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Fire response and seedling emergence
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Mark Ooi
University of Wollongong

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FIRE RESPONSE AND SEEDLING EMERGENCE PATTERNS OF
LEUCOPOGON (EPACRIDACEAE) IN SOUTH-EASTERN
AUSTRALIA

A thesis submitted in partial fulfilment of the requirements
for the award of the degree

MASTER OF SCIENCE (HONOURS)

from

THE UNIVERSITY OF WOLLONGONG

by

Mark Ooi

B.Env.Sci

DEPARTMENT OF BIOLOGICAL SCIENCES

2002

CERTIFICATION

I, Mark Ooi, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Master of Science (Honours), in the Department of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Mark Ooi

18th December 2002

Smoke and fire at Heathcote National Park during the 1999 hazard reduction burn.

Abstract

There is a lack of understanding of the ecology of many Australian plant species. In fire prone habitat, natural fire regimes have shaped the evolution, and subsequently the demography and life history traits, of the associated flora. Critical life history stages, like germination and recruitment, are often linked to fire in species that occur in fire-prone habitats.

Knowledge of plant demography in relation to fire is important, particularly for threatened species. Management decisions are based on understanding the effect of factors such as fire frequency and season of burn and ensuring that the fire regimes implemented do not have a negative impact on the vegetation community.

The Epacridaceae are a large family of plants confined mainly to Australasia. Although common and widespread in fire-prone systems, epacrid ecology is poorly understood. *Leucopogon* is the largest genus within the Epacridaceae. The aims of this study were designed to improve the understanding of the demographic processes of *Leucopogon* in relation to fire. I addressed these aims by focussing on the threatened species *L. exolasius*, and some common congeners, *L. setiger*, *L. squamatus* and *L. ericoides*, in the fire-prone vegetation of the Sydney region in south-eastern Australia. Specifically, the questions asked were:

- (i) What is the fire response of established plants?
- (ii) Is there a delayed or seasonal component to seedling emergence?
- (iii) Are germination cues linked to the passage of fire?

Fire response and seedling emergence patterns were compared between species. Data were collected after four fire events between August 1999 and September 2002.

To determine fire response of the four study species, individuals were tagged and measured, then subsequently burned. Survivorship was monitored post-fire for up to 12 months.

All four study species were fire sensitive (classified as mortality after 100% leaf scorch). However, some plants survived in areas that remained unburnt after the low intensity burns. The proportion of established plants that survived was therefore dependent on fire patchiness. Topography, such as rocky outcrops, contributes to patchy fuel conditions and represents a mechanism for adult plant survival. This finding supports some studies that suggest that rare species, particularly obligate seeders, are concentrated in parts of the landscape where fires are less frequent. The rare species, *L. exolasius*, occurs almost exclusively on rocky sandstone riparian hillsides where some individuals are likely to remain unburnt during low intensity burns.

In areas like the Sydney region, where large wildfires are a common event, recruitment from the seed bank would still be essential for the long term persistence of a species. In the event of two fires occurring in quick succession, a dormant seed bank could represent a buffer to population decline.

The role of fire on germination cues and seedling emergence was examined in three of the species (*L. ericoides* excluded) by monitoring the numbers of newly emerged *Leucopogon* seedlings over time. Permanent quadrats were established under mature plant canopies. After fire, quadrats were monitored approximately every three months, and the number of seedlings counted. Quadrats were also established in unburnt *L. exolasius* and *L. esquamatus* habitats.

All three *Leucopogon* species displayed a flush of seedling emergence after fire. Time elapsed until the onset of emergence differed between fires but not between *Leucopogon* species. Seedling emergence was restricted, in all *Leucopogon* species and after all fires, to the autumn (primarily late autumn) and winter period. The same seasonal pattern was found in unburnt habitat, though at much lower seedling densities. Emergence of *Leucopogon* species was delayed when compared with other fire sensitive species that co-occurred in the habitat.

These results indicate that the magnitude of delay to the onset of emergence is dependent upon the timing/season of the fire event. Also, combinations of fire-related and seasonal factors are necessary to maximise germination. A residual seed bank is left

after fire, with germination timing still linked to season, and some inter-fire recruitment may occur. Seasonal dormancy in *Leucopogon* is likely to have developed over evolutionary time scales, and although fire has provided a strong influence on germination cues, variable rainfall patterns in the Sydney region may have allowed the persistence of seasonal dormancy traits.

Results from the study were combined with data collected on species distribution, historical decline and threats, to make an assessment of the threatened species, *L. exolasius*, using a modified version of the IUCN Red List Criteria. The conclusion reached was the recommendation that the threat status of the species should be upgraded from vulnerable to endangered.

This research has several implications for the management of *L. exolasius*. Firstly, hazard reduction burns should primarily be conducted outside of the late autumn/winter period in *L. exolasius* habitat, to reduce the magnitude of delay of emergence after fire. Secondly, inter-fire intervals of greater than 10 years are recommended for the long-term persistence of *L. exolasius* populations. Primary juvenile periods are thought to be relatively long, and this amount of time is required for individuals to mature and replenish the seed bank. Finally, the threat status of the species on the Schedules of the NSW *Threatened Species Conservation Act* (1995) and the Commonwealth *Environment Protection and Biodiversity Conservation Act* (1999) should be changed from vulnerable to endangered.

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Chapter 1

Introduction

1.1 Demographic research and fire

The popularity of the use of plant populations in demographic studies is relatively recent (since Harper 1977) and subsequently there are many species for which even fundamental demographic data are unknown. In fire prone habitats, natural fire regimes have shaped the evolution, and hence the demography and life history traits, of the associated flora (Gill 1981; Keeley 1986; Naveh 1975, 1994). Critical life history stages, like germination and recruitment, are often linked to fire in species that occur in fire prone habitats (Naveh 1975; Whelan 1995).

1.1.1 Fire response

Before tackling the dynamics of plant demography, fundamental aspects of species biology must be understood. This includes, amongst other things, knowledge of a species response to natural disturbance regimes (Benson and McDougall 1995; Bell and Pate 1996). In areas like the Sydney region, fire-prone natural areas coexist with a large urban population. Fire management in areas close to the urban-bush interface, where the balance between protection of life and property and maintenance of biodiversity are at their most critical, is a difficult challenge. There is increasing pressure for more widespread and more frequent hazard reduction burning (Auld and Scott 1997; Bradstock *et al.* 1998). Understanding how a species copes and persists with any particular fire regime requires the fundamental knowledge of the response to fire of individual plants. Types of mechanisms include vegetative resprouting, fire-stimulated seed germination and fire-stimulated flowering or seed release (Bond and van Wilgen 1996). The simplest distinction for individual plant response, however, is between fire killed and resprouting species (Gill 1981; Whelan 1995). This knowledge is of intrinsic value and is important for flora conservation and management (Gill and Bradstock 1992).

Studies around the world have categorised plant response as either fire sensitive (seeders) or fire tolerant (resprouters) (Keeley 1986; Mooney and Hobbs 1986; le Maitre and Midgley 1992; Trabaud 1994). These descriptions relate to the plant's ability to persist after fire, by seed or by vegetative means, and most species tend to fall into one of these broad categories. However, the complexity of fire in a natural system must also be considered, with elements such as site effects, season, fire intensity and frequency taken into account. All of these elements can cause variation in a plant's response (Auld 1986; Gill and Bradstock 1992; Whelan 1995; Bond and van Wilgen 1996; Bell *et al.* 1996). Gill (1981) dealt with this complexity by developing a simple classification for the response of woody plant species to fire. He defined fire intensity 'biologically', using 100% leaf scorch of mature individuals as a level at which resprouting or plant death could be assessed. Bell *et al.* (1984) constructed a number of fire response categories, essentially 'obligate seeders' for plants killed by even low intensity fires and regenerating by seed and three categories of 'resprouters', to deal both with this complexity and with species displaying an intermediate response.

The evolutionary development and relative advantages of resprouters versus obligate seeders has been the subject of considerable study (see Whelan (1995) and references therein). Gill (1981) noted that resprouting or hard seededness, could be an adaptation, not only to fire, but also to other variables. Keeley and Zedler (1978) suggest that resprouting is less likely to be an adaptation selected by fire, but more an ancestral trait. They agreed with Wells (1969) that resprouting was less of a fire adapted trait than obligate seeding strategies. Resprouting can occur in habitats where fire is not a significant disturbance, to ensure, for example, survival after drought or frost (Bell *et al.* 1984). Trade-offs between resprouter and obligate seeder strategies have been investigated in other demographic areas. In general, it appears that seedlings of obligate seeders reach reproductive maturity faster than their resprouting counterparts, seedling mortality is higher in resprouters and fecundity lower (Whelan 1995; Bond and van Wilgen 1996). Other factors, such as multiple germination episodes during post-fire recruitment, have also been suggested as adaptive traits developed in obligate seeders as a risk spreading mechanism (Zammit and Westoby 1987a).

Attempting to explain the coexistence of resprouters and obligate seeders in the Californian chaparral, Keeley and Zedler (1978) studied the relative ability of congeneric species of resprouters and obligate seeders to survive fires and to establish seedlings after fire. Data on the species longevity and competitive ability between fires were also included. They concluded that areas with naturally higher frequency fire regimes contained greater proportions of obligate seeders. This point has been supported by other studies (e.g. Benson 1985; le Maitre and Midgley 1992; Clarke 2002) and suggests one way in which the composition of plant communities are adapted to certain fire regimes. Obligate seeding species have adapted to fire frequencies which exceed their primary juvenile period the majority of the time (Lamont *et al.* 1991) and as they are entirely dependant upon stored seed for regeneration, they are more vulnerable to local extinction as a result of increased fire frequency. Those species which resprout, although not completely immune, are generally more resilient to increased fire frequency, due to both adult plant survival as well as some recruitment from seed (Gill and Bradstock 1995).

A number of plant species, particularly obligate seeders, have been shown to decrease or become locally extinct as a result of increased fire frequency (e.g. Siddiqi *et al.* 1976; Ashton 1981; Gill and Bradstock 1995; Bradstock *et al.* 1997) The most vulnerable species are obligate seeders with a canopy stored seed bank, where even one short fire interval can cause local extinction (Keith 1996).

1.1.2 Germination cues

Fire can trigger dispersal from species with a canopy stored seed bank (known as bradyseporous species) (Whelan 1995) and enhance post-fire flowering and subsequent seed release (Bradstock 1995; Denham and Auld 2002). Species with a soil stored seed bank can have germination cues related to fire, such as heat (Gill 1981; Auld 1986; Auld and O'Connell 1991; Whelan 1995), smoke or smoke products (de Lange and Boucher 1990; Brown *et al.* 1993; Dixon *et al.* 1995; Keeley and Fotheringham 1997) or combinations of these (Keith 1997; Kenny 2000; Morris 2000). This can allow seedling emergence to occur as quickly as possible in a post-fire environment, where

there are increased resources available as well as reduced competition (Gill 1981; Keeley 1991; Whelan 1995; Bell 1999). A flush or pulse of seedling emergence post-fire can be a good indicator of this relationship (Auld 1986; Keeley 1991; Trabaud 1994; Auld and Tozer 1995; Tyler 1995).

1.1.3 Timing of emergence

In Mediterranean-type climates, the post-fire germination pulse coincides with a distinct cooler rainfall season (le Maitre and Midgley 1992; Trabaud 1994; Whelan 1995; Bell 1999). Seedling emergence is therefore delayed until suitable seasonal conditions arise and subsequently the season of burn can have pronounced effects on recruitment (Bond 1984; Bond and van Wilgen 1996; Lamont *et al.* 1991). The availability of soil moisture is often critical in determining the timing of seedling emergence (Cowling and Lamont 1987; Bradstock and O'Connell 1988; Keith *et al.* 2002).

In non-Mediterranean fire-prone habitats like south-eastern Australia, it has been hypothesised that the timing of seedling emergence occurs independently of season due to temporally variable rainfall patterns that are not strongly seasonal. Post-fire seedling emergence is therefore thought to occur as soon as soil moisture levels are sufficient, and fire season is thought to be of less importance to the timing of seedling emergence and subsequent recruitment (Bradstock and Bedward 1992; Whelan and York 1998). However, in other non-Mediterranean fire prone habitats, like the pine scrub forests of Florida, seedling establishment is confined mainly to spring, independent of the timing of the fire event (Lambert and Menges 1996; Carrington 1999; Carrington and Keeley 1999). It is likely that variation between species can exist, with some able to germinate immediately after fire and others delaying germination until additional conditions are met (Keeley 1995; Baskin and Baskin 1998; Maret and Wilson 2000).

A species with a seasonal emergence pattern post-fire could be considered to have a delayed emergence in areas with non-seasonal rainfall patterns, depending on the timing of the fire event. Seasonal and/or delayed emergence could result in competitive disadvantages for these species, particularly if co-occurring species have a quicker post-

fire recovery strategy. Measuring recruitment and survivorship in relation to post-fire climate after a series of fires is an important but under studied area (Gill 1981; Whelan 1995), both for understanding how species persist and for informed management decisions such as when to implement a prescribed burn (Gill and Bradstock 1992).

1.1.4 Demographic research and rarity

The word rarity, when used in terms of conservation status, is generally accepted as meaning ‘of limited abundance and distribution’ (Kunin and Gaston 1993; Gaston 1994; Bevill and Louda 1999). To gain an understanding of these limitations within a species, a demographic approach to study is fundamental (Harvey 1985; Schemske *et al.* 1994; Bevill and Louda 1999). By including a comparison of ecological traits between a rare species and some common congeners there is an increased ability to detect limiting factors within the rare species, as well as possibly enabling detection of broader ecological patterns (Kunin and Gaston 1993; Schemske *et al.* 1994; Pantone *et al.* 1995; Bevill and Louda 1999). An understanding of rarity is important for the conservation and management of rare plant species as well as for the development of ecological theory (Bevill and Louda 1999).

1.2 The genus *Leucopogon* (Epacridaceae)

The Epacridaceae are a large Family of plants confined mainly to Australasia, and closely related to the cosmopolitan Ericaceae family. Some broader definitions of this taxonomic group include Epacridaceae within Ericaceae (e.g. Kron 1996). Although a common and widespread understorey shrub component of temperate Australian heaths, woodlands and forests, the ecology of epacrids is poorly understood. What studies there are have largely been conducted in the Mediterranean-type climates of Australia’s south-west (e.g. Meney *et al.* 1994; Dixon *et al.* 1995; Bell and Pate 1996; Bell *et al.* 1996; Keighery 1996; Roche *et al.* 1997), whilst only a few recent studies have appeared from the non-Mediterranean Australian east coast (Keith 1997, 2002; Clarke *et al.* 2000; Gilmour *et al.* 2000).

Leucopogon is the largest genus within the Epacridaceae, with 230 species worldwide, and is part of the largest Tribe, Styphelieae. Two hundred mostly endemic species occur in Australia (Harden 1992). As with epacrids generally, there are few studies focusing solely on *Leucopogon*. The papers reviewed below however, include species of *Leucopogon* as a component of the study group.

1.3 Previous *Leucopogon* research

1.3.1 Fire response

In an overview of the Epacridaceae in Western Australia, Keighery (1996) found that a total of 66% of all western Australian epacrid species were killed by fire, a higher proportion than both the Proteaceae and Myrtaceae.

In a study by Fox (1988) at Myall Lakes in New South Wales, four species of *Leucopogon*, including *L. ericoides*, *L. lanceolatus*, *L. margarodes* and *L. virgatus* were classified into categories based on their mode of regeneration after fire. All four were classified as resprouters.

A number of south-west Australian *Leucopogon* species, including *L. conostephoides* and *L. verticillatus*, were the subject of studies by Bell and Pate (1996) and Bell *et al.* (1996) investigating growth, morphology and root anatomy in relation to fire response. Resprouter species were found to be generally multi-stemmed with large lignotuberous root stocks. Seeder species, which comprised 75% of the total species investigated, possessed a single main stem and a small root system. Seeder species commenced flowering at a younger age than their resprouting counterparts. Bell and Pate (1996) listed the time taken from germination to first flowering (primary juvenile period) for 24 south-western Australian Epacridaceae. All fifteen seeder species had flowered within three years whereas only one out of nine resprouters' had flowered after seven years.

1.3.2 Germination and dormancy breaking cues

Cues for breaking seed dormancy in *Leucopogon* or, in fact any members of Styphelieae, are not well understood. A number of studies have investigated germination response to fire and other related cues, particularly smoke. Clarke *et al.* (2000) applied smoke water to seeds of a number of species including *L. muticus*. At completion of the study there was no germination from either *L. muticus* or any of the other epacrids included in the study. Dixon *et al.* (1995) investigated the effect of different smoke application methods to a large range of south-west Australian species. Seven species of *Leucopogon* were included in this study. Only one of these species, *L. parviflorus*, germinated in glasshouse trials. There was marked variation among species in germination response in the field. *Leucopogon leptanthus* appeared in greatest numbers in quadrats smoked for greater than 60 minutes, whereas *L. conostephoides* and *L. striatus* showed reduced germination if smoked more than 30 minutes. *Leucopogon striatus* was also the only species to respond positively to smoked sand and smoked water but not smoke fumigant. Also in south-west Australia, Lloyd *et al.* (2000) found an increase of *in situ* germination of *Leucopogon* species after the application of concentrated smoke products as a foliar spray.

In a study in Victoria (Enright *et al.* 1997), *L. glacialis* responded well to smoke treatment and a wet heat treatment of soil samples germinated in ambient (uncontrolled) temperature glasshouse conditions. Heat shock is known to enhance germination in many hard seeded species by cracking the seed coat (e.g. Auld and O'Connell 1991). Heat shock as a dormancy-breaking cue in Epacridaceae, however, has been little studied. Enright *et al.* (1997) hypothesised that cracking of the seed coat is likely to have played a part in enhancing the germination of *L. glacialis*, though they added that aging of the seed coat over several years may be a pre-requisite. Previous unpublished laboratory trials mentioned in this study, which included heat application (60° – 120° C) on fresh *L. glacialis* seeds and other epacrid species, resulted in little or no germination even after pericarp removal. This added further support to their hypothesised need for seed ageing, though not necessarily for ageing specifically of the seed coat.

A study by Roche *et al.* (1997) involved the seed ageing of four *Leucopogon* species. Seeds of the four species were buried for one year, and then treated with smoke. This combination of treatments increased germination response significantly, compared to using the seed ageing or smoke treatments singly.

Studies by Bell *et al.* (1987) and Bell *et al.* (1995) investigated the effects of temperature, light and charcoal on the germination of a number of species in Western Australia. *Leucopogon* species used in these studies did not germinate. After testing with tetrazolium chloride, however, percentage viability of the seeds used was zero. The methods used for testing viability followed procedures from Lakon (1949).

1.3.3 Seed banks

Meney *et al.* (1994) included *L. striatus*, an obligate seeder, in their study of seed bank patterns after fire in south-west Australia. The authors' assumption that obligate seeding species would accumulate a persistent seed bank over time was not confirmed. There were large annual losses of seed due to rapid deterioration and loss of germinability. This, combined with high mortality of seedlings two to three years after fire, lead to seedling:parent ratios of less than one for *L. striatus*. This is a combination that could lead to local extinction if continued for a period of decades.

