnamomi* rather than being indicative of habitat preferences of *Banksia grandis*.

The aerial photographic record for the sites studied is consistent with the progressive decline of canopy species observed on dieback sites. Dieback appears to have begun adjacent to logging tracks prior to 1951 and spread rapidly downhill towards the creeks. Since 1951, there has been a slow progression of symptoms uphill, ranging from an average of about 1 m per year at sites 1 and 4 to about 2 m per year at site 10. Although *Banksia grandis* is absent from all but the most recent dieback zones, there are great differences in the survival of jarrah, particularly in areas affected in the last 30 years. At first, this appears to be related to the amount of salvage logging that has occurred - more jarrah have been removed from sites that have fewer surviving jarrah. However, the degree of salvage logging might be attributed to the survival of jarrah. That is, salvage logging may have only occurred on sites where jarrah died. The logging record and aerial photographic record are not helpful in providing evidence for either possibility. Accurate

recording of salvage logging operations and the prevention of salvage logging on some dieback sites would help in the evaluation of jarrah survival following the passage of *P. cinnamomi.*

If, as the evidence suggests, jarrah and *Banksia grandis* once dominated the pre-1951 dieback sites, then *P. cinnamomi,* the most likely agent in the decline of at least the *Banksia* canopy, has become rare in the surface soil and may be absent from some of the sites studied. The pathogen is still active at the dieback front and was easily located there with *in situ Banksia grandis* baits. It appears to become rare soon after the original and regenerating population of *Banksia grandis* have died, probably in the order of 10 years after the initial impact. This is consistent with the declines in disease potential reported by Weste et al (1973), Weste and Ashton (1994) and Duncan (1994) for Victorian forests and Blowes (1980) for the jarrah forest of Western Australia. Blowes (1980) regarded *P. cinnamomi* as a short-lived pathogen because it was difficult to find in soil around recently dead *Banksia grandis.*

Despite the scarcity or inactivity of *P. cinnamomi* in pre-1980 dieback zones on slopes (C and E), it was still located in five of the seven sites in one or both of these zones. It is not possible to tell if the pathogen has survived on the sites since the initial dieback event or if it has been re-introduced from soil attached to vehicles or feral pigs. However, its detection in *Leucopogon nutans* and *Xanthorrhoea preissii* roots after prolonged drought during summer suggests that the pathogen is capable of persistence in spite of unfavourable conditions. *P. cinnamomi* has previously been located in the roots of *Banksia grandis* (Shea 1979, Schild 1995) and *Dryandra sessilis* (Rockel et al 1982) after summer. It has also been isolated from the roots of plants not showing disease symptoms (*Hibbertia hypericoides, Kennedia coccinea* and *Lechenaultia biloba* in the jarrah forest (Shearer and Dillon 1995), and some species of the family Cyperaceae in Victoria (Phillips and Weste 1984)). Schild (1995) found that chlamydospores, the resting structure of *P. cinnamomi,* did not survive over summer in the surface soils of the jarrah forest away from drainage features. The persistence and regeneration on dieback

sites of a range of species that are known to be highly susceptible to infection (e.g.. *Daviesia decurrens, Leucopogon nutans, Pimelea suaveolens, Xanthorrhoea gracilis,* and *Xanthorrhoea preissii*) would allow the pathogen to survive in host tissue regardless of the ability of chlamydospores to survive in the soil. The potential for re-introduction of inoculum in sub-surface water flow over cap rock may also be important in the persistence and spread of *P. cinnamomi* on old dieback sites.

Although *P. cinnamomi* may persist on dieback sites in a range of tolerant and susceptible hosts, it is clearly not ubiquitous in such species. Potential tolerant hosts such as *Hibbertia hypericoides* and *Lechenaultia biloba* were abundant on the pre-1980 dieback sites studied. Despite this, *Phytophthora*-positive host plants, could not be located around *Phytophthora*-positive *Banksia grandis* in pre-1951 dieback zones. This is perhaps not surprising because not all root material in the soil surrounding the *Banksia grandis* baits could be excavated or plated out. However, the roots of the *Banksia grandis* baits had not extended far beyond their original containers. Wherever the inoculum came from that infected the baits, the roots of nearby plants were not an abundant source. In addition, *Banksia grandis* plants that were less than 3 m from *Banksia grandis* plants that tested positive for *P. cinnamomi* remained healthy and apparently unaffected throughout the trial at sites 9C, 9E, 10C and 23E.

Although *P. cinnamomi* was found on some pre-1980 sloping dieback sites it appears to be very localised. *P. cinnamomi* was not isolated from any of the *in situ Banksia grandis* on site 4E. However, it was isolated from a dying *Xanthorrhoea preissii* at that site in March, only 10 m from the row of *Banksia grandis*, although by that time only four *Banksia grandis* survived. Even at the active dieback fronts (zone G) where most recoveries were made, deaths of *Banksia grandis*, both planted and naturally occurring, were sporadic. At dieback fronts, mortality was greatest in the planted seedlings.

Very few highly susceptible species are eliminated immediately after *P. cinnamomi* enters unaffected vegetation. No highly susceptible species were absent from all dieback

quadrats in the boundary survey described in Chapter 2. This may indicate either that (i) some plants of highly susceptible species survive, (ii) some highly susceptible species regenerate quickly, or (iii) death is not rapid (i.e. not enough time had elapsed to detect complete elimination of a species). There are examples of each of these propositions in the jarrah forest.

(i) The age structure of *Xanthorrhoea preissii* populations demonstrates that some of the population of even the oldest dieback sites has survived the initial infestation. Populations in sloping dieback zones have continued to recruit at levels similar to unaffected vegetation, although there is an indication that the persistence of *P. cinnamomi* on dieback sites may affect survival. Although little is known about the age of *Macrozamia riedlei* and *Xanthorrhoea gracilis* plants, both species are thought to be extremely slow growing and probably demonstrate a persistence similar to *Xanthorrhoea preissii*. Large individuals of *Xanthorrhoea gracilis* were found in all zones. Large individuals of *Macrozamia riedlei* were found in zones A, F and G, the largest were in zone A.

(ii) Seedlings of *Banksia grandis* and *Dryandra sessilis* were observed at many recently-affected sites. Regeneration of other susceptible species from seed does not seem to be as pronounced, perhaps because some have special germination requirements, such as burning or passing through the digestive system of animals. At burnt recently-affected dieback sites there was evidence of germination of susceptible species such as *Adenanthos barbiger* and *Bossiaea aquifolium*. Species that apparently disappear quickly from dieback sites, such as *Persoonia longifolia* and *Leucopogon verticillatus*, possibly do so because of their poor capacity to germinate coupled with their great susceptibility to infection from *P. cinnamomi*.

(iii) The third proposition is self-evident if the pre-1951 dieback sites studied once had vegetation similar to the unaffected sites studied. Although there were no species absent from all dieback sites in the boundary study (Chapter 2), many were either absent from

pre-1951 dieback sites or present in only one or two sites. Slow death of jarrah on dieback sites is recognised (Shearer and Tippett 1989). It is possible that other species of intermediate susceptibility are infected at the time of the initial dieback yet persist until they succumb to the disease or environmental factors such as drought some years later.

The patterns of regeneration and survival evident on dieback slopes do not seem to be the same as those occurring on the creek edges (zone A). Jarrah is not renowned as a species of wet sites. Its much better recruitment at creek edges compared with sloping sites of similar dieback age, as found in this study, would not have been expected. The boundary between zones A and C, defined on most sites by a change in soil texture and gravel content in the surface layer, corresponds well with the boundary between abundant jarrah recruitment and poor jarrah recruitment, suggesting that there is something about the zone A environment that favours recruitment. Four species known to be susceptible to infection by *P. cinnamomi* were found much more frequently in zone A sites than in adjoining zone C sites: jarrah, *Lomandra sonderi, Macrozamia riedlei, Platysace compressa*. Fourteen of the 53 species that were found significantly less frequently in pre-1951 dieback quadrats on slopes (zone C) than in unaffected vegetation (zone F) (Table 2.7, page 52) were much more frequently found in zone A than in zone C: *Comesperma virgatum*, jarrah, *Kennedia coccinea, Leptomeria cunninghamii, Logania serpyllifolia, Lomandra sonderi, Monotaxis occidentalis, Opercularia echinocephala, Pentapeltis peltigera, Platysace compressa, Pteridium esculentum, Scaevola calliptera, Stylidium junceum, Tetrarrhena laevis*. Species with dead plants were less frequently found in zone A quadrats than in zones C and E. Whilst this might be attributable in some cases to low densities in zone A, *Xanthorrhoea gracilis* was not at all rare there. *Xanthorrhoea gracilis* was one of the species regarded by Shearer and Dillon (1995) as being most susceptible to infection by *P. cinnamomi*. Since some zone A sites have abundant *P. cinnamomi*, the absence of deaths of this species in zone A is puzzling.

Zone A surface soils remain moist well into summer. This favours the survival of *P. cinnamomi*. For this reason, *P. cinnamomi* is often isolated in valley bottoms throughout the year but on slopes mainly in spring (Shearer and Shea 1987, Schild 1995). The moist soils of valley bottoms in summer are also likely to permit plant species with shallow root systems to grow for longer periods. The prolonged growth, coupled with a reduced drought stress, may enable some species to repair damage done by *P. cinnamomi*. The novel hypothesis that prolonging conditions favourable for *P. cinnamomi* growth and survival also improves the capacity of host plants to cope with *P. cinnamomi* is worth consideration.

Differences in the frequency of susceptible and apparently dieback-sensitive species between zone A and zones C and E were most pronounced in sites where zone A had a dense cover of young bullich. The cover of litter and understorey vegetation on the sites containing bullich was great despite being burnt in a prescribed fire only two years before. The Ashburner system of farming in Queensland uses organic soil amendments such as plant litter to suppress *P. cimamomi* activity and allow avocado trees to grow in *P. cinnamomi*-infested soils (Broadbent and Baker 1975). The amount of organic matter in zone A topsoil may also be important in the appparent suppression of *P. cinnamomi* activity.

Further investigation is warranted in zone A sites for possible genetic resistance in susceptible species (see Chapter 6) and agents that might be suppressive to *P. cinnamomi*. The red clay loam soils of deeper valleys in the jarrah forest have been shown to suppress *P. cinnamomi* activity (Sochacki 1982) partly as a result of an antagonistic microflora (Malajczuk 1979). *P. cinnamomi* was found to survive for longer in red loam soils than in the sandy gravel soils of forest slopes (Sochacki 1982). The orange loam soils of the upper valleys of Myara forest block may have similar properties to the soils of the deeper valleys further downslope.

The paradoxical population structure of *Xanthorrhoea preissii* in zone A is also worth further investigation. The tallest, and therefore probably the oldest, individuals of this species occur in

zone A, yet the zone has the lowest density and poorest recruitment (expressed either as % of the population or total plants) of any zone. As burning promotes flowering in this species, poor recruitment might be explained if the incidence of fire had diminished in zone A. Research into fire scars in *Xanthorrhoea preissii*, currently under way, indicates that fire frequency in the jarrah forest has diminished since European settlement (David Ward, CALM, pers. comm.). Since creek edges are wet for longer periods than slopes, fire frequency would be naturally lower there. A further reduction in fire frequency may have more or less eliminated fire from creek edge vegetation. In addition, most of the prescribed burning now done in the forest occurs in spring when creek edge soils are wet. At that time the vegetation tends not to burn (Ross Mead, CALM, pers. comm.). Prescribed fires in spring do sometimes burn the edges of stream zones, however. Most zone A quadrats had been burnt in the 1993 control fire at all sites studied. From aerial photographs, the seven zone A sites studied appear to have been burnt in the severe wildfire of 1961.

Changes in fire frequency alone seem unlikely to explain the occurrence in zone A of *Xanthorrhoea preissii* plants in the two tallest classes, which were absent from other zones. The restriction of tall plants to valley bottoms could mean either that (i) individuals in the tallest classes in the other zones have been removed, (ii) plants of this species grow faster in low topographic positions, (iii) high topographic positions have not favoured the species for as long as low topographic positions, or (iv) plants live longer in low topographic positions. The second of these possibilities was found to be unlikely by determining the age of plants throughout the topographic profile, using the technique of Lamont and Downes (1979). There was no difference between the mean width of annual stem waves of plants in zones A and C and E. Therefore, plants of similar height in each zone are likely to be of similar age. Although logging activities tend to knock over some *Xanthorrhoea preissii* and it is conceivable that a catastrophic fire might have destroyed plants on slopes while sparing those in the damper valleys, the complete absence of the tallest height categories from all zones on slopes at all seven sites is curious. The combination of older individuals and poorer recruitment in zone A may be a consequence of one or many factors such as changes in climate, fire frequency and intensity, or soil moisture characteristics. The valleys studied may

have become wetter following dieback and the consequent decrease in tree density. Increases in stream flow are temporarily associated with logging (Borg et al 1987). They might be permanent when tree regeneration is poor upslope.

The sequence of aerial photographs available for Myara block between 1941 and 1994 shows clearly that there have been major structural changes along creeks. In 1941 black and white photos, the creeks have a darker tone and coarser texture than adjoining slopes. This is still evident in 1994 colour photography and is probably indicative of the different understorey compositions of creeks and slopes and the thicker understorey in the creeks. It is difficult to tell if the area of understorey vegetation has changed since 1941. The tree canopy in 1941 was open and appears to comprise mainly large trees. It is impossible to determine which species were present from the photos but from inspections of stumps and the size of trees still growing on creek edges, jarrah, marri, blackbutt and bullich were all present at that time. Apart from some valley bottoms where trees were absent in 1941 and are still absent, the canopy of many creeks is now closed and composed largely of young trees of all four species, especially bullich. No record of the growth rate of bullich could be found in the available literature perhaps because it is not a tree of commercial interest. The diameter increment at breast height of two bullich trees that fell over near my study sites was about 2 cm per year. Both trees were about 25 years old. The apparent growth rate of the young bullich measured is much greater than the long-term growth rate reported for jarrah, but at the upper range for young jarrah growing on good sites (Abbott and Loneragan 1983). From such growth rates and my interpretation of aerial photographs, as much as 99.5% of the bullich population at the edges of creeks may have appeared within the past 40 years or so. This finding is consistent with the population structure shown in Figure 3.28, where there is a substantial gap in the DOB distribution greater than 70 cm. Such a distribution might indicate that survival to the largest classes is a rare event or that most of a population has died. Bullich is generally regarded as being more fire-sensitive than other eucalypts in the jarrah forest. I can find no reference to support this view and there were no obvious deaths, even of juveniles, resulting from the prescribed burn in Myara block in 1993. Fire sensitivity is probably assumed from the thin gum bark, gum barked eucalypts sometimes being more sensitive than stringybark

eucalypts (Gill 1993). Massive fire scars on some older trees attest to its greater reaction to fire than species such as jarrah or marri. If bullich is fire-sensitive, an occasional intense fire in drainage systems may greatly reduce the density of the standing population. If the growth rate measured for the two fallen bullich is representative, all of the < 70 cm DOB trees could have been recruited since the 1961 bushfire, which is likely to have been the most severe since records commenced in 1937. A similar process of population death from intense fire, massive recruitment from seed, and extreme self-thinning has been described by Ashton (1981) in Victoria for *Eucalyptus regnans*, another gum-barked species. The aerial photographic evidence for a relationship between the 1961 bushfire and structural changes is compelling in Myara block. Within the limitations of photo resolution, there is little change in structure between 1941 and 1960. On 1968 photos, there are obvious dead trees in many drainage lines. Although it is impossible to attribute their death to the fire, many of the stags are still standing and they are clearly not jarrah, which may otherwise have been affected by *P. cinnamomi* or waterlogging. Although the scale of 1980 photos make interpretation of the forest canopy in the creek difficult, the structural changes are obvious by the time of the 1994 photos.

An increasing wetness of valley bottoms may have contributed to bullich recruitment at creek edges and the occurrence of solitary young bullich some distance upslope from drainage lines on dieback sites. Bullich grow naturally on wet sites. Extensive dieback on the slopes of Myara block during of the 1940s and possibly logging operations there during the 1960s, are likely to have allowed more water to percolate through slope soils into valley bottoms. The repositioning of many logging tracks in Myara block upslope from creeks in the last 40 years (which is obvious from the aerial photographs) and the occurrence of only young bullich on and beyond the original creek-side tracks is circumstantial evidence for the increasing wetness of the creeks and nearby slopes. The changing distribution of jarrah in valleys is also likely to be evidence of an increasing wetness. Jarrah are not commonly found in valley communities (Havel 1975). I found large jarrah stumps in one valley bottom in Karnet forest block (adjacent to Myara block - AMG MK 104138). The valley is now occupied by wetland species such as *Agonis*

linearifolia and *Banksia littoralis*. There is no jarrah recruitment on the valley bottom, adjacent to the stumps, but there is massive recruitment occurring at the edges of the *Agonis*-dominated community.

Massive bullich recruitment is not confined to creek edges. It extends well into creek communities, and so increasing wetness alone is unlikely to explain the structural change. The substantial recruitment of jarrah and marri as well as bullich on creek edges suggests that factors in addition to fire and increasing wetness are important in the current development of creek vegetation. The monitoring of creek vegetation would be worthwhile, not only for exploring some of the processes occurring in the structural dominants, but for explaining the behaviour of *P. cinnamomi* and its hosts there.

The distribution of plant deaths and the species involved were largely those expected if *P. cinnamomi* was to be the primary cause, although deaths in zone A were less than expected given the frequency of *P. cinnamomi* detection. The infrequent death of *Lomandra sonderi* in zone G (dieback front) is consistent with the observations of Shearer and Dillon (1995) that, although the species appeared to be very susceptible to infection, it was infrequently found dead in active dieback areas. The infrequent death of *Banksia grandis* in zone E is probably associated with its low density in that zone. However, because of its great susceptibility to infection, the infrequency of death might also indicate that *P. cinnamomi* activity declines rapidly with age of dieback. This is consistent with the small number of positive *P. cinnamomi* recoveries from *Banksia grandis* baits obtained in this zone. It is also logical. Once the mature *Banksia grandis* are killed, the volume of susceptible tissue must plummet on recent dieback sites. The probability of infection is also likely to decline close to active dieback fronts, allowing *Banksia grandis* regeneration to occur for some years. Most of the new *Banksia grandis* roots will be near the soil surface where fluctuations in temperature and moisture severely limit the period of *P. cinnamomi* activity. The absence of *Banksia grandis* from zone C and its rarity in zone E suggests that its extinction on infested sites is inevitable.

The jarrah forest is a complex ecosystem, of which little is so far known. Whilst *P. cinnamomi* is clearly associated with a large proportion of plant deaths in the jarrah forest, it is not solely responsible. For the maintenance of all jarrah forest species it is important that as many factors involved in plant mortality and survival as possible are considered. For instance, although the rate of recruitment of *Xanthorrhoea preissii* on sloping dieback sites appears to exceed the rate of death, additional pressures could shift the balance in the direction of population death. Leaf chlorosis in single branches, described above for some *Xanthorrhoea preissii* plants, is not consistent with symptoms observed in *Phytophthora*-affected plants, which are completely killed. The extent of this malaise is unknown, although shed branches in *Xanthorrhoea preissii* are common. Logging and the natural fall of tree branches would explain some shedding. If the "single branch disease" were affecting *Xanthorrhoea preissii* often and widely in the forest, its impact would be greatest on dieback sites, where infection by *P. cinnamomi* is also possible and the difference between the rate of recruitment and death is least. An additional ailment may be enough to shift *Xanthorrhoea preissii* towards local extinction. In the case of *Macrozamia riedlei*, many deaths are occurring in unaffected forest. Deaths occur in all age / size categories, in a range of canopy cover, and in burnt and unburnt vegetation. Natural causes such as cohort senescence (in the sense of Mueller-Dombois 1987), canopy gap requirements or burning effects seem unlikely to explain these deaths. Frequent deaths of *Macrozamia riedlei* in unaffected vegetation require further investigation. Although the species is susceptible to infection by *P. cinnamomi*, it is not renowned as a indicator of imminent dieback. Its death at least 50 m from the dieback front when no *Banksia grandis* were dying seems unlikely to have been caused by *P. cinnamomi*. One dead *Macrozamia riedlei* plant from unaffected vegetation at Site 23 was excavated to a depth of about 0.5 m. Fragments of stem and coralloid roots were collected and plated onto *Phytophthora*-selective agar, but *P. cinnamomi* was not recovered. This is perhaps not surprising since *P. cinnamomi* is rarely found in dead *Macrozamia riedlei* plants and the principal roots of the plant sampled were not reached. However, the plant, although severely damaged during the excavation, resprouted from the remaining stem during the following summer (Figure 3.34). None of the other dead *Macrozamia riedlei* at the

site resprouted. This may suggest that a foliar or stem apex pathogen was involved. The concentration of efforts in the forest to minimize the spread of *P. cinnamomi*, such as the application of the fungicide phosphonate, may not be effective in protecting populations of *Macrozamia riedlei*. The deaths of *Daviesia decurrens* in unaffected vegetation may also involve another pathogen, although senescence cannot be ruled out.

Figure 3.34 A *Macrozamia riedlei* resprout. The above-ground portion of the plant appeared completely dead when the stem and coralloid roots were excavated.

Drought during especially dry summers probably causes some death. Trees around granite outcrops appear particularly prone. Death from drought can be deceptive, however. Shrubs and herbs growing on and around granite outcrops regularly die off over summer but regenerate with the first rain. *Hibbertia hypericoides* displays the same deception on dieback sites. In the very dry summer of 1994 / 95, large areas of this species, the dominant of many dieback sites, died completely above ground (Figure 3.35). At the site pictured, all plants regenerated in the following June after rain in late May. The distribution of apparently dead *Hibbertia hypericoides* plants during summer had not been uniform. There were no "deaths" in unaffected vegetation and there were patches of "survivors" under marri

within the dieback zone. This is somewhat unexpected if water deficit alone is to explain the patterns because the water deficit in soils has been found to be greater under a forest canopy in summer than in the open (Stoneman et al 1995).

Figure 3.35 A dieback site in Churchman forest block in early autumn 1995 after an especially dry and hot summer. The grey shrubs in the foreground are *Hibbertia hypericoides*. All of the foliage appeared dead at that time. However, all shrubs resprouted after the first rain in May.

The evidence presented in Chapters 2 and 3 suggests that *P. cinnamomi* acts most aggressively on *Banksia grandis* at the dieback front. Other susceptible species may or may not be killed at this time, and in most species some of the population survives. Regeneration occurs of species that reproduce readily from seed. Inoculum levels of *P. cinnamomi* decline rapidly because their main food source, *Banksia grandis* roots, have almost disappeared. *Banksia grandis* seedlings are gradually removed from the vegetation. There are sporadic deaths of other susceptible species. The persistence of susceptible species originally present in the vegetation will depend on their degree of survival after the initial impact and their ability to reproduce or to be dispersed onto dieback sites, germinate and survive. Most susceptible species have demonstrated some capacity to persist despite dieback.

CHAPTER 4: THE SUSCEPTIBILITY AND SPATIAL ARRANGEMENT OF SPECIES LESS FREQUENT ON DIEBACK SITES

4.1 Introduction

Species found less frequently on pre-1951 dieback sites (Table 2.7, page 52), may be less frequent for biotic reasons (e.g. death following infection by *Phytophthora cinnamomi*), abiotic reasons (e.g. death because of environmental changes following canopy loss on dieback sites, as suggested by Wills 1993) or because differences in space were unrelated to differences in time in the space for time substitution study (Chapter 2). Of the 53 species in Table 2.7, *P. cinnamomi* has been isolated from dead plants of 14 species (Shearer and Dillon 1995) and from 18 species overall. Although *P. cinnamomi* is not necessarily the only factor involved in their decline, if indeed they have declined, it is at least a likely suspect.

In this Chapter, I investigate the distribution of some species found less frequently on dieback sites. Although the mechanisms of species decline due to structural change might require lengthy study, an association of their distribution on dieback sites with features more commonly found in unaffected vegetation (such as shade and abundant litter) might provide preliminary evidence of such an effect.

I also assess the susceptibility of a range of species found to be less frequent on dieback sites to infection by *P. cinnamomi*. The susceptibility (or non-susceptibility) of most of these species has not been reported. It is possible that they have simply been overlooked in the search for *P. cinnamomi* hosts. The small number of plants available for testing in this study greatly limited the quantitative evaluation of species susceptibility. The pathogenicity tests I performed were therefore designed to determine if species could be infected with *P. cinnamomi* and whether they could be killed in its presence. The failure to observe infection or death would not preclude *P. cinnamomi* as an agent causing decline in the species tested. Similarly, glasshouse observations of infection and death

need not mean that *P. cinnamomi* causes species decline. However, species becoming infected and dying in association with *P. cinnamomi* are likely to be worthy of greater attention in the field.

4.2 Methods

4.2.1 Spatial Distribution of Species Less Frequent on Dieback Sites

Two pre-1951 dieback sites (sites 4 and 10), where a range of species less frequent on pre-1951 dieback sites persisted, were chosen for study. *P. cinnamomi* had been isolated from *in situ Banksia grandis* baits at site 10 but not at site 4 (Table 3.2, page 84). Plot corners were first marked with flagging tape. Tree trunks were not used as plot corners. One tree at each site was assigned an arbitrary grid reference. All trees within the plots were located and numbered using a 50 m fibreglass tape and compass. Magnetic interference on the upper parts of both sites meant that all compass bearings had to be taken from the lower parts of the sites. Each tree was tied to at least two other trees as a check of its position. For each tree, diameter over bark (DOB) and crown dimensions were recorded. The plot at site 4 was determined by triangulation to be 1070 m^2 and the plot at site 10 to be 1008 m^2.

The positions of plants that were significantly less frequent (Table 2.7, including jarrah as lignotuberous seedlings) or less dense (Table 2.3) on dieback sites were located by tape and compass from trees in the lower parts of sites, where there was minimal magnetic aberration. The positions of the long-lived perennials *Macrozamia riedlei* and *Xanthorrhoea preissii* were also located. To minimize magnetic discrepancy, as few trees as possible, and mostly those which had been used for referencing other trees, were used as reference points.

Stylidium amoenum was especially abundant at site 10. Many plants of this species had recently died when the site was first inspected. Such an abundance of live and dead plants was not observed at any other pre-1951 dieback site. This allowed for other measurements to be made of its population: flowering / not flowering; dead / alive; % of litter in contact with plants.

4.2.2 Pathogenicity Tests

Pathogenicity testing of *P. cinnamomi* on species less frequent on dieback sites (Table 2.7, page 52) was limited by the availability of plants to test. Only a few species were available from Alcoa's Marrinup Nursery as nursery stock. Attempts were made to grow a range of species from seed supplied by Marrinup Nursery. Germination occurred in *Acacia urophylla, Hovea chorizemifolia, Kennedia coccinea, Labichea punctata, Stylidium junceum, Tetratheca hirsuta* (one plant) and *Thysanotus multiflorus* after application of 10% smoky water solution, which has been found to stimulate germination of a range of jarrah forest species (Dixon et al 1995). There was no germination of *Leptomeria cunninghamii, Stylidium amoenum* and *Tetrarrhena laevis*. Two species appeared in a soil seed bank trial (*Hibbertia rhadinopoda* and *Xanthosia candida*) and were used. Most species tested were transplanted from dieback-free forest, in which mining was imminent. This proved to be surprisingly successful. Plants were removed with a mattock and packed tightly into large, deep plastic trays. One layer of plants was placed in each tray. As much soil as possible was kept attached to the plants, although with the gravelly soils, some plants were effectively removed with bare roots. When this occurred, additional soil was removed and packed around the roots. The trays were watered when each transplant was added and again thoroughly when the tray was full so that the soil was saturated but no free water was visible. The following day, the transplants were potted in a commercial sand and bark potting mix and placed in a glasshouse with an automatic watering system. Plants were watered twice daily for five minutes.

Transplanting was attempted in June and November 1995. There was no obvious difference in the success of the two transplantings, although different species were removed on each occasion making comparison difficult. The only species that failed to transplant were *Patersonia babianoides* and *Trichocline spathulata*. There were a few apparent losses of other species. Although they were thrown out, they may not have been dead. *Pentapeltis peltigera* and *Clematis pubescens*, species with large underground storage organs were damaged during transplanting, wilted soon after potting but resprouted some weeks later.

Plants of *Comesperma virgatum*, which were harvested in June, shed their leaves and did not produce new shoots from the upper stems until late spring.

The species tested, their origin and stage of development are listed in Table 4.1. All species are perennials. Two types of control were used for the pathogenicity tests. The first was a control on plant health. An equal number of plants of each species tested were placed in the same glasshouse under the same conditions but not inoculated with *P. cinnamomi*. Only one plant was available for three species (*Dampiera linearis, Hibbertia huegelii* and *Lomandra caespitosa*), and so there was no control on plant health. The second control was on the pathogenicity of *P. cinnamomi*. Four species known for their susceptibility to infection (*Banksia grandis, Hibbertia commutata, Lomandra sonderi* and *Macrozamia riedlei*) and one species known for its field-resistance (marri) were included in the trial. These species vary in their field response to *P. cinnamomi* and probably therefore in their susceptibility. *Banksia grandis* and *Hibbertia commutata* (syn. *H. montana*) were found by Shearer and Dillon (1995) to be frequently infected and frequently dead on active dieback sites, *Lomandra sonderi* was frequently infected but infrequently dead and *Macrozamia riedlei* was frequently dead but *P. cinnamomi* was infrequently recovered. *Gompholobium polymorphum* and *Lepidosperma squamatum* were included in the trial because many deaths of these species had been seen at some dieback sites and they were common at the sites where transplants were obtained.

Control plants and plants to be infected were transferred to a glasshouse used for *P. cinnamomi* research in December 1995 to acclimatize prior to inoculation. The glasshouse is temperature-controlled and has an automatic watering system. Despite this, it experiences large temperature fluctuations in summer. Shadecloth was placed over the glasshouse in early summer to reduce the diurnal temperature fluctuation. Air temperature was measured hourly with four probes of a data logger for another experiment in the same glasshouse during much of the trial. 99% of hourly temperature readings were between 14.8°C and 35.8°C. The watering system failed for a week at the end of December. A few plants did not recover and were replaced. Pots were watered three times per day for 10 minutes with a 360° micro

sprayer. This was reduced to three times per day for 5 minutes in mid-April. Under this watering regime, soils were kept moist but were not waterlogged.