Viability of seeds from four resprouting *Leucopogon* species from south-west Australia decreased by between 13.5% and 76% over one year of soil storage (Roche *et al.* 1997). In the same study, a mixture of soil stored seed ageing plus smoke application increased germination response in all four species. Dormancy release over time is inextricably related to a loss of total viable seed bank size. The total available viable seed after one year of soil storage is likely to be significantly lower than the initial available viable seed. Knowledge of the longevity of a seed bank is of particular relevance to understanding a species' persistence after disturbance, especially with regards to maintaining numbers within a population of obligate seeders. Subsequent management and conservation of these species, for example setting a minimum time interval between fires, is also dependent on such information.

1.3.4 Other studies

Keighery (1996) gave an overview of aspects of the distribution, biology and conservation of the Epacridaceae in Western Australia. He made notes on pollinators and dispersal agents, as well as general information on flowering times, fire response, preferred soil types and susceptibility to *Phytophthora cinnamomi*. High levels of endemism were noted within the family. *Leucopogon* species were reported to have relatively unspecialised flowers. Over 20 different bee species from 11 genera are major pollinators, with flies, butterflies, wasps and moths minor but significant pollinators.

Fleshy fruited species like *Leucopogon* were reported to be dispersed mainly by birds. The importance of other known dispersers such as ants, reptiles and mammals, was unknown. In a study in the Sydney region by Westoby *et al.* (1990), however, six *Leucopogon* species, including *L. esquamatus* and *L. amplexicaulis*, were categorised as primarily ant dispersed. Rates of removal by ants of *L. lanceolatus*, a fleshy fruited species, were just as rapid as for those species with elaiosome-bearing seeds (French and Westoby 1996).

There are further studies looking at other aspects of the biology of *Leucopogon*. Reed (1989) compared soil and leaf total nitrogen against intensity of ericoid mycorrhizal infection in *L. juniperinus* and found no relation. Interestingly, mycorrhiza-forming fungi were found in the endocarp of *Styphelia tubiflora*, leading to speculation that breakdown of the endocarp and subsequent germination could be assisted by this association. Hingston (1999) studied bee visitor profiles of plants in three vegetation types in southern Tasmania. He found that the presence of species with nectariferous flowers, like *Leucopogon*, enhanced the pollination of nectarless species in the same area. In vitro propagation of *L. obtectus* was achieved by Bunn *et al.* (1989). Due to the difficulty in germinating many Styphelieae, other propagation methods have been researched both for horticultural and conservation reasons. Finally, taxonomic papers revising the genus *Leucopogon* have established the identity of new species (Powell and Robertson 1993) and investigated generic concepts (e.g. Kron 1996; Powell *et al.* 1997; Taaffe *et al.* 2001).

1.3.5 Summary of previous *Leucopogon* research

The studies outlined above give some insight into the biology of this genus.

Leucopogon species are confined mainly to temperate fire-prone habitats and can either resprout or be killed by fire. Obligate seeders studied in south-western Australia have a much shorter juvenile period than resprouters. Flowers are pollinated by a wide variety of insects. There is some indication from Western Australian studies that seed viability may be low, or that viability testing methods may be inadequate. Seed dormancy is complex, with fresh seed maintaining high levels of dormancy even after application of fire related cues or other experimental treatments, such as varying temperature and light regimes. Dormancy of seeds stored within the soil seed bank may be broken by fire cues, however, longevity of seed viability is variable. Seed dispersal can be carried out by birds, and also ants, reptiles and mammals, however the relative importance of these agents is unknown. Overall, detailed knowledge of the majority of *Leucopogon* species is lacking and there is a particular lack of knowledge for species from eastern Australia.

1.4 Aims of this study

This study investigated the adult response to fire, the post-fire germination response and the temporal distribution of seedling emergence of species within the genus *Leucopogon* after several fires between 1999 and 2002. The work was based in the fire-prone vegetation of the Sydney region in south-eastern Australia. Study species include the threatened *L. exolasius* and the more common congeners *L. setiger*, *L. esquamatus* and *L. ericoides*. Fundamental knowledge of fire related life history traits such as adult fire response and germination response are lacking for these species. Anecdotal evidence (Maloney 1979; Fox *et al.* 1987; Benson and McDougall 1995; D. Keith, pers. comm.) and a recent study (Keith 2002) suggest that post-fire germination in many species within the Epacridaceae is delayed. Specifically the questions posed in this study were:

- (i) What response do individual plants and plant populations have to fire?
- (ii) Is there a delayed or seasonal component to seedling emergence?
- (iii) Are germination cues linked to the passage of fire, inferred by a flush of germination post-fire?

Chapter 2

Study species and site description

2.1 Study species

Four species were investigated during this study, all within the genus *Leucopogon*. Three of these (*L. setiger*, *L. esquamatus* and *L. ericoides*) are common and widespread, while the fourth (*L. exolasius*) is a threatened species with a restricted distribution (New South Wales (NSW) *Threatened Species Conservation Act* 1995; Briggs and Leigh 1996; *Environment Protection and Biodiversity Conservation Act* 1999). *Leucopogon* is the largest genus within the family Epacridaceae and is part of the Tribe Styphelieae. The Styphelieae are characterised by drupaceous fruit, whereas all other taxa in the family have capsular fruit, usually with many small seeds.

Little is known about the demographic processes of the study species. Although the common congeners have occasionally been included within broad community level investigations, the threatened *L. exolasius* has not previously been the subject of any ecological study. In fact, demographic and population dynamics data are generally inadequate for most rare plant species (Kunin and Gaston 1993; Gaston 1994).

2.1.1 *Leucopogon exolasius*

A description of *L. exolasius* (F. Muell.) F. Muell. ex Benth. from the Flora of NSW by Harden, G.J. (ed) (1992) is as follows:

“Erect shrub to 1 m high; branchlets pubescent. Leaves oblong-linear or elliptic, 5.2-14.3 mm long, 1.2-2.4 mm wide; margins recurved or revolute, toothed to ciliate towards apex; lamina discolorous, scabrous to sparsely hispid, upper surface convex, lower surface striate-ribbed; petiole 0.3-0.5 mm long. Flowers spreading to pendent, 1-3 plus rudiment in spikes to 14 mm long, white; peduncles 2.5-5.3 mm long; bracteoles 1.6-1.9 mm long. Sepals 4.2-5.2 mm long. Corolla tube 3.1-3.6 mm long, often sparsely villous outside, pubescent near throat inside; lobes 4-5.4 mm long, villous

outside. Fruit ellipsoid, 4.4-4.8 mm long, glabrous, finely ribbed.” (see Figure 2.1a)

Leucopogon exolasius (F. Muell.) F. Muell. ex Benth. is a threatened species, listed as vulnerable under the NSW *Threatened Species Conservation Act* (1995), vulnerable under the Commonwealth *Environment Protection and Biodiversity Conservation Act* 1999, and 2VC- in ROTAP [(2) Geographic range in Australia less than 100 km, (V) Vulnerable, (C) with at least one population reserved, of unknown size (Briggs and Leigh 1996)]. The species is endemic to the southern Sydney region of New South Wales and occurs within two conservation reserves, Heathcote National Park and Dharawal State Recreation Area. Other locations include Holsworthy Army Range and non-reserve land along the Georges River near Campbelltown. Recent surveys along the Georges River (including Georges River National Park) and in Royal National Park failed to detect plants in locations recorded in earlier collections of the species (pre-1920s). It is possible that these populations are now extinct. In the case of the Royal National Park record, it was discovered that an incorrectly labelled specimen had been placed on the database. The location details state Stokes Creek, which is actually in Dharawal State Recreation Area to the south. Also, there has been one collection from the Grose River area in the Blue Mountains made in the late 1800s. No further collections have been made from this area or any nearby since and it is possible that this population is now extinct.

Whatever the inaccuracies in specific data, there has been a historical decline in the range of this species due to urban development. Overall there are approximately 12 known extant locations, ranging from Minto (34° 03'S, 150° 53'E) in the north to the Avon catchment (34° 25'S, 150° 44'E) in the south. There has been no assessment of number of individuals at these locations.

2.1.2 *Leucopogon setiger*

A description of *L. setiger* R. Br. from the Flora of NSW by Harden, G.J. (ed) (1992) is as follows:

“An erect to spreading shrub, 0.3-1.5 m high; branchlets scabrous. Leaves lanceolate to elliptic, 7-10 mm long, 1.4-2.1 mm wide; margins entire or minutely toothed towards apex; lamina usually glabrous, flat to convex on upper surface, lower surface finely striate-veined; petiole absent. Flowers spreading to pendent, 1 or 2 plus rudiment, in 10-16 mm long spikes, white; peduncles 4-9.5 mm long; bracteoles 1.1-1.5 mm long. Sepals 2.7-4.2 mm long. Corolla tube 2.3-3 mm long, internally sparsely hairy over upper half; lobes 2.6-4 mm long. Fruit ellipsoid, c. 4.2 mm long, dry, glabrous, yellow to green. Flowers July-Oct.” (see Figure 2.1b)

Leucopogon setiger R. Br. is widespread from the coast to the mountains around Sydney and the Hunter Valley areas and extends to the central western slopes (Harden 1992). It is endemic to New South Wales. Morphologically, it is very similar to *L. exolasius*, growing to a similar size and producing similarly sized fleshy yellow drupes. It can occur in similar habitats to *L. exolasius* but does not co-occur at any of the sites used in this study.

2.1.3 *Leucopogon esquamatus*

A description of *L. esquamatus* R. Br. from the Flora of NSW by Harden, G.J. (ed) (1992) is as follows:

“Slender shrub, to 1 m high; branchlets glabrous or finely hispid. Leaves mainly elliptic, sometimes obovate, 7-15 mm long, 2-3.3 mm wide; margins minutely toothed towards apex; lamina discolorous, glabrous, \pm flat, lower surface faintly striate; petiole c. 1 mm long. Flowers erect, solitary plus rudiment or often 2 together in upper leaf axils, white; peduncles to 1.5 mm long; bracteoles 1.2-1.5 mm long. Sepals 2.1-2.5 mm long. Corolla tube 1-1.5 mm long, glabrous; lobes 2.3-2.9 mm long, internally densely bearded on upper two-thirds with hairs reflexed. Fruit cylindrical, 3.8-4.5 mm long, glabrous, brown. Flowers Aug.-Sept.” (see Figure 2.1c).

Leucopogon esquamatus R. Br. is also widespread, occurring from the coast to the mountains, although more common from coastal heaths. Its range extends from the north coast of New South Wales, south to Victoria and into Tasmania (Harden 1992). It has a smaller stature than either *L. exolasius* or *L. setiger* and produces a smaller drupe with a membranous coat.

(a)

(b)

Figure 2.1: (a) *Leucopogon exolasius* in flower at Lake Eckersley, Heathcote National Park and (b) *Leucopogon setiger* in bud at Flat Rock Creek, Royal National Park.

(c)

Figure 2.1 (continued): (c) *Leucopogon esquamatus* in bud at Sarahs Knob, Heathcote National Park.

2.1.4 *Leucopogon ericoides*

A description of *L. ericoides* (Smith) R. Br. from the Flora of NSW by Harden, G.J. (ed) (1992) is as follows:

“Slender shrub, to 0.9 m high; branchlets finely pubescent. Leaves oblong to rarely elliptic, 4.2-15.5 mm long, 0.7-2.3 mm wide, margins recurved to revolute, entire; lamina concolorous, glabrous or finely pubescent, upper surface convex, lower surface faintly striate-veined; petiole absent. Flowers erect, 1-11 in 4-9 mm long spikes, white to pinkish; peduncles to 1-3 mm long; bracteoles 0.9-1.5 mm long. Sepals 1.4-2.1 mm long. Corolla tube 1.5-2.2 mm long, finely pubescent inside at throat; lobes 1.4-2 mm long. Fruit often curved obovoid, 2.4-5.7 mm long, prominently ridged, sparsely hairy, flat-topped, turning brown. Flowers July-Oct.”

Leucopogon ericoides (Smith) R. Br. is a common and widespread species from the coast to the mountains. It covers a range from Byron Bay in the north of New South

Wales, south into Victoria, South Australia and Tasmania. This species has only been included in the fire response section of the study.

2.2 Study sites

Study sites were located in the southern outskirts of Sydney, New South Wales within Royal National Park (34° 03'S, 151° 03'E) and Heathcote National Park (34° 07'S, 150° 58'E) (Figure 2.2). Royal National Park covers an area of approximately 15 000 ha and is bordered by the Pacific Ocean, Hacking River and Princes Highway with residential areas scattered along the boundaries in the north and west. Heathcote National Park is approximately 2 250 ha in area and is bordered by the Woronora River and Holsworth Military Area to the west and Woronora Catchment area in the south. The Princes Highway and Heathcote Road bound the east and north respectively, with scattered residential areas along these boundaries (Figure 2.2). Both parks occur at the south-eastern section of the Sydney Basin. A small amount of data were collected opportunistically from Garigal National Park (33° 46'S, 151° 14'E) in Sydney's north.

Eight sites were established within the southern Sydney study areas, two sites for *L. exolasius*, two sites for *L. setiger*, and four sites for *L. esquamatus* (Table 2.1). Data for *L. ericoides* were collected from one of the *L. setiger* sites (Flat Rock Creek in Royal National Park). A ninth site, the third for *L. setiger*, was established at Garigal.

2.2.1 *Leucopogon exolasius*

Leucopogon exolasius generally occurs in woodland to open forest (as defined by Specht 1970) on banks and slopes above rivers or creeklines. Study sites for this species were established at Dingo (near the Dingo Tunnel) and Lake Eckersley within Heathcote National Park. Sites were situated on slopes above the Woronora River, on a fairly steep gradient with areas of outcropping sandstone. Both sites were situated near a track used by Sydney Water for pipeline maintenance and as a fire trail. The

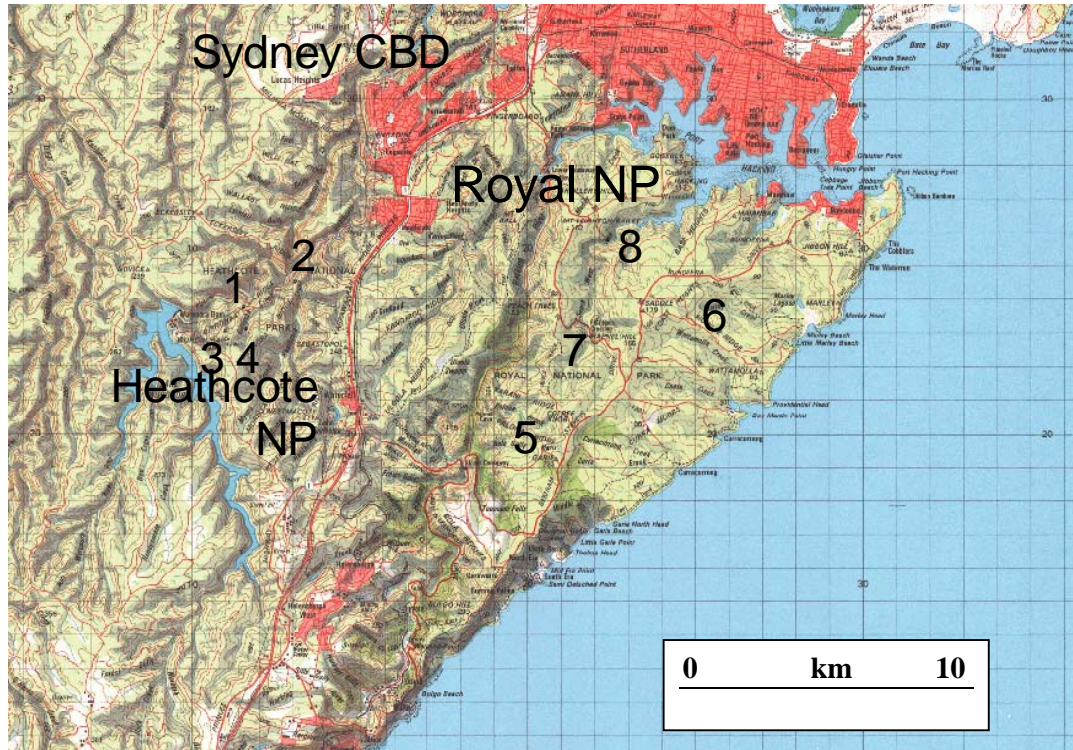


Figure 2.2: Location of the eight study sites within Heathcote and Royal National Parks in southern Sydney, New South Wales. National Park areas are represented by stipples (NB. the Royal National Park area in this figure also includes Garawarra SRA). Sites are represented as follows: (1) *L. exolasius* Dingo (2) *L. exolasius* Lake Eckersley (3) *L. esquamatus* Sarahs 1 (4) *L. esquamatus* Sarahs 2 (5) *L. esquamatus* Garie Trig (6) *L. esquamatus* Bundeena Road (7) *L. setiger* Flat Rock Creek (8) *L. setiger* Winifred Falls. Site (9) *L. setiger* at Garigal is outside the limits of this map.

L. exolasius populations extended from approximately 150 metres above the river bank, downslope and across the river into the Holsworthy Military area on the opposite bank.

Table 2.1: Study species, number of sites, year of fires affecting the site, type of fire (PB = prescribed burn, WF = wildfire) and vegetation structure (after Specht, 1970). NB. Not all fires burnt 100% of sites, therefore some were subject to multiple burns. Site numbers follow those from Figure 2.2.

The vegetation structure consisted of open woodland with canopy species dominated by *Angophora costata*, *Eucalyptus gummifera*, *E. agglomerata*, *Banksia serrata* and *Allocasuarina littoralis*. The understorey is quite open and contains a diverse mix of species. Dominant shrubs include *Acacia hispidula*, *Persoonia pinifolia*, *Doryanthes excelsa*, *Dodonaea triquetra*, *Hibbertia acicularis*, *Hakea dactyloides* and *Bossiaea heterophylla*.

2.2.2 *Leucopogon setiger*

Leucopogon setiger occurs in dry sclerophyll forest and occasionally in heath. Study sites were established at Flat Rock Creek and Winifred Falls, both within Royal National Park. The Flat Rock Creek site was located approximately 100 metres above

the creek, nestled in amongst sandstone outcrops on a gradual gradient. The Winifred Falls site was located approximately 200 metres above South West Arm Creek on a similar gradient. The dominant overstorey species again was *Angophora costata* with a mixed and relatively dense understorey including *Acacia terminalis*, *A. ulicifolia*, *Grevillea mucronulata*, *Doryanthes excelsa*, *Leucopogon ericoides* and *Dodonaea triquetra*. The Garigal National Park site contained a few individuals on skeletal soils on a sandstone platform. Dominant species included *Banksia ericifolia* and *Styphelia tubiflora*.

2.2.3 *Leucopogon esquamatus*

Leucopogon esquamatus is common in heath and can also be found in woodlands and on skeletal soils on sandstone outcrops. Two study sites were established at Sarahs Knob within Heathcote National Park and a further two at Garie Trig and Bundeena Road in Royal National Park. The Sarahs (1) site was situated on a gentle slope within damp heath with areas of outcropping sandstone. *Banksia ericifolia* and *Hakea* species up to 3 m dominated the shrub layer. The ground layer had greater than 70% cover of the sedge *Restio fastigiatus*. Sarahs (2) was less heathy, occurring amongst sandstone outcrops, with the occasional *Eucalyptus squamosa* or *Angophora costata* as overstorey. Ground cover was relatively sparse. *Leucopogon esquamatus* individuals were often concentrated at the edges of sandstone outcrops at both sites. The sites at Royal National Park were very similar in composition to Sarahs (1), with the exception of an additional dominant shrub species, *Persoonia lanceolata*.

2.2.4 *Leucopogon ericoides*

Leucopogon ericoides occurs in dry sclerophyll forest and heath. A single study site was established at Flat Rock Creek, within the *L. setiger* study site (see 2.2.2, above).

2.3 Climate

Temperature and rainfall data were collected from Holsworthy and Lucas Heights weather stations. Lucas Heights weather station is approximately five kilometres north of the study sites at Heathcote and 10 kilometres north-west of the study sites at Royal. Holsworthy weather station is approximately five kilometres north of the Lucas Heights station. The climate in this part of Australia is temperate with no dry season (using a modified version of the Köppen classification system) (Stern *et al.* 2000). Average annual rainfall for the area is approximately 1050 mm (average from 43 years of collected data) distributed relatively evenly throughout the year. Higher monthly rainfall averages occur in March and June. Lower averages occur in July and September (Figure 2.3). Average summer temperatures (max/min) are approximately 26°/18° C and average winter temperatures approximately 16°/7° C.

During the study period, from July 1999 to July 2002, rainfall levels were highly variable. There were very low levels of rainfall (all < 20 mm) in February 1999, August 2000, June, September and December 2001, and April and June 2002. All of these were well below monthly averages from the long term dataset. High levels of rainfall, well above long term averages (all > 100 mm) occurred in July and October 1999, March and November 2000, January and July 2001, and February 2002 (Figure 2.3). It is generally considered that a weak pattern of high summer/low winter rainfall exists in the Sydney region. Although there is a vague trend showing this over long term records, high levels of variability exist, as found over the three years of this study. Very low levels of summer rainfall were recorded in February 2000 and December 2001. Conversely, relatively high levels of rainfall were recorded during July 1999 and July 2001.

Temperatures during the study period did not vary too much from the long term mean. Most mean temperature levels from each month of the study period (both maximum and minimum) fell within 3°C of long term averages. Variation within each month was still quite high, as is shown by highest maximum and lowest minimum temperatures in each month (Figure 2.4). To gain an idea of the day-to-day variation in temperatures experienced at the sites, extra data were collected using a Tinytalk II temperature logger

(Gemini Data Loggers, UK) during the winter of 2001 at Heathcote National Park. Data from this logger revealed that June was the coldest month, with a daily average of 6.5° C. More than 30% of the time, temperature was less than 5° C, with minima often below 2° C.

2.4 Fires

Prior to the study, all sites within Heathcote National Park had not been burnt for at least 30 years. Sites at Royal National Park had all burnt during the 1994 wildfires, and subsequently had remained unburnt for approximately seven years prior to the study. The Garigal National Park site was last burnt in 1990.

Prescribed burns were conducted in August 1999 (winter) and April 2001 (autumn) in Heathcote National Park. A large scale wildfire occurred in December/January 2001/02 (summer), burning portions of both Heathcote and Royal National Parks. A small amount of data was also collected after a wildfire at Garigal National Park in October 2000.

2.4.1 Prescribed burn – August 1999

The prescribed burn conducted in 1999 was of very low intensity and was very patchy. Ambient air temperature was less than 14° C. Scorch heights at the *L. exolasius* Dingo site were generally less than 1 m or very occasionally between 1 and 2 m. Litter was only partially consumed. Fires at the *L. esquamatus* sites at Sarahs Knob were also of low intensity. Due to the vegetation being more heathy at Sarahs (1), scorch heights were very low. The predominance of a dense uniform sedge ground-cover however, ensured a complete burn. The burn at Sarahs (2) was much patchier and large sections of the plot remained unburnt.

2.4.2 Prescribed burn – April 2001

The 2001 prescribed burn was of greater intensity, carried out on a steeper slope in warmer ambient temperatures than the 1999 burn. Scorch heights were over 2 m high and all ground litter was consumed. Only the *L. exolasius* Lake Eckersley study site was burnt during this fire.

2.4.3 Wildfire – December/January 2001/02

The December/January 2001/02 wildfire was of extremely high intensity in some areas of both parks (Figure 2.5a), but this intensity was patchy (Figure 2.5b). At Heathcote National Park, most remaining unburnt areas at all sites were burnt. A high intensity fire burnt the *L. exolasius* Dingo site. Leaves were consumed up to 2 m and scorch heights reached 8 to 10 m. The Lake Eckersley site was also burnt but with a lower intensity. Rocky outcrops and patchier vegetation would have contributed to this. Litter was consumed and scorch heights reached 2 to 3 metres. It should be noted that some areas burnt by the 1999 and 2001 hazard reduction fires burnt again during the wildfire.

Lower intensity burns occurred in large sections of Royal National Park during the 2001/02 wildfires, possibly due to a combination of backburning operations or fires burning at night during lower ambient air temperatures. Fire at the *L. setiger* site at Flat Rock Creek was patchy, with scorch heights between 1 and 3 metres and litter mostly consumed. The *L. esquamatus* Garie Trig site received a similar patchy burn with scorch heights again approximately between 1 m and 3 m. Whole areas at both sites, up to approximately 10 x 10 metres in size, were left completely unburnt.

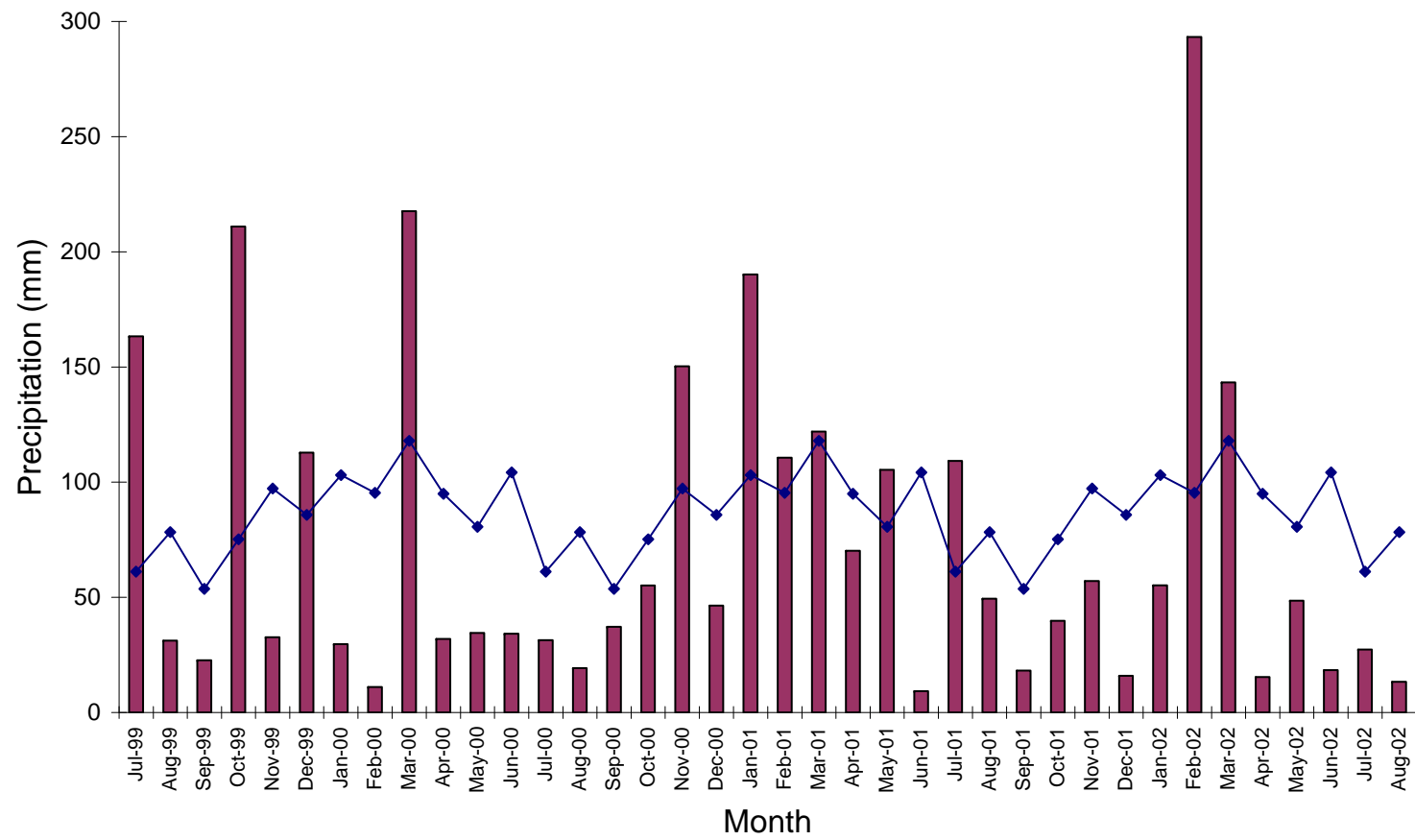


Figure 2.3: Rainfall data from the Lucas Heights weather station. Columns represent monthly averages recorded during the study period, whilst the line represents monthly averages from the long term data set (~43 years of data).

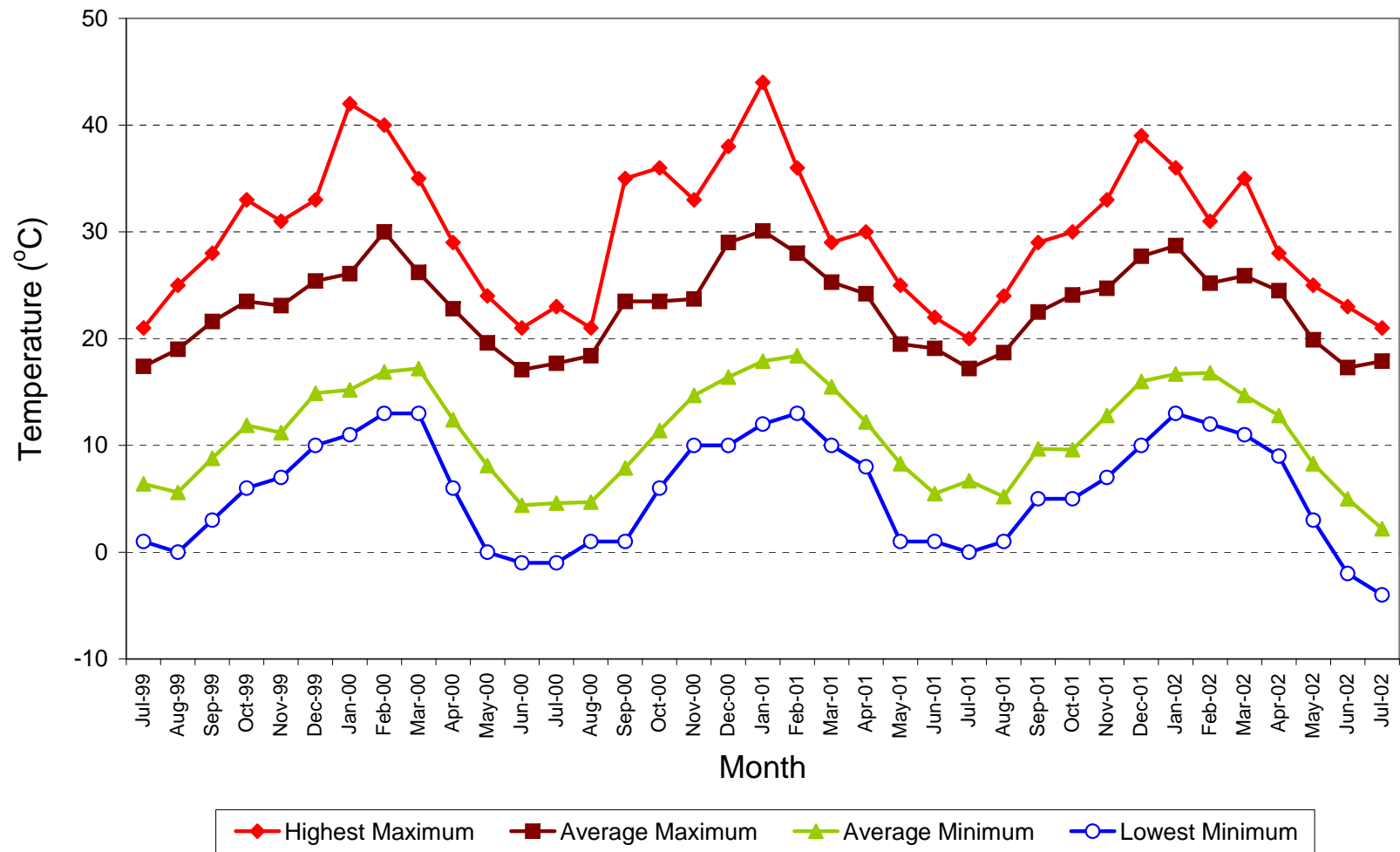


Figure 2.4: Temperature data from Holsworthy weather station for the study period July 1999 to July 2002.

(a)

(b)

Figure 2.5: Vegetation in Heathcote National Park after **(a)** high intensity fire, where leaves on all shrubs have been consumed, and **(b)** low intensity fire, where large areas can be seen remaining completely unburnt.

Chapter 3

Fire response

3.1 Introduction

Knowledge of an individual plant's response to fire is essential to gain an understanding of how populations persist in fire-prone ecosystems and how resilient a species is to any particular fire regime. In fire-prone urban environments like Sydney, prescribed burning is a common tool used for managing areas of bush, both for reducing fuel load for the protection of life and property (Conroy 1996; McLoughlin 1998), and for the maintenance of biodiversity (Benson 1985; Keith 1996). Rare or threatened species are of particular concern when striving to maintain biodiversity. In the Sydney region, these are often concentrated around urban areas, where clearing and development have destroyed large areas of habitat (Auld and Scott 1997). Fire management in areas close to the urban-bush interface is a difficult challenge. At these locations, the balance between protection of life and property and maintenance of biodiversity are at their most critical. There is increasing pressure for more widespread and more frequent hazard reduction burning (Auld and Scott 1997; Bradstock *et al.* 1998; Whelan 2002).

A hazard reduction burn to be carried out at Heathcote National Park provided the initial opportunity for this study. The threatened species *Leucopogon exolasius* occurred within one of the blocks planned for burning. Determining whether the burn was likely to have an impact on threatened species is a requirement under the NSW *Threatened Species Conservation Act* (1995). This requires knowledge of basic life history traits, such as fire response, of all threatened species within the block. Initial investigations revealed that the fire response of *L. exolasius*, along with the responses of a number of other *Leucopogon* species, were unknown. With over 2000 plant species in the Sydney region, gathering this type of information, particularly where there are knowledge gaps, is an important step towards successful monitoring and management of plant species in fire-prone areas (Gill and Bradstock 1992).

The simplest distinction of individual plant fire response is between fire killed and resprouting species (Gill 1981; Whelan 1995). Fire killed, or obligate seeding species

have adapted to fire frequencies that exceed their primary juvenile period the majority of the time (Lamont *et al.* 1991). Consequently they are entirely dependent upon stored seed for regeneration and are more vulnerable to local extinction as a result of increased fire frequency. Those species which resprout, although not completely immune, are generally more resilient to increased fire frequency, due to both adult plant survival as well as some recruitment from seed (Gill and Bradstock 1995).

A number of common congeners were chosen along with *L. exolasius* to assess their fire response. This was done to enable a comparison between rare and common congeners.

The aims of this part of the study were as follows.

- (i) To determine the effects of fire on individuals and local populations of the threatened species *Leucopogon exolasius* and three common congeners *L. setiger*, *L. esquamatus* and *L. ericoides*.
- (ii) Where possible, to compare the effects of variation in fire intensities on the study species' fire response.

3.2 Methods

To determine the fire response, localities containing the study species were identified and encompassed by a 30 x 15 metre plot pre-fire. All individuals within the plot were tagged using stainless steel wire stakes with numbered brass tags. Previous work had shown that numbers on the brass tags were still easily identifiable post-fire. Height (or stem length if not vertical), basal diameter, canopy area and the presence or absence of buds or flowers were noted. To increase the number of adult individuals surveyed, a number of plants were also randomly selected and tagged outside each plot. After fire, monitoring of post-fire survival was conducted at two-monthly intervals. Percentage of canopy scorch was visually assessed and recorded. Plants receiving 100% leaf scorch were surveyed for any indication of resprouting as a measure of their fire sensitivity. Plants not receiving 100% scorch were noted for percentage of leaf canopy scorched, and survival was scored over time. Species were considered fire-sensitive if adult and juvenile individuals receiving 100% leaf scorch did not survive (see Gill 1981). Gill

(1981) specified adult plants for assessment, partly due to the ease of monitoring. However, both juveniles and adults of the study species were easily observable. Juveniles were distinguished from seedlings in this analysis by the presence of a woody stem and adults were distinguished by the presence of buds or flowers. Where possible, the numbers of seedlings surviving the fire were also assessed.

3.3 Results

All four species were fire sensitive with all plants receiving 100% leaf scorch killed (Table 3.1). This was observed even after very low intensity fires in 1999 and, in some areas, after the 2001/02 fires. All four study species would therefore be classified as obligate seeders, dependent on seeds for post-fire regeneration.

3.3.1 *Leucopogon exolasius*

Leucopogon exolasius was found to be fire sensitive. A few individuals were killed with less than 50% leaf scorch (Table 3.1). The majority of individuals with less than 100% leaf scorch were concentrated in areas containing minimal ground litter and a large amount of sandstone outcropping. Survival of *L. exolasius* individuals occurred in both of the areas burnt by prescribed fires, in most cases due to their location in vegetation that did not burn, but in a few cases after leaf scorch of 50% or less. During the 1999 hazard reduction burn at Dingo site, it was observed that *L. exolasius* individuals were not very flammable even after the direct application of flame. Individuals that survived after partial leaf canopy scorch were still able to produce flowers and fruit the following season.

A very small proportion of tagged seedlings managed to survive after prescribed fire, again as a result of being in patches left unburnt. One out of the eight tagged seedlings survived the 1999 fire and one out of the 11 tagged seedlings survived the 2001 fire. All killed seedlings were consumed by the fire.

Some areas burnt during the 1999 and 2001 prescribed burns were also partially burnt again by the subsequent 2001/02 wildfire. The wildfire in these sections was of a lower intensity and patchy compared to areas that did not get burnt by the previous hazard reduction fire. Seedlings that had emerged after the original prescribed burns were significantly affected by the wildfire. Approximately 20% of these seedlings were killed at Lake Eckersley and 60% were killed at the Dingo site. Surviving seedlings were restricted to areas that were not burnt by the wildfire. Adults surviving the prescribed fire at Lake Eckersley were also killed by the subsequent wildfire. No seedlings from previously unburnt habitat survived the 2001/02 wildfire at either site. All of these were completely consumed by the fire.

3.3.2 *Leucopogon esquamatus*

This species was also fire sensitive. Due to its smaller stature, even low intensity fire caused 100% leaf scorch for the majority of tagged plants in areas that were burnt (Table 3.1). After the 1999 burn, most survivors at Sarahs (1) and Sarahs (2) occurred in habitat which had not been burnt, again due to patchy fire. Surviving individuals were concentrated at sandstone outcrop edges where there was a limited amount of litter accumulated.

The 2001/02 wildfire at Sarahs (2) killed all tagged plants as well as plants that had survived the original 1999 prescribed fire. All 35 tagged seedlings, which had emerged after the earlier prescribed burns, were also killed.

3.3.3 *Leucopogon setiger* and *Leucopogon ericoides*

The 2001/02 wildfire at Flat Rock Creek, where both of these species were present, was of quite low intensity and patchy. Mortality was still complete and the majority of tagged plants received 100% leaf scorch (Table 3.1). Areas were left completely unburnt just outside the plot with a number of individuals of both species surviving.