Table 4.1. Number of plants inoculated, source, age, and stage of development for species inoculated with *P. cinnamomi* in glasshouse trial; [a] Source: C = grown from cuttings, S = grown from seed, SS = grew in soil seed bank trial using soil collected in jarrah forest, T = transplanted from forest, X = tissue cultured; [b] Stage of development: 1 = only first few leaves present, 2 = many leaves present but not at reproductive stage, 3 = at size where flowering might occur, 4 = plant in flower prior to experiment

Species	Plants inoculated	Source [a]	Age (years)	Stage of development [b]
Acacia urophylla	5	S	0.5	2
Agrostocrinum scabrum	2	T	unknown	4
Amphipogon amphipogonoides	4	T	unknown	4
Banksia grandis	5	S	1	2
Boronia fastigiata	5	C	1	4
Clematis pubescens	2	T	unknown	4
Comesperma virgatum	2	T	unknown	3
Dampiera linearis	1	T	unknown	3
Gompholobium polymorphum	1	T	unknown	4
Hibbertia commutata	5	C	2	4
Hibbertia huegelii	1	T	unknown	1
Hibbertia rhadinopoda	2	SS	0.3	1
Hovea chorizemifolia	4	S	0.5	1
Hybanthus floribundus	3	T	unknown	4
Kennedia coccinea	4	S	0.5	2
Labichea punctata	32	S	0.5	1
Lepidosperma squamatum	3	T	unknown	4
Logania serpyllifolia	1	T	unknown	4
Lomandra caespitosa	1	T	unknown	4
Lomandra integra	1	X	2	4
Lomandra sonderi	3	T	unknown	4
Macrozamia riedlei	5	S	2	1
Marri	5	S	1.5	2
Mesomelaena graciliceps	3	T	unknown	4
Opercularia echinocephala	2	T	unknown	4
Opercularia vaginata	1	T	unknown	3
Pentapeltis peltigera	2	T	unknown	4
Scaevola calliptera	5	C	2	4
Stylidium amoenum	6	T	unknown	4
Stylidium junceum	c. 250	S	0.5	1
Tetrarrhena laevis	4	T	unknown	4
Tetratheca hirsuta	1	S	0.5	1
Tetratheca hirsuta	2	T	unknown	4
Thysanotus multiflorus	4	S	0.5	2
Xanthosia candida	1	SS	0.3	1

The soils were inoculated using *Banksia grandis* plugs. The plugs were inoculated with isolate MP 116 on the 8th of December 1995. This isolate was found to be of medium virulence by Hüberli (1995). The method of infecting *Banksia grandis* tissue for use as an inoculum source in soils was adapted from that used by Sochaki (1982). Young stems of wild *Banksia grandis* were obtained from sites in the jarrah forest where mining was imminent. The stems were cut into pieces about 3 cm in length and placed with a small amount of water into 2 l conical flasks. The flasks were autoclaved for 20 minutes at 121°C on each of three successive days. An agar plate containing a pure culture of isolate MP 116 was then added to each flask. The flasks were incubated at 23°C for seven weeks and shaken occasionally to facilitate spread of *P. cinnamomi* through the plugs. Plugs were placed in pots on the 23rd of January 1996. One half to two plugs were placed in pots depending on the size of the pots. The plugs were inserted vertically into the soil about 1 cm below the soil surface. Controls used to compare plant health were placed on a separate bench. *Kennedia coccinea*, a vigorous twining plant, was pruned whenever it began to grow over adjoining plants.

Plants were inspected every few days. When an inoculated plant died, it was removed from its pot and as much of its roots and lower stem as possible plated onto *Phytophthora*-selective agar (described in Chapter 3). Lesions were recorded. For species with obvious lesions, material was chosen for plating within and around the lesion. For species without obvious lesions, material was chosen at random. Plates were inspected over the following days for the presence of *P. cinnamomi*. It was sometimes difficult to tell when a plant was dead. A few looked in poor health compared with the controls but did not die. A few died back completely but resprouted at the same time. Plants were not harvested unless death seemed certain.

The trial was stopped 128 days after inoculation. Stem and root pieces of all plants in infected pots were then plated onto *Phytophthora*-selective agar. A portion of each inoculum plug was also plated out. The roots of control plants were inspected for comparison if there were lesions apparent on inoculated plants. Control plants were not

sampled for the presence of *P. cinnamomi*. If *P. cinnamomi* had been found in control plants, the hygiene of the experiment could have been described as poor but the results would have been unchanged. The survival of *Banksia grandis* plants on the control bench throughout the trial was strong evidence that *P. cinnamomi* was absent.

4.3 Data Analysis

4.3.1 Spatial Distribution of Species Less Frequent on Dieback Sites

The intention of this study was to determine if non-susceptible species found less frequently on dieback sites are randomly distributed or aggregated in relation to shade and litter cover. Although areas of shade might occur around fallen branches and under a range of tall plants, most would be associated with trees, since the understorey of most dieback sites is extremely sparse. The area close to trees on dieback sites would provide the most comparable environment in litter, shade, and water usage to non-dieback vegetation.

Tests for aggregation, randomness or regularity in plant populations have been devised by Ripley (1977) and Diggle (1983) and are used widely in ecology (e.g. West 1984, Hatton 1989a, Gibson and Brown 1991). Whilst these tests would assess the distribution of the species sampled against the null hypothesis of complete spatial randomness, further tests would be required to relate the distributions to those of the trees present, for it is conceivable that two species could have completely spatially random distributions while having coincident distributions. Conventional statistics have been employed in studies comparing the distribution of two entities in space. For instance, after finding that sweet briar distribution was aggregated when trees were present, Hatton (1989b) investigated the relationship between tree distribution and sweet briar dispersal units by making counts of units beneath canopies and away from canopies. Differences were analysed by t-test. Harrington et al (1981) used frequency measures to relate the distribution of species to canopy and gap in *Eucalyptus populnea* woodland. Since the

purpose of the current study was not to detect aggregation *per se*, a simple comparative statistic is probably adequate for at least a preliminary investigation of species distribution.

A simple test of randomness would be to compare the mean distance of plants of each species to their nearest trees with the mean distance of a set of random points to nearest trees. For this it is essential to have a reliable set of random numbers. The random number generator used (Microsoft Excel™ 4.0a) was tested using the simple checks described by Manly (1991). 100,000 random numbers from 0 to 1 were generated with the Excel™ function RAND. The mean, variance and correlation co-efficient of successive sets of 10,000 numbers was calculated. Chi-square statistics and their significance were determined for the frequencies of numbers in sub-sets of 0.1 for each set.

For the analysis of the spatial distribution data, a set of random grid references was generated equal in number to the total number of plants located within each sample (237 in site 4 and 2656 in site 10). Because the sample plots were irregularly shaped, I first tested trigonometrically whether a random point was within the plot. The distance of each valid random point and each species point to the nearest tree was then calculated. The random point and species distances were divided into classes of 0.25 m and tested for their goodness of fit (G-test) to a normal distribution. The null hypothesis that distances were normally distributed was rejected. This is not surprising since species are more likely to have a Poisson-like distribution. However, square root and log transformed data did not make the distribution normal. A non-parametric test (the Wilcoxon two-sample test) was therefore used to compare means.

In a study such as this, a significant difference between the mean distance of a species and a set of random points need not mean that a species is more likely or less likely to occur near trees. The problems associated with interpreting the results of spatial studies are illustrated below.

In Figure 4.1, 20 trees and 100 species have been placed randomly on a site using the Excel™ random number generator. Since the species were randomly generated, a comparison of the species with enough random points should show that the species are not clustered around the trees.

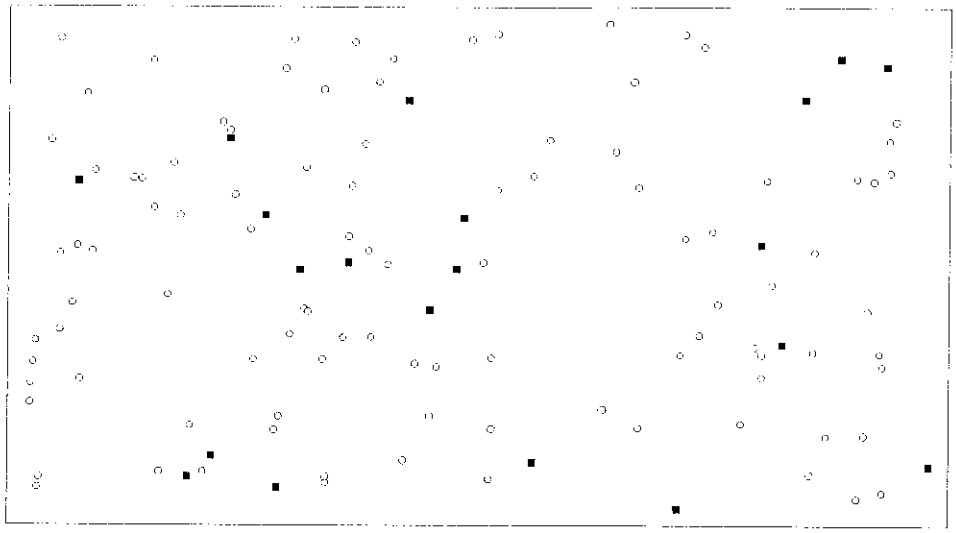


Figure 4.1 A random distribution: 20 trees (squares) and 100 individuals (circles).

However, in reality, many species, including the trees present, disperse their propagules only short distances from parent plants or spread by vegetative means. Such species will tend to have a clustered distribution. In Figure 4.2, the 100 species have been clustered into 10 groups using random seed numbers to limit their distribution to within 10 units in the x and y axes. Aggregation near trees appears possible for the hypothetical species shown.

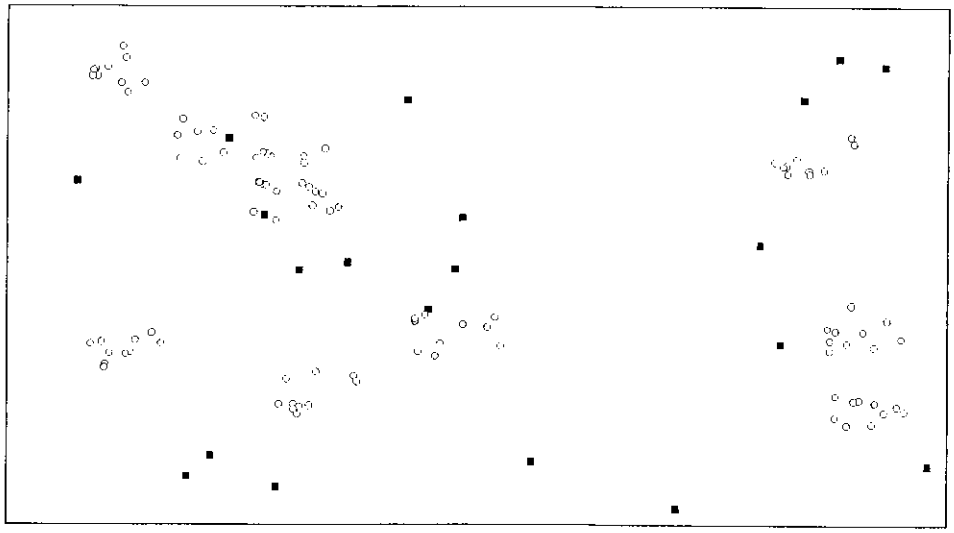


Figure 4.2 A clustered species distribution: 20 trees (squares) as in Figure 4.1 and 10 clusters each of 10 individuals (open circles).

The fewer the clusters the greater the likelihood of a significant difference being found. This is illustrated in the extreme case of a single cluster of 100 plants (Figure 4.3), again generated using random seed numbers to limit the distribution to within 10 units. In a comparison of the mean distance of this hypothetical species with the mean distance of a set of random numbers from the whole site, the difference would surely be significant, even though the position of the species may have nothing to do with the position of trees.

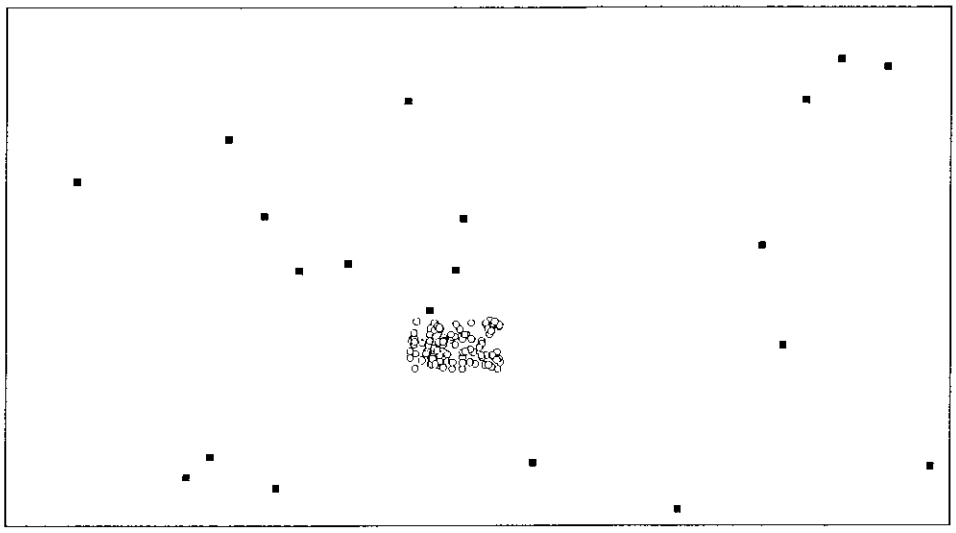


Figure 4.3 Clustered distribution: 20 trees (squares) as in Figure 4.1 and 1 cluster of 100 individuals (open circles).

The potential effect of sample edges on data interpretation is emphasized in (Figure 4.4). The 100 species positions were generated from random numbers between 0 and 100 for the x axis and random numbers between 90 and 100 for the y axis. An interpretation of the significance of the distribution of these species compared with that of random points for the whole plot is limited by the nearby boundary. That is, these species can only be adequately assessed if the distribution of trees beyond the boundary is known.

To minimize the risk of mis-interpreting the distribution of species with clustered distributions, random points were used for comparison only if they were closest to the same trees as the species. That is, comparisons between random points and species points were only made close to where the species grew. To minimize the risk of mis-interpreting the distribution of species near plot boundaries, the position of trees nearest to the boundary but outside it were also determined.

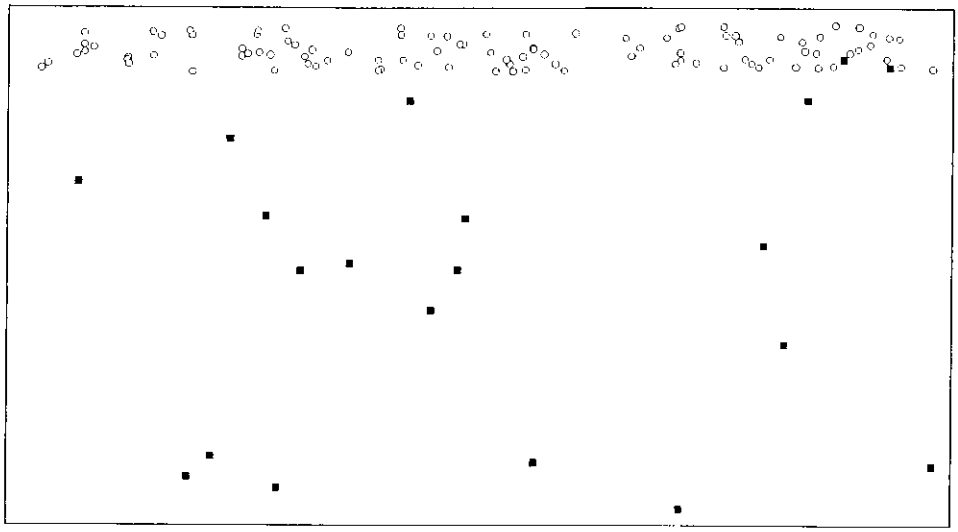


Figure 4.4 Edge effects: 20 trees (squares) as in Figure 4.1 and 100 individuals (open circles) along one edge.

4.4 Results

4.4.1 Spatial Distribution of Species Less Frequent on Dieback Sites

Random Number Generator

The Excel™ random number generator was found to be satisfactory (Table 4.2). The means and variances were close to the expected values. Six out of the ten correlation coefficients (r) were zero to two places. The largest was 0.015. The χ^2 statistic for the differences between expected and observed frequencies within 0.1 ranges were all not significantly large at $P<0.05$.

Table 4.2. Statistics for sets of 10,000 random numbers between 0 and 1 generated using the Excel™ function Rand.

	Sets of 10,000 random numbers										
	1	2	3	4	5	6	7	8	9	10	expected
mean	0.501	0.501	0.499	0.503	0.501	0.497	0.500	0.503	0.499	0.497	0.500
variance	0.084	0.082	0.084	0.084	0.083	0.083	0.083	0.083	0.084	0.083	0.083
r	-0.00	0.00	0.00	0.00	-0.01	-0.00	0.01	-0.02	-0.01	0.00	0.00
χ^2	10.3	5.0	2.5	13.0	14.9	9.0	8.6	16.0	7.1	7.1	< 16.9

Species Distributions

Fifteen of the 19 species measured on sites 4 and 10 occurred closer to trees than expected (Table 4.3). The fifteen species included two (*Lomandra sonderi* and *Platysace compressa*), which are known to be susceptible to infection by *P. cinnamomi.* All species measured at both sites, except *Xanthosia candida*, were either significantly closer to trees or not significantly closer to trees at both sites. The four species not significantly closer to trees than random points (*Adenanthos barbiger*, jarrah (lignotuberous seedlings), *Macrozamia riedlei* and *Xanthorrhoea preissii*) are known to be susceptible to infection by *P. cinnamomi.* No species was significantly further from trees than the set of random points used for comparison.

Table 4.3. Average distance (m) to nearest tree for species and random points; n = number of points used in test; significance of difference as determined by Wilcoxon two sample test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	SITE 10					SITE 4				
	species		random pt.			species		random pt.		
Species	dist.	n	dist.	n		dist.	n	dist.	n	
Adenanthos barbiger	3.11	*82*	3.21	*1895*		4.25	*16*	4.07	*181*	
Agrostocrinum scabrum	1.93	*41*	2.71	*678*	**					
Amphipogon amphipog.	2.04	*180*	3.17	*1848*	***	2.98	*17*	4.33	*60*	*
Boronia fastigiata	1.94	*24*	3.09	*953*	***					
Jarrah (seedlings)	3.41	*146*	3.30	*2303*		3.12	*8*	4.20	*63*	
Hovea chorizemifolia	2.32	*73*	3.05	*1610*	***	2.46	*46*	3.88	*135*	***
Logania serpyllifolia	2.03	*25*	3.12	*296*	***					
Lomandra sonderi	2.65	*99*	3.24	*1949*	**					
Macrozamia riedlei	4.24	*14*	3.61	*831*						
Opercularia echinocephala	2.11	*83*	3.20	*1541*	***					
Opercularia vaginata						2.24	*21*	4.45	*112*	***
Pentapeltis peltigera	2.05	*83*	3.06	*1468*	***	2.57	*35*	3.84	*82*	**
Platysace compressa	2.22	*77*	3.15	*1862*	***					
Scaevola calliptera	2.69	*84*	3.56	*428*	***					
Stylidium amoenum	2.34	*763*	3.16	*2313*	***	2.67	*12*	4.49	*30*	**
Stylidium junceum	1.94	*44*	3.14	*851*	***					
Trichocline spathulata						2.19	*33*	3.99	*132*	***
Xanthosia candida	2.33	*88*	3.09	*1217*	***	3.15	*31*	4.11	*94*	
Xanthorrhoea preissii						4.81	*16*	4.45	*152*	

The distributions of species not associated with trees and species associated with trees are shown for site 4 in Figures 4.5 and 4.6 respectively.

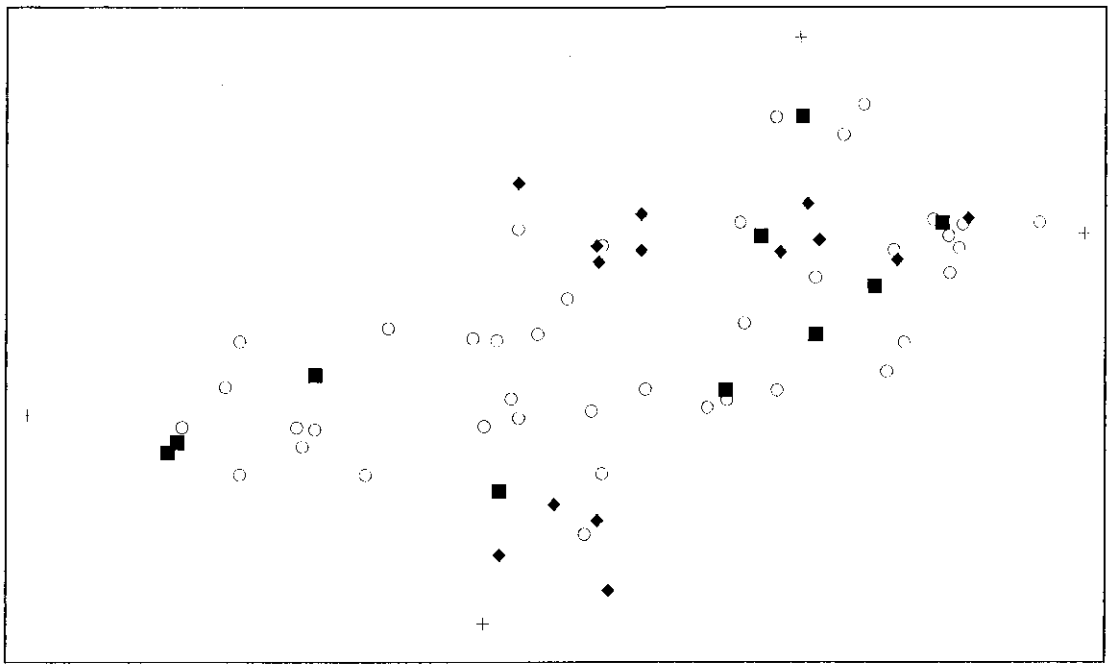


Figure 4.5 Species not associated with trees at site 4 (*Adenanthos barbiger*, jarrah seedlings, *Xanthorrhoea preissii*). ■ Trees > 20 cm DOB; ◆ Trees ≤ 20 cm DOB; O Plants of species listed; + Plot corners. Scale (approx.) 1 : 400

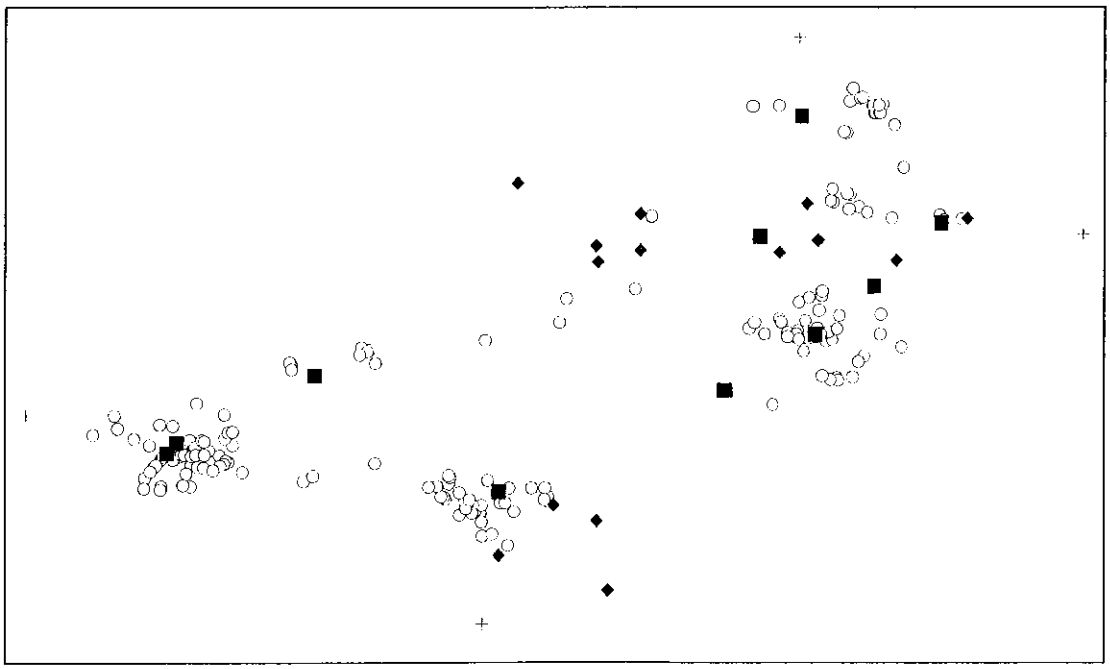


Figure 4.6 Species associated with trees at site 4 (*Amphipogon amphipogonoides, Hovea chorizemifolia, Opercularia vaginata, Pentapeltis peltigera, Stylidium amoenum, Trichocline spathulata, Xanthosia candida*). ■ Trees > 20 cm DOB; ◆ Trees ≤ 20 cm DOB; O Plants of species listed; + Plot corners. Scale (approx.) 1 : 400

Species Distributions and Tree Size

As discussed in Chapter 3, the diameter over bark at breast height (DOB) of trees that established on pre-1951 dieback sites after the dieback event is unlikely to be much more than 20 cm. To test if the species that grow closer to trees than expected also grew closer to trees that were probably on the site at the time of dieback than to trees that had probably established since dieback, the number of trees with DOB > 20 and DOB ≤ 20 closest to species with significant differences in Table 4.3 (observed) and random points (expected) was calculated. The significance of differences between observed and expected was determined by a G-test for goodness of fit. The differences were significant at both sites (Table 4.4). The species that grow significantly closer to trees than expected also grow closer to trees of DOB > 20 cm than expected.

Table 4.4. Goodness of fit (G-test) for observed number of plants significant in Table 4.3 that were closest to trees of ≤ 20 cm DOB or > 20 cm DOB versus expected DOB values as determined by proportioning random points; * $P < 0.05$, ** $P < 0.01$.

	DOB ≤ 20 cm		DOB >20 cm			Random
	observed	expected	observed	expected		points
Site 4	22	42	142	125	**	237
Site 10	803	848	861	816	*	2656

Species Distributions and Tree Type

To test if the significant species grow closer to one species of tree (jarrah or marri), the G-test of goodness of fit was used to assess the significance of differences between the number of significant species closest to each tree (observed) and the number of random points closest to each tree (expected) (Table 4.5).

Table 4.5. Goodness of fit (G-test) for number of significant species and random points closest to species of nearest tree; * $P < 0.05$.

	Jarrah		Marri			Random
	observed	expected	observed	expected		points
Site 4	27	28	137	136		237
Site 10	826	777	838	887	*	2656

At site 10, species that were found to grow closer to trees than expected also grow closer to jarrah than to marri. Such a difference might occur naturally if the marri happened to be arranged at the edge of large treeless areas. In this case, the average distance of random points to the closest marri would be greater than the average distance of random points to jarrah. At site 10 this is not so. The average distance of random points to their closest marri is 3.20 m compared with 3.18 m to jarrah. The two values are not significantly different as determined by a Wilcoxon two sample test. At site 10 the apparent occurrence of tree-aggregated species closer to jarrah than to marri is either real or co-incidental.

Stylidium amoenum *Survival and Flowering*

Live plants of *Stylidium amoenum* were more likely to occur close to trees than were dead plants (Table 4.6). Mean litter cover was greater around live plants (83%) than around dead plants (65%). This might be expected since live plants occurred closer to trees and therefore a large source of litter.

Table 4.6. Mean distance of live and dead *Stylidium amoenum* to nearest tree. Significance of difference determined by Wilcoxon two sample test.

	Distance (m)	n
Live Plants	2.34	763
Dead Plants	3.09	233
	P<0.001	

Plants of *Stylidium amoenum* were more likely to flower near trees in the spring of 1995 than away from trees (Table 4.7). 29% of plants flowered.

Table 4.7. Mean distance of flowering and non-flowering *Stylidium amoenum* to nearest tree. Significance of difference determined by Wilcoxon two sample test.

	Distance (m)	n
Flowering Plants	1.97	222
Non-flowering Plants	2.49	541
	P<0.01	

4.4.2 Pathogenicity Tests

The first death after inoculation occurred in *Hibbertia rhadinopoda*. If *P. cinnamomi* was present in dead plants, it was isolated from at least half of the plant segments plated for all species, except *Lomandra sonderi*, in which *P. cinnamomi* seemed to be rare (Figure 4.7).

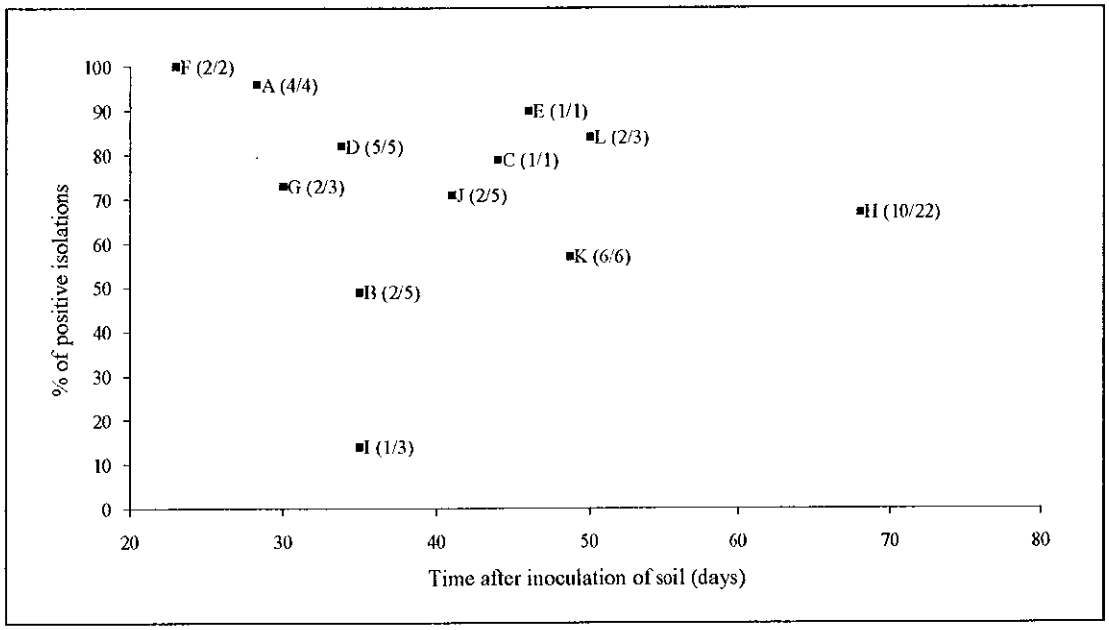


Figure 4.7 Chronology of plant deaths in which *P. cinnamomi* was isolated. The mean time after inoculation (days) is plotted against the % of plant pieces plated onto selective agar from which *P. cinnamomi* grew. Species: A *Banksia grandis*; B *Boronia fastigiata*; C *Gompholobium polymorphum*; D *Hibbertia commutata*; E *Hibbertia huegelii*; F *Hibbertia rhadinopoda*; G *Hybanthus floribundus*; H *Labichea punctata*; I *Lomandra sonderi*; J *Scaevola calliptera*; K *Stylidium amoenum*; L *Tetratheca hirsuta*. The number of plants containing *P. cinnamomi* and the total number of plants inoculated are shown in parentheses

Deaths were recorded in 15 out of the 34 species tested (Table 4.8). *P. cinnamomi* was isolated from dead plants of 13 species and from 25 species overall. *P. cinnamomi* was isolated from three of the positive controls (*Banksia grandis, Hibbertia commutata* and *Lomandra sonderi*) but also from the negative control (marri). It was not isolated from *Macrozamia riedlei*, a species found to contain *P. cinnamomi* in dead plants in the field (Shearer and Dillon 1995). The presence of lesions did not guarantee *P. cinnamomi* isolation, although it was certainly isolated from most lesioned areas. The only species, with more than one plant inoculated, for which all plants died and *P. cinnamomi* was isolated from them were *Hibbertia commutata, Hibbertia rhadinopoda* and *Stylidium amoenum*.

Table 4.8. The number of plants and plant pieces testing positive (+ve) for *P. cinnamomi* from plants that died or survived during the pathogenicity test. Plant pieces refers to the number of plant parts plated onto selective agar. [a] One *Banksia grandis* plant did not die. It was retained for cloning for its potential resistance to *P. cinnamomi*. [b] Live *Stylidium junceum* plants were not plated out. There were more than 250 plants in the tray. [c] Grown from seed. [d] Transplants. § indicates a species that was not known to be susceptible to infection by *P. cinnamomi*.