Table 3.1 Fire response data for four *Leucopogon* species

Columns indicate the number of adult and juvenile plants tagged, the proportion killed by fire, and the proportions killed due to 100% leaf scorch and due to less than 100% leaf scorch.

Species and site		No. of plants tagged (burn year in brackets)	Percentage of total killed by fire (%)	Percentage of total with 100% leaf scorch (%)	Percentage killed with 100% leaf scorch (%)	Percentage of total with < 100% leaf scorch	Percentage killed with < 100% leaf scorch
<i>L. exolasius</i>	Dingo	33 (1999)	81	69	100	31	40
		50 (2001/02)	100	100	100	0	0
	Lake Eckersley	46 (2001)	93	78	100	22	70
		71 (2001/02)	99	97	100	3	50
<i>L. esquamatus</i>	Sarah's 1	52 (1999)	89	89	100	11	0
	Sarah's 2	43 (1999)	86	51	100	49	71
		15 (2001/02)	100	100	100	0	0
<i>L. setiger</i>	Garigal	15 (2000)	93	73	100	27	75
	Flat Rock	69 (2001/02)	100	91	100	9	100
<i>L. ericoides</i>	Flat Rock	55 (2001/02)	100	91	100	9	100

Figure 3.1: *Leucopogon setiger* at the Garigal site. Unscorched sections of the canopy (with seed collecting bags) still flowered and produced viable seed the following season after fire.

Only 15 *L. setiger* individuals were tagged at the Garigal site. Survivors received less than 50% leaf scorch. Unscorched sections of leaf canopy continued to flower and produce fruit the following season (Figure 3.1).

3.4 Discussion

This study identified all four species as fire sensitive after low intensity hazard reduction burns and after a higher intensity wildfire. It also identified a mechanism for individual plant persistence after low intensity fire. Consequently, although the species are categorised as obligate seeders, the survival of some individuals within the landscape can provide a level of population persistence, particularly after low intensity fire. A number of plants survived after low levels of leaf canopy scorch, or in areas with minimal leaf litter that consequently remained unburnt, after low intensity burns. The level of survival of established plants is therefore dependent on fire patchiness.

The fire response of nearly 50% of the Epacridaceae in the Sydney region is unknown and the majority of the known responses have come from anecdotal observations (see Benson and McDougall 1995). This study has identified the previously unknown response of *L. exolasius*, confirmed previous anecdotal reports regarding *L. esquamatus* and *L. setiger*, and added another piece of information about *L. ericoides*. *Leucopogon ericoides* had previously been recorded as both an obligate seeder and a resprouter (see Benson and McDougall 1995 and references therein) in two separate studies. Regeneration of all four study species at all of the study sites is dependent primarily upon seeds, which are held in a soil-stored seed bank (M. Ooi, pers. obs.).

The functional classification of plants can be very useful, enabling broader scale predictions about vegetation dynamics (Gitay and Noble 1997). To understand these dynamics in fire-prone habitats, knowledge of the persistence of individual plants under various fire regimes is of particular importance. Obligate seeders, such as the four species studied, are particularly at risk to population declines by an increased fire frequency (Gill and Bradstock 1995; Whelan 1995; Keith 1996; NSW Scientific Committee 2000). This is especially problematic for species that are slow growing (i.e.

those with a long primary juvenile period) (Bond 1997), as post-fire recruits may be killed before they reach maturity and subsequently do not contribute towards replenishing the seed bank. A species' long term persistence is therefore dependant upon the seed bank although possibly, in the shorter term, also on individuals which survive a fire event.

There has been no investigation of the persistence or function of the seed banks of the four study species. Many studies, however, have shown that a number of species in fire-prone habitats cue seed dormancy to the passage of fire, ensuring a flush of seedling emergence in the immediate post-fire environment (Auld and Tozer 1995; Tyler 1995). There has been some evidence of fire-related cues breaking dormancy in seeds of *Leucopogon* species in Victoria (Enright *et al.* 1997) and Western Australia (e.g. Lloyd *et al.* 2000), however other studies have found either no response or variable levels of germination of *Leucopogon* species after application of fire cues (e.g. Dixon *et al.* 1995; Clarke *et al.* 2000). Seed bank longevity has also been investigated in *Leucopogon* species in south-western Australia. Roche *et al.* (1997) found that seed bank longevity varied between four *Leucopogon* species, with results ranging from 13.5% to 76% loss of viability over one year. The variability in the response of different *Leucopogon* species makes it difficult to infer dynamics from other studies, and suggests that further work at a species specific level is necessary to understand seed bank dynamics of the four species from this study. Gaining an understanding of seed bank dynamics can further help to establish management guidelines for obligate seeding species, and this is of particular importance for threatened species such as *L. exolasius*.

Study populations of all four species have shown some level of above-ground persistence after low intensity fires, primarily as a result of fire patchiness and subsequent survival in unburnt patches. A small percentage of individuals were also able to survive with between 25% and 50% leaf scorch. Low intensity fires are a result of a number of factors including low ambient temperatures, low wind speed, high fuel moisture and topography (Whelan 1995). Observations made during this study suggest that litter patchiness contributes to patchy and lower intensity fires and subsequently contributes towards a mechanism for adult plant survival within a population. There are

several factors that could lead to high levels of litter patchiness and subsequent patchy fires.

Litter patchiness can result from recent prescribed fires. A key finding from this study is that wildfire was carried through areas burnt only 0.7 and 2.3 years previously. Although the subsequent wildfire was very patchy in these areas, between 20% and 100% of recently emerged seedlings were killed.

At both *L. exolasius* sites, patchy fuel conditions occurred due to a large number of exposed sandstone outcrops (Figure 3.2a), whilst low levels of litter were maintained at parts of the *L. esquamatus* and *L. setiger* sites, around the edges of larger exposed sandstone platforms (Figure 3.2b). The majority of these areas remained completely unburnt during the low intensity burns, and individuals within them survived. Higher intensity fires experienced at the *L. exolasius* and *L. esquamatus* sites however, left no survivors. Clarke (2002) has suggested that vegetation on rocky outcrops in the Sydney region is subjected to lower fire frequencies.

Steep gradients, causing regular disturbance and movement of litter, also appeared to contribute to patchy fuel levels. In fire-prone habitat like the ones studied, it would seem likely that surface material movement would affect fire behaviour. Piles of litter were accumulated in “sinks” or slight depressions in the ground, while steep convex areas were often completely bare. At the northern edge of the *L. exolasius* Dingo site, the gradient was artificially increased due to the proximity of a track embankment. Litter levels here were very low.

Topography therefore may have played a part in the survival of individual plants in this study but only during lower intensity fires. It is unlikely that the survival of adult individuals in fire shadows is significant for the long term persistence of a population, due to the regular occurrence of higher intensity fires. However, it does provide some opportunity for survival in the landscape, even if all other regenerative sources are depleted (Whelan *et al.* 2002). This mechanism could provide a buffer to population decline, particularly in the event of two low intensity fires occurring in quick succession.

If a continuing high frequency fire regime were to be implemented, it is likely that adult survivorship after fire would only reduce the rate of decline rather than prevent it (Keith 1996). Many shrub species in the Sydney region have a primary juvenile period of greater than 10 years (Benson 1985; Whelan 2002). A frequent fire regime would prevent new seedlings from reaching their primary juvenile period and subsequently contributing to the maintenance of the seed bank. Under this regime, seed banks would eventually become exhausted. Also, any unplanned fire of a higher intensity occurring during this type of regime (Keith 1996), would cause high levels or complete mortality amongst established plants. With no surviving established plants as a buffer, local extinction would result.

Resprouting plant populations are more likely to persist in the event of increased fire frequency, due to a rapid recovery and lower levels of adult mortality. Keeley and Zedler (1978) hypothesised that areas with higher fire frequencies supported vegetation with higher proportions of resprouters whilst those with lower fire frequencies supported more obligate seeders. A recent study by Clarke (2002), found that there were much higher proportions of obligate seeders on less frequently burnt rocky outcrop vegetation, than in vegetation in more frequently burnt adjacent forest. Similarity in the species composition within the two habitats, at genus and family level, added evidence to the influencing role of fire frequency on community fire response traits. The rocky outcrops were considered to maintain fire shadows due to the physical barrier of bare rock, whilst higher fire frequencies in adjacent forest removed or reduced the abundance of obligate seeders.

Gill and Bradstock (1995) suggest that rare plant species, particularly obligate seeders, are concentrated in parts of the landscape where fires are less common. They propose that an increase in fire frequency over time may cause the local extinction of susceptible species, with remnant populations persisting only in areas where at least some of the fire events are avoided. The rare species *L. exolasius* occurs almost exclusively on rocky sandstone riparian hillsides (Fairley and Moore 1989; Benson and McDougall 1995), and during this study these conditions appeared to assist by leaving individuals unburnt during low intensity burns. Although the common congeners studied can also occur in

this habitat type, they are not restricted to it. It is outside the scope of this study to be able to confirm whether fire shadows maintain remnant populations of the rare species' studied. However, in some localised areas of *L. exolasius* habitat after this study, surviving adults may be the only source of persistence, due to the death of the majority of post prescribed fire seedlings after subsequent wildfire.

Studies investigating fire shadows or refugia, and the survival of fauna, are much more numerous (Keith *et al.* 2002; Whelan *et al.* 2002) than those for flora (Williams and Gill 1995). Quantitative studies of the importance of unburnt patches of habitat to flora communities, including rare species within them, would therefore contribute greatly to our understanding of vegetation dynamics in fire prone systems.

(a)

Figure 3.2 (a) Sandstone outcropping exposed after the high intensity wildfire in December/January 2001/02 at Heathcote National Park. During lower intensity fire, these outcrops provided a buffer from fire, and plants growing amongst them remained unburnt

Figure 3.2 (b) Surviving shrubs on the edge of a sandstone platform, at front and in the background, after fire at Garigal National Park. Low levels of fuel at the platform edge reduces fire intensity and increases fire patchiness.

Chapter 4

Seedling emergence patterns of three *Leucopogon* species

4.1 Introduction

The persistence of obligate-seeding plant populations is dependent primarily upon regeneration from seed (Whelan 1995). Seed banks of the four study species are all thought to be soil-stored, as found in other studies investigating *Leucopogon* species (Enright *et al.* 1997; Roche *et al.* 1997). However, little is known about the dynamics of the seed banks of the four study species, or how persistent they are. Many species from fire-prone environments cue their seed dormancy and subsequent germination to the passage of fire so as to enable a flush of seedling emergence in the immediate post-fire environment (Auld 1986; Keeley 1991; Trabaud 1994; Auld and Tozer 1995; Tyler 1995). The post-fire environment can be beneficial to seedling survival and growth due to increased availability of resources, as well as reduced competition and relative freedom from herbivory (Gill 1981; Keeley 1991; Whelan 1995; Bell 1999). Cues for breaking seed dormancy have not yet been resolved for *Leucopogon* species.

If fire is a cue for germination, aspects of fire intensity, frequency and season are all potentially important determinants of seed bank dynamics. For example, there is some evidence that low intensity fires may not provide adequate heat to break dormancy in seeds that are released from dormancy by a heat shock mechanism (e.g. Auld 1987; Keith 1996). If fire frequency is too high, obligate seeding populations can decline, with post-fire cohorts unable to mature and replenish the seed bank (Bradstock *et al.* 1998). Conversely, if fire frequency is too low, populations may decline, especially if seed bank longevity is limited and there is no inter-fire recruitment. Significant inter-fire recruitment appears to be very uncommon in Australian heathlands, and has been recorded only at low levels in some Australian forest communities (Keith 1996).

It is possible that season of burn could affect subsequent recruitment success (de Lange and Boucher 1993). Species with short-lived seed banks could require seed input from the current season prior to a burn for sufficient recruitment to occur (Benson 1985; Brown and Whelan 1999). Anecdotal evidence (Maloney 1979, Fox *et al.* 1987, Benson

and McDougall 1995; D. Keith, pers. comm.) and a recent study (Keith 2002) suggest that post-fire germination in many species within the Epacridaceae is delayed, sometimes by up to two years. Season of burn is thought to play a part in delayed germination in Mediterranean-type climates (Whelan 1995). Highly predictable burning season with following reliable winter rains ensures that emergence occurs during the onset of the wet season. In south-eastern Australia, rainfall patterns are somewhat aseasonal and it has been hypothesised that fire season effects are not predictable because of this (Bradstock and Bedward 1992). Whelan and York (1998) similarly suggested that season of burn is unlikely to affect the emergence patterns of *Hakea sericea* and *Petrophile sessilis* in the Sydney region due to highly variable rainfall. However, in other fire-prone habitats with variable rainfall, such as in Florida, post-fire emergence patterns for many species is delayed by up to 10 months and this can depend on the season of burn (Carrington and Keeley 1999).

In this chapter, I investigate the patterns of seedling emergence post-fire and in unburnt habitat. Both the timing of the onset of post-fire emergence and temporal patterns of emergence of three *Leucopogon* species after several fires between 1999 and 2002 were quantified. Germination of seeds of species within the Epacridaceae family is very difficult according to both horticultural studies and other laboratory trials (e.g. Maloney 1979; Beardsell and Richards 1987; Fox *et al.* 1987; Bell *et al.* 1995), particularly with species within the Styphelieae. Applications of simulated fire cues (heat, smoke and combinations) in laboratory trials on many Styphelieae have produced few positive results (Dixon *et al.* 1995; Clarke *et al.* 2000; M. Ooi, unpubl. data). *In situ* applications of fire related stimulus (Meney *et al.* 1994; Lloyd *et al.* 2000) or studies replicating *in situ* environments by having fluctuating seasonal temperature regimes (Enright *et al.* 1997; Roche *et al.* 1997) have had more positive results for a number of *Leucopogon* species. Consequently, to determine whether fire plays a role in breaking dormancy in the study species, *in situ* monitoring of post-fire emergence was carried out.

Study species were the threatened *L. exolasius* and the more common congeners *L. setiger* and *L. esquamatus*. Fundamental knowledge of fire related life history traits, such as post-fire germination response, is lacking for these species. Specifically the questions posed in this part of the study were:

- (i) Is there a delayed or seasonal component to seedling emergence?
- (ii) Are germination cues linked to the passage of fire, inferred by a flush of germination post-fire?

4.2 Methods

Permanent 1m x 1m quadrats were located under or near canopies of randomly selected mature individuals of the three study species, *L. exolasius*, *L. setiger* and *L. esquamatus*. The study relied on hazard-reduction burns and a large wildfire, so the design of the emergence experiments was somewhat opportunistic. Quadrats initially assigned to an unburnt category were subsequently burnt and some planned for burning were not, in fact, burned. The number of quadrats at each site therefore varied over time. Data were collected after fires in August 1999, October 2000, April 2001 and December/January 2001/02. For each site, the numbers of burnt quadrats and the year in which they were burnt are shown in Table 4.1. A map showing the site locations is provided in Chapter 2 (Figure 2.2). Emergence patterns were assessed over three fires for *L. exolasius*, two fires for *L. esquamatus* and two fires for *L. setiger*. Only a small amount of data was collected for *L. setiger* after the October 2000 fire at Garigal National Park.

Previous work (M. Ooi, unpubl. data) had shown that the numbers of flowers or fruit produced were strongly correlated with canopy area (*L. exolasius* $r = 0.71$; *L. esquamatus* $r = 0.99$; *L. setiger* $r = 0.84$). For each species, I ensured that canopy areas at each of the plots used for comparison, were similar. This was done to help standardise the likely seed input to the soil in the sites.

In burnt plots, quadrats were established either pre-fire or immediately post-fire. Patterns of emergence in the absence of fire were also recorded for *L. exolasius* and *L. esquamatus*. All quadrats were a maximum of 1 m from the canopy edge, where seedling emergence had been observed during previous visits (M. Ooi, pers. obs.).

Study species	Number of sites	No. of quadrats for emergence	
		Burnt (year burnt)	Unburnt
<i>L. exolasius</i>	Site 1 – Dingo	20 (1999)	30
		24 (2001/02)	
	Site 2 – Lake Eckersley	21 (2001)	30
		15 (2001/02)	
<i>L. esquamatus</i>	Site 3 – Sarahs 1	10 (1999)	10
		10 (2001/02)	
	Site 4 – Sarahs 2	8 (1999)	10
		10 (2001/02)	
	Site 5 – Garie Trig	10 (2001/02)	-
	Site 6 – Bundeena Rd	-	10
<i>L. setiger</i>	Site 7 – Flat Rock Ck	10 (2001/02)	10
	Site 8 – Winifred Falls	10 (2001/02)	10
	Site 9 – Garigal	5 (2000)	-

Table 4.1: Number of burnt quadrats monitored after each fire, the fire event in which they were burnt, and the number of quadrats monitored in unburnt habitat, during investigation of emergence patterns of the three study species.

After the December/January 2001/02 fire, seedlings of other species, including a number of Fabaceae, *Grevillea* spp., *Banksia* spp., and *Hakea* spp. were also recorded during each census. This enabled comparisons of speed of emergence between *Leucopogon* species and other species to be made.

Quadrats were monitored for seedling emergence within the first two to three months post-fire, and subsequently approximately every three months after that. I considered that this frequency would not miss significant emergence, because between 60% and 100% of seedlings were found to survive their first three months (M. Ooi, unpubl. data). Also, many of those not surviving remained withered but identifiable. New seedlings were tagged and measured at each census (Figure 4.1). Plots were monitored for a minimum

Figure4.1: *Leucopogon setiger* seedling (approx. 3 cm tall) tagged with a stainless steel stake at the Flat Rock Creek site, Royal National Park. The seed is still attached to the end of the cotyledons.

of nine months (after the December/January 2001/02 fire) to a maximum of three years (after the August 1999 fire and unburnt plots).

For each species, I counted the number of new seedlings at each census. Census dates after different fires were not always closely synchronised between all sites and all species, but differences usually did not exceed four weeks. Meteorological data were collected from Lucas Heights and Holsworthy weather stations, both within 10 km of all study sites. Emergence data were used to investigate several aspects of germination and seedling dynamics, as discussed below.

4.2.1 Temporal distribution of emergence

This part of the study was designed to ascertain the speed to onset and temporal distribution of emergence in *Leucopogon* species post-fire.

To compare speed of emergence and therefore test whether or not post-fire emergence is delayed in the three *Leucopogon* species, emergence data were transformed by assigning each quadrat a time (t) to first recorded seedling emergence post-fire (i.e. number of months post-fire). Only those quadrats that eventually included the species of interest were used in the analysis. To standardise times across all species and fires, emergence recorded in the first census was assigned $t = 3$ months, as the initial census always occurred within three months of the fire event. The second census was assigned $t = 6$ months, the third census $t = 9$ months and the fourth census $t = 12$ months. Actual census times occurred within four weeks of the assigned time. The same transformations were made for the other species recorded.

The time (t) was recorded for each quadrat, for each species, in each site. The t values were used to compare:

- (i) across fires for each species
- (ii) between *Leucopogon* species
- (iii) *Leucopogon* species and other species

Data did not meet the assumptions for parametric analysis even after transformation, so the significance of differences was tested using Kruskal-Wallis tests. If the Kruskal-Wallis test was significant, all possible pairwise comparisons between samples were made using the Dwass-Steel-Critchlow-Fligner post hoc procedure (Critchlow and Fligner 1991).