	Died				Survived			
	Plants		Plant pieces		Plants		Plant pieces	
Species	total	+ve	total	+ve	total	+ve	total	+ve
Acacia urophylla §					5	2	43	3
Agrostocrinum scabrum §					2	2	30	15
Amphipogon amphipogonoi. §					4	0	82	0
Banksia grandis	4	4	77	74	*a*			
Boronia fastigiata §	2	2	34	33	3	1	44	6
Clematis pubescens §					2	0	30	0
Comesperma virgatum §	1	0	22	0	1	1	5	2
Dampiera linearis					1	0	11	0
Gompholobium polymorph. §	1	1	22	18				
Hibbertia commutata	5	5	125	104				
Hibbertia huegelii §	1	1	20	18				
Hibbertia rhadinopoda §	2	2	19	19				
Hovea chorizemifolia §					4	1	39	1
Hybanthus floribundus §	3	2	25	11				
Kennedia coccinea	1	0	15	0	3	2	57	7
Labichea punctata §	22	10	33	22	10	0	49	0
Lepidosperma squamatum §					3	0	47	0
Logania serpyllifolia §					1	1	4	1
Lomandra caespitosa §					1	1	16	2
Lomandra integra §					1	1	14	1
Lomandra sonderi	1	1	29	4	2	0	42	0
Macrozamia riedlei					5	0	85	0
Marri					5	3	74	12
Mesomelaena graciliceps §					3	0	50	0
Opercularia echinocephala					2	0	28	0
Opercularia vaginata §					1	0	18	0
Pentapeltis peltigera §					2	0	15	0
Scaevola calliptera §	2	2	84	60	3	0	75	0
Stylidium amoenum §	6	6	115	66				
Stylidium junceum §	50	19	50	19	*b*			
Tetrarrhena laevis §					4	2	50	3
Tetratheca hirsuta [c]	1	1	10	9				
Tetratheca hirsuta [d]	1	1	15	12	1	0	13	0
Thysanotus multiflorus §					4	2	46	2
Xanthosia candida					1	0	2	0

P. cinnamomi was isolated from 21 of the 27 species tested that were found less frequently on pre-1951 dieback sites. This includes *Lomandra caespitosa* and *Lomandra integra*, which are part of the *Lomandra caespitosa* "group" recognised in Chapter 2. Sixteen of the 20 species were not previously known to be susceptible to infection by *P. cinnamomi*. Seven of these 16 species died during the trial and *P. cinnamomi* was isolated from them.

P. cinnamomi was isolated from all inoculated *Banksia* plugs after the trial.

4.4.3 Symptoms of Plants in Inoculated Soils

Acacia urophylla (MIMOSACEAE)

The leaves of all inoculated plants and some control plants developed yellow spots during the trial. There were no deaths. *P. cinnamomi* was isolated from two of the five plants.

Agrostocrinum scabrum (LILIACEAE)

The inoculated plants died back completely during the trial but resprouted. The control plant did not die back. The leaves of the inoculated plants were beginning to discolour when the trial was stopped. At that time, the base of the stems was very discoloured compared with the control plant. *P. cinnamomi* was isolated from both plants.

Amphipogon amphipogonoides (POACEAE)

One inoculated plant died back substantially but slowly. It had very few green leaves by end of trial. This plant had many blackened roots, which tested negative for *P. cinnamomi*. Other plants showed no apparent symptoms. All plants tested negative for *P. cinnamomi*.

Banksia grandis (PROTEACEAE)

Four of the five plants in inoculated soil developed massive lesions (Figure 4.8). Within a few days of the appearance of the lesions above the soil surface, the plants died and *P. cinnamomi* was readily isolated from root and stem tissue. These plants had died within 35 days of inoculation. One plant failed to die during the trial and showed no symptoms

of infection. Its inoculum plug tested positive at the end of the trial. The plant was set aside for its possible resistance to *P. cinnamomi* infection. It was still alive nine months after inoculation.

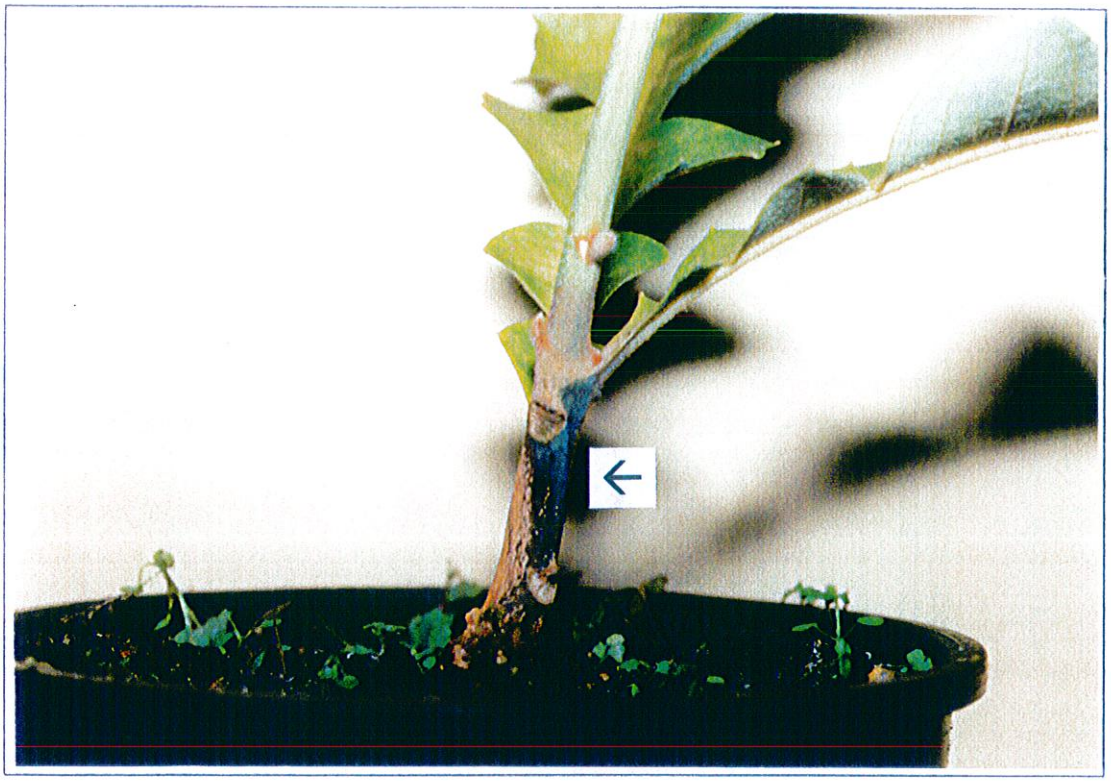


Figure 4.8 A lesion (indicated with an arrow) at the stem base of a *Banksia grandis* plant. The leaves lost their greenness the day after the photo was taken and *P. cinnamomi* was isolated from all pieces of stem and root plated onto selective agar.

Boronia fastigiata (RUTACEAE)

Two inoculated plants died very suddenly. Within one day they shed their leaved and lost turgour. Although the roots of this species are light coloured, lesions were not obvious yet *P. cinnamomi* was found in most root pieces randomly selected for plating. The other inoculated plants remained healthy, although one of these tested positive for *P. cinnamomi*.

Clematis pubescens (RANUNCULACEAE)

Both inoculated plants died back completely soon after inoculation but resprouted. The larger of the two plants had substantial darkening of its tuber and some roots when it was harvested but tested negative for *P. cinnamomi*.

Comesperma virgatum (POLYGALACEAE)

Both inoculated plants died back during the trial, gradually shedding leaves from the top to the bottom. It was difficult to tell when the plants were dead as the control plant also died back before resprouting from the stem. One of the inoculated plants was harvested during the trial and the other at the end of the trial. The one that was harvested at the end of the trial had resprouted after dying back. At the end of the trial it was beginning to shed leaves again and tested positive for *P. cinnamomi*. The first plant harvested tested negative for *P. cinnamomi*.

Dampiera linearis (GOODENIACEAE)

There was no control plant for this species. However, the inoculated plant appeared healthier at the end of the trial than at the beginning, when it was still recovering from transplanting. *P. cinnamomi* was not isolated although the entire plant was plated.

Gompholobium polymorphum (FABACEAE)

The one inoculated plant died and had lesions on its roots and lower stem. *P. cinnamomi* was found in most root and stem pieces plated onto agar.

Hibbertia commutata (DILLENIACEAE)

All inoculated plants died and yielded *P. cinnamomi*. Leaf discolouration was gradual and it took several weeks from first symptoms to complete death. The roots and lower stem of infected plants were completely blackened within, unlike the control plants.

Hibbertia huegelii (DILLENIACEAE)

This species showed similar symptoms to *Hibbertia commutata*. Death was slow and *P. cinnamomi* isolated from the majority of roots and stem.

Hibbertia rhadinopoda (DILLENIACEAE)

Death in both plants of this species was rapid. The roots and stems were lesioned and all pieces plated onto selective agar returned *P. cinnamomi*.

Hovea chorizemifolia (FABACEAE)

The inoculated plants and controls, which were at the seedling stage, did not grow during the trial. The leaves of three of the four inoculated plants were chlorotic when harvested but the control plants were also chlorotic. *P. cinnamomi* was isolated from a single piece of one inoculated plant.

Hybanthus floribundus (VIOLACEAE)

Plants of this species were in poor condition after transplanting. The control plant died several weeks after the inoculated plants so it was not surprising that *P. cinnamomi* could not be isolated from one of the plants in inoculated soil, yet had been readily isolated from the others. *P. cinnamomi* was recovered from roots with obvious lesions (Figure 4.9).

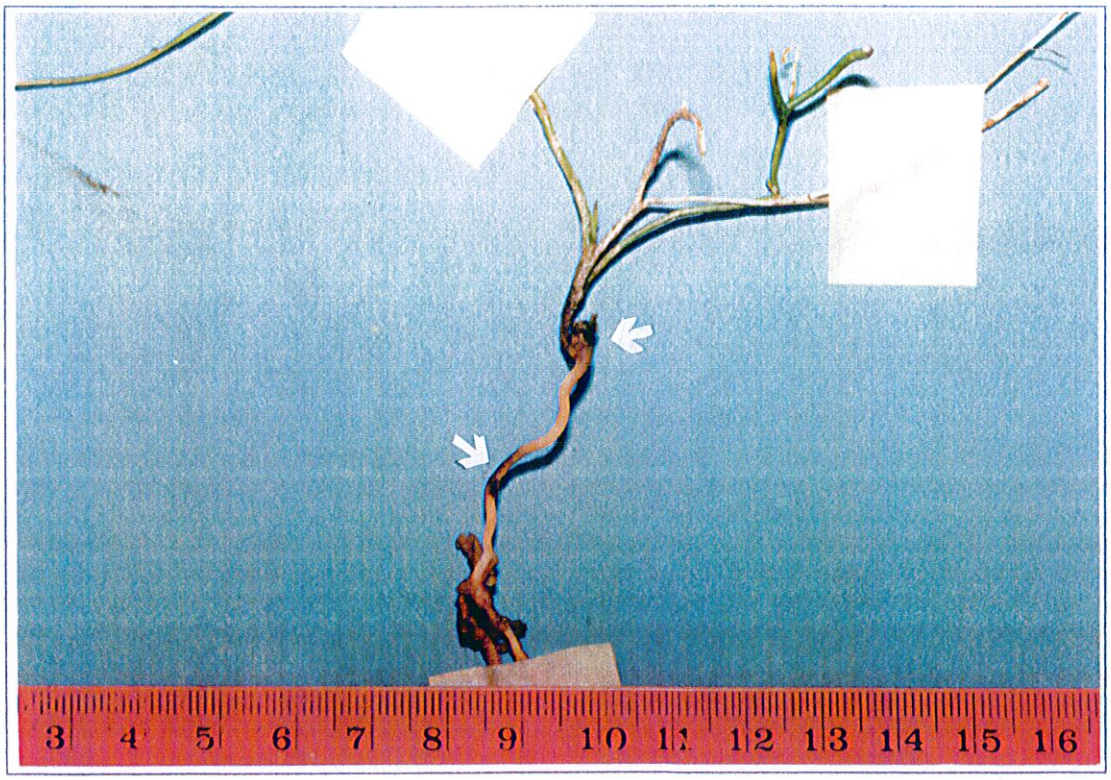


Figure 4.9 The root (with periderm removed) and lower stem of *Hybanthus floribundus*. *P. cinnamomi* was isolated from the lesioned area in the middle portion of the root and at the base of the stem (indicated by arrows). Part of the stem remained green although all of the plant's leaves had withered and been shed.

Kennedia coccinea (FABACEAE)

One plant in inoculated soil apparently died early in the trial, although on closer examination there was some green tissue left and the plant may have recovered had it been left. All but one of plants in inoculated soil had chlorotic leaves throughout the trial. However, many of the control plants, and others that had been germinated at the same time, were equally chlorotic. *P. cinnamomi* was found in two of the three plants that survived the inoculation.

Labichea punctata (CAESALPINIACEAE)

This species was grown from seed with about 10 seedlings per tube. Tubes were inoculated six months after germination. Control and inoculated seedlings were chlorotic throughout the trial and grew slowly. The only difference between control and inoculated plants at the time of harvest, was that the latter had shed some of their leaves. *P. cinnamomi* was only isolated from plants that shed their leaves during the trial and were assumed to have died.

Lepidosperma squamatum (CYPERACEAE)

Some leaves died on inoculated and control plants. Otherwise, plants remained healthy and *P. cinnamomi* could not be located in tissue plated onto selective agar.

Logania serpyllifolia (LOGANIACEAE)

The single plant inoculated died back completely above ground twice and resprouted. The second resprout was less vigorous than the first and had become chlorotic by the end of the trial. *P. cinnamomi* was found in one root.

Lomandra caespitosa (XANTHORRHOEACEAE)

The inoculated plant appeared healthy throughout the trial and flowered during summer. Some roots of its massive root system were discoloured but not obviously lesioned. There was no control plant for this species to see if the root discolouration found was unusual. *P. cinnamomi* was isolated .

Lomandra integra (XANTHORRHOEACEAE)

Although the inoculated plant appeared healthy when harvested at the end of the trial, most of its root tips were blackened. Only one of 14 root pieces yielded *P. cinnamomi*. The control plant did not have similar root discolouration.

Lomandra sonderi (XANTHORRHOEACEAE)

There was some leaf death in two of the three inoculated pots but none in the control pots. The plant that was harvested during the trial was found to be not completely dead. It had several dead shoots but a new healthy shoot was about to emerge. *P. cinnamomi* was isolated from only four of 29 pieces plated onto selective agar from this plant.

Macrozamia riedlei (CYCADACEAE)

One plant growing in inoculated soil had a completely rotten secondary tap root. *P. cinnamomi* could not be isolated from the rotten tissue or surrounding tissue or from the other plants inoculated.

Marri (MYRTACEAE)

Inoculated plants remained healthy. There was some localised darkening of roots but this did not appear to be associated with detection of *P. cinnamomi*. *P. cinnamomi* was isolated from three of the five plants.

Mesomelaena graciliceps (CYPERACEAE)

This species responded poorly to transplanting, although none of the inoculated plants or control plants died. There was no observable difference between inoculated and control plants and *P. cinnamomi* could not be isolated.

Opercularia echinocephala (RUBIACEAE)

The two plants growing in inoculated soil flowered during the trial. They displayed no obvious signs of stress and *P. cinnamomi* was not isolated.

Opercularia vaginata (RUBIACEAE)

The single inoculated plant grew progressively healthier during the trial as it recovered from transplanting. *P. cinnamomi* could not be found in plated tissue.

Pentapeltis peltigera (APIACEAE)

Both plants in inoculated soil died back after transplanting, as had the control plant. All three recovered and flowered over summer during the trial. The lower half of the tuber of one of the inoculated plants was rotten when harvested. The tissue was soft and mushy and there was very little root material emanating from it. The entire root and tuber system of this plant were plated out but *P. cinnamomi* was not isolated.

Scaevola calliptera (GOODENIACEAE)

This species had a massive root system, which produced many new shoots. The two plants from which *P. cinnamomi* was isolated took a long time to die completely. Some shoots would die while others remained apparently unaffected. The roots were not obviously lesioned but were entirely a different colour from control plant roots. *P. cinnamomi* was not found in the small sample of roots from live plants plated out at the end of the trial.

Stylidium amoenum (STYLIDIACEAE)

All plants died centrifugally. The leaf bases first lost all pigment. The outer parts of the leaves then became chlorotic over a period of one to two weeks (Figure 4.10). Infected tissue was obviously discoloured, especially in the stem and upper root. *P. cinnamomi* was found in more than half of the root and stem pieces plated onto selective agar.

Stylidium junceum (STYLIDIACEAE)

Infection of soil for this species was done in a tray of about 250 seedlings. Although all seed had been planted at the same time and emergence occurred over a short period, plant size varied enormously. Many small and large plants died during the trial. Dead plants harvested during the first two months of the trial tested negative for *P. cinnamomi*. No further dead plants were harvested until the trial was stopped. Most then tested positive for *P. cinnamomi*. The leaves of dead plants first became chlorotic, then orange to brown before they fell off. Live plants were not plated out at the end of the trial.

Figure 4.10 (a) A healthy (control) plant of *Stylidium amoenum*.

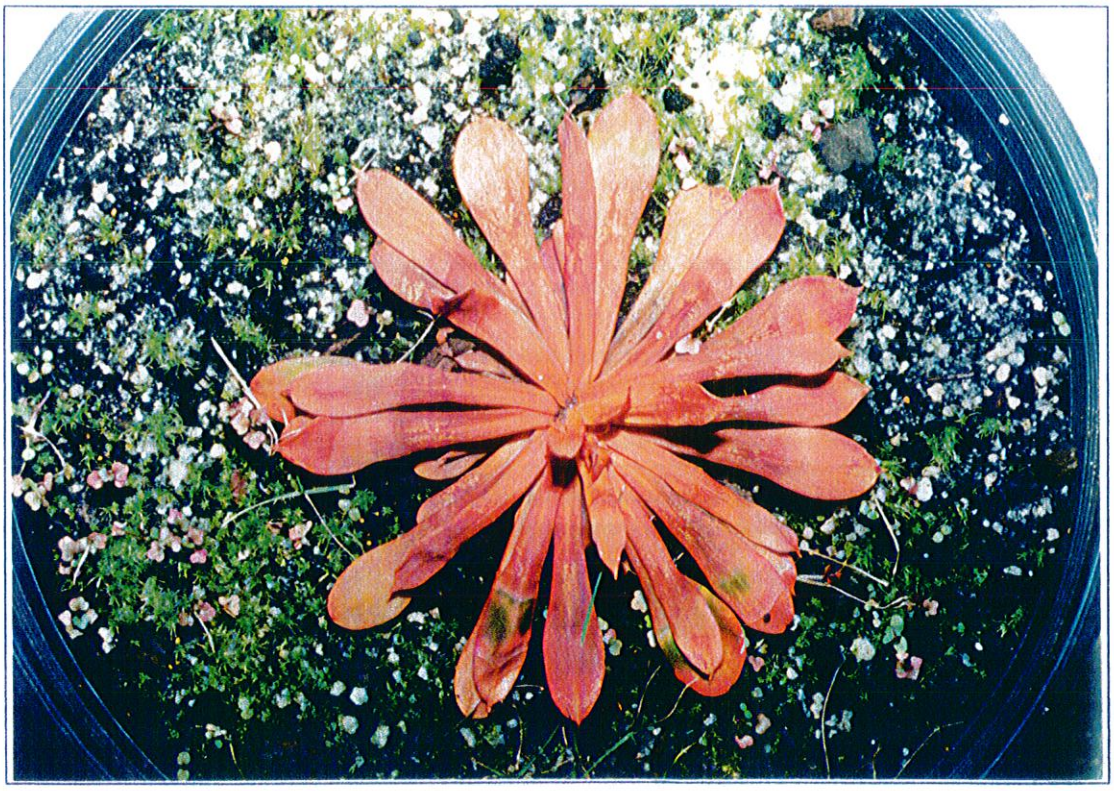


Figure 4.10 (b) A dead plant of *Stylidium amoenum* that had been growing in soil inoculated with *P. cinnamomi*. *P. cinnamomi* was isolated from the stem and roots.

Tetrarrhena laevis (POACEAE)

Soil-inoculated and control plants grew vigorously and some flowered. There were no deaths. The root tissue of plants in inoculated soil had discoloured patches but these were not obviously associated with *P. cinnamomi* when the agar plates were inspected. *P. cinnamomi* was isolated from two of four plants tested.

Tetratheca hirsuta (TREMANDRACEAE)

Two inoculated plants died. One had been grown from seed, the other transplanted. *P. cinnamomi* was isolated from most of the plant pieces plated. Lesions on roots and lower stem were obvious. Death occurred suddenly, following chlorosis of the leaves, which were quickly shed. A third inoculated plant obtained by transplanting did not die and *P. cinnamomi* could not be isolated from it.

Thysanotus multiflorus (LILIACEAE)

None of the inoculated or control plants died. All put on abundant growth during the trial. Although *P. cinnamomi* was isolated rarely from plants from inoculated soil, there were clear differences between infected and control plants. The leaf tips of plants in infected soil withered and many roots of these plants had patches of dark tissue. P. cinnamomi was isolated from two of the four plants in inoculated soil.

Xanthosia candida (APIACEAE)

The soil-inoculated and control plants both appeared healthy at the end of the trial. *P. cinnamomi* was not isolated.

4.5 Discussion

The propositions outlined at the beginning of this Chapter, that species less frequent on dieback sites but not known to be susceptible to infection by *P. cinnamomi* could be either susceptible to infection by *P. cinnamomi* or affected by structural site changes, proved not to be mutually exclusive. Some species appear to be both susceptible to infection by *P. cinnamomi* and spatially arranged close to the former structural

dominants on dieback sites. This could mean either that such species are affected by *P. cinnamomi* and structural changes or that structural changes exacerbate the effects of *P. cinnamomi*. The latter proposition is attractive because it suggests that the activity of *P. cinnamomi* is less under trees, and old trees in particular. Suppression of *P. cinnamomi* activity by litter application, and the increased antagonistic microbial activity which it puts into the soil, has been demonstrated by Nesbitt et al (1979) and Duncan (1994). Litter is only abundant on old dieback sites around trees, and the older and larger the tree, the more litter is usually generated. Whilst *P. cinnamomi* suppression associated with litter may occur on dieback sites, changes to the physical environment in addition to the activity of *P. cinnamomi*, where it persists, seem more likely to explain the deaths of a species such as *Stylidium amoenum* on dieback sites. Multiple deaths of this species were observed in a tree clearing trial on a site (in Torrens Road, north of Dwellingup) where *P. cinnamomi* was presumed to be absent (Figure 4.11).

Figure 4.11 Clumps of dead *Stylidium amoenum* at an experimental site in Torrens Road north of Dwellingup. The majority of trees had been removed. *P. cinnamomi* was presumed to be absent.

4.5.1 Spatial Distribution of Species Less Frequent on Dieback Sites

The current distribution of some understorey species on dieback sites may be related to the survival of canopy species following the initial dieback event. These understorey species were found to grow closer to trees that were likely to have been present at that time of dieback. When the size of the canopy of these trees is considered, the significance of finding that some species grow closer to large trees than to small trees must be much greater. The canopy of trees with DOB > 20 cm was 4.6 times greater in area on average at site 10 than the canopy of trees with DOB ≤ 20 cm. If the tree-aggregated species had been responding to differences in shade alone, they should logically have been further from the large DOB trees than the small DOB trees, since all measurements of species positions were made to tree trunks.

Healthy plants of most of the species found to occur near trees also grew at great distance from trees at both sites, in spaces under logs with minimal litter cover and beneath tall *Xanthorrhoea preissii* plants. This suggests that the trees alone are not responsible for the spatial segregation. The logs are likely to have been on the site since soon after the dieback event, which occurred in the 1940s. Extensive salvage logging occurred in the vicinity in the 1950s. The tall *Xanthorrhoea preissii* plants would certainly have been present at the time of dieback, based on the relationship between age and stem height (Lamont and Downes 1979). It is possible that the persistence of species found to grow close to trees is a function of the persistence of objects (including trees, other long-lived plants and logs) that provide shade following dieback.

The distributions recorded may arise because plants of some species die when exposed to an altered light and temperature environment. The greater mortality of *Stylidium amoenum* with increasing distance from trees is evidence for such a process. Alternatively, the segregation of these species may relate to their failure to recruit. *Stylidium amoenum* flowered less with increasing distance from trees. Presumably, less

seed of this species would fall onto soils away from trees as a consequence, decreasing its likelihood of germination, establishment and persistence.

Removal of the tree layer increases the quantity of light reaching the forest floor (Stoneman et al 1995) and its quality (e.g. Oleson 1992, Endler 1993), increases fluctuations in temperature and moisture at the soil surface (Shea 1977), diminishes litter production and reduces the protection of understorey plants and soils from forces such as wind, frost and heavy rain or hail. These changes in the physical and biological environment may lead to plant population changes in a multitude of ways. Differences in light environment may effect plant survival, growth, susceptibility to fungal attack (Grime 1966) and germination (Rokich and Bell 1995). Plant processes such as germination, rate of growth, time of emergence and flowering may be linked to soil and air temperature (Collins et al 1985). On dieback sites in the jarrah forest, a raised soil surface temperature might also increase the period of *P. cinnamomi* activity amongst plants with shallow roots. Extreme summer temperatures at the soil surface might be lethal to seeds unprotected by the litter or gravel mulch. The greatest fluctuations resulting from evaporation are likely to occur at the surface, and so drought might be experienced mostly by shallow rooted species (mainly herbs) on dieback sites in summer. Litter may be important to plants for its mulching qualities, which reduces temperature and water content fluctuations of surface soil, its nutrient store, which will ultimately be cycled to living plants (Facelli and Pickett 1991), and its shading of seeds, many of which have a dark requirement for germination in the jarrah forest (Rokich and Bell 1995). Erosion by wind and rain, which clearly occurs to a larger extent on dieback sites than unaffected forest, is likely to remove much of the seed stored in the organic rich top few mm of soil. This would have greatest effect on any species that die as a result of the initial dieback impact, from *P. cinnamomi* or canopy loss, and rely on soil-stored seed for regeneration.

The measures of spatial arrangement used in the present study are likely to be extremely simplistic. The light environment on the forest floor around a single tree in isolation will change with the time of day and the time of year. The light environment around many, irregularly arranged trees will be extraordinarily complex. Microtopography and an

uneven distribution of ground flora and litter add significantly to the complexity. There appeared to be some evidence on site 10 of plant pattern associated with an uneven light environment. Around one tree with large canopy gaps to the west and north, the canopy dependent understorey species measured occurred commonly on the western side of the tree but rarely on the northern side. The northern side would have been in full sun for most of the day during all of the year. The western side would have been shaded until early afternoon during summer.

Many studies of patch dynamics in northern hemisphere forests have reported an increase in species diversity, cover or abundance following the creation of artificial or natural canopy gaps (e.g. Davison and Forman 1982, Metzger and Schultz 1984, Monk and Gabrielson 1985, Moore and Vankat 1986, Collins and Pickett 1988, Hughes et al 1988, Rieners 1992). Such increases are attributed to the sudden availability of additional resources. The fluctuating populations produce pattern in the forest, which can be related to disturbance frequency, duration and size. Few studies seem to have found or suggested that canopy opening might be detrimental to some species (e.g. Davison and Formann 1982, Collins et al 1985). At first, the occurrence of many canopy-dependent understorey species in the jarrah forest would seem to indicate that plant-disturbance processes are different there from those operating in some northern hemisphere forests. This need not be the case, however. Firstly, the presence of light intolerant species does not preclude detrimental effects occurring after natural opening of the canopy. Plant losses need only be temporary and invasion could occur from peripheral shaded habitat. Alternatively, and more likely, canopy gap creation need not result in many or any plant deaths. If it did, the species identified in this study that grow near trees would be far less common in the forest than they appear now to be because the majority of the forest has been logged twice. However, the jarrah forest has at least two gap species, which limit the duration of the gap. The first is jarrah. In mature forest, there is a latent population of lignotuberous jarrah seedlings, which are well placed to make use of the newly available resources when space becomes available. The seedlings may be long-lived (Abbott and Loneragan 1986). Their well-developed lignotuber enables them to survive periodic fires.

The second gap species is *Banksia grandis* (see Chapter 2, Discussion). This species is fast growing and may become very dense in open canopy sites. On sites where *Banksia grandis* is already abundant, the fall or senescence of a mature jarrah or marri would not necessarily create much of a gap for understorey species. Most fires would have only a short-term impact on canopy gap size. Rapid regeneration of eucalypt foliage, the release and germination of serotinous *Banksia grandis* seeds, the resprouting of *Banksia grandis* in cool and moderate fires, and the activation of short-lived leguminous shrubs quickly close the canopy, at least for ground flora species. The presence of a productive middle storey and an upper storey that responds rapidly to disturbance has probably long-protected gap-sensitive understorey species. The susceptibility of both of these storeys to *P. cinnamomi* has exposed understorey species to a light environment that is naturally rare and short in duration in the jarrah forest.

For most species, a distribution closer to trees than expected on dieback sites is probably related to structural changes following dieback. *Lomandra sonderi* may be an exception. It is often found growing in rings around stumps and stump holes on dieback sites and unaffected sites. This might suggest that it is dispersed by birds or some other animal that has an association with trees.

Three of the four species that did not grow closer to trees than expected are known to be long-lived: jarrah (lignotuberous seedlings), *Macrozamia riedlei* and *Xanthorrhoea preissii*. The independence of the position of the latter two species is logical. Old plants would have established in their current position before some of the current trees to which measurements were made. The pattern of lignotuberous jarrah seedlings, however, is not intuitive. Offspring of plants establish close to their parents unless they are dispersed by some agent such as wind or animals. Such dispersal mechanisms have not been reported in jarrah, although ants and mammals do gather and consume much of the seed produced (Abbott and Loneragan 1986) and seed falling from lateral branches at great height might be expected to land some distance from the parent trunk. The distribution of the lignotuberous jarrah seedlings might be explained by the processes of germination and

germinant survival. Stoneman and Dell (1994) found that jarrah seed germinated more readily under a forest canopy. However, seedling mortality is less when the canopy is removed (Stoneman et al 1994). On a very open dieback site, such as site 10, germination of jarrah seed may be rare but when germination does occur, the germinants that have established some distance from parent trees may be more likely to survive.

Obvious questions arising from the spatial study presented are why was a species such as *Stylidium amoenum* abundant on site 10 when it was absent or rare on most other pre-1951 dieback sites? and why had 23% of the population at site 10 suddenly died? Deaths had presumably occurred in the last few years because the site was burnt in 1993. An answer to the first question is not obvious although differences in the abundance and activity of *P. cinnamomi* over time may have been important because *S. amoenum* appears to be especially susceptible to infection. The answer to the second question may relate partly to the recent death of a jarrah near the centre of the plot. There were many deaths immediately to the north of this tree. It and its neighbouring trees to the west would have provided shade to these *Stylidium amoenum* plants from about midday onwards during most of summer and autumn. Mortality might also have been influenced by the activity of *P. cinnamomi*. The two positive *Banksia grandis* baits from site 10 were located in the area of greatest *Stylidium amoenum* mortality.

4.5.2 Pathogenicity Tests

The pathogenicity tests were not expected to give a quantitative assessment of the susceptibility of species to infection by *P. cinnamomi*. They were also not expected to give an indication of how the species would respond to *P. cinnamomi* in the field. *P. cinnamomi* was isolated from 24 of the 34 species tested (71%). It was isolated from three of the five marri plants tested. Marri is apparently unaffected by *P. cinnamomi* in the field, although it has been isolated from young dead plants in bauxite mine rehabilitation in the jarrah forest (Hardy et al 1996). The three infected marri plants remained healthy in the glasshouse despite the presence of *P. cinnamomi*. Some species

may have become infected simply because of the high inoculum levels in the pots and the prolonged period of *P. cinnamomi* activity, which would not have been experienced in the wild. Despite this, infection was not inevitable, at least for the duration of the trial, because *P. cinnamomi* could not be isolated from almost 30% of species. From the time to death and % isolation of *P. cinnamomi* in the *Banksia grandis* and *Hibbertia commutata* controls, an association of *P. cinnamomi* in the field seems likely with *Agrostocrinum scabrum, Boronia fastigiata, Gompholobium polymorphum, Hibbertia huegelii, Hibbertia rhadinopoda, Hybanthus floribundus, Labichea punctata, Scaevola calliptera, Stylidium amoenum, Stylidium junceum* and *Tetratheca hirsuta*. The relationship between susceptibility and species survival in the field need not be a linear one. Population density at the time *P. cinnamomi* enters unaffected vegetation is likely to be an important factor in such a relationship. *Comesperma virgatum*, which was found to be susceptible to infection but not easily killed in the glasshouse, has an unusual distribution in the wild. Plants are widely spaced and solitary. It would take very few deaths in this species to significantly reduce its distribution and restrict its ability to reproduce. Field studies are required to test associations between susceptibility, species death and population decline in the wild.