Temporal emergence patterns were subsequently followed for up to three years, in both burnt and unburnt habitat. The mean numbers of new seedlings appearing at each census were plotted. Census times were standardised for most sites and fires by categorising data into four time periods; December – February, March – mid-May, mid-May – August and September – November. Time categories were moved forward one month

for all Royal National Park sites data after the December/January 2001/02 fire (*L. esquamatus* Garie, *L. setiger* Flat Rock and *L. setiger* Winifred Falls) due to late completion of the census.

For *L. esquamatus* plots burnt in 1999, no data were collected between February and August due to injury to the author. The majority of the seedling pulse recorded in August 2000 was therefore assumed to have occurred within three months of the census, due to the size of the seedlings and the low numbers of withered seedlings present. Larger seedlings, based on growth rate data from previous work (M. Ooi, unpubl. data) were assigned to the earlier March – mid May time category.

Similar methods were used to determine how recently seedlings had emerged at other sites. During the census, notes were made on the stage of development of the seedlings recorded. Categories included cotyledons only, cotyledons plus a few true leaves, and a tuft of true leaves. These notes enabled a finer assessment of which part of the season that seedlings were emerging.

4.2.2 Determination of a post-fire emergence flush

A flush of seedlings post-fire is indicative of dormancy-breaking cues related to fire. Total seedling emergence post-fire was compared with pre-fire data, when available, as well as comparing burnt and nearby unburnt plots to determine if there was a relative flush of emergence. Data used for these comparisons were from immediately after the August census where possible, as this was found to include the time of peak seedling emergence. Pre-fire data from both *L. esquamatus* sites burnt in 1999 were collected in late June 1999 and it was therefore assumed that a slight underestimate was obtained. As data did not meet the assumptions for parametric analysis, statistical comparisons of seedling densities were made using a Wilcoxon signed ranks test for pre-fire versus post-fire data. A Mann-Whitney U test was used for burnt and unburnt seedling density comparisons. The Mann-Whitney U test was also used for pre-fire versus post-fire comparisons at the *L. esquamatus* burnt plot Sarahs (2), due to the small number of quadrats burnt.

4.3 Results

4.3.1 Temporal distribution of emergence

(a) *Leucopogon exolasius*

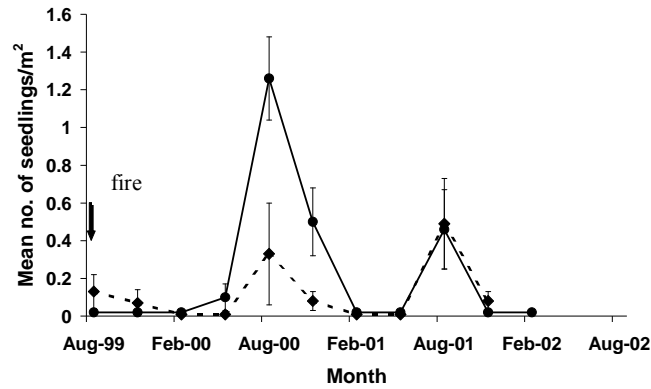
Speed of emergence (time taken to the onset of emergence in a quadrat) post-fire differed significantly between the three fire events (Kruskal-Wallis test, $P < 0.0001$) (Table 4.2). There were no significant differences between sites within the December/January 2001/02 fire.

Fire event	No. quadrats with <i>L. exolasius</i>	Mean time (t) to onset of emergence (months)
August 1999	17	11.6 ± 0.4
April 2001	20	3.5 ± 0.2
Dec/Jan 2001/02	32	6.9 ± 0.2

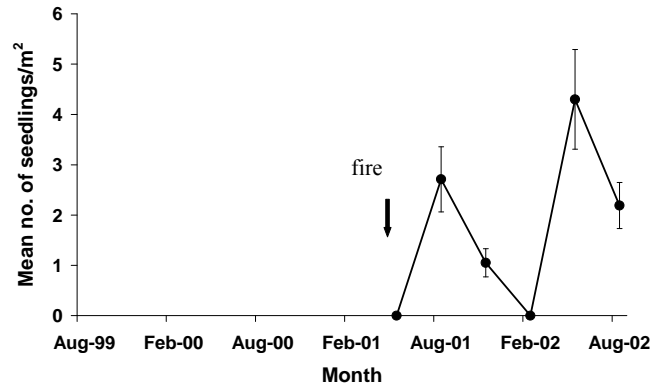
Table 4.2: Mean time (t) to the onset of emergence of *L. exolasius* after the three fire events. The numbers of quadrats are those which included *L. exolasius* seedlings.

The first *L. exolasius* seedling emergence after the August 1999 (winter) burn was observed 10 months post-fire, during the May 2000 census. Peak emergence occurred 10 to 12 months post-fire (1.26 ± 0.22 seedlings/m²) (mean \pm 1SE). After the April 2001 (autumn) burn, first emergence was recorded only two months post-fire, with the peak occurring two to five months post-fire (2.71 ± 0.81 seedlings/m²). Subsequent pulses of emergence were recorded in plots followed for longer than one year (Figure 4.2a & b). At the Dingo site, the magnitude of the subsequent pulses was significantly smaller and peaked between May and August 2001, 21 to 24 months post-fire. At the Lake Eckersley site, subsequent emergence pulses were recorded in both May and September 2002, 14 to 17 months post-fire. Over 50% of seedlings recorded in the May census were at the cotyledon only stage and are presumed to have emerged in May, close to the census time. The magnitude of the secondary pulses at Lake Eckersley did not differ significantly from the initial pulse.

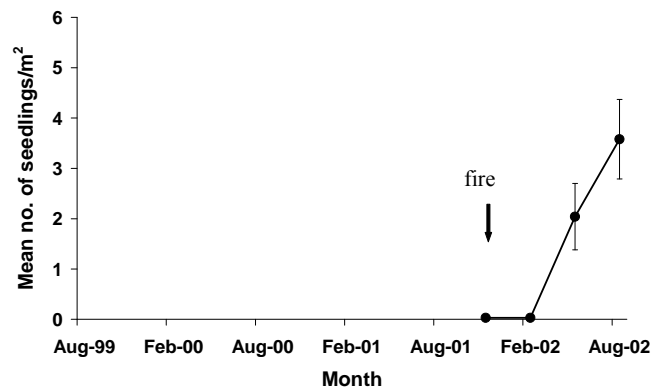
(a)



(b)



(c)



(d)

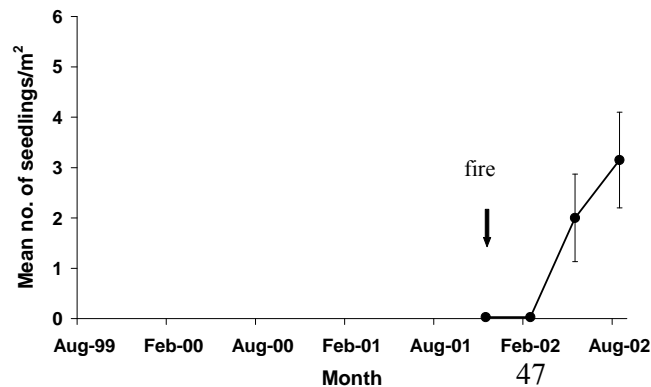


Figure 4.2 Temporal patterns of new emergence for *Leucopogon exolasius* at (a) Dingo site after fire in August 1999 (solid line), and in unburnt habitat between 1999 and 2001 (dotted line), (b) Lake Eckersley after fire in April 2001, (c) Dingo site after fire in Dec/Jan 2001/02 and (d) Lake Eckersley after fire in Dec/Jan 2001/02. Data are mean number of newly emerged seedlings at each census. (Note that scale on y axes differ).

Replicate sites were not burnt during either of the above burns, but the germination peaks in unburnt habitat, coincided with emergence at the burnt sites (Figure 4.2a).

Timing of emergence at the replicate sites after the December/January 2001/02 fire did not differ significantly (Figure 4.2c & d). The onset of emergence of *L. exolasius* differed significantly to that of other species (Fabaceae, *Grevillea* spp. and *Hakea* sp.) after the December/January 2001/02 (Kruskal-Wallis, $P < 0.0001$), with *L. exolasius* emergence being comparatively delayed (Figure 4.3).

After the December/January 2001/02 (summer) fire, the first observed emergence occurred in late May (Dingo 2.04 ± 0.66 seedlings/m²; Lake Eckersley 2.00 ± 0.87 seedlings/m²), between three and five months post-fire and peaked between six and nine months post-fire (Dingo 3.58 ± 0.79 seedlings/m²; Lake Eckersley 3.15 ± 0.95 seedlings/m²) when the study was terminated. Timing and magnitude of germination were very similar at the two replicate *L. exolasius* sites. Census dates during this year were a few weeks later than previous years, and greater than 50% of the total seedlings recorded were newly emerged (cotyledons only) in the March – mid May census. This would suggest that peak emergence again was restricted close to the census time, in May.

(b) *Leucopogon esquamatus*

The time taken to reach the onset of emergence post-fire differed significantly between the fire events for *L. esquamatus* (Kruskal-Wallis test, $P = 0.0001$) (Table 4.3), but there were no significant differences between sites within each fire.

Fire event	No. quadrats with <i>L. esquamatus</i>	Mean time (t) to onset of emergence (months)
August 1999	15	11.6 ± 0.3
Dec/Jan 2001/02	32	6.0 ± 0.2

Table 4.3: Mean time (t) to the onset of emergence of *L. esquamatus* after the three fire events. The numbers of quadrats are those which included *L. esquamatus* seedlings.

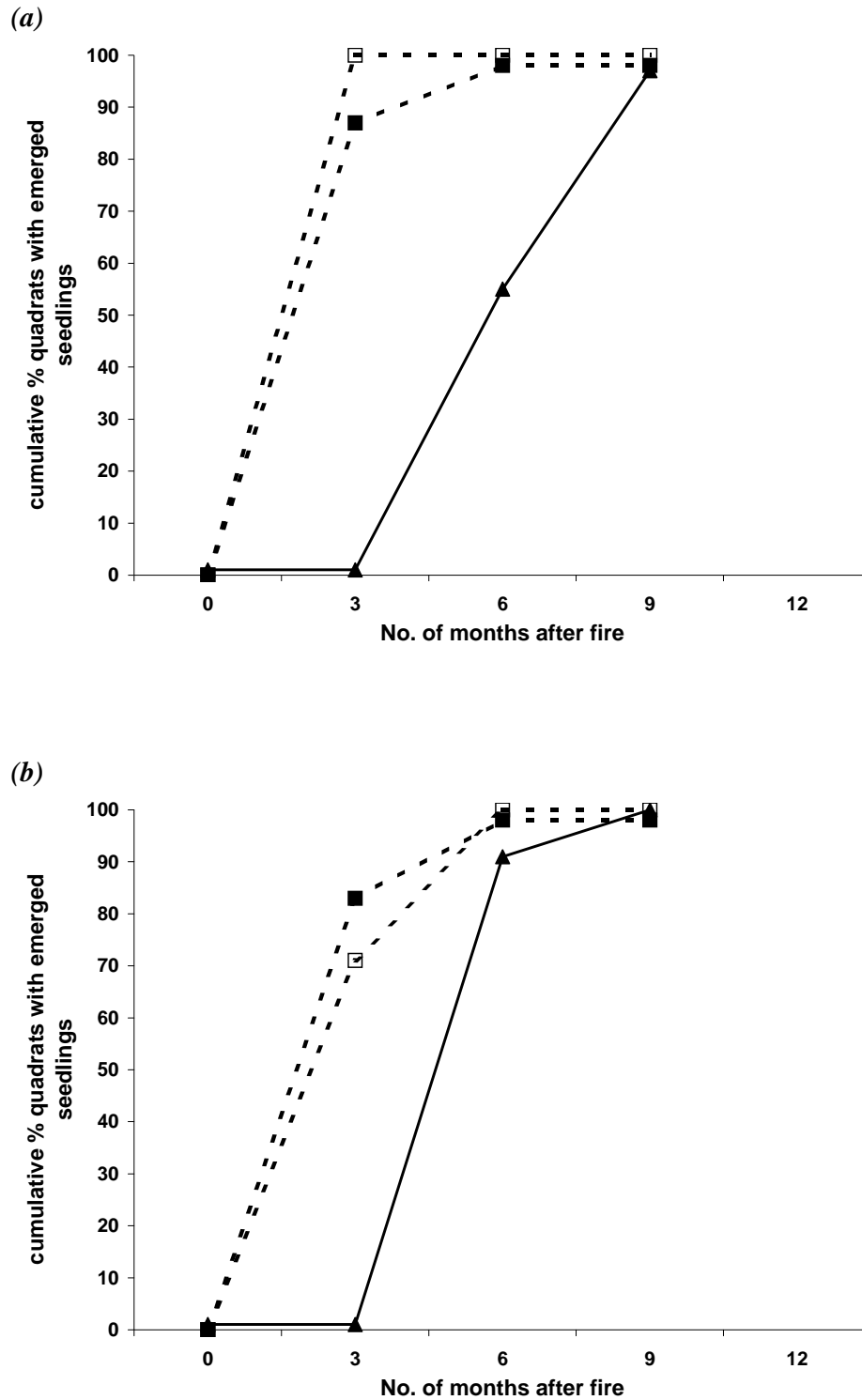


Figure 4.3 Cumulative percentage of quadrats with emerged seedlings at each census time after fire for (a) *L. exolasius* (solid line), combined Fabaceae (■) and *Hakea dactyloides* (□) at the Dingo site and (b) *L. exolasius* (solid line), combined Fabaceae (■) and *Grevillea* spp. (□) at the Lake Eckersley site.

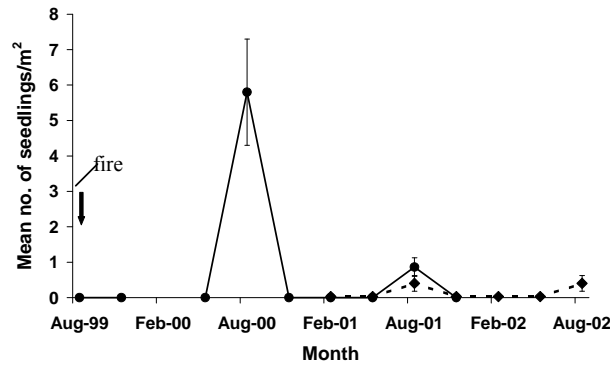
After the August 1999 (winter) fire, no *L. esquamatus* emergence was recorded up until January 2000, four months post-fire, at either site. Plots were not censused again until August 2000, when a large number of new seedlings were recorded. Peak emergence therefore occurred at some time between the January and August 2000 census, four to 12 months post-fire (Sarabs (1) 11.60 ± 1.49 seedlings/m²; Sarabs (2) 5.80 ± 1.59 seedlings/m²). It was assumed that the time of emergence was closer to the August census date, inferred by the size of the seedlings, the lack of any withered seedling remnants and the continuing emergence after August. A small number of seedlings observed, however, were much larger than the assumed August 2000 cohort. It is likely that some earlier emergence had also occurred. This was judged by the amount of time taken by the August 2000 cohort to reach a similar size (M. Ooi, unpubl. data). The number of larger seedlings observed in the area was 0.5 ± 0.3 seedlings/m². A second, much smaller pulse, was observed the following year between May and August 2001, 21 to 24 months post-fire (Figure 4.4a & b).

Timing of emergence in unburnt plots was synchronised with emergence peaks in the burnt plots. Magnitude of the seedling densities in unburnt habitat was low compared to seedling densities from the first pulse after fire in burnt habitats (Figure 4.4a).

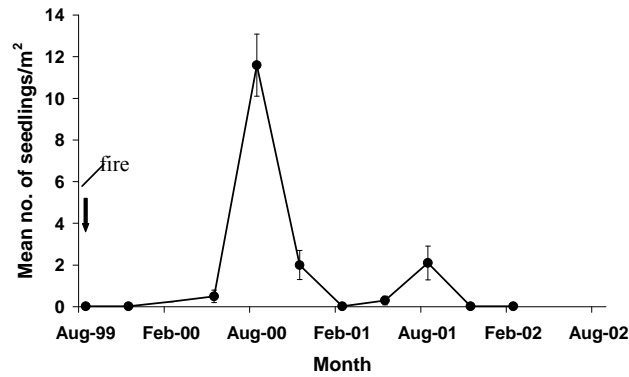
First emergence after the December 2001/02 (summer) was not recorded until the May/June 2002 census, five to six months post-fire (Garie 7.80 ± 2.29 seedlings/m²; Sarabs (2) 5.11 ± 1.27 seedlings/m²). Similar densities of new emergence were recorded after nine months (Garie 4.60 ± 1.78 seedlings/m²; Sarabs (2) 5.78 ± 1.98 seedlings/m²) when the study was terminated (Figure 4.4c & d). The emergence peak at the Garie site was recorded earlier than the Sarabs (2) peak, however the census occurred a few weeks later at the Garie site.

As with *L. exolasius*, a significant difference was found between the time to first emergence of *L. esquamatus* and those of other species (Fabaceae, *Grevillea* spp. *Hakea* sp. and *Banksia* spp.) after the December/January 2001/02 fire (Kruskal-Wallis test, $P < 0.0001$), with *L. esquamatus* emergence occurring significantly later (Figure 4.5).

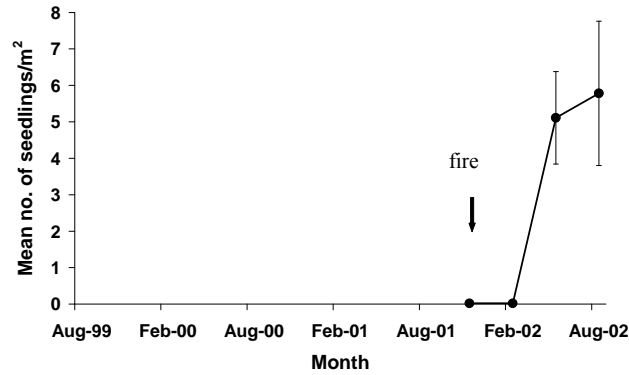
(a)



(b)



(c)



(d)

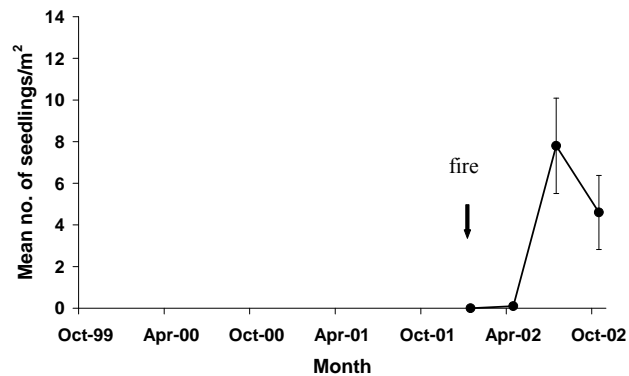


Figure 4.4 Temporal patterns of new emergence for *Leucopogon esquamatus* at (a) the Sarahs (2) site (solid line) after fire in August 1999, and in unburnt habitat between 2001 and 2002 (dotted line), (b) the Sarahs (1) site after fire in August 1999, (c) the Sarahs (2) site after fire in Dec/Jan 2001/02 and (d) the Garie Trig site after fire in Dec/Jan 2001/02. Data are mean number of newly emerged seedlings at each census. (Note that scale on y axes differ).