The failure of one *Banksia grandis* plant to die and the limited isolation of *P. cinnamomi* from species such as *Lomandra sonderi* and *Macrozamia riedlei*, which are known to be susceptible, places doubt on the meaning of negative results in this study. Species testing negative may have (i) been resistant to infection under the conditions of the tests, (ii) been resistant to infection only for the genetic sample of plants that were used, (iii) had insufficient material plated out to guarantee detection, or (iv) contained populations of the pathogen that could not be detected with the isolation procedures used (i.e. *P. cinnamomi* was dormant). The trials may also have been run for too short a period. Although a different inoculation method was used, about 15% of *Banksia grandis* plants growing in soil inoculated with *P. cinnamomi* survived for 395 days in the pathogenicity tests of McCredie et al (1985). To attach maximal certainty to negative results, pathogenicity tests of *P. cinnamomi* should be set up and run for long periods using large

numbers of plants obtained from large numbers of areas. The results then need to be compared with plant death and isolation of *P. cinnamomi* under field conditions. The surviving *Banksia grandis*, for instance, may have been genetically less susceptible to infection than the other four plants tested. Under field conditions, however, less of its tissue may have been infected by *P. cinnamomi*, yet it may have still succumbed during periods of water stress during summer.

The rapid death and great isolation of *P. cinnamomi* from some plants of *Banksia grandis, Boronia fastigiata, Labichea punctata, Scaevola calliptera* and *Tetratheca hirsuta* and survival and poor or no isolation of *P. cinnamomi* from other plants of the same species may indicate great intraspecific variation in resistance to infection. Further research is warranted.

Caution needs to be exercised in the interpretation of results from any susceptibility assessment. Table 4.9 shows the findings of this and previous studies of the susceptibility of marri and *Tetratheca hirsuta* to infection by *P. cinnamomi*.

Table 4.9. Findings on the susceptibility of marri and *Tetratheca hirsuta*.

Study	Study type	Marri	*Tetratheca hirsuta*
Podger (1968)	Field search		*P. cinnamomi* isolated from about 25% of root tissue sampled of *T. viminea* (syn. *T. hirsuta*)
Podger and Batini (1971)	Pot trial	*P. cinnamomi* not isolated in pot trial; one plant died	
Shearer and Dillon (1995)	Field search	Plants did not die and *P. cinnamomi* was not isolated	Plants did not die and *P. cinnamomi* was not isolated
This study	Pot trial	*P. cinnamomi* isolated from three of five plants; no plants died	*P. cinnamomi* isolated from two of three plants; two plants died

If the current study had been the first to assess the susceptibility of marri, and had done so in isolation from field studies, the species may have been regarded as very susceptible. Field searches would have shown that the species was insensitive to the pathogen even if it were indeed commonly infected. *Tetratheca hirsuta* was regarded by Shearer and Dillon (1995) as comparatively resistant to infection because no deaths were observed in active dieback areas. No dead plants were found in the current study either, although the species was found to be significantly less abundant in dieback sites in the dieback boundary study described in Chapter 2. Whilst the current study has shown that not all species prone to death following infection are killed during the initial impact, and Podger (1968) did not state whether the plants he sampled were dead or alive, an alternative explanation is possible for the apparent discrepancy. In the glasshouse pathogenicity test, the leaves of *Tetratheca hirsuta* plants dropped off soon after chlorosis. Death was very rapid. This small sub-shrub would be very difficult to identify once it died and the chances of finding dead plants with leaves still attached would be slim. In addition, the species appears to produce seed of low germinability (Bell et al 1993, personal observations), or at least seed with special germination requirements. Unlike *Banksia grandis*, it may not go through a phase of rapid regeneration following dieback. *Tetratheca hirsuta* is probably very susceptible to infection by *P. cinnamomi* and disappears quickly following dieback associated with *P. cinnamomi*.

Assessment of susceptibility is likely to be best in field studies of active dieback sites, where sites are monitored frequently and plants of inconspicuous species tagged. The following types of studies may locate many susceptible species but are open to mis-interpretation in isolation: (i) studies where deaths are recorded in the field but no association is made with *P. cinnamomi*; (ii) studies where dieback sites are visited once or rarely; (iii) studies done solely in the glasshouse. The isolate of *P. cinnamomi* used for inoculation may also influence the results obtained in pathogenicity tests (Hüberli 1995).

Based on published lists of *P. cinnamomi* isolation from host plants (Podger 1968, Titze and Palzer 1969, Gardner and Rokich 1987, Shearer and Dillon 1995, 1996b), the

current study appears to be the first to record infection by *P. cinnamomi* of species in the families Caesalpiniaceae, Polygalaceae, Stylidiaceae, and Violaceae and in the genera *Agrostocrinum, Comesperma, Hybanthus, Labichea, Logania, Scaevola, Stylidium, Tetrarrhena,* and *Thysanotus*. Some species of Stylidiaceae appear to be highly susceptible to infection.

Given enough time in contact with the pathogen and suitable conditions for invasion, perhaps all species can become infected with *P. cinnamomi*. Such a proposition would be difficult to prove or disprove. However, from the results presented in this Chapter, there are clearly inter- and intra-species differences in the time taken for the display of symptoms and in the degree of infection. The capacity for infection by *P. cinnamomi* in some of the species studied, whilst not providing proof of cause for their low frequency on pre-1951 dieback sites, at least identifies an additional area for further investigation.

Twenty-one of the 27 species tested in this study that were not previously known to be susceptible to *P. cinnamomi* infection, became infected. The host range for *P. cinnamomi* may be much greater than recognised in the northern jarrah forest.

CHAPTER 5: THE ORIGIN OF SPECIES MORE FREQUENT ON DIEBACK SITES

5.1 Introduction

Species may be have been found more frequently on pre-1951 dieback sites because they were more common on these sites before dieback than in the unaffected vegetation sampled (i.e. the basic assumption of the space for time substitution study was invalid) or the species have increased in number since dieback. If species have increased in number since dieback, their progenitors may have been (i) on the sites at the time of dieback, (ii) in other vegetation types nearby or (iii) outside the jarrah forest altogether. The common occurrence in unaffected vegetation of some of the species found more frequently in pre-1951 dieback vegetation suggests that examples of the first possibility occur. The third possibility is clearly the case for non-Australian plants. Unlike the species found less frequently on dieback sites, of which 17% were not present on pre-1951 dieback sites, 40% of species more frequent on pre-1951 dieback sites were not present in unaffected vegetation or were exotic species that would not have occurred there. Since dieback sites are likely to be wetter now than before dieback, when they were covered with water-hungry trees, the movement upslope of species that previously inhabited creek bottoms is plausible. The opening of the canopy might also attract a suite of species from more open plant communities of the jarrah forest such as those on granite outcrops.

The search for the origin of species found more frequently in pre-1951 dieback sites is not esoteric. If these species are a normal, yet rare, component of the jarrah-dominated communities studied, dieback after 40 years may have only resulted in a redistribution of species abundance with the loss of perhaps three or four species. In this case, some rare species have become abundant and some abundant species have become rare, and the overall effect of dieback on species diversity is not great. The small differences recorded in species / quadrat between unaffected and pre-1951 dieback vegetation (Table 2.5, page 48), and the occurrence in pre-1951 dieback vegetation of most species found

in unaffected vegetation support this proposition. However, if many species have invaded following dieback, initially, there is likely to have been a substantial decrease in species richness.

In this chapter, I present the results of an investigation into the natural distribution of some species that were found more frequently on pre-1951 dieback sites. The density of the species was first measured along transects through dieback fronts into unaffected vegetation to check that the differences found in frequency were also evident in density. The soil seed bank was then sampled to determine if species not present above ground in unaffected vegetation were simply latent. The presence of a latent seed bank would have indicated that the gap processes found to operate in many northern hemisphere forests, whereby some species only appear in canopy gaps created by disturbance, were well developed in the northern jarrah forest. The possible origin of species not obviously present in the unaffected vegetation is discussed.

5.2 Methods

5.2.1 Species Density

Species density was measured along transects through dieback fronts at six sites in spring 1995. The sites were those (except site 10) used in Chapter 3. A point was chosen at the dieback front where there was at least 200 m of dieback and unaffected vegetation on either side. One density measurement was taken at distances of approximately 10, 50, 90 and 130 m from the dieback boundary into dieback and unaffected vegetation at each site. At site 4 the samples at 90 and 130 m on the unaffected side were increased by about 20 m because a narrow strip of ironstone vegetation occurred about 90 m from the dieback front. The samples in dieback vegetation 10, 50 and 130 m from the dieback front were in zones G, E and C respectively. The sample in dieback vegetation 90 m from the dieback front was commonly near the boundary between zones C and E.

At each sampling point, a modified point-centred quarter method was used to measure density of selected species. This was based on the method described by Cottam and Curtis (1956), which involves measuring the distance from a point to the nearest individual of a species in four pre-determined segments of a sampling area. The density is then the square of the mean distance per unit area. This plotless method was modified because, if species were absent in unaffected forest, as some were expected to be, the search area would have been enormous, especially 130 m from the dieback front. An arbitrary cut-off, which gave a sampling area of 400 m^2, was used to save time in searching. Species not found in a segment were given the value 11.28 m. Densities were then calculated as:

$$\textbf{Density} = (400 \div (\textbf{Mean Distance})^2) \cdot \pi \quad \text{plants / 400 } m^2$$

This meant that if a species was not found in any segment its density was zero for the sample.

Species were selected for sampling if they were widespread at the six sites. Distance to nearest tree, tree cover and bare ground cover were also recorded.

5.2.2 Soil Seed Bank

Ten soil samples were collected randomly from each density sample point with a trowel in early February 1996. The first sample was taken 5 paces from the central point. Subsequent samples were taken every three paces in a circle around the central point. The trowel was put obliquely into the soil to remove about the top 2 cm. The 10 samples were bulked. The area sampled at each point was estimated to be 0.08 m^2. On average, 2.5 kg of soil was removed to represent each point.

The bulked soil was placed into seed flats over a thin layer of sand and bark potting mix above a water absorbent cloth. One tray was used for each bulked sample. Each tray was treated with Fongarid™ at the recommended rate for seed flats to kill or suppress any *P. cinnamomi* present. Trays were then placed in an air-conditioned glasshouse with an

automatic watering system. The following day each tray was watered with smoky water supplied by Alcoa's Marrinup Nursery (10 ml of smoky water in 90 ml of tap water per tray) and left to soak overnight to stimulate germination of smoke-sensitive species (Dixon et al 1995). Trays were inspected frequently. When germination commenced, seedlings were counted and removed if they could be identified. *Centrolepis aristata*, one of the species investigated in the field survey, occurred as a weed in the glasshouse. Although its abundance in the glasshouse might have been quantified by having trays of sterile soil as controls, most interest pertained to its presence or absence in soils from unaffected quadrats, where it had not been found above-ground. Because of this, no significance could be given to the occurrence of this species in soils of unaffected quadrats.

The experiment was done primarily to detect species, mainly annuals, not present above-ground in unaffected vegetation. Since a small area was sampled, only abundant species such as these could be expected to germinate. Heat treatment of half the soils, which has been done in other soil-seed bank studies in the jarrah forest (Vlahos and Bell 1986, Grant 1993), would have triggered the germination of heat sensitive seeds. Although this would have allowed for a better comparison of overall seed density with the other studies, species with heat-sensitive seeds were not of interest (i.e. species with heat-sensitive seeds are not likely to be annuals) and space was not available in the glasshouse for an additional 48 heat-treated seed flats.

5.2.3 Origin of Species More Frequent on Dieback Sites

Alternative origins were investigated for species that were rarely found or were not found in unaffected vegetation. Other vegetation types in the vicinity of the study area were searched. The frequency of the species in creek edge and ironstone gravel vegetation had already been determined (Chapters 2 and 3). Granite outcrops, which are structurally more similar to dieback vegetation than other communities nearby and possible sources of the annual species, are abundant in the study area. However, most granite outcrops are traversed by forestry tracks. Annual species on these granite

outcrops might have been introduced via the tracks. One of the largest granite outcrops in Myara forest block (see Figure 3.1 for location) was searched in November 1995 for species found to be more frequent on dieback sites. It is one of the few outcrops in the vicinity that does not have a road adjacent to it.

The origin of species that have been dispersed by human activities can sometimes be traced by inspecting herbaria records. If a species was not collected during early botanical expeditions to an area but had been collected widely in another area prior to the expeditions, there is circumstantial evidence for its introduction. There were many botanical expeditions in south-western Western Australia in the mid 19th Century. Unfortunately, an herbarium was not established in Western Australia until early this Century and most earlier collections left the State for Europe or Melbourne (MEL) (Green 1990). Nineteenth Century collections held at MEL of the following species that were found more frequently on pre-1951 dieback sites were checked for their date and location by Mr Neville Walsh (National Herbarium of Victoria): *Centrolepis aristata, Hyalosperma cotula, Isotoma hypocrateriformis, Levenhookia pusilla, Levenhookia stipitata, Millotia tenuifolia, Neurachne alopecuroidea, Podolepis gracilis, Podotheca angustifolia, Pterochaeta paniculata, Waitzia nitida.*

5.3 Results

5.3.1 Species Density

All but two of the species measured had a significantly greater density in dieback vegetation than in unaffected vegetation as determined using a Wilcoxon two sample test for all quadrats within sites where a species occurred (Table 5.1). Tree density was significantly greater in unaffected vegetation ($P < 0.001$).

Table 5.1. Mean density of species measured in all dieback quadrats and all unaffected quadrats. Significance of differences was determined by a Wilcoxon two sample test. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Species	Dieback (plants / 400 m^2)	Unaffected (plants / 400 m^2)	P
Acacia barbinervis	9.9	4.8	*
Astroloma pallidum	5.9	3.2	*
Baeckea camphorosmae	5.7	0.4	*
Burchardia umbellata	6.3	0.3	**
Centrolepis aristata	43.6	0.0	*
Dryandra lindleyana	38.7	211.0	
Gompholobium knightianum	243.1	73.1	**
Haemodorum spp.	83.5	0.9	***
Hakea lissocarpha	2.6	0.0	*
Hypocalymma angustifolium	70.9	0.9	**
Isotoma hypocrateriformis	9.2	0.0	***
Lechenaultia biloba	400.0	104.4	*
Levenhookia pusilla	1680.6	0.2	***
Lobelia spp.	1.3	0.0	**
Millotia tenuifolia	945.0	0.1	***
Neurachne alopecuroidea	8.1	0.0	*
Phyllanthus calycinus	294.5	0.8	
Pterochaeta paniculata	21304.9	0.0	***
Tetraria octandra	98.1	1.8	*
Tripterococcus brunonis	23.1	0.1	***
Eucalyptus spp. (Trees)	3.1	11.5	***

As expected, there were differences between species in their distribution or abundance along the transect. Species may be placed into one of three groups:

(i) Species abundant on the dieback side of the boundary and rare or absent in unaffected vegetation (Figure 5.1). Most of these species have their greatest abundance at least 50 m from the dieback boundary into dieback vegetation. *Levenhookia pusilla* was only present in unaffected vegetation more than 50 m from the dieback front at site 4 adjacent to a narrow strip of unaffected ironstone vegetation, where it was relatively abundant.

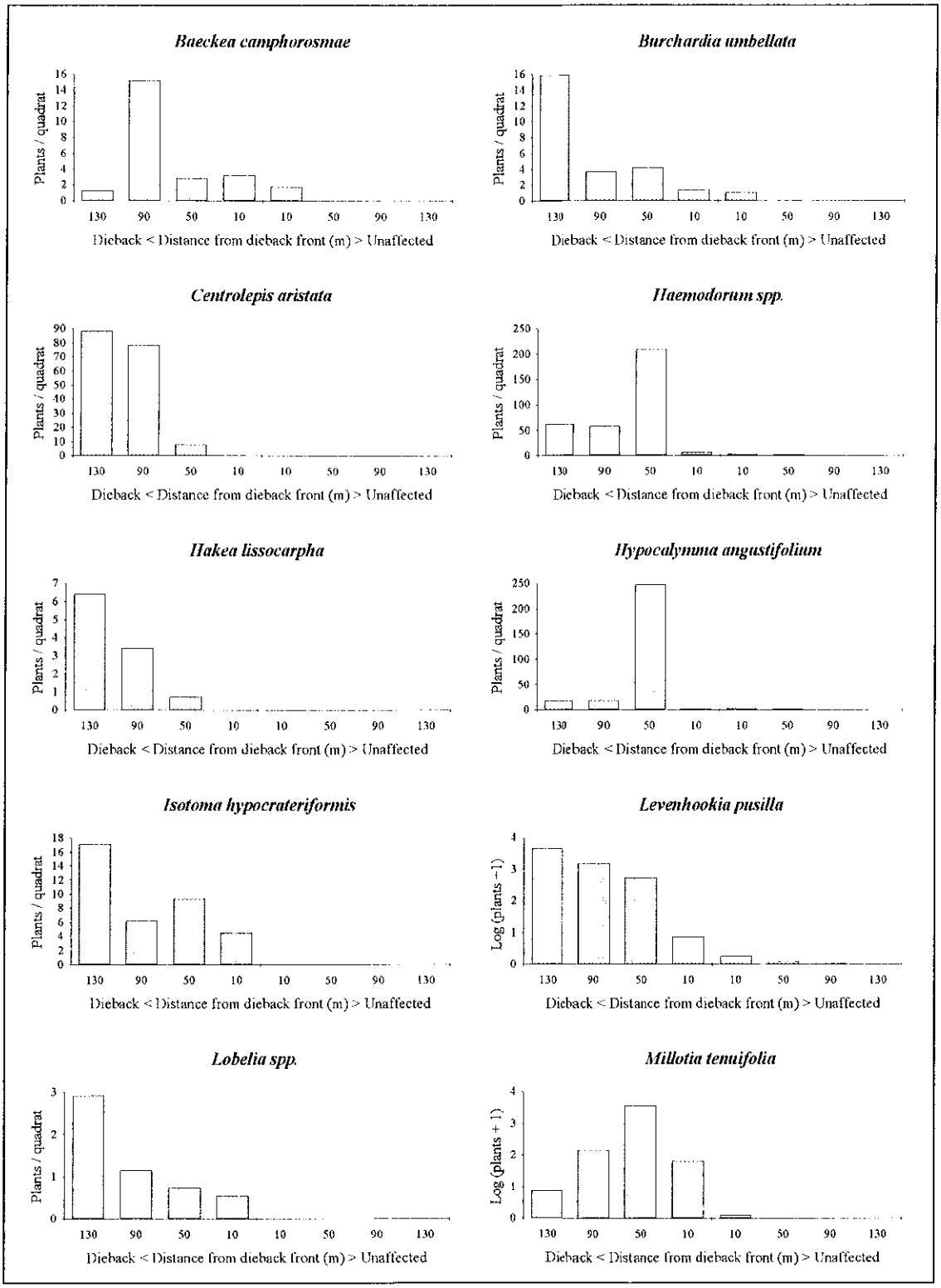


Figure 5.1 Mean density (plants / 400 m^2) along transects through dieback fronts for species abundant on the dieback side of the boundary and rare or absent in unaffected vegetation.

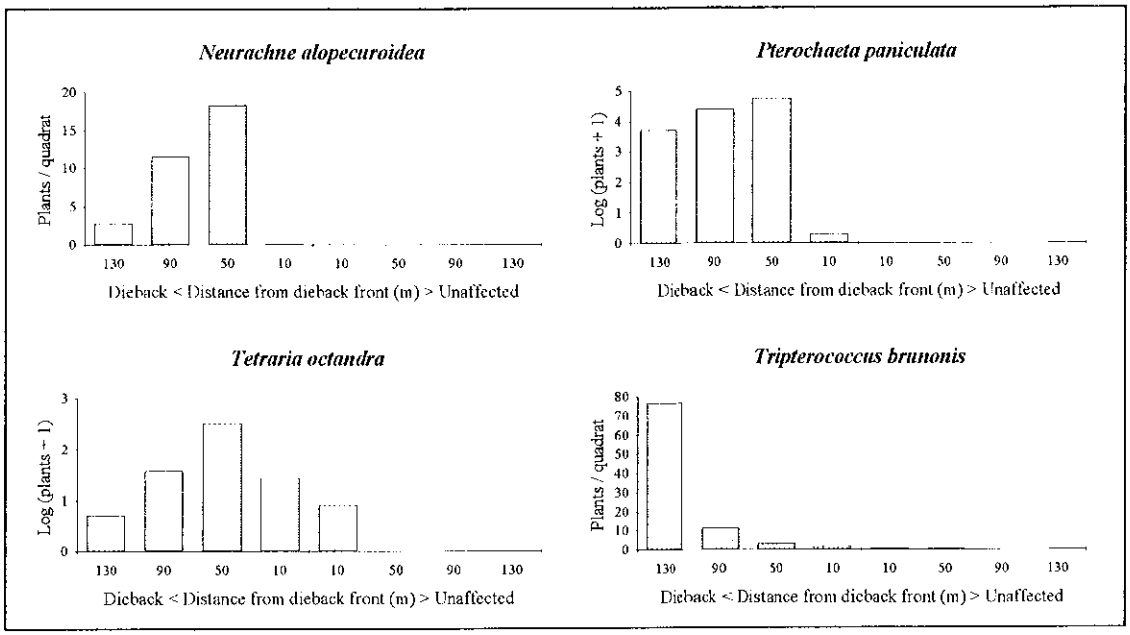


Figure 5.1 (cont.) Mean density (plants / 400 m^2) along transects through dieback fronts for species abundant on the dieback side of the boundary and rare or absent in unaffected vegetation.

(ii) Species present and abundant throughout unaffected vegetation but more abundant in dieback vegetation (Figure 5.2). *Phyllanthus calycinus*, although not more significantly abundant overall, probably belongs in this group. It is significantly more abundant in dieback vegetation when only the samples at 50, 90 and 130 m on both sides of the boundary are compared ($P < 0.05$).

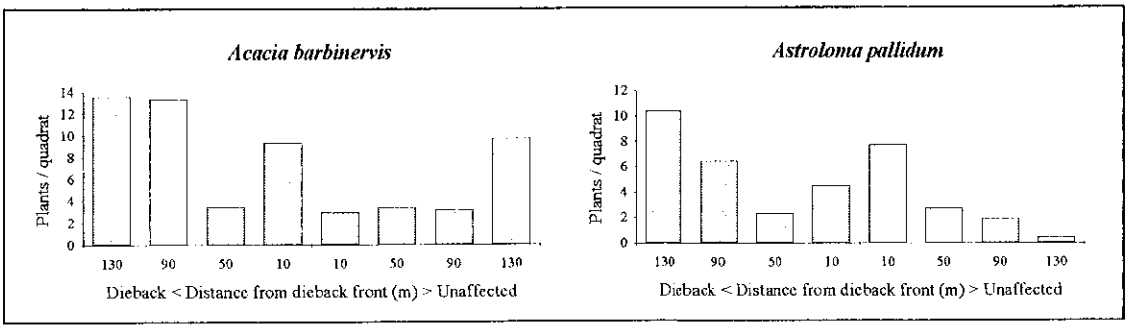


Figure 5.2 Mean density (plants / 400 m^2) along transects through dieback fronts for species present and abundant throughout unaffected vegetation but more abundant in dieback vegetation.

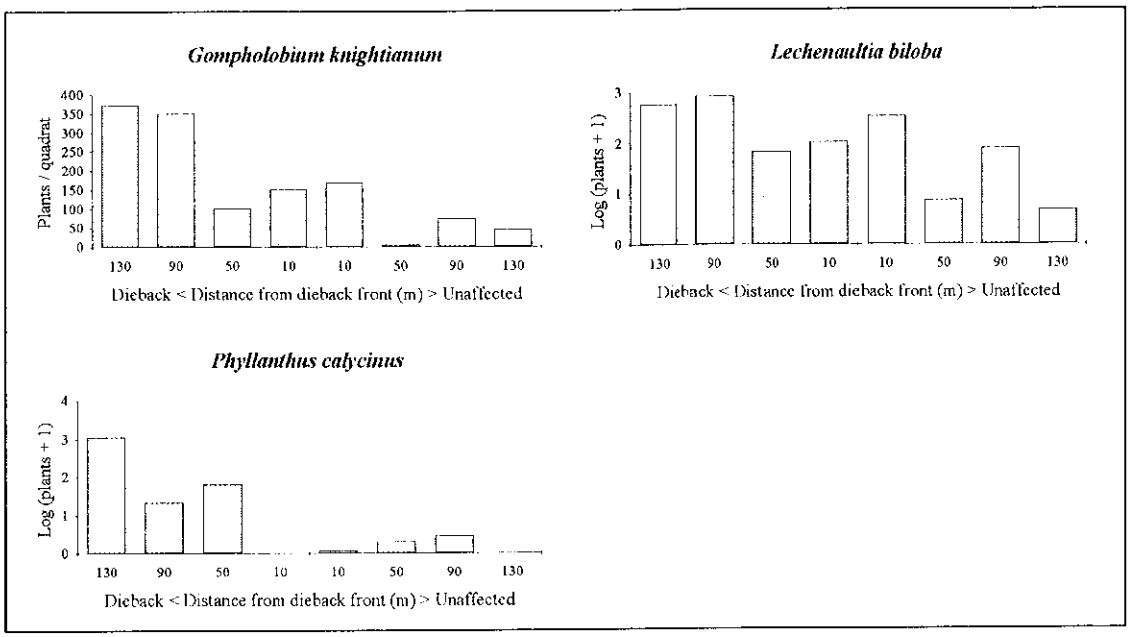


Figure 5.2 (cont.) Mean density (plants / 400 m^2) along transects through dieback fronts for species present and abundant throughout unaffected vegetation but more abundant in dieback vegetation.

(iii) Species not more abundant in dieback vegetation (Figure 5.3). The apparent abundance of *Dryandra lindleyana* is solely attributable to dense stands in two samples.

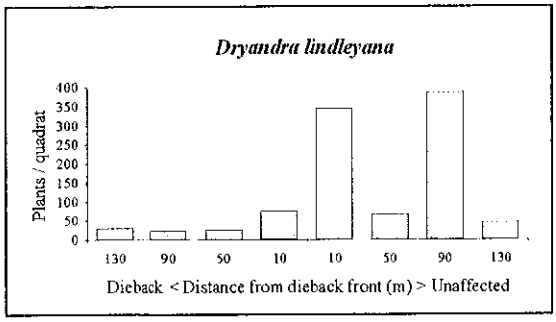


Figure 5.3 Mean density (plants / 400 m^2) along transects through dieback fronts for *Dryandra lindleyana*.

Although not more abundant in the dieback vegetation sampled, *Dryandra lindleyana* was still more frequent in dieback vegetation (Figure 5.4), as it was found to be in Chapter 2.

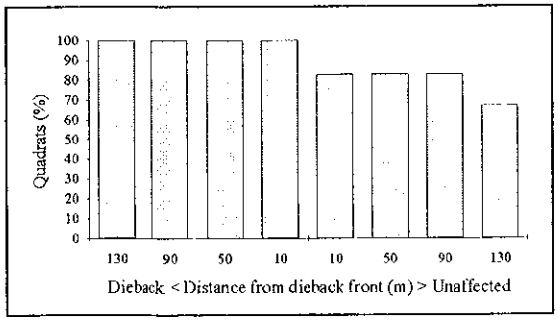


Figure 5.4 % of quadrats containing *Dryandra lindleyana* at each distance along transects through dieback boundaries.

The annual species in group (i) above appeared to be least abundant under trees and most abundant in large patches of bare ground. The abundance of one of these annual species, *Pterochaeta paniculata*, was correlated with the amount of bare ground on dieback sites ($r = 0.56$; $P < 0.05$) (Figure 5.5).

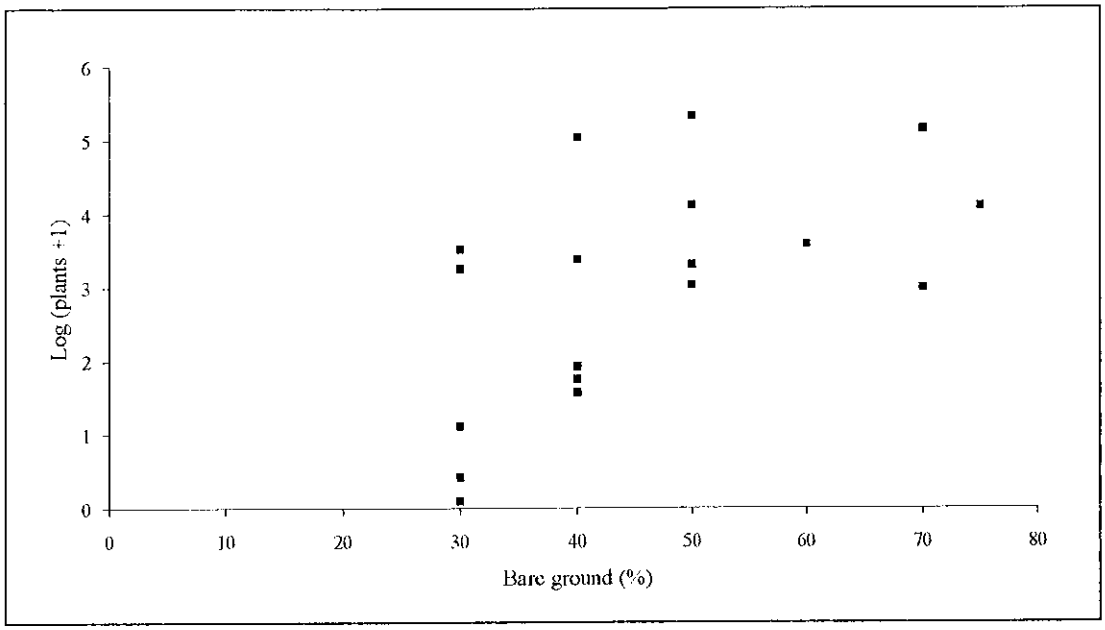


Figure 5.5 The density of *Pterochaeta paniculata* ($\log_{10}$ (plants / 400 m^2 + 1)) plotted against the cover of bare ground (%).

5.3.2 Soil Seed Bank

Despite watering, there was no germination in the soil seed bank trays until early April 1996. The majority of germinants appeared between May and July. Sporadic germination occurred until observations of the trays ceased in November 1996. Seedlings of *Bossiaea ornata* and *Trymalium ledifolium* were the last observed to emerge, in October.

Germinants of 46 species were identified in the soil sampled, 35 in dieback samples and 28 in samples from unaffected vegetation. The soil seed bank data are summarized in Table 5.2. The average expressed seed density was 449 germinants m^{-2} in dieback quadrats and 58 germinants m^{-2} in unaffected quadrats. This does not include the seed of species that would be stimulated by heat treatment (e.g. some legumes). The majority of

germinants in the dieback samples were annual species: 86% in soil samples from dieback quadrats compared with 46% in soil samples from unaffected quadrats.

Table 5.2. Density of species germinating in more than one soil sample in the soil seed bank trial and their frequency (% of trays containing germinants). * = introduced species.