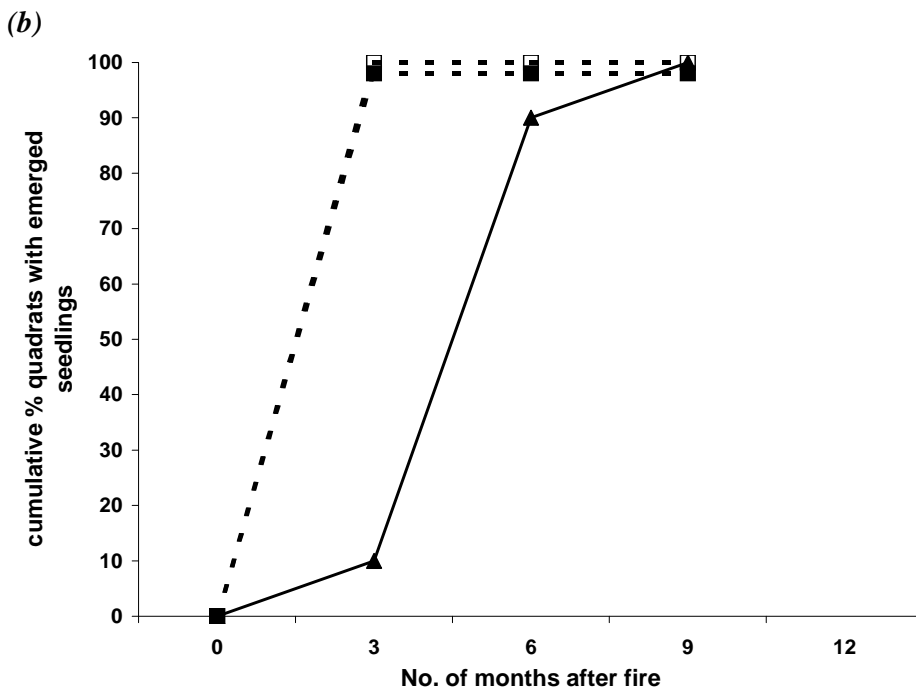
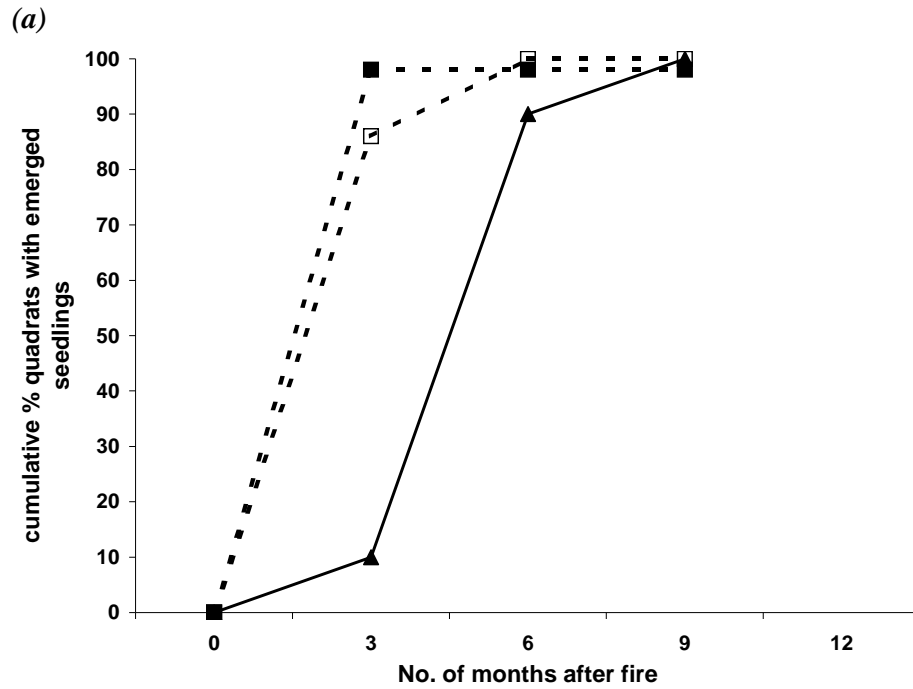


Figure 4.5 Cumulative percentage of quadrats with emerged seedlings at each census time after fire for (a) *L. esquamatus* (solid line), combined Fabaceae and (also *Banksia ericifolia*) (■) and *Grevillea* spp. (□) at the Sarahs (2) site and (b) *L. esquamatus* (solid line), combined Fabaceae (■) and *Banksia* spp. (□) at the Garie Trig site.

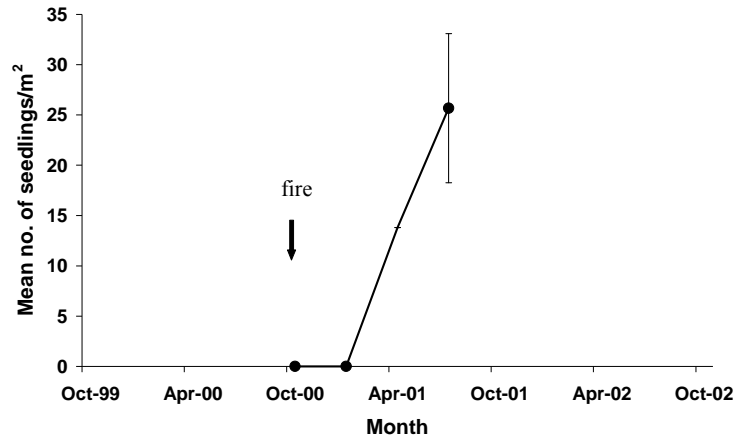
(c) *Leucopogon setiger*

The *L. setiger* Garigal site was censused on only three dates. No emergence was recorded immediately after the fire in November 2000 or four months post-fire. Large numbers of seedlings were recorded at the last census, 10 months post-fire (Figure 4.6a). The peak therefore occurred between four and 10 months post-fire (25.67 ± 7.42 seedlings/m²). Anecdotal observations of another Epacridaceae species at the site, *Styphelia tubiflora*, revealed that a large number of seedlings had emerged within the first four months post-fire.

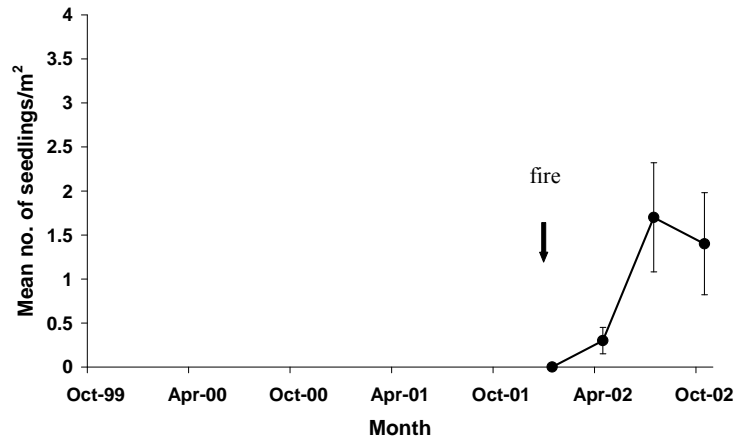
There were no significant differences between the timing of emergence at replicate sites of *L. setiger* after the December/January 2001/02 fire. No *L. setiger* emergence was recorded until the April census. Small numbers of seedlings emerged at Flat Rock Ck (0.30 ± 0.15 seedlings/m²) and Winifred Falls (1.00 ± 0.79 seedlings/m²) three to four months post-fire. The peak pulse of emergence occurred between April and June (Flat Rock Ck 1.70 ± 0.62 seedlings/m²; Winifred Falls 2.20 ± 1.16 seedlings/m²), four to six months post-fire, with a further sizeable pulse (Flat Rock Ck 1.40 ± 0.58 seedlings/m²; Winifred Falls 1.10 ± 0.67 seedlings/m²) recorded six to eight months post-fire (Figure 4.6b & c). A number of newly emerged seedlings were present at both sites during the April – June census. Over 50% of seedlings recorded in this census had cotyledons only and are likely to have emerged close to the census date, in May or June. The following July – September census contained similar levels of emergence, though seedlings measured during this census were at a more developed stage, suggesting emergence earlier in the season.

There were significant differences in time to onset of emergence between *L. setiger* and other species (Fabaceae and *Grevillea mucronulata*) (Kruskal-Wallis, $P = 0.0004$) indicating a delayed emergence for *L. setiger* after the December/January 2001/02 fire (Figure 4.7).

(a)



(b)



(c)

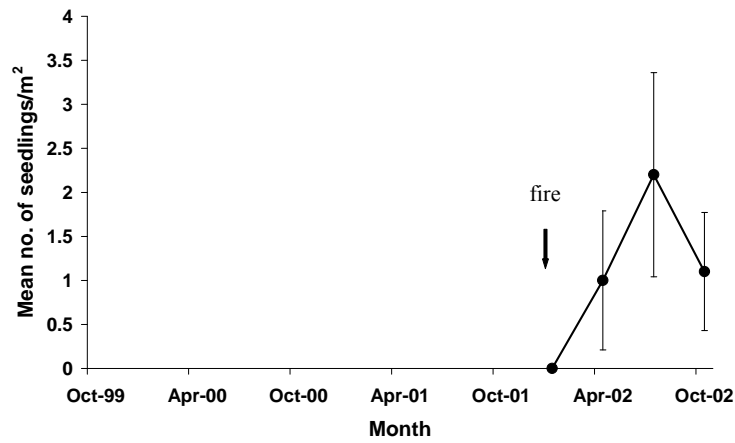


Figure 4.6: Temporal patterns of new emergence for *Leucopogon setiger* at (a) Garigal after fire in October 2000. Emergence patterns at (b) the Flat Rock Creek site and (c) the Winifred Falls site are from after the Dec/Jan 2001/02 fire. Data are mean number of newly emerged seedlings at each census.

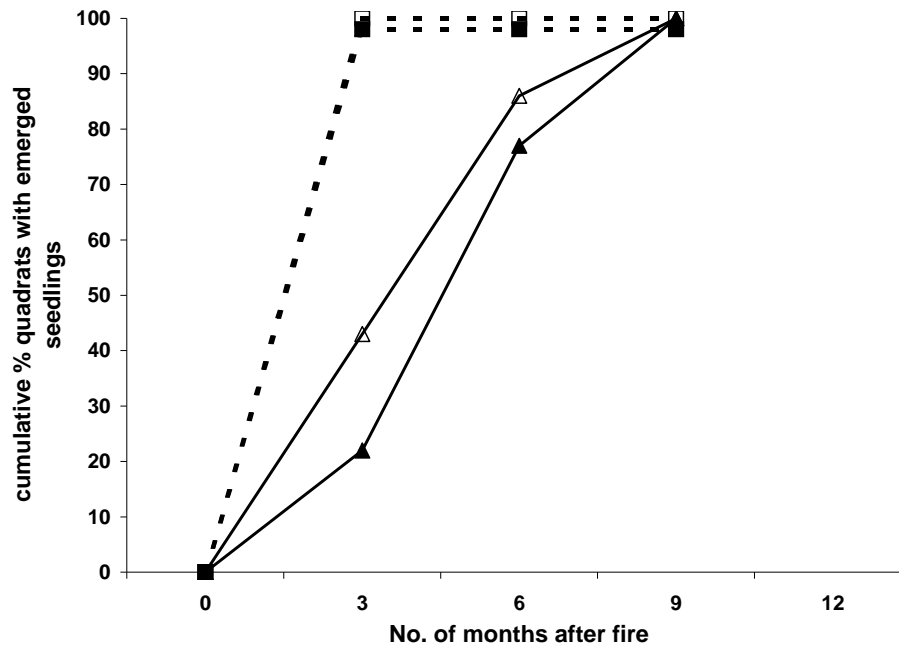


Figure 4.7 Cumulative percentage of quadrats with emerged seedlings at each census time after fire for *L. setiger* (solid line) at Flat Rock Creek (▲) and Winifred Falls (△), and other species (dotted line) combined Fabaceae (■) and *Grevillea mucronulata* (□).

(d) Summary of results and rainfall

The results for the three *Leucopogon* species shows that speed of emergence differed significantly between fire events. There were no significant differences between replicate sites within each fire. The speed of emergence of the *Leucopogon* species differed significantly to that of other species (including Fabaceae, *Grevillea* spp. and *Hakea* spp.) after the December/January 2001/02 fire, with *Leucopogon* emergence being comparatively delayed.

All three *Leucopogon* species monitored produced a peak pulse of emergence post-fire during the May/June – August period, with emergence trailing off during the August/September – November period. This occurred despite the fact that the fires occurred in different seasons. Although sometimes up to five times smaller, secondary emergence pulses post-fire and emergence in unburnt habitat, displayed the same temporal pattern.

Typical of the region, rainfall varied considerably over the study period. After the August 1999 (winter) burn high rainfall events occurred in October 1999, only two months post-fire (more than triple the long term monthly average), and March 2000 (double the long term monthly average) (see Figure 2.2). However, no significant emergence was recorded until August 2000, the following winter. After the December/January 2001/02 (summer) fire, exceptionally high rainfall occurred in February 2002 (triple the long-term monthly average) but peak emergence was recorded either in the autumn or winter periods. Rainfall in the 2002 winter period was approximately four times lower than the long-term average.

4.3.2 Post-fire emergence flush

Seedling densities at all *L. exolasius* and *L. esquamatus* sites recorded before the fires, and in the plots established in unburnt areas, were uniformly low over all years. There were no seedlings recorded at unburnt *L. setiger* sites. Post-fire seedling densities were significantly higher for all species at all sites, compared both to pre-fire data (Figure 4.8) or to adjacent unburnt habitat densities (Figure 4.9).

(a) *Leucopogon exolasius*

For *L. exolasius*, mean seedling density before the August 1999 fire at Dingo site was low (0.23 ± 0.12 seedlings/m²). Post-fire seedling densities recorded after August 2000 (1.67 ± 0.41 seedlings/m²) were significantly higher (Wilcoxon signed ranks test, $P = 0.01$). In adjacent unburnt habitat, mean seedling density (0.23 ± 0.12 seedlings/m²) was also significantly lower than the post-fire densities (Mann-Whitney U test, $P \leq 0.01$). Significantly higher post-fire seedling densities (4.5 ± 1.56 seedlings/m²) were also found after the April 2001 fire, with pre-fire densities very low at 0.1 ± 0.1 seedlings/m² (Wilcoxon signed ranks test, $P = 0.004$) (Figure 4.8a). There was no significant difference found between post-fire seedling densities at any of the sites (Kruskal-Wallis test, $P = 0.1053$).

(b) *Leucopogon esquamatus*

Leucopogon esquamatus mean seedling density before the August 1999 fire at Sarahs (1) was low (0.70 ± 0.30 seedlings/m²). A flush of post-fire seedling emergence (13.50 ± 2.21 seedlings/m²) was significantly larger (Wilcoxon signed ranks test, $P = 0.004$). At Sarahs (2), post-fire densities (5.8 ± 1.59 seedlings/m²) were also significantly greater than pre-fire (0.4 ± 0.4 seedlings/m²) (Mann-Whitney U test, $P = 0.03$). The same result was obtained after the December/January 2001/02 fire at Sarahs (2), with pre-fire densities at 0.4 ± 0.22 seedlings/m² and post-fire densities at 11.56 ± 3.56 seedlings/m² (Wilcoxon signed ranks test, $P = 0.0078$) (Figure 4.8b). Post-fire densities were significantly higher at Garie Trig (12.50 ± 3.98 seedlings/m²) after the December 2001 fire compared to unburnt habitat (0.40 ± 0.22 seedlings/m²) (Mann-Whitney U test, $P < 0.0001$) (Figure 4.9a).

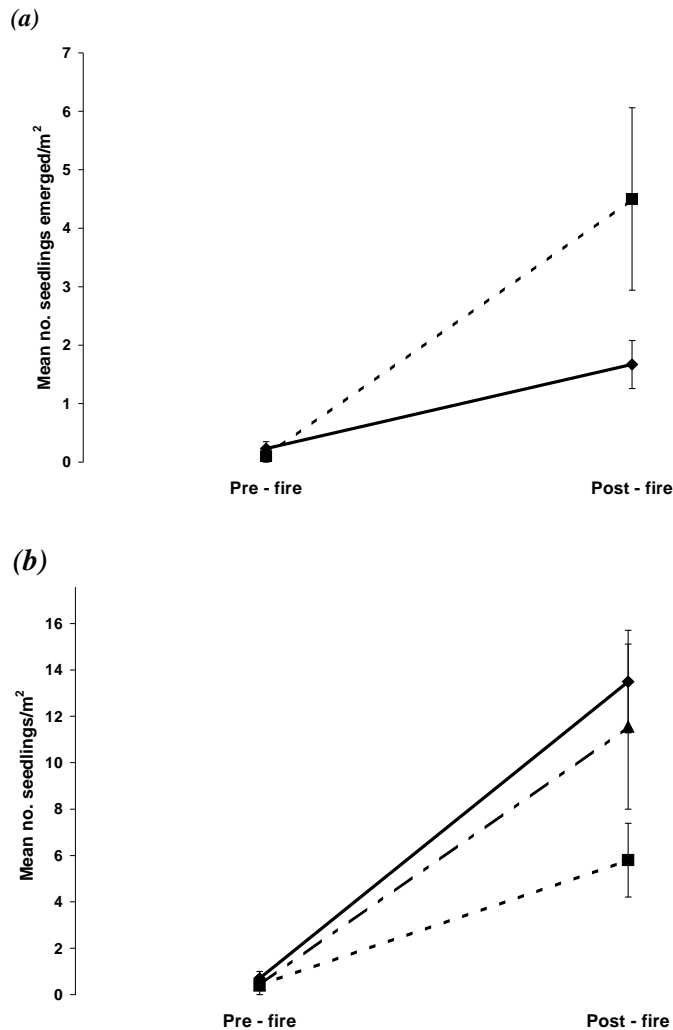
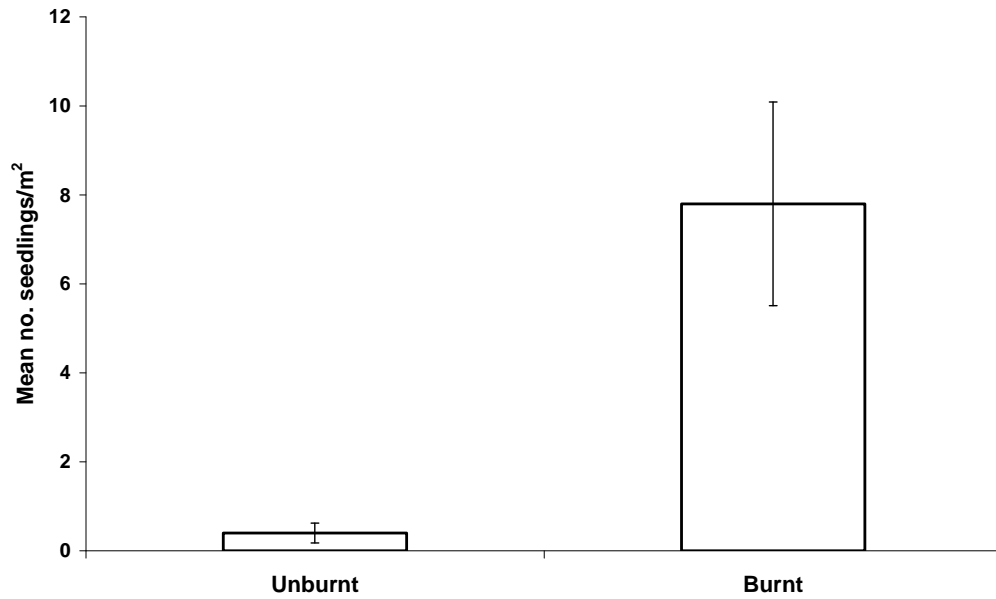


Figure 4.8: Post-fire flush of seedling emergence indicated by significantly higher post-fire seedling densities compared to pre-fire densities for (a) *Leucopogon exolasius* after fires in August 1999 at Dingo site (solid line) and April 2001 at Lake Eckersley (dotted line) and (b) *Leucopogon esquamatus* after fires in August 1999 at Sarahs (1) (solid line) and Sarahs (2) (dotted line). Pre and post-fire densities after the December/January 2001/02 fire at Sarahs (2) are also shown (dot/dash line).