Species	Density seeds m^{-2}		Frequency % of trays (n = 28)	
	Dieback	Unaffected	Dieback	Unaffected
Bossiaea ornata	0.0	1.6	0	11
Centrolepis aristata	34.4	1.0	39	4
Chamaescilla corymbosa	10.4	3.1	25	7
Conostylis setosa	2.6	0.5	14	4
Hibbertia rhadinopoda	1.0	0.5	4	4
Hydrocotyle sp.	19.3	1.0	39	7
Levenhookia pusilla	289.6	12.5	64	11
Levenhookia stipitata	4.2	2.6	14	7
Millotia tenuifolia	7.3	0.0	32	0
Opercularia echinocephala	0.5	1.6	4	11
Pentapeltis peltigera	0.5	0.5	4	4
Platysace compressa	3.1	4.7	14	25
Pterochaeta paniculata	18.2	0.0	29	0
**Senecio vulgaris*	1.0	0.0	7	0
Siloxerus multiflorus	4.2	0.0	7	0
Sphaerolobium medium	0.0	1.0	0	7
Stylidium calcaratum	6.8	7.3	11	11
Stylidium hispidum	19.8	6.3	54	21
Stylidium junceum	1.6	0.5	11	4
Tetraria capillaris	0.0	1.6	0	11
Thysanotus thyrsoideus	1.0	2.6	7	11
Xanthosia candida	4.2	1.0	14	7
Xanthosia ciliata	3.1	1.0	7	7
Xanthosia huegelii	2.1	0.0	11	0

None of the species that were rare or absent above-ground in unaffected quadrats germinated widely in soils from unaffected quadrats. *Levenhookia pusilla*, which had been found above-ground at one site, germinated from soil samples in unaffected vegetation (130 m from the dieback boundary) at two sites, in low numbers. One plant of *Centrolepis aristata* appeared in soil collected 130 m from the dieback front in unaffected vegetation but, as discussed above, no significance can be placed on it.

There was a similar pattern of distribution for seed and field plant density for three species, which were common germinants (Figure 5.6). Although a massive extrapolation is required to convert the density of plants in the area of the soil samples (0.08 m²) to the area of the above-ground measurements (400 m²), the differences between soil-seed density and above-ground density for the three species in Figure 5.6 are curious. The magnitude of seed and field plant densities are similar in *Pterochaeta paniculata* but disparate in *Levenhookia pusilla* and *Millotia tenuifolia*. This may indicate that there is a greater mortality of seedlings in the latter two species or that their seed does not all germinate in the year of production.

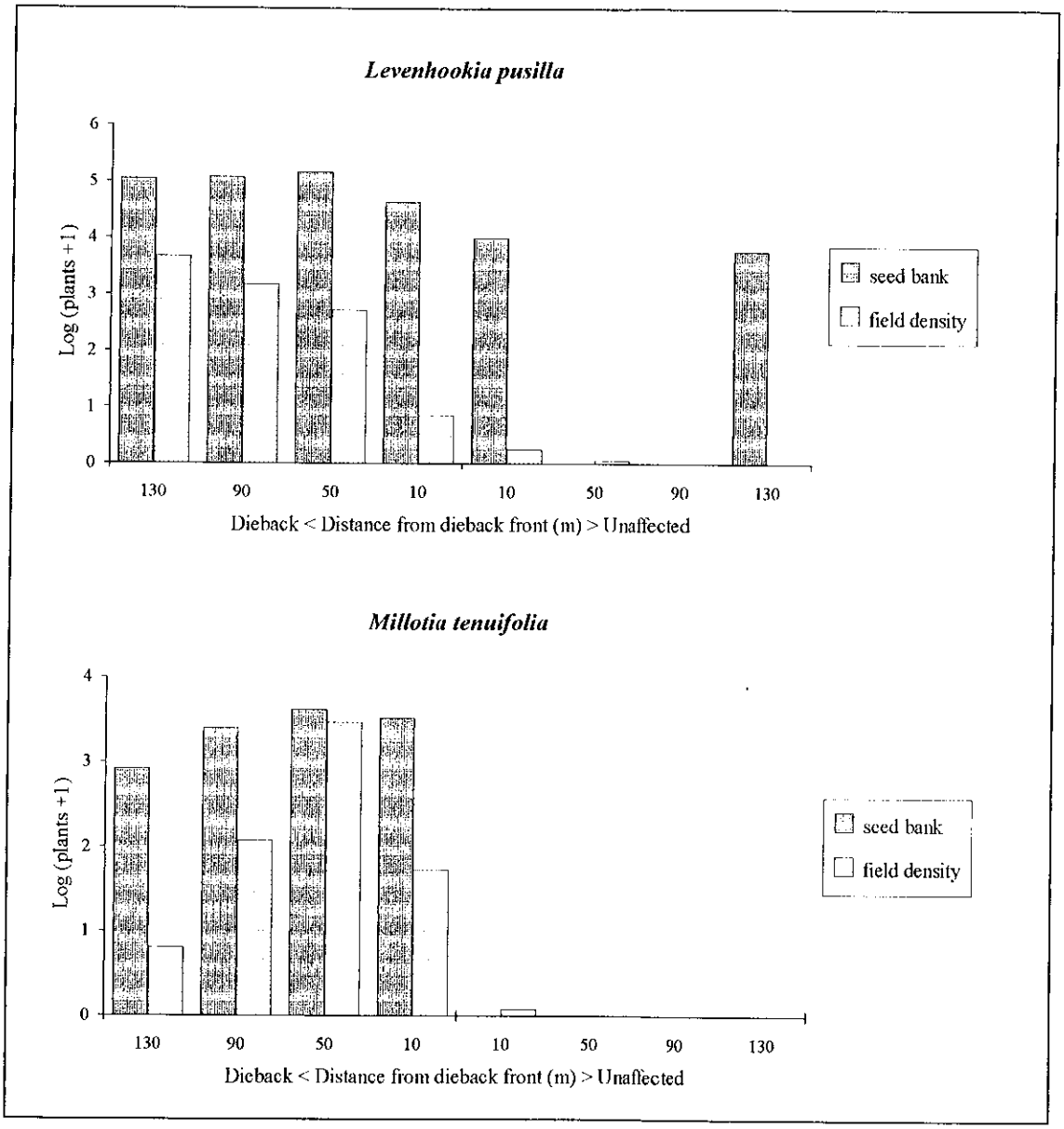


Figure 5.6 Density (plants / 400 m²) for quadrats in the field and soil seed bank samples (extrapolated) along transects through the dieback front at six sites for *Levenhookia pusilla, Millotia tenuifolia* and *Pterochaeta paniculata*.

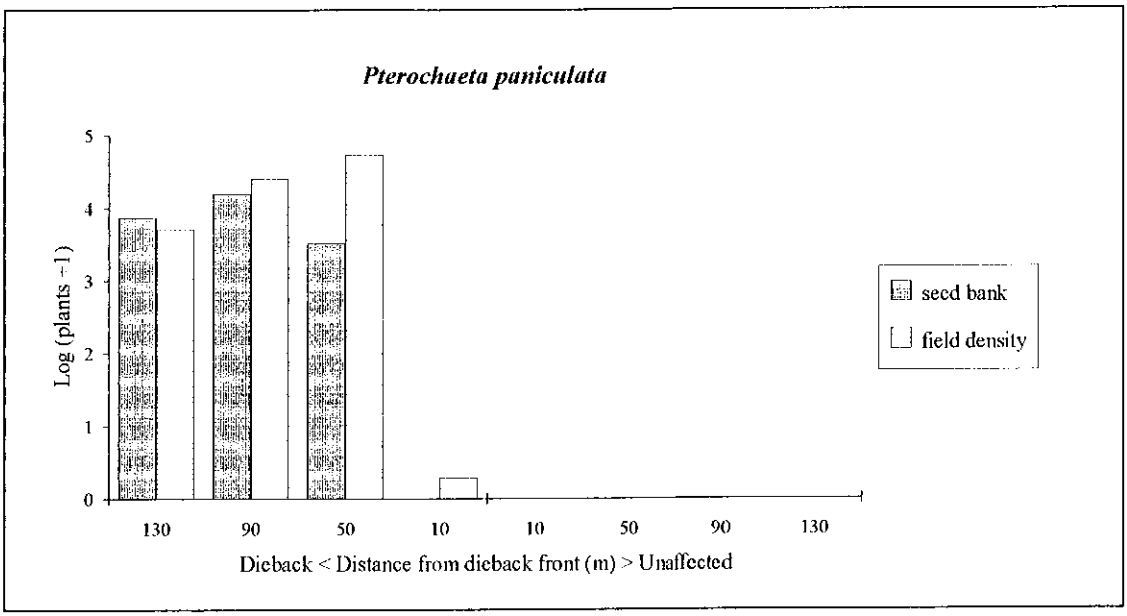


Figure 5.6 (cont.) Density (plants / 400 m²) for quadrats in the field and soil seed bank samples (extrapolated) along transects through the dieback front at six sites for *Levenhookia pusilla, Millotia tenuifolia* and *Pterochaeta paniculata*.

5.3.3 Origin of Species More Frequent on Dieback Sites

Of the 30 species found more frequently on pre-1951 dieback sites that occur rarely in unaffected vegetation (Table 2.6, page 50; native species with a % frequency of < 10 in unaffected quadrats used in the comparison with pre-1951 quadrats), only two (*Gompholobium marginatum* and *Hypolaena exsulca*) were found more frequently in pre-1951 dieback creek edge vegetation (zone A) than in sloping pre-1951 dieback vegetation (zone C) (Figure 5.7). Three other species had a similar frequency in both zones (*Mesomelaena tetragona, Olearia paucidentata* and *Stipa* spp.).

Five of the 30 species were present in both quadrats sampled on unaffected sites with an ironstone-dominated soil surface (*Isotoma hypocrateriformis, Laxmannia squarrosa, Levenhookia pusilla, Millotia tenuifolia* and *Pterochaeta paniculata*).

Three of the 30 species were present on or around the undisturbed granite outcrop inspected: *Baeckea camphorosmae, Isotoma hypocrateriformis, Levenhookia pusilla*. *Levenhookia pusilla* was uncommon.

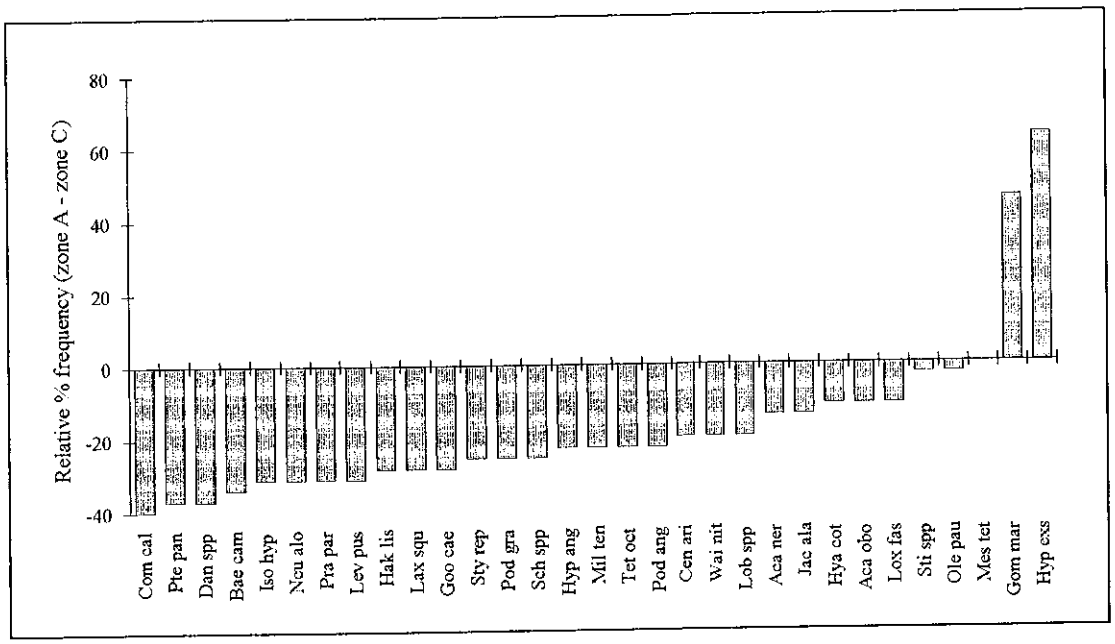


Figure 5.7 Relative % frequency (zone A - zone C) of species rarely found in unaffected vegetation. Species names are abbreviated with the first three letters of the genus and species. The full names are given in Table 2.6, page 52.

Despite the limited geographical information provided with many 19th Century collections, all of the species searched for at the National Herbarium of Victoria (MEL) appear to have been collected in or around the Darling Ranges (northern jarrah forest) at the time of early botanical expeditions. Many of the species have earlier collections from the Perth and Albany areas. The earliest collections of the species housed at MEL are:

Centrolepis aristata	"Valleys of the Darling Range" 1877, although two earlier records were from Albany area 1867
Hyalosperma cotula	"Jarrah forests between York and Perth" 1877, "Pinjarrah, very frequent" 1877
Isotoma hypocrateriformis	"Valleys of the jarrah forests between York and Perth" 1877, but collected to north and south of Perth in 1871
Levenhookia pusilla	"Upper Darling Range" 1857, "Maddington" near Perth 1839, and widespread in south-west by 1877
Levenhookia stipitata	"Jarrah forests Swan R" 1877, "Serpentine R" 1877
Millotia tenuifolia	"Upper Swan" 1883, earlier collection (1867) from Albany

Neurachne alopecuroidea	Earliest jarrah forest collection is 1881, early records from Albany area (1867)
Podolepis gracilis	"Darling Ra. moist places" (early 19th Century collection, no date); "Swan R" (1843), "near Serpentine R." (1886)
Podotheca angustifolia	"Swan R" 1844, "E. sources of Swan R." 1889
Pterochaeta paniculata	"jarrah country Darling Ra, south of Swan River" 1877"; "flats, sandy ground less sterile, Serpentine R". 1877
Waitzia nitida	"Swan R." (pre 1840), not obviously from jarrah forest areas until 1890s

The type of *Pterochaeta paniculata* is a 1839-40 collection from "Maddington", a suburb of Perth.

5.4 Discussion

Many of the species found more frequently on pre-1951 dieback sites were probably present in the vegetation at the time of the initial dieback event (e.g. species shown in Figures 5.2 and 5.3 above). These species may favour the enhanced light environment of dieback sites and increase in abundance with the loss of canopy, much as gap-dependant species do in some northern hemisphere forests. One jarrah forest species, *Lechenaultia biloba*, is often most profuse along roadsides, where there is abundant light and little competition from other perennial species. Rather than increasing in abundance, a species such as *Dryandra lindleyana* may have a different distribution on dieback sites. A clumped distribution in unaffected vegetation and a scattered distribution in dieback vegetation would explain the patterns found. The abundance of some species shown in Figure 5.2 increases with age of dieback. This suggests that there is a lag between dieback and species increases. This would be expected because none of these species are known to regenerate prolifically from seed.

A small number of species found more frequently on pre-1951 dieback sites and largely absent in unaffected vegetation appear to have come from creek edge vegetation, perhaps as sloping dieback sites have become wetter. The origin of the remainder is unclear. Three possibilities might be considered.

(i) The presence of a mesic vegetation zone between creek edges and slopes prior to dieback, which contained the species now frequently found on dieback sites, could explain the patterns found. However, there is no evidence of such a zone in areas where unaffected vegetation still extends to near the edge of creek zones.

(ii) The species may have been components of the much more open creek communities present at the time of the first dieback (see Chapter 3, Discussion). With the closing of the canopy, they have simply been forced uphill. This proposition may be impossible to test because the structural changes in creek communities are complete and the species in question are now abundant on the adjacent dieback sites. If creek communities were ever to become open again and had abundant bare ground, similar in cover to the present dieback sites on slopes, the annual species now growing on sloping dieback sites may invade regardless of whether they had originated in the creeks before dieback or come from outside the jarrah forest. Although, from the aerial photographic record, creek vegetation once had an open canopy, there is no evidence that the understorey was equally open. The presence of a thick shrub layer of *Agonis linearifolia,* which is presently common in many of the creek communities in the study area, may have been inhibitory to species such as *Pterochaeta paniculata*, which show a preference for bare ground (see Figure 5.5 above).

(iii) The species may have come from vegetation types in the Darling Ranges with open canopies, such as granite outcrop and ironstone vegetation. Many of these species are annuals. Characteristics of many annual species are large seed production and high germinability (Grime 1979). The common passage of forestry tracks through or beside granite outcrops and the use of ironstone gravels in road construction would have facilitated the spread of such species.

Granite outcrops and ironstone soils are widespread in the jarrah forest, although they occupy little area. The obvious question arising from the proposition that species invaded dieback sites from granite outcrops and ironstone vegetation is why did invasion not occur into the remainder of the forest prior to the introduction of *P. cinnamomi*? The answer may lie in the theories of jarrah forest processes put forward in Chapter 4. Opportunities for invasion may be limited because the canopies of the upper and middle storeys of the jarrah forest are resilient. The presence of a productive middle storey of *Banksia grandis* would limit the size of canopy openings following natural disturbances such as tree senescence or tree fall. Openings are also quickly filled after fire. The correlation of *Pterochaeta paniculata* density with bare ground cover on dieback sites supports this contention and suggests that some species may become rare or disappear if and when the canopy closes on dieback sites.

The possibility that the species not found in unaffected forest have been introduced from beyond the jarrah forest in the Darling Ranges cannot be discounted, although it probably cannot be proven either. The early collection in the jarrah forest of these species does not mean they were not introduced. Bentham (1863-78), in the first comprehensive Australian Flora, lists more than 20 grass and 20 daisy weed species less than 100 years after European settlement and less than 50 years after the establishment of major population centres. By the 1870s, when many of the species investigated were collected from the jarrah forest, there was trade in jarrah timber and movement of timber and people through the forest between settlements in Perth, York and Albany. The most likely invaders amongst the species are the annuals. The annual reproductive strategy is commonly found in species that colonize disturbed and open ground (Grime 1979). Hobbs and Atkins (1991) found that the representation of annual weed species was greater in woodlands of the arid Western Australian wheatbelt, where the canopy was open, than in dense shrublands nearby. Unlike the current study, however, they found that annual species favoured litter-covered ground in open areas rather than bare ground. A large proportion of temperate Australian weeds are annuals. Almost one quarter of weeds of native vegetation in Victoria are annuals (Carr et al 1992). The fact that most

of the annuals of dieback sites are native to Australia does not preclude them from being weeds of Australian vegetation. The invasive nature of some Australian plants outside their normal range is well recognized (e.g. Humphries et al 1991, Carr et al 1992).

Absence cannot be proven by sampling. The non-occurrence of some species in unaffected vegetation in the Broad Quadrat Survey (Chapter 2), the Density Survey (Section 5.3.1) and the Soil Seed Bank Study (Section 5.3.2) does not mean that the species are absent in unaffected vegetation. They may be present in unaffected vegetation in extremely low numbers. Some species in the jarrah forest are difficult to propagate from seed. If this were reflected in the soil seed bank experiment, the non-appearance of a species may not equate to the non-occurrence of its seed. In addition, the area of soil that can physically be tested for its seed bank is extremely small so there is a tendency to locate species that are most abundant as well as most germinable. From the information presented in this thesis, at least 30 native species either occur in very low numbers or do not occur naturally in unaffected vegetation dominated by jarrah and *Banksia grandis* in the northern jarrah forest. (Table 5.3).

Vlahos and Bell (1986) found that 35% of the soil seed density of the sites they sampled in the northern jarrah forest comprised annual species, some of which were the focus of the current study. Almost two-thirds of the species appearing in their soil samples were annuals. The dieback status of the sites sampled by Vlahos and Bell (1986) was not reported, and so few comparisons can be made between their study and mine. If their sites had been affected by dieback, their mean seed density of 767 seeds m^{-2} is not especially different from the 448 seeds m^{-2} I recorded, considering that their soils were heat-treated to stimulate fire-sensitive seeds. Grant (1993) found a much lower seed density and species representation (especially of annual species) in jarrah forest soils than Vlahos and Bell (1986), although his values were intermediate between my findings for soils from unaffected sites and those reported by Vlahos and Bell (1986). The low seed densities found in my soils from unaffected vegetation are consistent with the overwhelming dominance of resprouting species in the jarrah forest.

Table 5.3 The ratio of samples (unaffected / pre-1951 dieback) of species that either occur in very low numbers or do not occur naturally in unaffected vegetation dominated by jarrah and *Banksia grandis* in the northern jarrah forest, and their possible origin. The values given for the broad quadrat survey are % frequencies for unaffected and pre-1951 dieback. The values given for the density survey and soil seed bank study are numbers of samples in which a species was recorded. The samples 10 m from the dieback boundary have been excluded for the purpose of this table. n/s = not searched for in density survey. n/g = no germinants observed in soil seed bank study.

Species	Broad Quadrat Survey (ratio of samples: unaffected / dieback)	Density Survey	Soil Seed Bank Study	Origin
Acacia nervosa	6 / 25	n/s	n/g	Unknown
Acacia obovata	0 / 12	n/s	n/g	Unknown
Baeckea camphorosmae	7 / 58	0 / 7	n/g	Granite
Centrolepis aristata	0 / 30	0 / 7	1 / 10	Unknown
Comesperma calymega	2 / 35	n/s	n/g	Unknown
Gompholobium marginatum	2 / 30	n/s	n/g	Creeks
Goodenia caerulea	6 / 37	n/s	n/g	Unknown
Hakea lissocarpha	2 / 48	0 / 6	n/g	Unknown
Hyalosperma cotula	4 / 27	n/s	n/g	Unknown
Hypolaena exsulca	4 / 17	n/s	n/g	Creeks
Isotoma hypocrateriformis	0 / 73	0 / 15	n/g	Ironstone / Granite
Jacksonia alata	0 / 15	n/s	n/g	Unknown
Laxmannia squarrosa	0 / 33	n/s	n/g	Ironstone
Levenhookia spp.	6 / 82	2 / 18	2 / 15	Ironstone / Granite
Levenhookia stipitata	0 / 10	n/s	0 / 3	Unknown
Lobelia spp.	0 / 17	0 / 6	n/g	Unknown
Loxocarya fasciculata	2 / 20	n/s	n/g	Unknown
Mesomelaena tetragona	0 / 32	n/s	n/g	Creeks
Millotia tenuifolia	6 / 28	0 / 14	0 / 8	Ironstone
Neurachne alopecuroidea	2 / 50	0 / 5	n/g	Unknown
Olearia paucidentata	0 / 15	n/s	0 / 1	Creeks
Podolepis gracilis	0 / 20	n/s	n/g	Unknown
Podotheca angustifolia	0 / 20	n/s	0 / 1	Unknown
Prasophyllum parvifolium	0 / 23	n/s	n/g	Unknown
Pterochaeta paniculata	7 / 95	0 / 17	0 / 8	Ironstone
Schoenus spp.	0 / 27	n/s	n/g	Unknown
Stipa spp.	0 / 25	n/s	n/g	Creeks
Stylidium repens	0 / 23	n/s	n/g	Unknown
Waitzia nitida	0 / 32	n/s	0 / 1	Unknown
Xanthosia huegelii	0 / 7	n/s	0 / 3	Unknown

The species germinating in the soil samples were not entirely as expected. Although some annual species were abundant, others (e.g. **Aira cupaniana, Isotoma hypocrateriformis, Podolepis gracilis*) were absent, though widespread on the sites

sampled. *Stylidium hispidum* was the third most common germinant on dieback sites. Although the density of this species was not measured, its representation in the soil seed bank is likely to be many times greater than its field density. This suggests either that (i) it has a large seed reserve in the soil, which may have been triggered by the application of smoky water, (ii) that it produces large quantities of germinable seed, which in the field are perhaps substantially reduced by predation, or (iii) that, if most seeds germinate, many seedlings do not reach maturity. Although the susceptibility of *Stylidium hispidum* was not measured in the pathogenicity trials (Chapter 4), prolific seed production or soil seed store would be effective mechanisms of persistence were it susceptible. The occurrence of *Hibbertia rhadinopoda* and *Platysace compressa* in the seed bank may also be indicative of persistence mechanisms. Both species are commonly found dead on dieback sites (Figure 3.31, page 115) and both are susceptible to infection. *Hibbertia rhadinopoda* was found as frequently on pre-1951 dieback sites as on unaffected sites (Chapter 2). If the species is killed by *P. cinnamomi*, as the small sample in the pathogenicity test suggests (Chapter 4), and it has a capacity for rapid regeneration from seed, it may be a key species in facilitating the survival of *P. cinnamomi* on the dieback sites studied.

Although the investigation into the origin of species found more frequently in pre-1951 dieback vegetation than in unaffected vegetation was inconclusive, the reproductive characteristics of some species and their apparent absence from unaffected vegetation suggest that substantial invasion has occurred after dieback. The vegetation of pre-1951 dieback sites is, to some degree, alien, and not just a redistribution of species already present.

A knowledge of the presence or absence of invading species is important in the interpretation of data on species richness obtained through space for time substitution. The effect of dieback on species richness might be assessed at more than one scale, for example: (i) the number of species / quadrat; (ii) the number of species in a geographic region such as the jarrah forest; or (iii) the number of species in existence. On the

smallest of these scales, it would be easy to conclude from Table 2.5 (page 48) and Figure 3.9 (page 91) that dieback has had little effect. By removing possible invading species, however, there are 14 fewer species / quadrat in pre-1951 dieback sites than in unaffected vegetation. If many species have invaded dieback sites, species richness at the quadrat level was greatly reduced soon after the initial dieback event.

At the regional scale, it could be argued that, if invasion has occurred, many or most of the invaders have come from within the region, based on the searches made of the herbarium records. In this case, dieback has changed abundance and distribution but, since few species found frequently in unaffected vegetation are absent from pre-1951 dieback vegetation, it may not have greatly changed diversity. Time will be the only test of this proposition. *P. cinnamomi* may have been in the forest for too short a period to evaluate the long-term prospects of susceptible jarrah forest species. Regional and total extinctions may yet occur.

CHAPTER 6: PERSISTENCE MECHANISMS OF SUSCEPTIBLE SPECIES ON DIEBACK SITES

6.1 Introduction

Dieback-sensitive species might persist on dieback sites by surviving the initial impact or recolonizing afterwards. Survival might occur because of chance (i.e. plants of a susceptible species were missed by the pathogen) or some form of resistance in the plants to the effects of *P. cinnamomi*. For species that are not killed by *P. cinnamomi* in the field, resistance is believed to occur because of an ability to cope with the pathogen rather than an ability to prevent penetration of the pathogen (Cahill et al 1993). Susceptibility of field populations of jarrah to infection by *P. cinnamomi* has been demonstrated to range from highly susceptible to highly resistant (McComb et al 1991). The level of resistance is genetically controlled (Stukely and Crane 1994). The restriction of *P. cinnamomi* development in the least susceptible lines of jarrah is similar to that which occurs in generally field resistant species such as marri and some sedges (Cahill et al 1993). Since jarrah may experience large water deficits over summer (Crombie et al 1988), an ability of jarrah to limit the impact of the pathogen within its tissue may mean the difference between survival and death at times of normal stress.

Recolonization of susceptible species on dieback sites clearly occurs. Numerous *Banksia grandis* seedlings are readily found in winter at dieback fronts amongst dead mature *Banksia grandis* plants. Although the seedlings do not seem to persist, based on their absence from older dieback sites, the germination event demonstrates that germination and establishment need not be prevented if seed of species killed by *P. cinnamomi* can persist in the soil or be dispersed to dieback sites. The occurrence of some species on old dieback sites might be explained in part by their reproductive capacity and dispersal mechanisms. *Dryandra sessilis* is believed to be an aggressive colonizer of open, dieback sites once jarrah and *Banksia grandis* have been killed (Rockel et al 1982). The species

is highly susceptible to infection by *P. cinnamomi* and is often found dead on active dieback sites (Shearer and Dillon 1995). It has been shown to harbour *P. cinnamomi* in its roots over summer (Rockel et al 1982). Since *Dryandra sessilis* does not have special inherent dispersal mechanisms and animal dispersal vectors are not known for its seed, seed dormancy might be expected to be important in its apparent success. The colonizing ability and susceptibility of *Dryandra sessilis* are thought to be evidence of cycles of epidemic and recovery on dieback sites (Wills 1993). An understanding of the reproductive characteristics of *Dryandra sessilis* may be valuable in predicting future patterns of infection and vegetation on dieback sites.

In this chapter, I present the results of a study of the relative resistance of populations of several susceptible species that persist on dieback sites. The possible role of reproductive strategies in the persistence of susceptible species is investigated and discussed, using *Dryandra sessilis* as an example.

6.2 Methods

6.2.1 Resistance

Intra-specific differences in the susceptibility of plants to infection by *P. cinnamomi* are usually investigated by introducing the pathogen under the bark of a plant and measuring its rate of movement. The best method for investigating such differences is *in situ,* on the roots of living plants. *In situ* inoculation in unaffected vegetation is not usually permitted because of the risk of contamination to soils. The exposure of roots in the field also involves some disturbance. In large plants, such as trees, this might not interfere with the plant's function. With small plants, however, disturbance of this scale may affect the rate of *P. cinnamomi* movement. Although an inverse relationship between plant stress (as measured by water deficits) and movement of *P. cinnamomi* in plant tissue has been found in jarrah (Tippett et al 1987), the effect of plant stress on *P. cinnamomi* activity is unknown for other species in the jarrah forest. Field experiments of this type are not

easily controlled. Excision of roots followed by *in situ* inoculation is an alternative approach. For many deep-rooted species this is impractical. For these reasons, *in situ* or *ex situ* inoculation of stem tissue is commonly performed (e.g.. McCredie et al 1985, Tippett et al. 1985, Shearer et al 1987). *Ex situ* stem inoculation was used in the present study. The reliability of this method has not been thoroughly tested. However, Shearer et al (1987) found that the rate of colonization in excised roots of jarrah and *Banksia grandis* was correlated with the *in situ* rate of colonization in inoculated stems. Hüberli (1995) found that significant differences could occur in the relative pathogenicity of some *P. cinnamomi* isolates when applied to stems *in situ* and *ex situ*, although within the same isolate there was generally correlation between *in situ* and *ex situ* colonization rates.

The sites selected for study were all in Myara forest block. The site numbers referred to are shown in Figure 3.1. Some sites had been burnt two years earlier, whilst others had not been burnt for at least eight years.

Stems of species to be tested were cut with secateurs on two sampling dates (30 August and 13 September 1995). The species and sites sampled on the second date were determined from the measurements of *P. cinnamomi* colonization from under-bark inoculation of the first sampling. This was fortuitous rather than planned because a maximum number of stems were collected on the first date that could logistically be processed for under-bark inoculation. The species, zones and number of sites sampled are listed in Table 6.1. When a species was sampled from a dieback zone (A or C) a sample was also taken from the unaffected part of the site (zone F). Additional samples were made for *Adenanthos barbiger* from four unaffected sites and for jarrah from an unaffected creek edge site dominated by bullich (Myara forest block, AMG MK 115077). All species are known to be susceptible to infection and all persist to some extent on dieback sites. *Hibbertia hypericoides* was included because it seems to be ultimately unaffected by the pathogen, occurring widely as a dominant of dieback sites. Resistance could have been an important mechanism in its success.

Table 6.1. The number of populations of species tested in each zone by under-bark inoculation for measurement of relative resistance to *P. cinnamomi* movement in stem tissue. The letters used for zones are those described in Chapter 3 except that zone H represents unaffected zone A vegetation.

	Zone			
Species	A	C	F	H
Adenanthos barbiger		3	7	
Bossiaea ornata		1	1	
Hibbertia hypericoides		2	2	
Jarrah	5	5	5	1
Petrophile striata		1	1	

Between 20 and 30 stems were cut of each species in each population. One stem was cut per plant. Foliage was trimmed from the stems immediately after removal. The cut stems were placed in a damp hessian bag, which was put in an ice box containing frozen plastic blocks beneath a layer of newspaper. Jarrah stems were taken from plants less than 2 m tall. Uniformly young stems were sought but were not always available, especially in sites that had not been burnt. At one site with a burning boundary across zones A and C, an equal number of jarrah stems was collected on both sides of the boundary to investigate whether fire could have influenced the susceptibility of tissue to *P. cinnamomi* spread.

The following day, the stems were trimmed into 20 cm lengths and the remaining side branches and foliage were removed. The top and bottom were dipped in molten wax to seal the conducting tissues. When the wax had dried the entire stems were surface sterilised with 70% alcohol. When this dried, a small cut was made under the bark in the middle of each stem section and a disk of Mira cloth, which had been colonized with a *P. cinnamomi* isolate of medium virulence (isolate MP 116), was placed beneath it. The inoculated section was then wrapped in parafilm. The stems from each sample were placed in sterilized plastic trays on paper towels moistened with deionized water. The trays were put in plastic bags, sealed, and stored in the dark at 23°C for about one week (6.65 days for stems collected at the first harvest and 6.81 days for stems collected at the second). The trays were then removed and put into a 4°C coldroom.