(a)



(b)

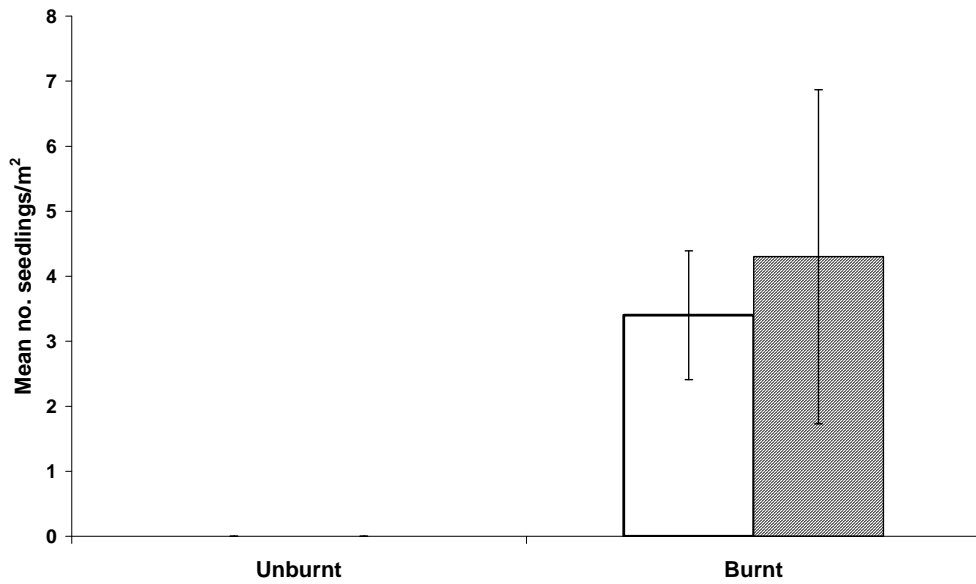


Figure 4.9: Post-fire flush of seedling emergence indicated by significantly higher seedling densities at burnt compared to nearby unburnt habitat after the December/January 2001/02 fires for: (a) *Leucopogon esquamatus* at Garie Trig and (b) *Leucopogon setiger* at Flat Rock Creek (□) and Winifred Falls (▨).

There was no significant difference between post-fire seedling flushes between fires or between sites (Kruskal-Wallis, $P = 0.3481$).

(c) *Leucopogon setiger*

For *Leucopogon setiger*, comparisons could only be made between burnt and unburnt habitat. No seedlings were found in unburnt habitat. Mean number of seedlings were significantly higher in burnt habitat after the 2001/02 wildfire for both Flat Rock Creek (3.40 ± 0.99 seedlings/m²; Mann-Whitney U test $P = 0.001$) and Winifred Falls (4.30 ± 2.57 seedlings/m²; Mann-Whitney U test $P = 0.003$) (Figure 4.9b).

4.4 Discussion

All three species displayed a flush of germination post-fire, implying that dormancy breaking cues are related to fire. This also provides evidence for the existence of a persistent soil-stored seed bank (Keeley 1995). Delayed and regular annual emergence was observed in this study. The timing of the annual emergence pulse correlated with a late-autumn/winter season. The season of seedling emergence remained the same irrespective of the season of burn. Emergence patterns in unburnt habitat, investigated with both *L. exolasius* and *L. esquamatus*, were also restricted to a similarly timed annual pulse. It therefore appears that the magnitude of the delay to post-fire emergence was dependant upon the timing of the fire event.

4.4.1 The post-fire emergence flush and seed dormancy

A flush of seedlings post-fire indicates dormancy-breaking cues related either directly or indirectly to fire (Tyler 1995). Direct cues have been well documented and studies on south-eastern Australian species have shown that heat shock, particularly for hard-seeded species (e.g. Auld 1986; Auld and O Connell 1991), or combinations of heat, smoke and other mechanisms such as dark (e.g. Keith 1997; Kenny 2000; Morris 2000)

can break seed dormancy. Indirect effects of fire have not been as well investigated in south-eastern Australia, although Auld and Bradstock (1996) found that soil temperatures increased sufficiently in recently burnt sites to break dormancy in legume species in the residual seed bank. Other indirect effects include increased fluctuations of soil temperatures (Brits 1986) and reduced competition (Tyler 1995).

Identifying specific dormancy-breaking cues from a post-fire flush of emergence is not possible but some inferences may be made. Initial post-fire pulses of emergence recorded at all sites after all fires were significantly higher than subsequent pulses, except at the *L. exolasius* Lake Eckersley site after the autumn 2001 fire. At this site, the subsequent emergence pulse was not significantly different to the initial one. I suggest that the close proximity of these quadrats to the summer 2001/02 fires might have provided a stimulus for increased germination. As these quadrats were not burnt themselves, it is possible that another fire stimulus, such as smoke, could have enhanced germination (e.g. Dixon *et al.* 1995).

With evidence from this study of both a flush of emergence post-fire and delayed and regular seasonal emergence, it is likely that a combination of fire related cues and abiotic seasonal factors is necessary to maximise germination. Seeds with a primary dormancy followed by a type of imposed secondary dormancy (termed “physiological dormancy”, see Baskin and Baskin 1998) would produce the type of emergence patterns observed.

Dormancy may be broken by overcoming physical, morphological or physiological barriers. Physical dormancy is often overcome by heat shock in fire-prone vegetation and has been well studied in this region due to the number of hard seeded species and the fire prone environment (e.g. Auld and O’Connell 1991). Morphological dormancy occurs when the embryo is underdeveloped. Embryos must grow before germination can take place and this requires specific, usually seasonal temperature stratification (Baskin and Baskin 1998). Physiological dormancy is caused by a physiological inhibition mechanism within the embryo. Physiological dormancy can be broken before, after or concurrently with morphological dormancy and is similarly dependent on stratification, and possibly smoke (Baskin and Baskin 1998). A secondary physiological

dormancy can be imposed after dispersal by factors such as dark. Keeley (1987) found that this form of dormancy could be overcome by using charred wood as a treatment in germination trials.

Seasonal aspects of germination ecology have received comparatively little attention in the heath and forest species of south-eastern Australia (although see Sonia and Heslehurst 1978; Bradstock and Bedward 1992). This may be due to the predominance of fire as a disturbance mechanism, the lack of “extreme” temperatures regimes (e.g. compared to those occurring in arid areas), and the lack of a defined rainfall period (e.g. compared to those with Mediterranean-type climates). However, results from my study suggest that seasonal factors play an important role in the germination ecology of these species. With highly variable annual rainfall, seasonal temperature variation may be an important dormancy regulator in the three study species. A number of other species from this region may also work in a similar way, with other studies implying a similar germination pattern. These include *Grevillea caleyi*, *Kunzea* spp. (Auld *et al.* 2000), *Banksia ericifolia*, *Petrophile pulchella* (Bradstock and O’Connell 1988) *Banksia integrifolia*, *B. serrata* and *B. aemula* (Sonia and Heslehurst 1978). Species that have previously been considered as ‘hard to germinate’ or as having delayed emergence may also require seasonal treatments, and include *Persoonia* spp., *Hibbertia* spp., members of the Rutaceae and other members of the Epacridaceae. Further investigations using germination trials are necessary to understand these mechanisms more thoroughly.

4.4.2 Inter-fire emergence

Germination outside the initial post-fire flush was also recorded during this study. Smaller annual pulses two to three years post-fire were found at *L. exolasius* and *L. esquamatus* sites, the only sites followed for more than one year. This indicated the existence of a residual seed bank, with germination timing remaining linked to season. Decreasing levels of seedling recruitment with time since fire are a feature of Australian heathlands (Keith *et al.* 2002).

Emergence spread over a longer time period has been suggested as a risk-spreading mechanism in some bradysporous species like *Banksia ericifolia* and *B. serrata* (Zammit and Westoby 1987a; Whelan *et al.* 1998) and also in *Epacris stuartii*, a species with soil-stored seed banks (Keith 2002). Risk-spreading can act as a buffer for population recovery, particularly in the event of a poor recruitment season in the first year post-fire. The effectiveness of subsequent emergence pulses as a risk-spreading mechanism for the study species is unknown.

The results also revealed low levels of seedling emergence in long unburnt habitat, particularly at sites with the threatened species *L. exolasius* and to a lesser extent, more open *L. esquamatus* sites. Recruitment in unburnt habitat has rarely been recorded in Australian heath or woodlands (Keith 1996), although low levels of inter-fire germination and recruitment in *Banksia* species have been found by Whelan *et al.* (1998) and Zammit and Westoby (1987b, 1988) in the same region as this study, and Witkowski *et al.* (1991) in south-western Australia. In other fire-prone habitats, like the Californian chaparral, germination in the absence of fire is more common (Keeley 1987, Zammit and Zedler 1994), with many species able to germinate and recruit in areas as a result of other forms of disturbance.

Germination and recruitment of *Banksia serrata* was found by Whelan *et al.* (1998) to be mainly confined to sites where the understorey was open and there was frequent soil disturbance. *Leucopogon exolasius* habitat occurs along riparian areas, which are typically steep with rocky outcrops. Soil disturbance in riparian areas has been documented as a significant factor affecting germination (Pickup *et al.* 2003). A range of plant sizes including seedlings, juveniles and adults occur at both *L. exolasius* sites (M. Ooi, unpubl. data), neither of which had been burnt in over 30 years. Also seedlings were observed clustered around recently senesced individuals at one unburnt *L. exolasius* site (M. Ooi, pers. obs.). At the *L. esquamatus* sites that had previously been unburnt for 30 years, a number of juveniles and seedlings were recorded pre-fire. These factors suggest that the observed low levels of seedling emergence are leading to some recruitment in the inter-fire period. This recruitment may be enough to replace senesced adults in long unburnt habitat, and indeed may be enhanced due to the openings created by senescent individuals.

4.4.3 Seasonal emergence patterns

Emergence of all three *Leucopogon* species was delayed, with the magnitude of delay dependent upon the timing of the fire event. Post-fire emergence of many species in the study region occurs as soon as significant moisture is available (Auld 1986; Bradstock and Bedward 1992; Auld and Tozer 1995; Whelan and York 1998). However, all three species delayed emergence until the onset of the autumn or winter period, irrespective of earlier significant rainfall. Other species monitored, including those with known fire cues such as members of the Fabaceae and *Grevillea* spp., displayed peaks of emergence within the first three months post-fire.

The seasonal pattern of seedling emergence observed in this study does not appear to have been recorded previously in the fire-prone areas of south-eastern Australia, although there has been some inference of this possibility, based on optimal germination temperatures (e.g. Bradstock 1985), seasonal loss of dormancy (Auld *et al.* 2000) and simulated data, suggesting emergence is more likely to fail after autumn/winter fires than after spring/summer fires (Bradstock and Bedward 1992). Seasonal emergence is a common phenomenon in many Mediterranean-type habitats, where it is considered that germination coincides with a distinct winter rainfall period (le Maitre and Midgley 1992; Trabaud 1994; Whelan 1995; Bell 1999). Rainfall in the Sydney region, however, is highly variable.

The Californian chaparral climate is typically Mediterranean. The predominant fire season is June to October (summer to early autumn) and the majority of seedling emergence occurs in spring (Carrington and Keeley 1999). As sprout growth is limited by drought immediately after the June to October fire season, and then by winter temperatures, delayed post-fire emergence occurs concurrently with resprouting. The seasonal delay in seedling emergence in these habitats is therefore not expected to be disadvantageous (Carrington and Keeley 1999). In the Sydney region, fire season straddles spring and summer, with 85% of fires occurring between August and January and the majority of large burns occurring between October and January (Conroy 1996; McLoughlin 1998). For many species, post-fire seedling emergence occurs mainly as soon as soil moisture levels are sufficient (e.g. Auld 1986; Auld and Tozer 1995;

Whelan and York 1998) whilst resprouting also commences quickly (Purdie 1977). Supporting this, data from my study revealed that several Fabaceae, *Grevillea* spp., *Banksia* spp. and *Hakea* spp. had peak emergence in the first few months post-fire. Depending on the timing of the fire event, seedling emergence of the *Leucopogon* species studied could lag behind that of many other species by up to one year, possibly placing them at a competitive disadvantage.

Delayed emergence in the fire-prone vegetation of the south-east Australian region has rarely been documented, particularly in species with persistent seed banks. Species in the region with transient seed banks, like the pyrogenic flowerers *Doryanthes excelsa* and *Telopea speciosissima*, have a delayed emergence post-fire, comparable to that of the study species. Competitive disadvantages of delayed post-fire emergence potentially affecting these species are thought to be ameliorated by their large seed size, ensuring that seedlings have sufficient reserves to establish (Denham and Auld 2002). *Leucopogon* species are small seeded, and the reduction in resources, such as nutrients, light and moisture, by faster growing neighbours, may produce a competitive disadvantage. This disadvantage would increase with an increase in the magnitude of delay.

Previous studies have shown that delayed post-disturbance emergence can disadvantage subsequent growth and survival of seedlings (e.g. Jones *et al.* 1997). Timing of emergence separated by only a few weeks can be enough to affect subsequent survival and recruitment in some habitats (Jones *et al.* 1997). The potential advantages or disadvantages of delayed emergence in *Leucopogon* species in fire-prone habitats remain to be investigated. Such investigations should ideally include comparisons of mortality within cohorts (i.e. seedlings whose emergence times are separated by a few weeks), comparisons between successive annual cohorts, and comparisons between cohorts subjected to different burning seasons, with replication across sites and a range of fires.

Although some form of dormancy may be the explanation for delayed emergence, it is unclear why it occurs and persists in a habitat with such variable rainfall. Several possible reasons are worthy of discussion.

4.4.4 Evolution and persistence of seasonal dormancy

Investigating emergence patterns in comparable habitats may reveal some clues as to the occurrence of seasonal dormancy in aseasonal rainfall regions. Delayed and seasonal emergence has been found post-fire in the sand pine scrub of Florida (Carrington and Keeley 1999). Like south-eastern Australia, this region does not have a Mediterranean-type climate, but instead has variable rainfall annually, with a slightly higher proportion (~ 65%) falling in summer (Whelan 1985). Fires have a return interval of between 10 and 100 years (Carrington 1999) and typically occur in spring and early summer, whilst seedling establishment within the community generally occurs in spring, possibly as a result of adaptations to the slightly higher summer rainfall pattern. Seedling establishment can therefore be delayed for up to 10 months (Carrington and Keeley 1999). Seasonal conditions are considered the primary cause for the evolution of dormancy, particularly in areas suffering from low or variable rainfall (Baskin and Baskin 1998). From 14 000 years to about 12,000 years ago, Florida was marked by a high degree of climatic variability, with increased seasonality and other climatic extremes (Delcourt and Delcourt 1993). Approximately 5 000 years ago, all of the components of the modern southern forests communities were established (Whelan 1985). It is considered likely that many components of the current Florida pine communities could have developed germination cued strongly to season. However, although delayed as a result of seasonal emergence, some species still display a post-fire flush of germination. Carrington and Keeley (1999) suggested that the indirect effects of fire, such as canopy gaps and subsequent increased levels of light and nutrients, are likely to cause this post-fire flush in the Florida sand pine scrub, rather than direct fire effects. Other mechanisms, such as hurricanes, have been a regular disturbance force in sand pine communities, and these have perhaps been more responsible than fire for large scale stand replacement (Stanturf *et al.* 2002). Many species have therefore evolved under the influence of other significant disturbance patterns and although able to persist in a fire-prone habitat, do not have germination cues adapted to it.

Fire-prone habitats have existed in Australia at least since the late Tertiary (Walker and Singh 1981) and there is evidence of much earlier significant fire events (e.g. Glasspool 2000). It would seem unlikely that fire has not had a long influence on determining

germination cues. Climatic variability may still have had an influence on Australian flora and although this would not be as prominent due to such a significant fire history, some species may have maintained traits such as seasonal germination cues. From analysis of megafossil deposits, the Epacridaceae were represented in the Australian flora from the Oligocene (25-35 million years before present (m.y. BP)) onwards (Christophel 1995). Cooling temperatures up until the middle Miocene (15 m.y. BP) intensified climatic conditions from warmer and wetter to much more variable and drier (Walker and Singh 1981). There is also suggestion that during the Pliocene (around 2.6 m.y. BP) winter rainfall dominated the climate due to the intensification and movement north of the subtropical high-pressure belt (Bowler 1982). A significant amount of time under variable climatic conditions and winter dominant rainfall could plausibly have enabled epacrids to develop the seasonally based germination cues observed in this study. Similar, though perhaps not as sharply defined, seasonal dormancy mechanisms are also found in east coast *Banksia* species (Sonia and Heslehurst 1978; Bradstock and O'Connell 1988). Megafossil records show that *Banksia* species evolved at similar times to the Epacridaceae (Christophel 1995).

While this line of reasoning might explain how seasonal dormancy has developed, further questions are raised as to how these dormancy mechanisms are able to persist in south-eastern Australia. In Florida, germination does not seem to be strongly related to fire and there is a general, though quite variable, seasonal trend to spring emergence post-fire (Lambert and Menges 1996). In a study by Carrington (1999) in Florida sand pine scrub, prescribed burns were carried out in late spring (May). Seedlings of the herbaceous resprouter, *Eriogonum floridanum*, were recorded five weeks post-fire and new seedlings continued to emerge for up to two years. Seedlings of the fire sensitive woody shrub *Calamintha ashei* first emerged 10 months post-fire. Both of these species therefore emerged close to spring and displayed a significant flush of germination. Two resprouting woody shrubs, *Palafoxia feayi* and *Chapmannia floridana* produced much lower levels of emergence three weeks (spring) and five months (autumn) post-fire respectively. New *C. floridana* emergence was not recorded after 10 months (spring). In a study by Whelan (1985) in longleaf pine, prescribed burns were implemented in north-central Florida in April. No germination was recorded until summer, four months post-fire, when *Chapmannia floridana* seedlings emerged. Emergence of the two resprouters,

Liatris tenuifolia and *Berlandiera subacaulis*, began significantly after six months, in autumn. From these studies, it seems that some Florida species may have adapted germination cues more strongly to fire whereas others germinate more independently. With the dominance of other disturbance mechanisms in the sandpine scrub (Stanturf *et al.* 2002), and a fire history possibly shorter than that of the Australian continent, adaptations to fire may be less pronounced (Whelan 1985). Variable rainfall patterns may allow the multitude of germination responses to co-exist by providing sufficient moisture throughout the year.

In comparison, fire activity in south-eastern Australia has a much longer history and seems to have increased considerably in the last 120 000 years (Walker and Singh 1981). Consequently the majority of species in fire-prone habitats have germination cued to the passage of fire, with fewer species maintaining other dormancy mechanisms such as seasonal temperature requirements. Nevertheless those that have maintained these cues, such as the *Leucopogons* studied, are able to persist, possibly for the same reasons expressed for the Florida vegetation. The highly variable nature of the regions rainfall means that sufficient moisture is available for germination, irrespective of the timing of a fire or the season that germination is cued to.