Over the next two days, trays were removed in groups (by species and site), so that the amount of time samples that were to be compared spent in the cold room would be similar. For jarrah, the diameter of the stem at the wound was measured and an estimate of the % of periderm present made to determine if the age of the tissue influenced the rate of *P. cinnamomi* colonization in the tissue. Obvious lesions were measured in jarrah stems. This was generally only possible on sites that had been burnt, since burning initiates new growth. Stems from these sites were green and fleshy. Each stem was cut into 0.5 cm cross sections above the infected wound, 18 sections for each stem. The cut surface of each section was mounted on the selective agar medium described in Chapter 3 and incubated at 23°C. One plate was used per stem. Stem sections were numbered on the plate. Plates were inspected about 40 hours later and stem sections infected with *P. cinnamomi* noted using a light microscope. The plates were inspected again at about 60 hours. No further inspections were made because *P. cinnamomi* from infected stem sections was beginning to encroach on non-infected stem sections. The length of stem infected with *P. cinnamomi* was determined as the centre of the infected section furthest from the inoculation point (i.e. the piece next to the inoculation point was given the distance 2.5 mm, the piece next to it 7.5 mm etc.). The colonization rate for each section was then calculated as the length of infected stem (mm) divided by the incubation time (in days). One pair of trays containing *Hibbertia hypericoides* from Site 1 was inadvertently left in the cold room for two weeks and plated out with stems from the second harvest.

6.2.2 Reproductive Strategies in *Dryandra sessilis*

Dryandra sessilis is a shrub of the Family Proteaceae. In the jarrah forest it grows to a height of about 4 m. The species often grows in very dense stands on open sites, including disturbed areas such as gravel pits. In the Broad Quadrat Survey of Chapter 2, it was only found in abundance on dieback sites with ironstone surface gravels. The pale yellow flowers of *Dryandra sessilis*, which are clustered into terminal heads amongst the prickly leaves, are primarily pollinated by birds.

Germination

A single collection of 189 seeds of *Dryandra sessilis*, collected in January 1996 from Boddington, was available for germination studies (seedlot 960046, supplied by Alcoa Marrinup Nursery). The sample is small by seed testing standards so little emphasis could be placed on quantitative results. The purpose of the trial was to find if any dormancy could be found, which may enable the species to persist on dieback sites despite the series of epidemics that appears to eliminate *Banksia grandis*. The effect of depth of sowing was also investigated because, if seed could survive at depth and germinate after soil disturbance, recolonization might also occur. Germinable seed has been found up to 10 cm below the soil surface in the jarrah forest (Koch et al 1996).

The seed was placed in a 4°C fridge for two days. This was done in case the seed had a cold requirement for germination. Many jarrah forest seeds germinate at low temperatures (Bell and Bellairs 1992). Low temperatures are associated with the first prolonged rain after seed shed. There is likely to be some mechanism which protects seed from germination during sporadic summer rainfall events. If the mechanism involved exposure to low temperature, no germination would have occurred because the trial was commenced in mid-February, soon after the seed was collected. The seed was divided into two lots. The first lot of 99 seeds was sown in nine rows of 11 seeds on a layer of perlite in a seed flat, 2 cm below the final soil surface. The seeds were covered with vermiculite. The seed flat was placed in a temperature-controlled glasshouse with an automatic watering system. The use of two materials was designed to facilitate recovery of ungerminated seeds after the trial was over. The second seed lot of 90 seeds was placed in five 10 cm pots at three sowing depths - 0 cm (surface sown), 0.5 cm and 5 cm, making six seeds per sowing depth per pot. The pots were placed in the same glasshouse as the seed flat. A small amount of a 1994 seedlot was sown in a separate pot just below the soil surface in a sand and bark potting mix to test if germinability was maintained beyond one year.

Plants were counted as they emerged. After 114 days, more than one month after the last plant emerged, the tray and pots containing the 1996 seedlot were searched for germinated and ungerminated seeds. Ungerminated seeds were tested for viability using a standard tetrazolium test. The living parts of embryos stain in a 1% solution of tetrazolium chloride. The pattern of staining is indicative of the viability of seeds (MacKay 1972). A knowledge of the anatomy of the seed under investigation is crucial to the proper interpretation of the staining pattern. Staining may occur slowly if there is an almost impermeable testa. This could be mis-interpreted as incomplete staining. To obtain an understanding of the seed anatomy of *Dryandra sessilis* and the treatment of seeds required to obtain an adequate staining pattern, a number of seeds collected in 1994 were tested under a range of pre-treatments. Pre-treatments for the seeds were: soaking in water for 48 hours; soaking in water for 48 hours and testa removed; soaking in water for 48 hours and cotyledons separated; no pre-soaking; no pre-soaking and testa nicked. It proved to be impossible to remove the testa of unsoaked seeds. Seeds were then placed in a 1% tetrazolium chloride solution for 24 hours and examined under a dissecting microscope. Unsoaked seeds remained largely unstained. The most thorough staining was of seeds that had been soaked and the cotyledons separated or the testa removed. Because of the moist conditions in the pots and tray, the testa of the seeds from the germination trial were easily separated from the cotyledons before placement into a 1% tetrazolium chloride solution. After 24 hours, the cotyledons were separated and inspected under a dissecting microscope for their staining pattern.

Soil-seed Storage

The ability of *Dryandra sessilis* seed to persist in the soil beyond the year of production was investigated by collecting soil samples beneath a dense stand of mature *Dryandra sessilis* plants in early spring (September 1996). At that time, germination of seed shed in the previous year would have finished and the following year's seed would not have been produced. Soil and litter was collected under and around reproductive *Dryandra sessilis* plants at a site in Karnet forest block with a spade to a depth of about 5 cm. An area of

approximately 1.25 m^2 was sampled. The soil, weighing 25.3 kg in total, was passed through a 2 mm sieve. Because the soil was wet, this did not entirely separate the soil fraction. To locate ungerminated seeds, it was necessary to spread the gravel, plant litter and remaining soil in a thin layer and search it carefully. The viability of any ungerminated seeds found was to be tested by placement in a 1% tetrazolium chloride solution. This would not necessarily give an indication of the germinability of seeds. However, if a dormancy mechanism were involved in their non-germination beyond the first period of optimal germination conditions, their placement in soil in a glasshouse may not have detected any germination.

Seed Production

An estimate of *Dryandra sessilis* seed production was made at a site in Myara forest block containing a dense population, which had been burnt almost two and a half years earlier. Within a 100 m^2 quadrat, the number of reproductive plants was counted and an estimate of the number of follicle clusters on each plant was made. By extrapolation, the number of seeds produced in a typically dense stand could be estimated, with some assumptions.

6.3 Results

6.3.1 Resistance

Jarrah

There is a continuum of *P. cinnamomi* colonization rates in jarrah stems for the sites sampled (Figure 6.1). There is no obvious boundary in the rates where one group of populations might be thought of as more susceptible than another. However, apart from one zone A population (pre-1951 dieback in creek edge vegetation) (site 11), populations from unaffected sites (zone F) tend to have longer lesion lengths than populations from dieback sites. When the mean rates of *P. cinnamomi* colonization of

jarrah populations in dieback and unaffected sites are compared in a t-test, the difference is significant ($P < 0.01$). The four zone A populations with small colonization rates were dominated by bullich (*Eucalyptus megacarpa*). The zone A population with a relatively large colonization rate (site 11) was dominated by jarrah. The single unaffected population of jarrah from creek edge vegetation (zone H), which was dominated by bullich, had the fifth highest colonization rate overall, 6.76 ± 0.51 mm day $^{-1}$.

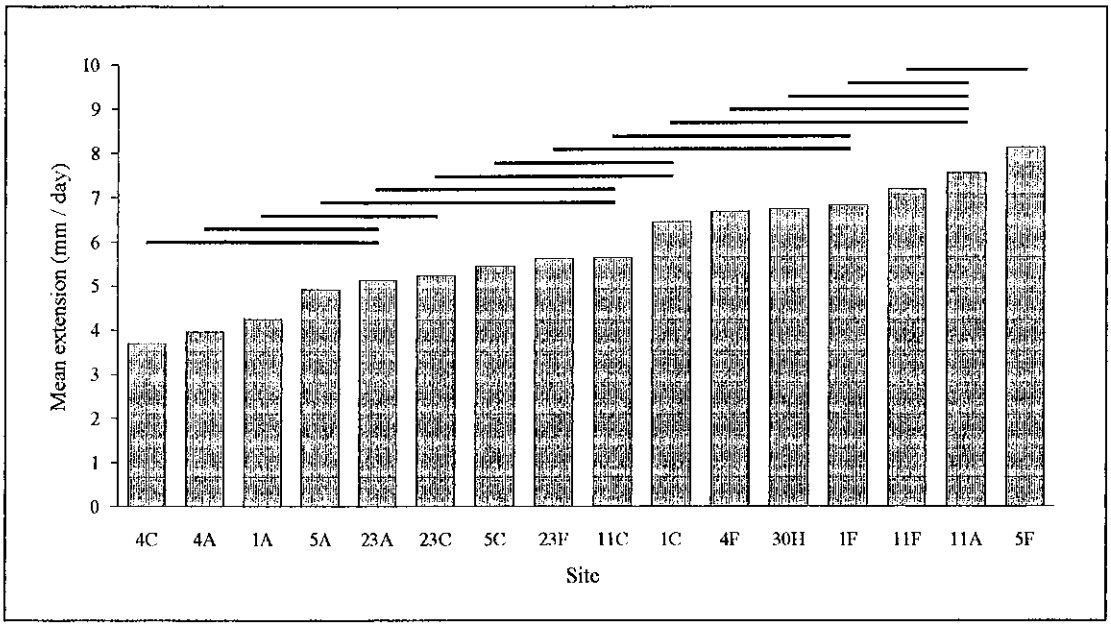


Figure 6.1 Mean colonization rate of *P. cinnamomi* in jarrah stems at each site sampled. Horizontal bars indicate that mean colonization rates for the sites below the bars are not significantly different as determined by a t-test.

There was no significant correlation between jarrah density and *P. cinnamomi* colonization rate in jarrah on dieback sites. The zone C jarrah population with the largest *P. cinnamomi* colonization rate (site 1) had the highest density of total jarrah, jarrah ≥ 20 cm DOB and jarrah < 20 cm DOB of the five zone C sites. The zone A population with the largest *P. cinnamomi* colonization rate (site 11) had the highest density of jarrah ≥ 20 cm of the five zone A sites.

P. cinnamomi colonization rate in jarrah was significantly correlated with stem diameter ($r = 0.17$; $P < 0.01$) and % of periderm on stem ($r = 0.12$; $P < 0.05$). These factors are unlikely to have affected the overall findings because sites at both ends of the resistance /

susceptibility continuum had a great within-site range of mean % of periderm and diameter of stem.

The mean *P. cinnamomi* colonization rate exceeded the mean lesion extension rate by 1.00 ± 0.28 mm / day for the four sites where lesions were measured. The difference may be greater than this because the most conservative measure of colonization possible was used in comparisons (i.e. 2.5 mm was subtracted from each colonization length, since the colonization length had been determined as the middle of the stem section furthest from the inoculation point). Lesion lengths were, on average, 65% of the length of stem found to have been infected by *P. cinnamomi* using the plating method.

There was no significant difference between *P. cinnamomi* colonization rate in burnt and unburnt sites (Table 6.2).

Table 6.2. Mean *P. cinnamomi* colonization rate and standard error for jarrah on burnt and unburnt sites; n = 12 in all samples. There was no significant difference between colonization rates in burnt and unburnt samples within zones as determined by a t-test.

	11A mm day $^{-1}$	11C mm day $^{-1}$
Burnt	7.81 ± 0.57	5.91 ± 0.80
Unburnt	7.33 ± 0.51	5.40 ± 0.48

Adenanthos barbiger

The *P. cinnamomi* colonization rate in *Adenanthos barbiger* was significantly greater in zone C than in zone F at the three sites where both zones were sampled (Table 6.3). However, when the rates of colonization for all zone C and zone F populations are compared, the difference in colonization rate is not significant, as determined using a t-test.

Table 6.3. *P. cinnamomi* colonization rates in *Adenanthos barbiger* (mm day $^{-1}$) and standard error for each site measured and all sites combined. DBS 1 and 2 are the sites in Myara forest block used in the dieback boundary survey (Chapter 2). Significance (P) of difference as determined by a t-test: * $P < 0.05$.

Site	Zone C (mm day $^{-1}$)	Zone F (mm day $^{-1}$)	P
1		2.59 ± 0.43	
4	1.70 ± 0.18	1.14 ± 0.19	*
5		2.33 ± 0.31	
11	2.92 ± 0.45	1.75 ± 0.25	*
23	3.07 ± 0.37	1.78 ± 0.40	*
DBS1		2.34 ± 0.29	
DBS2		3.61 ± 0.48	
All sites	2.56 ± 0.44	2.22 ± 0.30	n.s.

Other Species Tested

Four of the five other populations of zone C and zone F species tested had a significantly greater *P. cinnamomi* colonization rate in zone C (Table 6.4).

Table 6.4. *P. cinnamomi* colonization rate in other species sampled (mm / day) and standard error. The site number of the populations sampled is indicated in parentheses. Significance (P) of difference as determined by a t-test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s. not significant. *a* Samples from both zones for this species were stored at 4°C for two weeks before plating out.

Species (site)	Zone C (mm day $^{-1}$)	Zone F (mm day $^{-1}$)	P
Bossiaea ornata (1)	4.08 ± 0.45	1.32 ± 0.35	***
Hibbertia hypericoides (1)[a]	2.30 ± 0.30	1.40 ± 0.24	*
Hibbertia hypericoides (4)	2.19 ± 0.23	2.36 ± 0.28	ns
Leucopogon nutans (4)	8.63 ± 0.59	6.12 ± 0.58	**
Petrophile striata (1)	3.01 ± 0.58	5.19 ± 0.50	**

6.3.2 Reproductive Strategies in *Dryandra sessilis*

Germination

The first leaves of *Dryandra sessilis* appeared after about six weeks and there was no further emergence after 11 weeks. Germination probably occurred much earlier because the hypocotyl was noticed protruding from some seeds long before the cotyledons separated from the testa. The % of seedlings emerging diminished greatly below 0.5 cm (Figure 6.2).

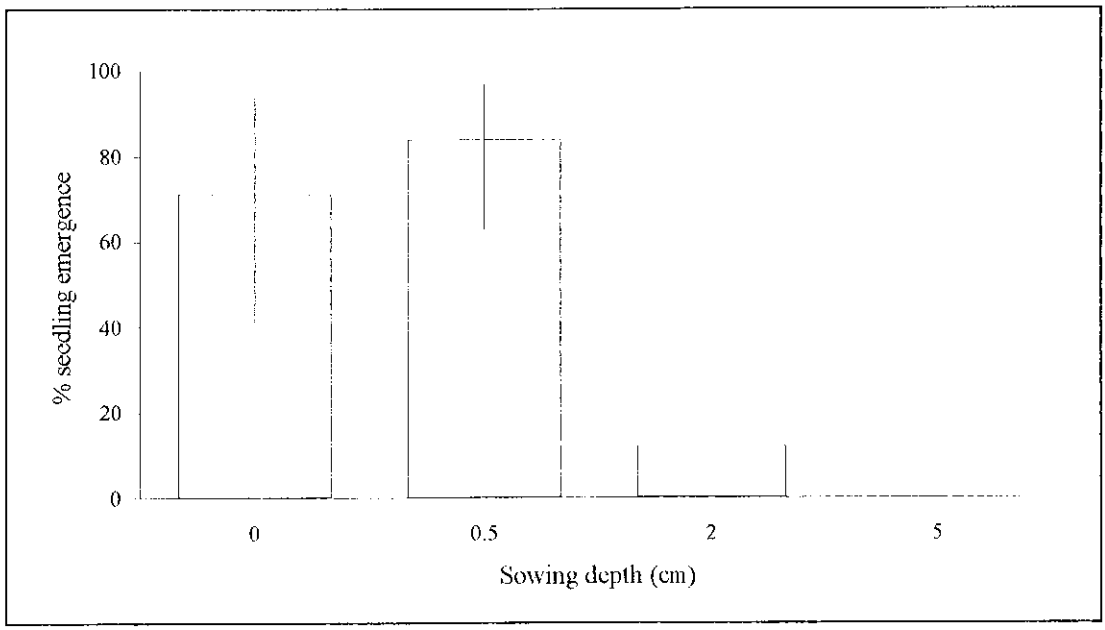


Figure 6.2 % seedling emergence at the four depths of sowing. 95% confidence limits are shown where these could be calculated. There was only one sample at 2 cm and there was no emergence at 5 cm.

Of all the seed sown, almost 70% had germinated. At the 2 cm and 5 cm depths, most germinants had died with minimal hypocotyl extension. On closer examination, some seeds were empty and there was no evidence of seed or seedling parts. Only two seeds of the 189 sown were found to be ungerminated but not empty. One had been surface sown and the other had been sown at 2 cm depth. These seeds were found not to be viable in the tetrazolium test. The surface sown seed had mushy cotyledons. These did not stain at all. The hypocotyl and areas of shoot and root meristem were stained. However, the

hypocotyl was clearly damaged and it was difficult to tell if all of the hypocotyl had been stained. The surface of the testa had a powdery appearance, unlike fresh seed or germinated seed sown below the soil surface. It is possible that the seed had been damaged by fungal growth. The hypocotyl and areas of shoot and root meristem of the seed from 2 cm depth had stained completely but only about 50 % of the cotyledons were stained.

Seed sown from the 1994 seedlot germinated readily.

Soil-seed storage

Nineteen ungerminated seeds were found in the soil sampled. All had been shed with their follicle. In all cases the follicle was closed, suggesting that the follicle was shed before maturity. Seventeen seeds showed signs of predation at the proximal end. The other two seeds were badly decayed. All of the follicles had holes at their point of attachment. None of the seeds would have been capable of germination.

Seed production

The 100 m^2 quadrat contained 50 reproductive plants. Plants as young as three years old had flowered and produced fruit. Because the recent growth of plants can be identified from stem scars, it is possible to determine which seed-bearing follicle clusters were produced in the past year. There were on average 37 follicle clusters on one year old branches of plants with a stem diameter at the base of ≥ 5 cm and 7 follicle clusters on year old branches of plants with a stem diameter at the base of < 5 cm. Clusters normally contained three follicles. Each follicle had potentially contained two seeds. Based on these figures, a stand such as that sampled could have produced up to 480,000 seeds per ha in the past year. The output of viable seed would have been much less than this because of seed predation, which appears to be substantial in this species. However, the potential seed production is clearly great in the typically dense stands of *Dryandra sessilis*.

6.4 Discussion

6.4.1 Resistance

Resistance to the movement of *P. cinnamomi* in stems appears to develop in jarrah populations on many dieback sites. That it does not develop on all dieback sites and is not related to jarrah density indicates that resistance has not been integral to the regeneration or survival of jarrah on dieback sites. Nevertheless, a diminished susceptibility may have contributed to greater recruitment of jarrah in zone A sites by decreasing the water deficits reported for jarrah during summer (Crombie et al 1988). Resistance to infection may be important in the long-term survival of jarrah. As a selective force in shaping plant communities floristically and structurally, the value of comparative resistance in jarrah populations may not yet be apparent.

P. cinnamomi colonization rate in stems does not appear to be well correlated with the field susceptibility of species. Colonization in *Adenanthos barbiger*, a species that is especially sensitive to infection, was amongst the lowest measured. In unaffected sites, colonization in jarrah, a species found by Shearer and Dillon (1995) to be of uncertain or variable susceptibility, was amongst the highest. *Leucopogon nutans* had the highest mean colonization rate of the species tested.

The significantly greater *P. cinnamomi* colonization rate in stems from plants of dieback sites, in the species measured other than jarrah, seems to be illogical. If a population naturally displayed a range of susceptibilities, the action of *P. cinnamomi* might remove the more susceptible plants. *P. cinnamomi* colonization would then be less in plants from dieback sites. If a population did not display a range of susceptibilities, *P. cinnamomi* colonization would be the same in dieback and unaffected vegetation. The antithesis of the first proposition should be that a significantly greater *P. cinnamomi* colonization on dieback sites indicates that *P. cinnamomi* is selectively killing resistant plants in a population. A mechanism for such a process is difficult to envisage. There are at least

two alternatives to this appraisal of *P. cinnamomi* action. Firstly, there might be a natural increase in resistance in the species measured with increasing distance from drainage features (i.e. from zone C to zone F). In this case, *P. cinnamomi* could remove the most susceptible individuals from zone C populations and zone F populations might still have significant lower *P. cinnamomi* colonization rates. Secondly, there may be discrete susceptible / resistant populations of species that occur in relatively small spaces. The data for *Adenanthos barbiger* support this to some extent, where there is great between-population variation in *P. cinnamomi* colonization rate. The mean colonization rate in stems from dieback site 4C, for instance, was lower than six of the seven mean colonization rates from unaffected sites but greater than the mean colonization rate on the seventh site, 4F. A third possibility, that *P. cinnamomi* operates differently in the stems of the species tested to the root tissue that it normally infects, is worth consideration.

The measurement of lesion length instead of *P. cinnamomi* colonization in the under-bark inoculations would not have given a true indication of the amount of tissue infected. In jarrah, lesions were, on average, only 65% of the length of infected tissue. Such *P. cinnamomi* colonization beyond the observed lesion in jarrah stems has been reported by Hüberli (1995).

The inadvertent delay in processing two trays of *Hibbertia hypericoides* stems demonstrates that *P. cinnamomi* can survive in plant tissue for at least two weeks at 4°C.

The comparative resistance found in jarrah on most of the dieback sites sampled is consistent with the propagation of disease resistant clones from field resistant jarrah of dieback sites (McComb et al 1994), and the prediction of Burdon (1991) that resistance to infection should occur at higher frequency in areas where a favourable environment has promoted disease expression. The absence of obvious resistance - susceptibility patterns in most of the other species studied suggests that such patterns are not universal. As a mechanism of persistence on dieback sites, resistance to infection is

undoubtedly invaluable. In jarrah, however, resistance has not been solely responsible for persistence.

6.4.2 Reproductive Strategies

Dryandra sessilis seed retains some degree of germinability and viability when stored for at least two years in dry conditions at room temperature. Although the seed sample tested for germinability and the soil sample searched for ungerminated seed were extremely small on the scale of annual seed production and plant population size, a large proportion of *Dryandra sessilis* seed and perhaps all of it appears to germinate or perish in the same year as it is shed. It is impossible to demonstrate the non-existence of a phenomenon by sampling so, to some extent, the sample sizes used are irrelevant. The response of the testa of *Dryandra sessilis* seed to soaking in water does provide further evidence, however. In the preliminary tetrazolium tests, the tough protective testa became soft after soaking in water and was easily damaged or removed. Unless seed germinated soon after the first winter rains, it would seem unlikely to survive predation and fungal attack in the wet winter soils of the jarrah forest. The available evidence suggests that there is no dormancy mechanism in *Dryandra sessilis* seed beyond the requirement of soil moisture and perhaps low temperature, to allow the seed to germinate when soil moisture is persistent.

The greater germination of *Dryandra sessilis* seed near the soil surface is consistent with that recorded for *Hakea amplexicaulis*, another proteaceous shrub (Grant 1993), and that expected of ruderal species, plants that commonly establish on disturbed, open ground (Grime 1979). The apparent preference of *Dryandra sessilis* plants for open sites, such as dieback areas, may relate to characteristics of the family Proteaceae. Many proteaceous species hold their seeds on the parent plant until a fire, when seeds are shed into an environment with abundant light. Rapid germination and establishment before the canopy closed again would give these species some advantage.

The high % germinability and viability of *Dryandra sessilis* seed, found in this study, has been reported previously by Fox et al (1987) and Bell et al (1993). There appears to be some variance in the literature, however, over the seed storage mechanism of the species and its response to fire. Bell et al (1993) indicate that *Dryandra sessilis* stores its seed on the plant, as many proteaceous species do, whereas Wrigley and Fagg (1987) and Lamont et al (1991) indicate that its seed is released on maturity. Wills (1993) suggests that the species is a prolific post-fire seeder, a claim that would be consistent with the retention of seed on the plant until its release following a fire. Although it is possible that some populations of *Dryandra sessilis* across its entire range store their seed on the plant, all populations that I have seen in the jarrah forest do not. Its prolific post-fire recruitment might relate more to the period of flowering, the reduction of competition following a fire, and the normal timing of fires rather than to its seed storage tendency. *Dryandra sessilis* commonly flowers from late winter until early summer. Seed seems to be shed mainly from mid to late summer. The most common fires in the forest are the cool prescribed burns in spring and wildfires in summer. Large *Dryandra sessilis* plants are not killed by cool prescribed burns. If spring fires do not damage flowers, the seed produced in summer will germinate in soil with very little competition. Even if all the flowers were damaged, the surviving plants will produce another crop of seed in the following year. A summer fire may simply facilitate the opening of follicles, again releasing seed to germinate into a low competition environment. If the adults were killed at that time, this would appear to be consistent with an obligate seeder that stored its seed on the plant. Hot fires in spring or autumn could be detrimental to a population of *Dryandra sessilis* if mature plants are killed. In spring, there would be no seed in the soil for regeneration, and in autumn, the seed capable of germination will be on or near the soil surface and is likely to be destroyed.

Unless a long-distance dispersal vector is found for *Dryandra sessilis* seed, the colonizing ability attributed to the species (Rockel et al 1982) may lie in its high % seed germinability, rapid growth (3 year old plants in the field were between 1 and 1.5 m tall), rapid reproduction and copious seed production.

Such effective reproduction and great susceptibility to infection by *P. cinnamomi* would be consistent with a species that contributed to the peaks and troughs of susceptible hosts in epidemic - recovery cycles hypothesized by Weste (1981) and Wills (1993). In fact, although there are other highly susceptible species growing on dieback sites, there seems to be no other with such a capacity to rapidly increase the abundance of host tissue in the soil. However, since there is no evidence of soil-seed storage in *Dryandra sessilis*, recovery would be slow or non-existent in a model involving annihilation of the standing population of *Dryandra sessilis* by *P. cinnamomi*. In reality, *P. cinnamomi* probably rarely eliminates entire populations of standing *Dryandra sessilis* plants. In the six sites studied by Rockel et al (1982), the mortality of *Dryandra sessilis* ranged from 7% to 83% of the population, with a mean of 25%. This suggests that the population is likely to rebuild quickly from surviving, reproductive plants within dieback sites.

Dryandra sessilis plants do not produce easily interpreted growth rings. Although it is possible to age young plants from seasonal growth scars on stems, large and presumably older plants are not easily aged. Despite this, it is clear that many plants of *Dryandra sessilis* survive on dieback sites for more than 10 years. Although these old plants may be survivors from previous epidemics, the enormous density of individuals more than 5 years old on many dieback sites suggests either that *P. cinnamomi* is extremely rare or absent on these sites or that *Dryandra sessilis* is not as susceptible as it is generally thought to be. The former proposition seems reasonable given the low frequency of *P. cinnamomi* recovery on pre-1951 dieback sites described in Chapter 3 and the rapid disappearance of *P. cinnamomi* under *Xanthorrhoea australis* plants reported by Duncan (1994).

The difference in the persistence of *Dryandra sessilis* and *Banksia grandis*, two species that are highly susceptible to infection by *P. cinnamomi* and that have highly germinable seed, probably lies in differences in the age of seed bearing plants. As mentioned earlier, three year old *Dryandra sessilis* plants have been observed to flower, although it is not known how old plants have to be to produce germinable seed. Abbott (1984b) reports that *Banksia grandis* plants do not produce seed until they are 30 to 40 years old.

Although I have seen a 15 year old *Banksia grandis* plant in the jarrah forest in flower, such a gap between germination and seed production may be too great to facilitate recruitment from post-dieback germinants on dieback sites.

Species that reproduce readily from seed and produce seed within a few years of germination are likely to persist on dieback sites. One such species is *Hibbertia rhadinopoda*. It commonly germinated in soil seed bank trials (Chapters 4 and 5, and possibly in Vlahos and Bell 1986 as *Hibbertia acerosa*), was commonly found dead on dieback sites (Figure 3.31, page 115) and appears to be highly susceptible to infection by *P. cinnamomi* (Chapter 4). Susceptible species that produce seed of low viability or require special germination conditions are likely to be less persistent. *Stylidium amoenum* seed is difficult to germinate. Bell et al (1993) report a germinability of 1%. In a preliminary germination test, I obtained one seedling from 200 seeds after application of smoky water, which is supposed to stimulate germination of many jarrah forest seeds (Dixon et al 1995). The seedling did not survive.

Although the susceptibility of *Stylidium hispidum* was not tested in Chapter 4, its abundant germination in the soil seed bank trial (Chapter 5) would compensate for plant losses were it susceptible. A soil seed store (i.e. seed dormancy) could enable susceptible species to persist by delaying germination until the level of *P. cinnamomi* diminishes.

Some jarrah forest species, mostly legumes, have hard-coated seed that is stimulated to germinate after fire (Bell et al 1993). Such seed is likely to be long-lived in the soil. A relationship between heat-stimulated seeds in susceptible species and persistence on dieback sites is not obvious, however. There are seven legumes in the list of species found less frequently on dieback sites (Table 2.7, page 52) and seven legumes in the list of species found equally frequently on dieback sites (Table 2.8, page 54). There are legumes susceptible to *P. cinnamomi* infection in both lists.

Gompholobium knightianum and *Trymalium ledifolium* are species of intermediate susceptibility (Shearer and Dillon 1995) with fire-stimulated seed (Bell et al 1993) that may benefit from a soil seed store. Vlahos and Bell (1986) found *Trymalium ledifolium* to be the shrub with the largest soil seed store in their study of jarrah forest seed banks. Both species produced abundant germinants on most of the burnt sites studied in Myara forest block in the present study.

Species that have long-distance dispersal agents are also likely to persist. The seed of *Leucopogon nutans*, a highly susceptible species that was frequently found on dieback sites (Chapter 2), is abundant in emu and rabbit droppings (T. Vigilante, University of Western Australia, pers. comm.). The fleshy seed of *Persoonia longifolia* is probably dispersed by birds. Although the species is almost totally eliminated on recent dieback sites and regenerates poorly there, it was occasionally found on older dieback sites (Figure 6.3). *Macrozamia riedlei* seed is also widely dispersed by brush-tail possums (Main 1981) and emus. I have observed masses of *Macrozamia riedlei* seed in emu pellets on granite outcrops and seedlings growing in tree stumps some distance from the ground.

Of the reproductive characteristics investigated for *Dryandra sessilis*, copious seed production within a few years of germination and the survival of part of the pre-dieback cohort are likely to be of greatest importance in the capacity of the species to persist in abundance on some dieback sites. Species with soil seed reserves or seed that is dispersed over long distances by animals may also be persistent on dieback sites. However, the persistence of so many susceptible species on dieback sites seems unlikely without the greatly diminished *P. cinnamomi* inoculum level occurring on dieback sites once all *Banksia grandis* plants die (Chapter 3).

Figure 6.3 A shrub of *Persoonia longifolia* (about 2 m tall) growing between a marri (left) and a dead jarrah (right) in the pre-1951 dieback part of site 5. The dieback front is about 200 m from the shrub, which is the only one growing beyond the front. It is not clear if the plant is a survivor or invader.

CHAPTER 7: SYNTHESIS

7.1 A Model of Vegetation Change Associated with Dieback in the Northern Jarrah Forest

7.1.1 Integral Components of the Model

Underwood (1990) describes a valid model as "any attempted explanation for existing observations ..... that actually explains the observations". From such models, hypotheses (predictions) can often be generated, then tested, and the model supported, rejected or refined (Underwood 1990). In these senses, a model is constructed below to explain the patterns recorded in the present study. Predictions about the future vegetation of dieback sites are presented, contingent on management practices. The predictions will only be evaluated by long-term monitoring.

The schematic model developed shows, in general terms, the factors involved in change from unaffected vegetation to pre-1951 dieback vegetation. The integral components of the model are discussed below.

Change

The key element of the model is change in vegetation. If change has not occurred, the model is illegitimate, regardless of how well it explains the observations made. Throughout the thesis, care has been taken to recognize the differences measured in the space for time studies as differences in space rather than changes in time. It could be argued that developing a model of vegetation change based on differences measured in space is a serious transgression of the principals outlined in the Methodology Rationale (Section 2.2). Evidence of change has been presented, however. The aerial photographic record indicates that structural change occurred on the sites studied. The structural changes could not be associated with fire or logging history. The current distribution of

unaffected vegetation and the persistence of jarrah stumps was suggestive that the dieback sites studied had at least the dominant elements at the time of dieback (Chapter 2). Nonetheless, the model presented below must be prefaced with the hypothesis that the differences measured in space are representative of change. Evidence to support or reject this hypothesis could be obtained by long-term monitoring of unaffected and recently-affected vegetation.

Presence of P. cinnamomi

The second key component of the model is the invasion of *P. cinnamomi*. If *P. cinnamomi* did not enter a site, the changes described are unlikely to occur. *P. cinnamomi* was found at the seven sites studied in Chapter 3, although it was not evenly distributed within each site. That it has been associated with the deaths of plants of many species in the jarrah forest is suggestive that it plays a significant role in vegetation changes, and that it has played a significant role in shaping the current vegetation of the dieback sites studied. The model would not preclude the direct impact of waterlogging on jarrah, proposed by Davison (1994), if *P. cinnamomi* was also in the system.

On-going Presence of P. cinnamomi

Although *P. cinnamomi* was found rarely on sloping pre-1951 dieback sites (zone C), it was present on three of the seven sloping pre-1951 dieback sites searched (Table 3.2, page 84). It is not known whether the *P. cinnamomi* found on these sites had been present continually since the initial infestation or had been re-introduced at some time after the initial infestation from active dieback fronts upslope. It is also not known whether *P. cinnamomi* was absent from the four sloping pre-1951 dieback sites in which *P. cinnamomi* was not isolated.

The model presented below assumes that *P. cinnamomi* can be present on dieback sites long after the initial infestation, regardless of whether it persists or is re-introduced from time to time. This is reasonable for the majority of old dieback sites in the jarrah forest,

which are close to active dieback fronts and, in some cases, bisected by unrestricted vehicle tracks. If *P. cinnamomi* was indeed absent from four of the pre-1951 dieback sites studied, the effects of its absence were not manifest. That is, susceptible species were not obviously more abundant on these four sites than on the other three.

Susceptibility to Infection by P. cinnamomi

There are differences in the probability that a plant of a species will be killed by *P. cinnamomi* infection. This is related to the susceptibility of the individual and the species. Some species become infected with *P. cinnamomi* in the field and die (Shearer and Dillon 1995). *Banksia grandis* is very susceptible to infection and plants of all ages are killed at the time of the introduction of the pathogen (Chapter 2), although disease escapes have occasionally been observed. Some degree of resistance to the spread of infection may be important in the chance of survival of an individual of a species that is normally highly susceptible to infection. Resistance at the population level may develop in jarrah after dieback but was not demonstrated in most other species tested (Chapter 6). The host range of *P. cinnamomi* is great (Chapter 4, Podger 1972). Some species are field-resistant, although they may be capable of being infected (Chapter 4, Shearer and Dillon 1995).

Sensitivity to Canopy Changes

Some species may be sensitive to the loss of canopy species regardless of whether they are susceptible to infection by *P. cinnamomi* (Chapter 4). Changes in the density of such species may be delayed for some time after *P. cinnamomi* enters a system. Although all mature *Banksia grandis* are likely to die quickly, jarrah may not die for years (Shearer and Tippett 1989). The massive input of *Banksia grandis* leaves into the litter layer soon after the death of standing plants may initially offer some protection to canopy-dependent species, regardless of the degree of canopy death.

Proportion of Population Killed

All plants of most susceptible species, except *Banksia grandis*, do not seem to be killed at the time of initial *P. cinnamomi* activity (Chapter 2). Chance may play a great part in this. Alternatively, *Banksia grandis* may be much more susceptible to infection and more likely to be killed than the majority of species. Although *P. cinnamomi* may survive in *Banksia grandis* tissue over summer (Shea 1979, Schild 1995), if it were to decline rapidly in abundance thereafter, as it has been shown to do in *Xanthorrhoea australis* in Victoria (Duncan 1994, Duncan and Keane 1996), the probability of infecting susceptible species nearby may also rapidly decline.

The chance of local extinction will be greatest for species that occur at low density. A species such as *Comesperma virgatum* may be affected for this reason. It was rarely found on pre-1951 dieback sites (Chapter 2) and was found to be susceptible to infection by *P. cinnamomi*, although perhaps not greatly so (Chapter 4). Although widespread in the jarrah forest, the species was rare on the scale of the quadrat sizes used in Chapter 2.

Capacity for Rapid Recruitment

Banksia grandis seedlings were commonly observed at active dieback fronts (Chapter 2). Without this capacity to recruit immediately after the death of the standing crop, the species would become extinct with the initial infestation. Other susceptible species displaying the capacity for rapid recruitment are jarrah, from lignotuberous seedlings, and *Dryandra sessilis* from seed (Chapter 6).

Incapacity for Reproduction

Although a species such as *Dryandra sessilis* is capable of substantial production of highly germinable seed, other species may not be so able. The seed of many species is difficult to germinate *ex situ*. In some cases, dormancy is only broken by the addition of

smoke-treated water (Dixon et al 1995), a possible indication that fire is an important trigger of their germination. If little germinable seed is produced by a species or the triggers needed for germination are not present, recruitment may not be possible after mature plants are killed by *P. cinnamomi*. The parasitic shrub, *Leptomeria cunninghamii*, may represent a special case of incapacity of reproduction if its host or hosts have been affected by *P. cinnamomi*.

Time to Reproduction

The capacity of a highly susceptible species to persist well beyond the initial impact may depend largely on the time it takes to reach maturity and reproduce, and the viability of its propagules. *Banksia grandis* may take at least 15 years to flower and produce seed (Chapter 6) and perhaps much longer in most cases (Abbott 1984b). The gap between post-dieback recruitment and seed production is clearly too great in *Banksia grandis*. The species was rarely found in pre-1980 dieback sites and not at all in pre-1951 dieback sites (Chapter 2).

Dryandra sessilis, on the other hand, may flower, and presumably produce viable seed, three years after germination. A capacity for such a rapid population turnover would be advantageous in a highly susceptible species. *Dryandra sessilis* is abundant on some old dieback sites, especially those with ironstone in the surface gravels (Chapters 2 and 6).

Other susceptible species, which have commonly germinated in soil seed bank studies, such as *Hibbertia rhadinopoda* and *Trymalium ledifolium* (Chapter 5, Vlahos and Bell 1986), may be similarly prolific and resilient in the presence of *P. cinnamomi*.

Invasion and Plant Density Increases

The death of dieback-sensitive species creates spaces for the establishment of dieback-tolerant species. There is evidence that some species, mainly annuals, were not present at the time of

dieback, although most were probably present in the vicinity (Chapter 5). These species have invaded. Other dieback-tolerant species were probably present in unaffected vegetation at the time of the initial infestation and have increased in abundance in response to the more open conditions. The probability that susceptible species will persist will be greater if they have effective dispersal mechanisms. *Leucopogon nutans* may be abundant on pre-1951 dieback sites for this reason (Chapter 6).

7.1.2 Factors Not Included in the Model

Creek Edge Vegetation

The model seeks to explain the patterns recorded. Although simplistic, it may do so effectively for sites with a jarrah overstorey and *Banksia grandis* middle storey. The creek edge vegetation studied (zone A in Chapter 3) differed in many ways from vegetation upslope. It was floristically distinct. There were fewer plant species deaths despite abundant *P. cinnamomi* at some sites. Some susceptible species were more abundant or more frequently found there than on adjoining vegetation upslope. Recruitment of jarrah was especially common along creeks edges but rare upslope. The model does not attempt to explain the patterns recorded in creek edge vegetation. This is partly because so little is known about unaffected creek edge vegetation. In addition, if resistance to infection in plants and pathogen suppression from soils are important in shaping creek edge communities, the factors listed in the model may not be as critical.

Disturbance

Since the seven sites used to construct the model were burnt or logged at the same times over the period covered by the model, there is justification for excluding such disturbances as factors affecting vegetation composition, even though, in isolation, they may have a profound effect on the floristic composition of dieback vegetation.

It would be difficult, in any case, to include logging and prescribed burning in a model of vegetation change in the jarrah forest. Little is known about their effects. Logging, and particularly that which occurred after the initial death of plants from *P. cinnamomi* infection, may have exacerbated the effects of dieback by removing trees that could have provided some protection for species apparently dependent on the forest canopy and by disturbing the ground layer and soil. The unrestricted movement of logging vehicles, in the time before an association between plant deaths and infection by *P. cinnamomi* was recognized, may have re-introduced *P. cinnamomi* to dieback sites where it had become scarce or absent. Prescribed burning may have moderated some effects of dieback by promoting seed germination in some species and flowering in others such as *Xanthorrhoea gracilis* and *Xanthorrhoea preissii*.

7.1.3 The Model

A schematic model of vegetation change associated with *P. cinnamomi*-related dieback for sloping jarrah forest sites with an understorey of *Banksia grandis* is presented in Figure 7.1. The model shows the vegetation at four times: (i) before the introduction of *P. cinnamomi* and at (ii) five, (iii) 10 and (iv) 50 years after dieback. Between (i) and (ii), there are many plant deaths, especially of *Banksia grandis*. Unusually large (hereafter called extreme) rainfall events may be important in the degree of jarrah death. Susceptible plants that are rare may become locally extinct. Regeneration of *Banksia grandis* occurs from seed so that five years after the dieback event the vegetation has changed structurally but not floristically (based on presence / absence of species). Between (ii) and (iii) the *Banksia grandis* cohort is slowly removed by *P. cinnamomi* activity until by about 10 years after dieback it is extinct because plants have not yet reached their reproductive age. There may be some invasions from off-site, especially if the site adjoins an older dieback area. Field-resistant species may begin to fill gaps left by dead plants and the bare ground that has appeared with the loss of litter producing species. *P. cinnamomi*-related deaths may still occur but *P. cinnamomi* is becoming uncommon. These processes continue to (iv), the 50 year old dieback site, where *P. cinnamomi* is now very isolated or absent. There is much bare ground.

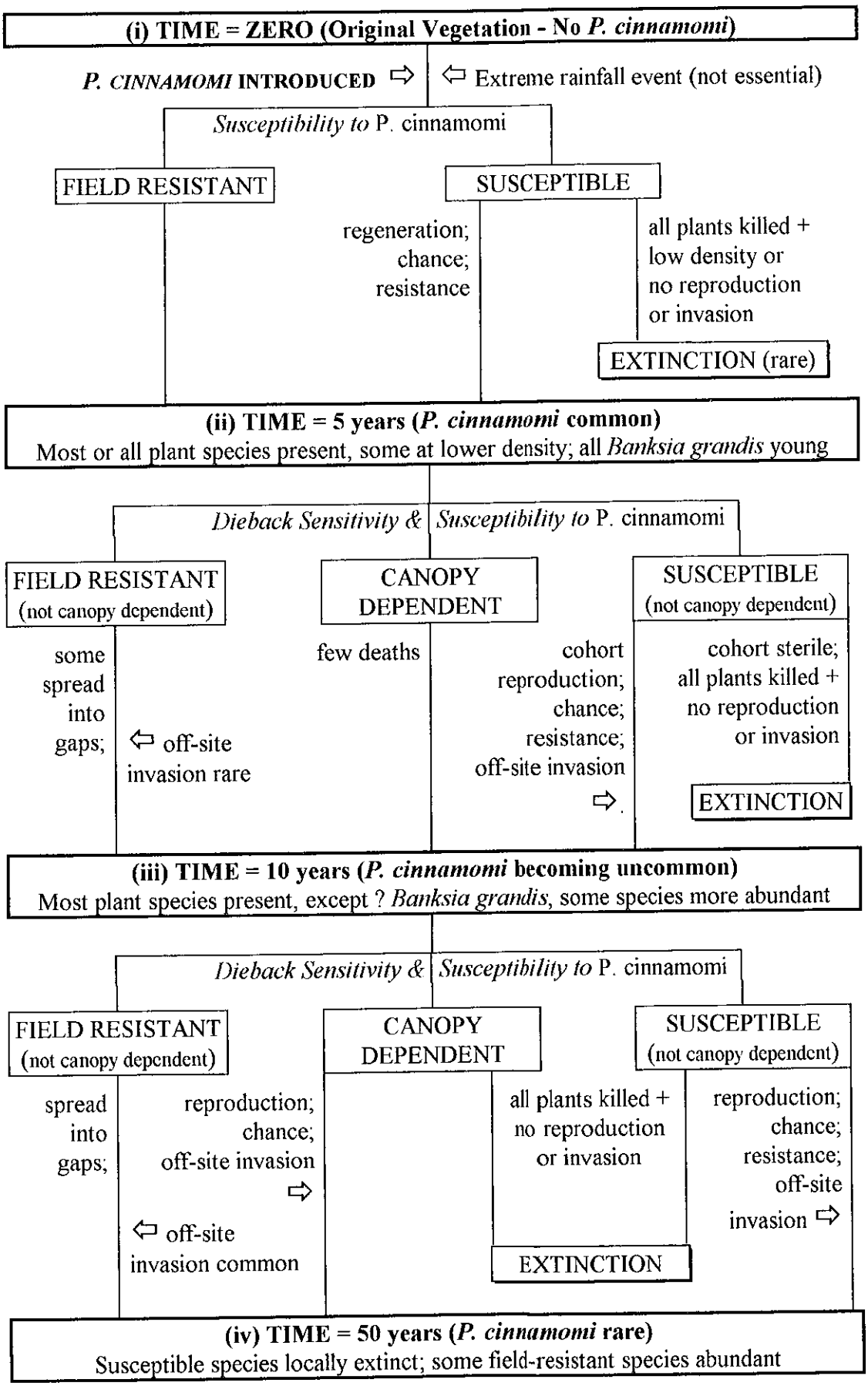


Figure 7.1 A model of changes in floristic composition associated with *P. cinnamomi* related dieback for sloping sites with gravelly surface soils and an understorey of *Banksia grandis* in the jarrah forest

Many annual species have invaded. Some species from creek edge vegetation have extended their range upslope. The number of *P. cinnamomi* susceptible and dieback-sensitive species present after 50 years depends on the relative magnitudes of mortality and recruitment. Factors such as reproductive capacity, soil seed store, persistence of a canopy, fire and dispersal of seeds by animals such as emus may be important in determining whether a species disappears or survives. Effective dispersal of seeds into the dieback site from unaffected vegetation beyond would allow species to become temporarily extinct. Other factors that have not been investigated in the present study, such as insect damage (Abbott 1992), other pathogens (Shearer 1994), changes in the size of pollinator populations (Wills and Keighery 1994), fire, logging and drought, may be enormously important in shaping dieback vegetation. However, they could only be included in the model with further research and long-term monitoring.

7.1.4 The Future of Dieback in the Northern Jarrah Forest

Dieback Frequency and Magnitude

The magnitude of dieback events in the jarrah forest is thought to be related to weather patterns. Under normal conditions, there is a short optimal period in spring and autumn for activity of *P. cinnamomi* near the soil surface. Plant deaths are sporadic and most commonly observed at dieback fronts. Occasionally, deaths occur in many, large patches. These are thought to be triggered by extreme rainfall events. Waterlogging, increased *P. cinnamomi* spread and activity, or a combination of factors may be the cause of plant deaths following such events (Shearer and Tippett 1989, Davison 1994).

Examples of dieback in large patches have been rare since the early 1980s, although there is anecdotal evidence of large-scale dieback events in each of the prior four decades (Batini and Hopkins 1972, McKinnell 1981, Shearer and Tippett 1989, Davison 1994). The recent rarity of large-scale dieback has been attributed to declining annual rainfall. Annual rainfall has generally been below average since the late 1960s (Shearer and

Tippett 1989). If major dieback events could be confidently associated with weather events, predictions might be made of future dieback frequency and magnitude based on the models of climate change being developed.

An association between extreme rainfall events and major dieback events is plausible, based on the available weather data and dieback information (see Appendix 2). However, such an association is impossible to demonstrate because of the imprecision of data on spatial and temporal dieback patterns. This is of little consequence because models of climate change do not predict the future frequency of extreme rainfall. There is, however, no indication that extreme rainfall events are likely to be less frequent. The future frequency of large-scale dieback events may be determined as much by the vegetation as by the frequency of extreme rainfall, if indeed extreme rainfall is important. The occurrence of vegetation prone to being affected by extreme rainfall events, either through waterlogging (Davison 1994) or the dispersal of *P. cinnamomi* propagules, has diminished greatly. Most of the areas in valleys and below forestry tracks, the key points for introduction of the pathogen, have already been affected.

Predictions of higher mean temperatures associated with global warming (Pittock and Allan 1990) are perhaps more important in the future of dieback. The period of optimal conditions for infection of hosts by *P. cinnamomi* may be extended as a result. Sporadic deaths would be more common and the advance of dieback fronts may accelerate.

The Future Vegetation of Dieback Sites

The future vegetation of dieback sites will depend, to some extent, on the amount of intervention from forest managers. The most obvious intervention would involve the planting of *P. cinnamomi*-resistant jarrah clones on dieback sites. The effect of such plantings on the composition of dieback sites might depend on the timing of their introduction. If they were planted soon after the death of standing jarrah, there may be fewer losses of canopy-dependent species, fewer invasions of gap-dependent annual and

weed species, and less invasion by species from creek vegetation. If they were planted long after the initial dieback event, for example on pre-1951 dieback sites, the proliferation of canopy-dependent species is likely to be slow, limited by the low density of canopy dependent species already on the site and the capacity of seed to be dispersed from sites where they are more abundant. Invading, gap-dependent annual species might decline. Once established, however, the disappearance of annual species is not guarantied. The persistence of these species will depend on the longevity of their seed banks or the occurrence of survival niches for adults. The efficacy of planting *P. cinnamomi*-resistant clones may be short-lived, of course, if the mortality of jarrah on dieback sites is primarily related to extreme rainfall events and the sensitivity of jarrah to the increased wetness of dieback sites, as suggested by Davison (1994).

In the absence of intervention, further change on the oldest dieback sites known is likely to be slow. Tree cover will increase with a possible concomitant increase in the abundance of canopy-dependent species and decrease in the cover of annual species. However, since the mean cover of marri on dieback sites more than 40 years since the initial impact was less than 10% (Table 3.11, page 93), substantial changes of this kind may not be obvious for many decades. A continued occurrence of *P. cinnamomi* will mean that some plants of susceptible species will become infected and die, especially if many susceptible species populations do not develop resistance on dieback sites, as suggested by the under-bark inoculation experiment of Chapter 6. Since *P. cinnamomi* seems to be rare on the pre-1951 sloping dieback sites studied and the susceptible species present do not reproduce prodigiously from seed, large epidemics are unlikely. The persistence of susceptible species will depend on the relative magnitudes of mortality (including that attributable to *P. cinnamomi*) and recruitment. A species such as *Xanthorrhoea preissii*, which appears to have recruited well on pre-1951 sloping dieback sites, will probably persist, whereas a species such as *Adenanthos barbiger*, the abundance of which was inversely correlated with the time since dieback, will probably disappear (Table 3.5, page 97). *Adenanthos barbiger* was already absent from one of the seven pre-1951 sloping dieback sites sampled.

This process of death (largely attributable to infection by *P. cinnamomi*) and recruitment that appears to be occurring sporadically on old dieback sites in the jarrah forest is effectively the epidemic - recovery cycle predicted by Weste (1981) and Wills (1993), on a small scale. Larger scale epidemic - recovery cycles are plausible but may prove to be uncommon in space and time. In the jarrah forest, the only species that has shown a tendency for rapid regeneration on dieback sites is *Dryandra sessilis*. As already discussed, it tends to be most prolific on sites with abundant ironstone in the surface gravels. On sites where it is abundant, many plants of *Dryandra sessilis* have clearly survived for more than a decade.

Regardless of intervention or non-intervention, amongst other factors, the ultimate floristic composition of a dieback site will depend on the continued occurrence of *P. cinnamomi* on the site and the availability of plant propagules for dispersal onto the site. The long-term occurrence of *P. cinnamomi* on dieback sites will be a function of the relative importance of three mechanisms: (i) re-introduction through the dispersal of propagules in sub-surface water flow, (ii) re-introduction of the pathogen by humans and other animals, and (iii) persistence through the continued co-incidence in space and time of host and pathogen. If host plants contribute at all to the long-term occurrence of *P. cinnamomi*, the pathogen will continue to shape the vegetation of dieback sites. However, if the dispersal of *P. cinnamomi* propagules in sub-surface water flow from dieback fronts upslope were solely responsible for the occurrence of *P. cinnamomi* downslope, *P. cinnamomi* would ultimately disappear from dieback sites. *P. cinnamomi* has been in the jarrah forest for a relatively short period. It is still in the process of working its way upslope from infested valleys. In Myara forest block, there were no catchments in which all vegetation had been infested. When catchments are completely infested, it will be worthwhile to monitor populations of *P. cinnamomi* across the landscape so that the relative importance of *P. cinnamomi* occurrence mechanisms may be assessed.

If *P. cinnamomi* were to disappear from dieback sites, natural regeneration may then accelerate for plant species with a source of propagules. Some species, such as *Banksia grandis*, are unlikely to regenerate. However, facilitated regeneration of species absent from completely affected catchments and with no natural source of propagules may be possible if re-introduction of the pathogen by humans and other animals could be prevented.

7.2 Recommendations for Further Research

Taxonomic investigations and floristic surveys are urgently required in the jarrah forest. There were many taxa found in the current study that did not adequately fit their published descriptions. These include the shrub *Hibbertia commutata,* which includes two or more variants of unknown taxonomic rank (Chapter 2). One variant was found commonly on dieback sites. If the dieback variant is a resistant genotype of *Hibbertia commutata*, it might be propagated for its re-introduction onto rehabilitated bauxite mine sites and for the long-term survival of this highly susceptible species. If, however, the dieback variant were a distinct taxon, *Hibbertia commutata* may wrongly be assessed as persistent on dieback sites. Differences in the susceptibility of a species such as *Hibbertia hypericoides* to infection by *P. cinnamomi* in separate geographic regions should be investigated for similar reasons (Chapter 2, Discussion). The jarrah forest, despite its proximity to the Perth metropolitan area and its use for forestry, bauxite mining and recreation, has had little attention paid to its flora and vegetation. The recent floristic survey by Gibson et al (1994) of the Swan Coastal Plain, which includes the Perth metropolitan area, located 81 species not previously known for the area, including 30 undescribed taxa and two species presumed to be extinct. In order to assess the changes that are occurring as a result of *P. cinnamomi* infestations in the jarrah forest, it is essential that we know what species occur there. Without this knowledge, it is possible that extinctions will occur because of *P. cinnamomi* before the plants species are found.

There is scope for much research on the creek edge vegetation (zone A). The frequent co-occurrence of some susceptible species and abundant *P. cinnamomi* in this vegetation could indicate that (i) there are agents in the soil that are antagonistic to *P. cinnamomi*, (ii) the susceptible species that grow in creek edges are comparatively resistant to *P. cinnamomi* infection, or (iii) plants are better able to cope with infection in an environment that remains wetter for longer. Investigations into the first of these possibilities might locate organisms that could be used in control of infestations. Investigations into the second of these possibilities might locate resistant genotypes that could be used in revegetation programs currently being done in bauxite mining areas. Research into the dynamics of bullich recruitment is needed so that appropriate protocols can be developed for prescribed burning in jarrah forest valleys. Data on the water usage of trees in the valleys may be useful. The change from a tall open forest of mature trees to a short closed forest of largely juvenile trees (Chapter 3, Discussion) and the apparent invasion of bullich upslope may have an effect on the amount of water discharged from forest creeks and available for use downstream.

Careful long-term monitoring of dieback over a large section of forest is required to elucidate possible correlations between major weather events and the magnitude and frequency of dieback events.

The differences recorded in space in the present study are so dramatic that there is little doubt that, in a relatively short time, dieback, associated largely with the infection of plants by *P. cinnamomi*, is catastrophic and causes great structural and floristic change. However, there is still much to know about the processes involved in change and about the importance of time in those processes. For instance, are the oldest dieback sites known in the forest indicative of long-term effects?, or is the epidemic still in its formative stages? Have the highly susceptible species survived the worst?, are they now in the process of re-building?, or are we about to witness their local extinction? Long-term ecological studies are crucial to an adequate understanding of dieback - the pathogen, its hosts and the complex environment they share. The immediate commencement of such studies is strongly recommended.

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APPENDIX 1: SPECIES AUTHORSHIP

* denotes introduced species; the number in parentheses is the collection number - to be lodged at PER (K.McDougall); Nomenclature follows Marchant et al (1987) except where otherwise referenced.

FERNS

DENNSTAEDTIACEAE
Pteridium esculentum (G. Forster) Cockayne

CYCADS

CYCADACEAE
Macrozamia riedlei (Fischer ex Gaudich.) C.Gardner

CONIFERS

PINACEAE
**Pinus* sp.

MONOCOTYLEDONS

CENTROLEPIDACEAE
Aphelia cyperoides R.Br.
Centrolepis aristata (R.Br.) Roemer & Schultes (326)

CYPERACEAE
Baumea sp.
Cyathochaeta avenacea Benth.
Lepidosperma angustatum R.Br. (250)
Lepidosperma squamatum Labill. (283)
Lepidosperma sp. F "group"
Mesomelaena graciliceps (C.B.Clarke) K.L. Wilson
Mesomelaena tetragona (R.Br.) Benth. (197)
Schoenus grammatophyllus F.Muell. (290)
Schoenus nanus (Nees) Benth. (307)
Tetraria capillaris (F.Muell.) J.Black (243, 256)
Tetraria octandra (Nees) Kuek.

HAEMODORACEAE
Anigozanthus manglesii D.Don (316)
Conostylis aculeata subsp. *preissii* (Endl.) J.Green (409)
Conostylis caricina Lindley (428)
Conostylis serrulata R.Br. (249)
Conostylis setigera R.Br. (198, 272)
Conostylis setosa Lindley
Haemodorum discolor T.Macfarl. (363) [Macfarlane 1987)]

IRIDACEAE
Orthrosanthus laxus (Endl.) Benth. (415)
Patersonia babianoides Benth.
Patersonia juncea Lindley (344)
Patersonia occidentalis R.Br.
Patersonia pygmaea Lindley
Patersonia rudis Endl.

LILIACEAE (Cronquist 1981)
Agrostocrinum scabrum (R.Br.) Baillon
Burchardia umbellata R.Br. (298)
Caesia occidentalis R.Br.
Caesia parviflora R.Br.
Chamaescilla corymbosa (R.Br.) Benth. (222)
Dianella revoluta R.Br. var. *divaricata* (R.Br.) R.Henderson [Henderson 1987]
Johnsonia lupulina R.Br. (334)
Laxmannia squarrosa Lindley (299)
Thysanotus arbuscula Baker (389)
Thysanotus dichotomus (Labill.) R.Br. (336)
Thysanotus multiflorus R.Br. (259)
Thysanotus patersonii R.Br. (262)
Thysanotus sparteus R.Br.
Thysanotus tenellus Endl.
Thysanotus thyrsoideus Baker
Thysanotus triandrus (Labill.) R.Br.
Tricoryne elatior R.Br.
Tricoryne humilis Endl. (333)

ORCHIDACEAE (the names given in Hoffman and Brown (1992) have been adopted)
Burnettia nigricans (R.Br.) Hopper & A.P.Brown
Caladenia flava R.Br.
Caladenia longicaudata Lindley
Caladenia marginata Lindley
Caladenia reptans Lindley
Cyanicula sericea (Lindley) Hopper & A.P.Brown
Diuris corymbosa Lindley
Diuris longifolia R.Br.
Elythranthera brunonis (Endl.) A.S.George
**Monadenia bracteata* (Sw.) Dur & Schinz
Paracalaena nigrita (J.Drummond ex Lindley) Blaxell
Prasophyllum elatum R.Br.
Prasophyllum parvifolium Lindley
Prasophyllum plumaeforme Fitz.
Pterostylis barbata Lindley
Pterostylis recurva Benth.
Thelymitra benthamiana H.G.Reichb.
Thelymitra crinita Lindley
Thelymitra macrophylla Lindley

POACEAE
**Aira cupaniana* Guss.
Amphipogon amphipogonoides (Steudel) Vick. (293)
Amphipogon debilis R.Br.
**Briza maxima* L.
**Briza minor* L.
Danthonia setacea Steudel
Dichelachne crinita (L.f.) J.D.Hook. (391)
Neurachne alopecuroidea R.Br.
Stipa campylachne Nees (313)
Stipa hemipogon Benth. (364)
Stipa mollis R.Br. (354)
Tetrarrhena laevis R.Br.
**Vulpia bromoides* (L.) Gray

RESTIONACEAE
Hypolaena exsulca R.Br.
Lepyrodia sp.
Loxocarya cinerea R.Br.
Loxocarya fasciculata (R.Br.) Benth.
Loxocarya flexuosa (R.Br.) Benth.
Restio spp.

XANTHORRHOEACEAE
Lomandra brittanii Choo (360)
Lomandra caespitosa (Benth.) Ewart (295)
Lomandra hermaphrodita (C.R.P. Andrews) C.Andrews
Lomandra integra T.Macfarl.
Lomandra micrantha (Endl.) Ewart
Lomandra nigricans T.Macfarl.
Lomandra preissii (Endl.) Ewart (315)
Lomandra purpurea (Endl.) Ewart (319)
Lomandra sonderi (F.Muell) Ewart (274)
Lomandra spartea (Endl.) Ewart
Xanthorrhoea gracilis Endl.
Xanthorrhoea preissii Endl.

DICOTYLEDONS

AMARANTHACEAE
Ptilotus declinatus Nees (339)
Ptilotus manglesii (Lindley) F. Muell.

APIACEAE
Actinotus glomeratus Benth. (288)
Daucus glochidiatus (Labill.) Fischer, C.Meyer & Ave Lall.
Hydrocotyle alata A.Rich.
Pentapeltis peltigera Bunge
Platysace compressa (Labill.) Norman (175)
Platysace tenuissima (Benth.) Norman (417)

APIACEAE (cont.)
Trachymene pilosa Smith (317)
Trachymene sp. A
Xanthosia atkinsoniana F.Muell. (218, 287)
Xanthosia candida (Benth.) Steudel
Xanthosia ciliata Hook.
Xanthosia huegelii (Benth.) Steudel

ASTERACEAE
Angianthus sp.
**Arctotheca calendula* (L.) Levyns
Craspedia variabilis Everett & Doust (279) [Everett and Doust 1992]
Hyalosperma cotula (Benth.) Wilson (245) [Wilson 1989]
**Hypochoeris glabra* L.
Lagenifera huegelii Benth.
Millotia tenuifolia Cass. (300)
Olearia paucidentata (Steetz) Benth. (199)
Pithocarpa pulchella Lindley
Podolepis gracilis Graham (357)
Podotheca angustifolia (Labill.) Less. (325)
Pterochaeta paniculata Steetz (327) [Wilson 1992b]
**Senecio vulgaris* L. (286)
Siloxerus multiflorus Nees [Entwisle 1995]
**Sonchus oleraceus* L.
Trichocline spathulata (DC.) J.H.Willis
**Ursinia anthemoides* (L.) Poiret
Waitzia nitida (Lindley) Paul G Wilson (351) [Wilson 1992a]

CAESALPINIACEAE
Labichea punctata Lindley (257, 322)

CAMPANULACEAE
Isotoma hypocrateriformis (R.Br.) Druce (366)
Lobelia rhombifolia Vriese
Lobelia rhytidosperma Benth.
Wahlenbergia aff. *multicaulis*

CASUARINACEAE
Allocasuarina fraseriana (Miq.) L. Johnson
Allocasuarina humilis (Otto & A.Dietr.) L. Johnson (229)

CRASSULACEAE
Crassula exserta (F.Reader) Ostenf.

DILLENIACEAE
Hibbertia amplexicaulis Steudel (292)
Hibbertia commutata Steudel (201)
Hibbertia glomerata Benth. (310, 413)
Hibbertia huegelii (Endl.) F.Muell.
Hibbertia hypericoides (DC.) Benth. (216)
Hibbertia quadricolor Domin (202)

DILLENIACEAE (cont.)
Hibbertia rhadinopoda F. Muell. (306, 343)

DROSERACEAE
Drosera barbigera Planchon (337)
Drosera erythrorhiza Lindley
Drosera macrantha Endl. (232, 405)
Drosera microphylla Endl. (414)
Drosera platystigma Lehm.
Drosera stolonifera Endl. (285)

EPACRIDACEAE
Andersonia latiflora (F.Muell.) Benth. (341)
Andersonia lehmanniana Sonder (169)
Astroloma ciliatum (Lindley) Druce (196)
Astroloma pallidum R.Br. (273)
Leucopogon capitellatus DC. (208, 219)
Leucopogon gracillimus DC. (235)
Leucopogon nutans E.Pritzel
Leucopogon oxycedrus Sonder (399)
Leucopogon propinquus R.Br. (401)
Leucopogon pulchellus Sonder (427)
Leucopogon verticillatus R.Br. (342)
Styphelia tenuiflora Benth.

EUPHORBIACEAE
Monotaxis occidentalis Endl.
Phyllanthus calycinus Labill.
Poranthera huegelii Klotzsch (282)
Poranthera microphylla Brongn.
Stachystemon vermicularis Planchon

FABACEAE
Bossiaea aquifolium Benth.
Bossiaea ornata Benth. (203, 226)
Bossiaea pulchella Meissner (260)
Chorizema rhombeum R.Br. (323)
Daviesia costata Cheel (281)
Daviesia decurrens Meissner (177)
Daviesia preissii Meissner
Daviesia rhombifolia Meissner
Dillwynia sp. A (227)
Gastrolobium villosum Benth. (261)
Gompholobium capitatum Cunn. (353)
Gompholobium knightianum Lindley (210, 254)
Gompholobium marginatum R.Br. (268)
Gompholobium polymorphum R.Br.
Gompholobium preissii Meissner (335)
Gompholobium venustum R.Br. (347)
Hovea chorizemifolia DC. (180)
Hovea trisperma Benth. (173, 230)

FABACEAE (cont.)
Jacksonia alata Benth. (314)
Kennedia coccinea (Curtis) Vent. (247)
Kennedia prostrata R.Br.
Mirbelia dilatata R.Br.
Nemcia spathulata (Benth.) Crisp (267) [Crisp and Weston 1987]
Pultenaea sp. (411)
Sphaerolobium linophyllum (Huegel) Benth. (392)
Sphaerolobium medium R.Br. (280)

GENTIANACEAE
**Centaurium erythraea* Rafn.

GOODENIACEAE
Dampiera alata Lindley (215)
Dampiera linearis R.Br. (237)
Goodenia caerulea R.Br. (393)
Goodenia incana R.Br. (385)
Lechenaultia biloba Lindley (166)
Scaevola calliptera Benth. (346)
Scaevola glandulifera DC. (387)
Scaevola pilosa Benth.
Scaevola platyphylla Lindley
Scaevola repens Vriese (388) [Carolin 1992]

HALORAGACEAE
Glischrocaryon aureum (Lindley) Orch.

LAMIACEAE
Hemiandra pungens R.Br. (244)
Hemigenia ramosissima Benth. (207)

LAURACEAE
Cassytha glabella R. Br.
Cassytha pomiformis Nees
Cassytha racemosa Nees

LOGANIACEAE
Logania campanulata R.Br. (383)
Logania serpyllifolia R.Br. (252)
Mitrasacme paradoxa R.Br.

LORANTHACEAE
Nuytsia floribunda (Labill.) R.Br.

MIMOSACEAE
Acacia alata R. Br. (181)
Acacia barbinervis Benth.
Acacia extensa Lindley (212)
Acacia lateriticola Maslin (214)
Acacia nervosa DC. (167)

MIMOSACEAE (cont.)
Acacia obovata Benth. (400)
Acacia pulchella R. Br. (191)
Acacia urophylla Benth. (174)
Acacia varia Maslin (206)
Acacia wildenowiana H.L.Wendl. (276)

MYRTACEAE
Agonis linearifolia (DC.) Schauer (359)
Baeckea camphorosmae Endl. (193)
Calothamnus rupestris Schauer
Calothamnus sanguineus Labill. (277)
Calytrix depressa (Turcz.) Benth. (367)
Calytrix leschenaultii (Schauer) Benth. (356)
Eucalyptus calophylla Lindley
Eucalyptus marginata Donn ex Smith
Eucalyptus megacarpa F.Muell.
Eucalyptus patens Benth.
Hypocalymma angustifolium Endl.(204)
Hypocalymma robustum Endl.
Leptospermum erubescens Schauer (241)
Verticordia insignis Endl.
Verticordia plumosa (Desf.) Druce

OLACACEAE
Olax benthamiana Miq. (234)

PITTOSPORACEAE
Billardiera floribunda (Putterl.) F.Muell.
Pronaya fraseri (Hook.) E.Bennett (394)

POLYGALACEAE
Comesperma calymega Labill.
Comesperma virgatum Labill. (209)

PROTEACEAE
Adenanthos barbiger Lindley (171)
Banksia grandis Willd.
Banksia littoralis R.Br.
Banksia sphaerocarpa R.Br. (263)
Conospermum capitatum R.Br.
Conospermum stoechadis Endl. (224)
Dryandra lindleyana (Labill.) R.Br. [George 1996]
Dryandra sessilis (Knight) Domin (221)
Grevillea bipinnatifida R.Br. (289)
Grevillea pilulifera (Lindley) Druce (404, 408)
Grevillea pulchella (R.Br.) Meissner (238)
Grevillea quercifolia R.Br. (239)
Grevillea synapheae R.Br. (304)
Grevillea wilsonii Cunn. (184)
Hakea amplexicaulis R.Br.(217)

PROTEACEAE (cont.)
Hakea cyclocarpa Lindley (269)
Hakea lissocarpha R.Br. (211)
Hakea ruscifolia Labill. (176)
Hakea stenocarpa R.Br. (309)
Hakea trifurcata (Smith) R.Br.
Hakea undulata R.Br.
Isopogon axillaris R.Br.
Isopogon crithmifolius R.Br. (270) [Foreman (1995)]
Isopogon sphaerocephalus Lindley (233)
Persoonia angustiflora Benth. (369)
Persoonia elliptica R.Br. (220)
Persoonia longifolia R.Br.
Petrophile linearis R.Br.
Petrophile media R.Br.
Petrophile striata R.Br.
Synaphea petiolaris R.Br.
Xylomelum occidentale R.Br.

RANUNCULACEAE
Clematis pubescens Huegel ex Endl.

RHAMNACEAE
Spyridium tridentatum (Steudel) Benth. (386)
Trymalium ledifolium Fenzl (178)

RUBIACEAE
Opercularia echinocephala Benth. (253)
Opercularia vaginata A.L.Juss. (264)

RUTACEAE
Boronia crenulata Smith
Boronia fastigiata Bartling (200)
Eriostemon spicatus A.Rich. (240)

SANTALACEAE
Leptomeria cunninghamii Miq. (255, 330)

STACKHOUSIACEAE
Stackhousia monogyna Labill. (265, 311, 340) [Barker 1984]
Tripterococcus brunonis Endl. (246)

STERCULIACEAE
Lasiopetalum floribundum Benth.
Lasiopetalum glabratum Paust

STYLIDIACEAE
Levenhookia preissii (Sonder) F.Muell. (358)
Levenhookia pusilla R.Br. (338)
Levenhookia stipitata F.Muell.
Stylidium amoenum R.Br.

STYLIDIACEAE (cont.)
Stylidium brunonianum Benth. (390)
Stylidium bulbiferum Benth.
Stylidium calcaratum R.Br. (258)
Stylidium diuroides Lindley (345, 380)
Stylidium hispidum Lindley (275)
Stylidium junceum R.Br. (251)
Stylidium lateriticola Kenneally [Kenneally 1992]
Stylidium lineatum Sonder (355)
Stylidium repens R.Br.
Stylidium schoenoides DC. (242, 271)

THYMELAEACEAE
Pimelea preissii Meissner (301)
Pimelea spectabilis Lindley (320)
Pimelea suaveolens Meissner (225)

TREMANDRACEAE
Tetratheca hirsuta Lindley (183, 205)

VIOLACEAE
Hybanthus floribundus (Lindley) F.Muell. (195)

APPENDIX 2: WEATHER PATTERNS AND DIEBACK

A2.1 Introduction

An association between rainfall, especially rainfall extremes, and dieback has been proposed via *P. cinnamomi* activity in Western Australia (Shearer and Tippett 1989) and Victoria (Tregonning and Fagg 1984), and between rainfall and waterlogging in conjunction with jarrah death in Western Australia (Davison 1994).

Rainfall, in association with temperature, is undoubtedly important in determining the duration of *P. cinnamomi* activity in surface soils of the jarrah forest. In normal or below average rainfall years, the effects of *P. cinnamomi* are seen as sporadic deaths at dieback fronts. Occasionally, there are extensive deaths of jarrah and other species. Whether these are caused primarily by *P. cinnamomi*, secondarily by *P. cinnamomi* in conjunction with waterlogging, or solely by waterlogging, their confirmed association with particular climatic events might allow some predictions to be made about future dieback epidemics based on models of climate change, currently being developed.

Pittock and Allan (1990) indicated that, within the severe limitations of the climatic models currently available for Western Australia, a continuing trend of below average rainfall associated with frontal systems in winter was likely. Predictions about the future summer rainfall pattern are less certain (Robert Allan, CSIRO Division of Atmospheric Research, pers. comm.). A temperature rise is expected as part of the global warming model. The effect of diminished winter rainfall could be exacerbated by increased evaporation (Pittock and Allan 1990). Davison (1994) suggests that there is a relationship between large rainfall events and extensive jarrah death. If large rainfall events were limited to winter, predictions might be made about the future frequency of major episodes of tree decline because winter rainfall is predicted to remain below average.

A2.2 The Timing of Major Dieback Events

The detection of correlation between weather patterns and major dieback events in the jarrah forest is difficult because dieback events are poorly documented in time and space. Shearer and Tippett (1989) report that, from anecdotal information, the peak of jarrah deaths occurred in the early 1960s, from aerial photographic investigations there were many deaths in the early 1970s, and from their personal experience there was a major dieback event between 1982 and 1984. Davison (1994) reports that there were many jarrah deaths in the late 1950s and mid 1960s. The period since 1984 has been benign for large-scale dieback. The only recorded large patch of jarrah to die in that period was near Byford in early 1993 (Dr. Ian Colquhoun, Alcoa of Australia, pers. comm.).

From my own investigations using aerial photographs (Chapter 3), large patches of apparently dead jarrah appeared in Myara and Karnet forest blocks between 1941 and 1951. These observations accord with the growing interest in dieback research at the end of the 1940s reported by Havel (1989). The patches grew substantially in size between 1951 and 1960, although by 1960 almost all trees had been removed from the sites by salvage logging so that it is difficult to tell if the trees died or were simply removed. Large patches of apparently dead jarrah were observed on aerial photos taken south of Dwellingup in 1958. It is not clear if these were recent deaths because the previous photography of the area was taken in 1943. However, the area was logged in the mid-1950s. Dead and dying jarrah were routinely removed from other parts of the forest. It seems possible that the apparently dead patches were not removed because they had not declined when the logging occurred. Changes occurring between 1960 and 1968 on the sites studied are difficult to interpret because of a severe bushfire in 1961.

From all sources, it seems that there were major dieback events involving extensive jarrah death in the 1940s, the late 1950s to mid 1960s, the early 1970s, and from 1982 to 1984. It also seems likely that there were notable dieback events in the 1920s, when patches of dead jarrah were first recorded.

A2.3 Weather Data

Weather data were obtained from the Perth office of the Bureau of Meteorology for rainfall (Jarrahdale from 1907 onwards with minor gaps in data, Dwellingup from 1935 onwards and complete except for January in 1961, and Karnet from 1963 onwards with some missing data) and temperature (Perth from 1935 onwards).

The rainfall models for south-western Western Australia (Pittock and Allan 1990) reflect the trend in rainfall in the jarrah forest over the past 30 years. Winter and annual rainfall have been consistently below average in that time (Figures A1 and A2). Summer rainfall has been above average for much of that period but appears to be declining again (Figure A3). There was a long period of below average summer rainfall between 1930 and the mid 1950s. The patterns for autumn and spring show great fluctuation over short periods.

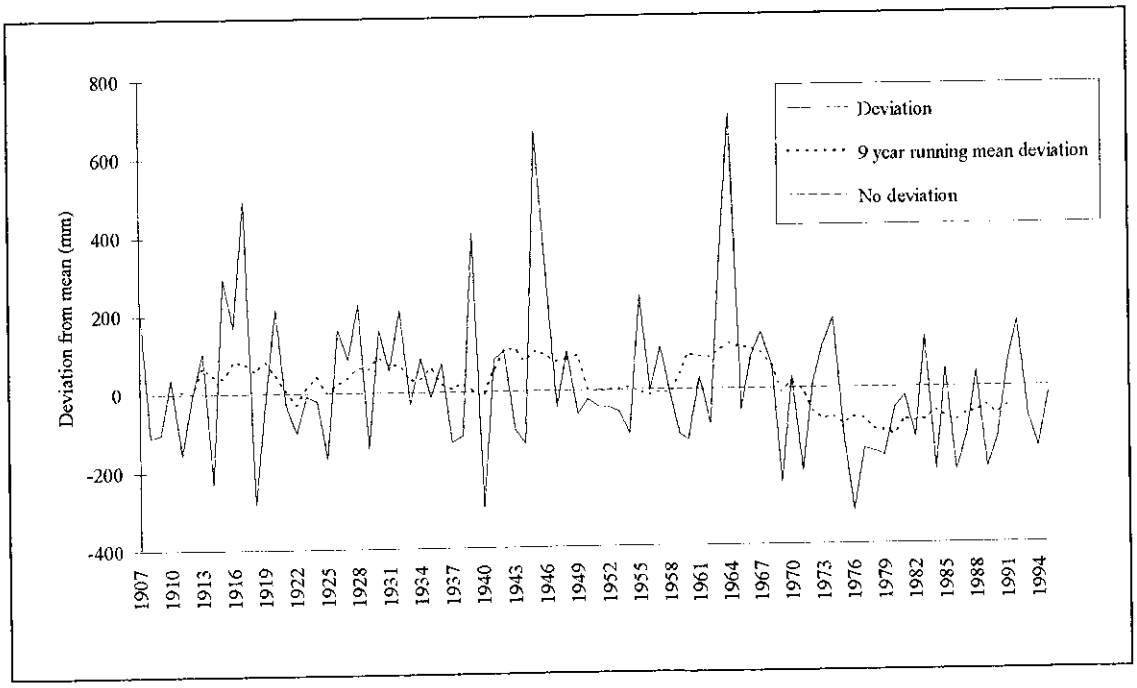

Figure A2 Deviation from long-term mean winter rainfall from 1907 to 1995 for combined data of Jarrahdale (1907 - 1934) and Dwellingup (1935 - 1995), and nine year running mean deviation.

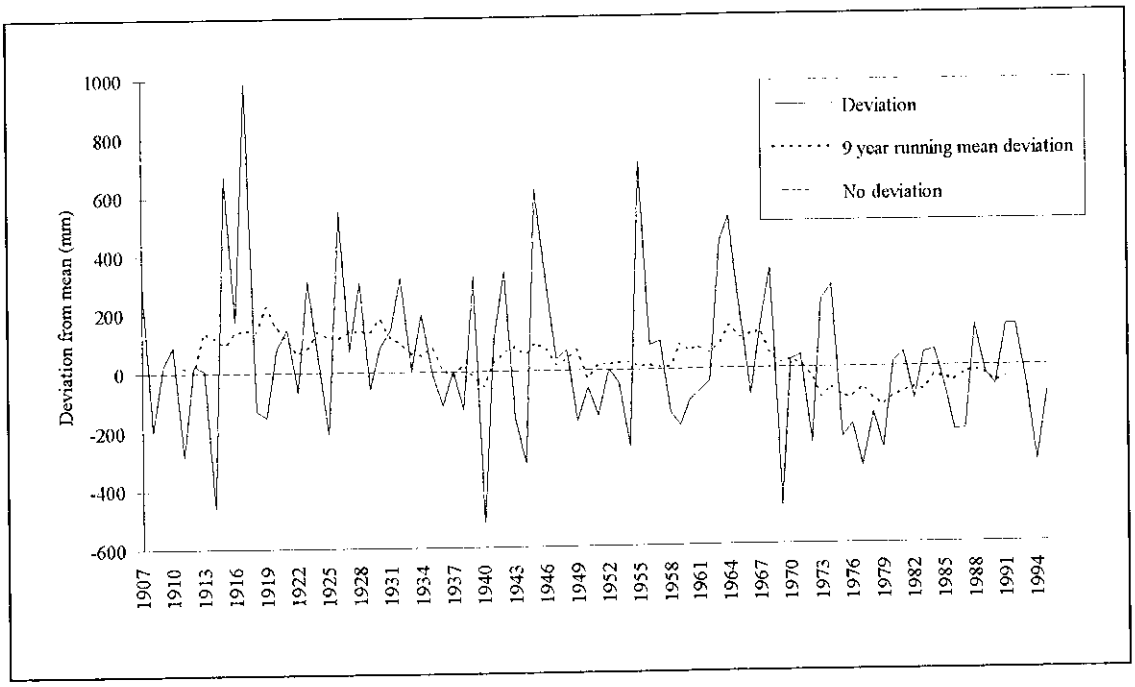

Figure A2 Deviation from long-term mean annual rainfall from 1907 to 1995 for combined data of Jarrahdale (1907 - 1934) and Dwellingup (1935 - 1995), and nine year running mean deviation.

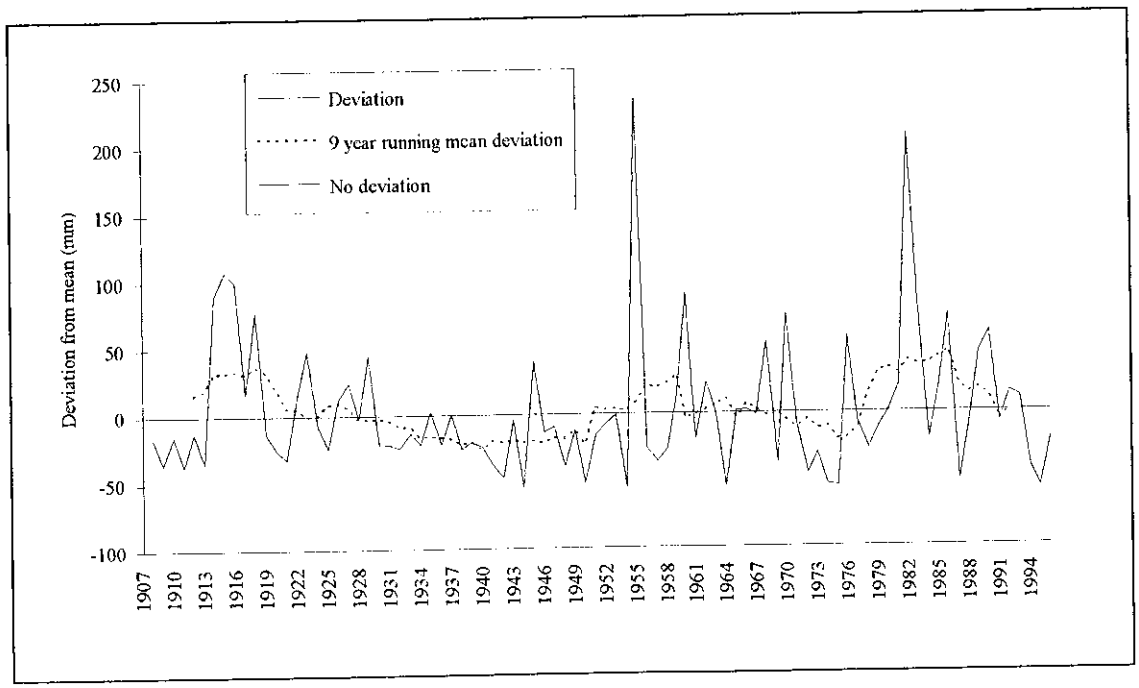

Figure A3 Deviation from long-term mean summer rainfall from 1907 to 1995 for combined data of Jarrahdale (1907 - 1934) and Dwellingup (1935 - 1995), and nine year running mean deviation.

It is not only the timing of major dieback events that is required for correlation with weather patterns. Although the average annual rainfalls for the three weather stations in the study area are similar (Dwellingup 1269 mm, Jarrahdale 1181 mm, Karnet 1220 mm

- see Figures 2.4 and 3.1 for locations), there are some notable differences in the magnitudes of extreme rain events between stations (Table A1). For instance, when Dwellingup received 159.8 mm in January 1982, its second highest summer rain event on record, Jarrahdale received only 58.2 mm. And when Jarrahdale received 109 mm in one day in February 1992, Dwellingup only had 23.9 mm. Such differences are not restricted to cyclonic events during the summer months. If major dieback events are associated with extraordinary weather events or combinations of weather events, the impact of such weather events is likely to be localised.

Table A1 Rain events of more than 90 mm in one day for Jarrahdale, Karnet and Dwellingup climate stations. Records for two day periods are shown where better accordance was achieved because apparent discrepancies may occur between stations for daily readings if the rain event occurs in the morning when readings are taken. The two day record for the January 1992 event is included to show the magnitude of the difference between records. * indicates that there is no record.

Year	Date	Jarrahdale (mm)	Karnet (mm)	Dwellingup (mm)
1939	July 25	95.5	*	111.8
1945	June 10	80.8	*	114.8
1945	June 18	85.1	*	99.8
1952	June 4,5	96	*	90.2
1955	February 17	106	*	177.5
1964	August 3,4	145	142.5	145.6
1967	June 26	127	145.8	37.1
1978	October 1,2	92	97.6	97.8
1980	April 20,21	95	55.8	59.6
1982	January 21	58.2	106.8	159.8
1982	January 21,22	78.2	151.8	208
1983	July 24,25	88	83	93
1984	April 30	48	52	93.4
1987	July 29	140	113	87.2
1992	February 9	109	30.4	23.9

A2.4 A Search for Correlation between Weather Patterns and Major Dieback Events

Detecting association between weather patterns and dieback patterns is complicated by the time jarrah may take to die after infection or other forms of stress. Shearer and Tippett (1989) report that jarrah may take five or more years to die after infection. There is therefore likely to be a lag between important weather events and major dieback events that involve many jarrah deaths.

Even if there were consistent weather patterns that produced large patches of dead jarrah between 1920 and 1970, the same patterns might not have produced dead patches since. Changes in forest hygiene practices since the 1960s may have influenced the rate of spread of *P. cinnamomi* and the number of large dieback events. In addition, the widespread death of jarrah around logging tracks and watercourses prior to 1970 may have significantly reduced the areas now prone to mass jarrah death.

Despite the limitations of associating dieback with weather patterns, extreme weather events have occurred at the times when major dieback events are thought to have been triggered. The second largest summer rainfall total at Dwellingup in 1981/82 preceded the last major dieback event in that area. The largest summer rainfall total in 1954/55 may have been related to reports of the peak of jarrah decline in the late 1950s (Davison (1994) and the frantic salvage logging of the 1950s (from personal observations of aerial photography). The third largest summer rainfall total in the summer of 1959 / 1960 may have exacerbated the malaise. The three largest summer rainfall totals are linked to single major rainfall events: 177.5 mm in one day in February 1955; 105.4 over two days in December/January 1959/60; 208 mm over two days in January 1982. Interestingly, Jarrahdale received little rain in January 1982 and there appear to be no major dieback sites in the Jarrahdale area attributed to the event.

Although exceptional summer rainfall has been implicated in outbreaks of dieback because of the potential activity of *Phytophthora* in the warmest months, summer rainfall

does not seem to adequately explain dieback events in the 1940s and early 1970s. The largest and second largest spring rainfall totals in 1971 and 1942 respectively were brought about by above average rainfall in September. There were no large single summer rainfall events in the late 1930s or 1940s and late 1960s. The largest summer rainfall for Dwellingup between 1936 and 1950 was 34.3 mm on the 11th of February 1937, the 16th highest summer rainfall between 1936 and 1996 at Dwellingup. At Jarrahdale, the largest summer rainfall day in these periods was 31.8 mm on the 25th of December 1945, the 13th highest summer rainfall in one day between 1936 and 1996. The highest November rainfall events in a single day did occur in that period at both stations, 64.3 mm at Dwellingup in 1946 and 58.7 mm at Jarrahdale in 1938. These are not exceptionally large daily totals when compared with the records for all months.

The three largest winter rainfall totals, however, occur at times that might link them to dieback events in the 1940s and early 1970s. The winters of 1945 and 1964 were exceptional. The rainfall in June 1945 at Dwellingup was 719.2 mm, 464.4 mm above average. This was followed by the second wettest August on record (211.7 mm above average). The winter of 1964 produced rainfall 436.1 mm in excess of the average. The winter of 1917, just prior to the first record of patchy jarrah death, was similarly exceptional and the third highest total on record for Jarrahdale (491.9 mm above average). This was coupled with a run of wet summers - four of the nine highest summer rainfall totals for Dwellingup and Jarrahdale stations combined are between 1914 and 1918. The three largest and three smallest range-standardized rainfall totals for each season at Dwellingup are shown in Figure A4. Although a relationship between extreme rainfall and dieback may be contentious, the absence of notable large rainfall events since the early 1980s is consistent with the lack of reported extreme dieback activity.

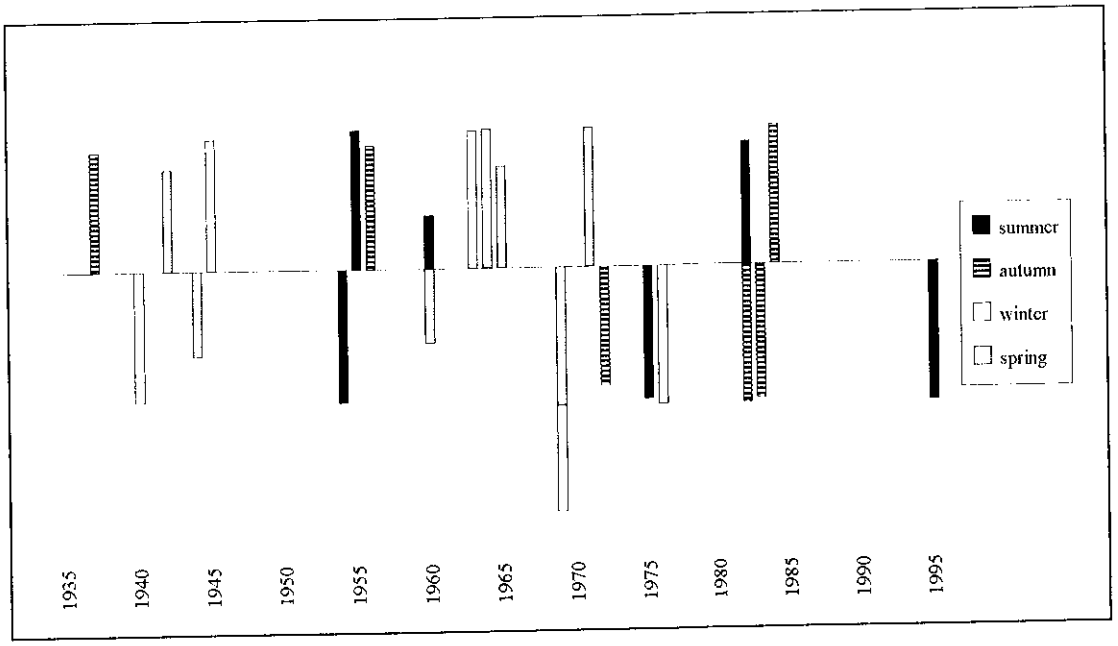

Figure A4 Three highest and three lowest rainfall totals for each season at Dwellingup since 1935. The totals are range-standardized.

A combination of notable climatic events may also be important. For example, the wettest August on record at Dwellingup (360 mm above average) occurred in 1955, in the same year as the largest summer rainfall total. Large rainfall events in 1945 and 1955 were preceded by dry summers. The large rainfall event at Dwellingup in early 1982 coincided with consecutive dry autumns. Temperature extremes may also be important. Five of the 12 hottest summers on record (for the Perth weather station) occurred in the late 1970s just before the wet summer of 1981 / 82 (Figure A5). Six of the 10 coldest winters since 1935 (for the Perth weather station) occurred between 1951 and 1960, a period of major dieback.

An association between past large rainfall events and major dieback events is plausible but impossible to demonstrate because of the imprecision of data on spatial and temporal dieback patterns.

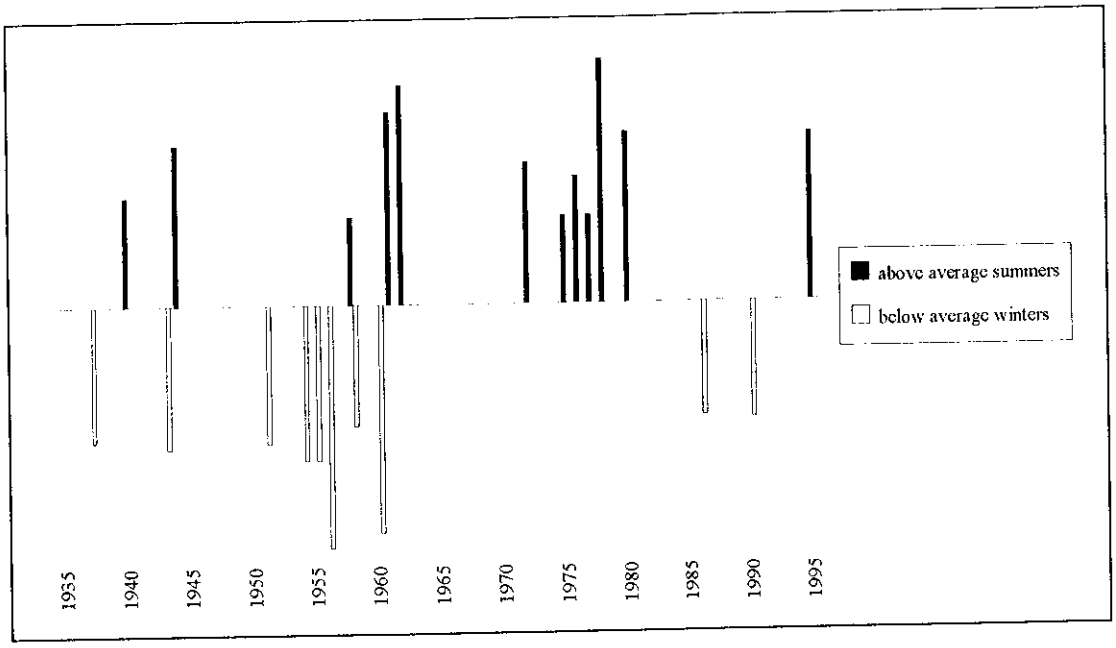

Figure A5 The timing of the ten highest and ten lowest mean temperatures for summer and winter at Dwellingup since 1935. Twelve high summer temperatures are shown because the tenth highest temperature value occurred on three occasions. The temperatures are range-standardized.