The predominantly spring/summer fire season in south-eastern Australia may not be optimal for rapid post-fire emergence in the *Leucopogon* species studied, but the species have persisted with this level of delay. It is unknown how sensitive the species are to an increase in the magnitude of delay, and subsequently an increase in the level of competitive disadvantage. The season of fire therefore, could play a more important role in the population dynamics of species like *Leucopogon*, with a seasonal emergence pulse, than species with a faster post-fire emergence response. This could be tested by experimentally manipulating cohorts of seedlings into habitats burnt during different seasons.

4.4.5 Conclusions

The investigation of emergence patterns revealed that the *Leucopogon* species studied have a regular annual emergence pulse which occurs both post-fire and in unburnt habitat. The regularity of this seasonal pulse, suggests that emergence will occur at the same time of the year irrespective of the timing/season of a fire event. The magnitude of the delay is therefore dependent upon fire season. Season of fire has previously been thought to have little effect on emergence patterns in areas like the study region in the short term, due to variable distribution of annual rainfall (Bradstock and Bedward 1992).

Leucopogon exolasius and *L. esquamatus* sites burnt in winter, an *L. exolasius* site burnt in autumn, and sites of all species burnt in summer produced peak emergence pulses in the following late autumn/winter period. Replication of season of fire was not possible and therefore results should be interpreted with some caution. However all post-fire emergence pulses were delayed to the same seasonal window irrespective not only of the season of burn, but also of significant rainfall earlier in the post-fire period.

These findings do not support the hypothesis put forward by Bradstock and Bedward (1992), suggesting that effects of fire season are not predictable in this region in the short term. The length of delay to the onset of emergence could be predicted from the season of burn. Fire stimulates the germination of these species but does not regulate the timing of germination. Unlike the rainfall induced variation in emergence patterns of *Hakea sericea* and *Petrophile sessilis* observed by Whelan and York (1998), this study suggests that factors other than sufficient moisture can be important in determining the timing of germination and subsequent emergence of *Leucopogon* species. In particular, seasonal temperature regimes combined with fire related cues might be the necessary factors that maximise germination in these *Leucopogon* species. These results highlight the continuing need and importance of species level ecological research with regards to fire season in south-eastern Australia.

Chapter 5

Discussion: implications for the assessment of threat status and for management of *Leucopogon exolasius*

5.1 Introduction and overview of study

The research presented in this study has contributed to the improved understanding of an important, though under-studied, component of temperate Australian vegetation. The aims of this study were to investigate four species within the genus *Leucopogon* in the fire-prone vegetation of south-eastern Australia. The four species, all occurring within the Sydney region, were the threatened *L. exolasius*, and the more common congeners *L. esquamatus*, *L. setiger* and *L. ericoides*. Specifically the questions were:

- (i) What is the response of individual plants and plant populations to fire?
- (ii) Is there a delayed or seasonal component to seedling emergence?
- (iii) Are germination cues linked to the passage of fire?

All four *Leucopogon* species, both the common taxa and the threatened species, were killed after 100% leaf scorch, and all were therefore classified as obligate seeders. A mechanism for individual plant persistence after low intensity fire was also identified. Consequently, although the species were categorised as obligate seeders, the survival of some individuals within the landscape provided a level of population persistence after low intensity fire. A number of plants survived in areas with minimal leaf litter that consequently remained unburnt, after low intensity burns. The level of survival of established plants was therefore considered to be dependent on fire patchiness. Topographic features, such as rocky sandstone outcrops, appeared to assist fire patchiness by creating breaks in the litter layer.

Post-fire emergence of seedlings was not immediate, but was delayed for up to 12 months. This pattern occurred after several fires, although the magnitude of the delay varied between fires (from two months to 12 months). There was a regular annual pulse of emergence in the same season of each year, after each fire. A similar annual pattern occurred in unburnt habitat, though seedlings were at lower densities.

A striking feature of the results is that emergence patterns were consistent between fires and between species. The season of germination appears to occur at late-autumn/early-winter, regardless of when the fire occurs. From this, I concluded that delayed post-fire emergence was dependant upon the timing of the fire event. Fire may stimulate germination of these species, but it does not regulate the timing of germination. A fire in late winter will therefore result in an 11-12 month delay for the germination season, whereas a fire in late summer will result in a shorter wait of approximately three to four months. Further research needs to be conducted to ascertain if delayed emergence affects subsequent recruitment of *Leucopogon* species. This may have implications for management, particularly for the season of implementing hazard reduction burns in habitat of the threatened species *L. exolasius*. Since European settlement, a shift away from spring/summer fires to higher levels of autumn/winter fires has begun (McLoughlin 1998).

A flush of germination post-fire indicated that the study species had seed dormancy cued, either directly or indirectly, to the passage of fire. Regular annual emergence patterns suggest that combinations of fire-related and abiotic factors are necessary for maximising emergence from the seed bank. Pulses of seedling emergence in subsequent years post-fire suggest that a proportion of the seed bank can remain after fire, and that germination cues remain linked to season. Subsequent or secondary pulses of emergence post-fire could also be a possible mechanism for risk spreading, in the event of failure of the initial post-fire seedling cohort. Evidence of germination in the absence of fire, also observed as a regular annual emergence pattern, indicated that some inter-fire recruitment is possible. The influence of season on seed dormancy and germination has rarely been considered in the Sydney region. This may be due to the predominance of fire, or the lack of extreme seasonal variation.

Many species, including those within the Epacridaceae, Rutaceae and Dilleniaceae, are simply classified as ‘difficult to germinate’ (e.g. Dixon *et al.* 1995). Seasonal regulation of seed dormancy requires further research, to investigate what role it plays in species from the Sydney region.

In this study, I specifically investigated features of the ecology of *Leucopogon* species relevant to understanding post-fire recovery mechanisms, and also possible processes that might threaten populations of the study species. In this chapter, I assess the status of *L. exolasius*, using both the World Conservation Union (IUCN) Red List Criteria (IUCN 1994, 2001) and a modified version of these criteria. Ecological data, combined with information such as the geographic distribution and rates of decline, are essential for the assessment of species via these schemes. I also discuss rarity of *L. exolasius* in relation to conclusions from this study. Finally I will investigate management options for the threatened species *L. exolasius* and propose suggestions for future research.

5.2 Possible causes of rarity of *Leucopogon exolasius*

All four species were categorised as obligate seeders after several fires in this study. All are therefore dependent on seeds for post-fire regeneration. Survival of some established plants within a population was also observed after low intensity fire. Topographical features, such as rock platforms at the edge of heath, or sandstone outcropping in riparian habitats, contributed to fire patchiness in low intensity fire, and the surviving individuals were in unburnt patches.

Some theories have suggested that increasing fire frequency could restrict obligate seeding species to fire shadows (Gill and Bradstock 1995; Clarke 2002), where at least some plants escape being burned in some fire events. This would particularly be the case if the species has a long primary juvenile period. Fire shadows would maintain longer inter-fire intervals, which would allow these species to mature, reproduce and replenish the seed bank. Anecdotal observations (M. Ooi, unpubl. data) suggest that *L. exolasius* has a primary juvenile period of at least 10 years, whereas *L. setiger* and *L. esquamatus* produce significant flowering within approximately four years post-fire. Further research is required to investigate the primary juvenile period for these species.

The rare species *L. exolasius* currently occurs almost exclusively on rocky sandstone riparian hillsides (Fairley and Moore 1989; Benson and McDougall 1995). The common congeners studied also occurred in habitats conducive to patchy fire but, unlike *L.*

exolasius, they were not restricted to such sites. Given the similarities in many features of this group of species, I hypothesise, based on my observations from sites with different times to last fire, that *L. exolasius* will be found to have a relatively long primary juvenile period. This feature confines it, more tightly than its congeners to microhabitats with lower frequency fire thus contributing to its restricted distribution and low abundance.

5.3 Assessing threat status using relevant findings from this study

Ranking of species according to their risk of extinction is central to conservation assessment (Akçakaya *et al.* 2000). Ranking and listing threatened taxa identifies those most urgently in need of management action, and those to which usually limited funding can be directed with the most effect (Keith 1998, Akçakaya *et al.* 2000).

Leucopogon exolasius is a threatened species, listed as ‘vulnerable’ under the NSW *Threatened Species Conservation Act* (1995) Schedule 2, ‘vulnerable’ under the Commonwealth *Environment Protection and Biodiversity Conservation Act* (1999), and 2VC- in ROTAP [(2) Geographic range in Australia less than 100 km, (V) Vulnerable, (C) with at least one population reserved, of unknown size (Briggs and Leigh 1996)]. Prior to this study, little was known about the ecology of this species or how to manage its populations, so the basis for its listing must be questioned. The reasons for its initial listing are unclear, and the possible causes of rarity have never been investigated.

Until the recent development of schemes for assessing extinction risk (e.g. Millsap *et al.* 1990; IUCN 1994), threatened species lists have typically been compiled using threat status based on qualitative decisions and expert opinion. This method is still applied, with lists such as ROTAP (Briggs and Leigh 1996), and it was the approach used to list species in New South Wales, prior to the implementation of the *Threatened Species Conservation Act* (1995). The benefits of a qualitative approach include its ease of application to a wide variety of taxa and modest data requirements (Chalson and Keith 1995; Todd and Burgman 1998). However, a quantitative approach to assessing extinction risk provides a more transparent and repeatable method. Decision rule

criteria, such as the IUCN Red List Criteria (IUCN 1994, 2001), include the use of quantified data. Due to the relatively recent introduction of threatened species legislation in many parts of the world, there is more scrutiny and debate over species listed as threatened (Keith 1998; Mace and Hudson 1999). Explicit, repeatable and precise listing criteria help to defend these listing decisions (Keith 1998).

The IUCN (1994) developed the Red List Criteria, a semi-quantitative method for assessing the threat status of a wide range of taxa. Under IUCN Red List Criteria, quantitative data regarding geographic range, population status and rates of decline are required. Information on habitat and life history characteristics is also required. There has been considerable analysis and assessment of the IUCN criteria (e.g. Keith 1998, Todd and Burgman 1998, Colyvan *et al.* 1999, Akçakaya *et al.* 2000, Gigon *et al.* 2000, Keith *et al.* 2000, Gärdenfors *et al.* 2001). Some analyses have led to modification, one example being RAREplants (Keith 1998), targeted at assessing vascular plants. A number of changes have been made (e.g. reducing the thresholds for geographical range). The Environmental Flora Network (EFN) has developed the RAREplants criteria further. Threat categories for both the IUCN and modified criteria are listed in Table 5.1. The EFN modified criteria, with departures from the IUCN criteria in italics, are shown in Table 5.2, whilst the original IUCN criteria are shown in Table 5.3. IUCN definitions are listed in Table 5.4.

An independent Scientific Committee reviews and maintains the Schedules of threatened taxa attached to the NSW *Threatened Species Conservation Act* (1995). Although assessment is based on a variety of advice, expert opinion and other information, the EFN modified IUCN criteria are used as an important tool in assessing the conservation status of plant species nominated.

Leucopogon exolasius was listed on Schedule 2 of the NSW *Threatened Species Conservation Act* (1995) prior to the implementation of the use of the EFN modified IUCN criteria by the NSW Scientific Committee. In this section, I collated the relevant findings from the study, as well as gathered distributional data from herbaria, historical records and targeted surveys, to enable an assessment of the threat status of *L. exolasius*

via the EFN modified IUCN criteria. Analysis of the relevant information is presented below.

5.3.1 Fire response

Leucopogon exolasius is fire sensitive. Fire sensitive species depend primarily on regeneration from seed. The transition from seed to seedling and subsequent recruitment to maturity are therefore critical life stages, and threats surrounding this life history stage, such as fire frequency, need to be assessed.

5.3.2 Distribution

The core distribution of the species occurs between the south-west outskirts of Sydney and the Illawarra region of NSW. The oldest records note the species as “near Camden” (1843), Grose River (1894), Como (1901), Woronora (1901) and Macquarie Fields to Campbelltown (1914). More recent collections have confirmed some of these locations. However, neither the Grose River nor the Como areas have produced subsequent collections. The Grose River location is highly disjunct, and with no further collections since 1894, it is quite possible that this population is extinct. Under the definitions from the NSW *Threatened Species Conservation Act* (1995), any population not confirmed for 50 years is considered as ‘presumed extinct’.

More recent collections have been made from the catchments of the Avon and Cataract dams and the Holsworthy Military Reserve. There is an unconfirmed record (no specimen lodged at any herbaria) from the north of Sydney, near Wisemans Ferry. I carried out targeted searches in remnant vegetation along sections of the Georges River and along the Hacking River in Royal National Park. No further populations of *L. exolasius* were found. Vegetation surveys carried out for a mapping study of western Sydney found *L. exolasius* in eight survey plots (M. Tozer, pers. comm.) but these were simply confirmation of older known locations, not new populations.

It is now possible to make an estimate of the species' extent of occurrence (EOO), one measure of distribution used under the IUCN definitions. All definitions of IUCN Red List (and the modified scheme) criteria such as EOO, are shown in Table 5.4. The other measure of distribution, area of occupancy (AOO) could not be calculated due to a lack of finer scale data. Using all confirmed locations only, an estimated EOO of 230 km² is reached. If the unconfirmed record in the north of Sydney is included, this estimate increases to 477 km². Extending the area to include the Grose River collection increases the EOO to approximately 2 680 km².

5.3.3 Population size and number of locations

Total population size is unknown. Some coarse estimates could be made for the two study sites but, as shown during my study, population numbers fluctuate dramatically due to the mortality of fire sensitive adults and pulses of recruitment after fires. There is nothing known about the size of populations at any of the other locations.

A total of 14 sub-populations and six locations have been estimated, as per IUCN definitions (see Table 5.4). The Heathcote National Park, Dharawal State Recreation Area, Cataract and Avon catchments, Holsworthy, and the Campbelltown area records are all considered as distinct locations under IUCN definitions. It is currently impossible to calculate how many of these would need to be included in order to contain 90% of the total population size (data used in the modified IUCN criteria). If it is assumed that all locations contain similar numbers of individuals, a conservative estimate of five populations is indicated.

5.3.4 Predicted and historical declines

A decline in the species' extent and quality of habitat and population size, particularly in the western parts of its range, has occurred. Historical records show that the species occurred extensively along the Georges River. Collecting notes by J. L. Boorman in 1914 state that the species was fairly common from Macquarie Fields to Campbelltown

on the south-west outskirts of present-day Sydney. More recent collections from the south-west locations confirm that the species is still extant. However, large areas of land have been cleared with the encroachment of urbanisation. Remaining bushland reserves in the south-west, containing this species, are quite fragmented (M. Ooi, pers. obs).

Notes from 1901 by E. Cheel show that the species also occurred in Como near the mouth of the Georges River in Sydney's south. The Como site has not been confirmed since the original 1901 collection. Como is now an urbanised area with some small stands of remnant vegetation. The majority of habitat would have been cleared between the original collection date and the present day.

Declines have obviously occurred in the distributional range and size of the population, as well as in the quality of habitat. However, quantifying the rate of decline is not possible from the data available.

5.3.5 Threats

Clearing along some sections of the Georges River would have led to the loss of individuals and habitat of *L. exolasius*. A number of populations occur on private property or land not managed for conservation. Clearing is therefore considered a threat to some of the populations. Nearly 30% of all plant species listed on the Schedules of the NSW *Threatened Species Conservation Act* (1995) are, or could become, threatened by clearing (NSW Scientific Committee 2001).

Results from this study have shown that *L. exolasius* is fire sensitive. It is hypothesised that the primary juvenile period of *L. exolasius* is at least 10 years. Also, a number of the *L. exolasius* populations occur on the urban fringe, where there is increasing pressure for more frequent hazard reduction burning (Auld and Scott 1997; Whelan 2002). Populations of the study species in these areas are at threat from an increased frequency fire regime, regardless of land tenure.

It is also possible that the season of burn may negatively affect the study species. Fires in mid-winter may delay post-fire emergence of *L. exolasius* by up to a year, due to the seasonal emergence patterns found during this study. A shift from a spring/summer historical fire regime (which would produce a much shorter time to emergence), to a regular late autumn/winter regime could constitute a threat to the species in the long term. Increasing the magnitude of the delay to emergence over the long term could put the *L. exolasius* seedlings at a competitive disadvantage. It has recently been reported that since European settlement, a shift away from spring/summer fires to higher levels of autumn/winter fires has occurred (McLoughlin 1998).

5.4 Assessment of *Leucopogon exolasius* against the EFN modified IUCN criteria

The five decision rules of the EFN modified IUCN criteria and the IUCN criteria are shown in Tables 5.2 and 5.3. Correct use of schemes such as these involves assessing the species against all rules. The species is assigned the threat status from the rule that returns the greatest assessment of risk. Threat categories are listed below in Table 5.1. If there are insufficient data for any particular assessment rule, then the category assigned for that rule is Data Deficient (DD). If data is not estimated as passing under the set threshold for any particular rule, or related sub-rules are not met, then the category assigned for that rule is Low Risk (LR). Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) assessments are assigned when data passes under the set thresholds and then meets the required number of additional sub-rules under any particular rule.

Incorporated into the assessment scheme is an allowance for uncertainty. Lower, best and upper estimates are made for each rule. With quantitative survey data, lower and upper bounds can be calculated. Issues such as unconfirmed locations for distributional data, however, can be dealt with using a precautionary approach. In the case where there is a lack of full scientific certainty, a precautionary approach invokes the principle that this should not be used as a reason for not listing a species as threatened. Using this

Table 5.1: Threat categories endorsed by the IUCN (2001). The categories generally accepted as indicating some level of threat are, (i) critically endangered (ii) endangered and (iii) vulnerable.

approach, the highest feasible estimate of risk under any particular rule should be used to assess threat status. A precautionary approach can also be applied to the scheme as a whole (Keith *et al.* 2000). For example, if a status of Low Risk has been assessed under one rule only, and all other rules are Data Deficient, a threat status of Low Risk would be counter-precautionary. In a case like this, Data Deficient would be a more precautionary assessment.

The threat status assigned after assessment of *L. exolasius* using both the IUCN Red List criteria and the EFN modified version of the IUCN criteria is **Endangered (EN)** via **Rule B**. Details of the full assessment are shown below.

Table 5.2: The Endangered Flora Network modified form of the rule set endorsed by IUCN (1994, 2001). The basic rules endorsed by IUCN (1994) are in ordinary type, with amendments in bold italics.

Table 5.3: Original IUCN Red List Criteria (IUCN 1994, 2001)

Table 5.4: Definitions used for applying the IUCN Red List Criteria (2001) and the EFN modified criteria.

Rule A: Rates of population decline - DD

There has obviously been some level of historical decline, as well as a likelihood of some level of future decline in extent, habitat quality and population size. However, it is not possible to quantify this with the data available.

Rule B: Distribution – EN (IUCN and EFN modified criteria)

The lower bound estimate of extent of occurrence is estimated at 230 km² (under the EFN threshold for EN of 500km² and the IUCN threshold of 5 000 km²). The more optimistic estimate of 477 km² is still under the threshold for endangered for both sets of criteria, whilst the most optimistic estimate of 2 680 km² is under the endangered threshold for the IUCN criteria but only under the threshold for vulnerable under the EFN modified criteria. There were no data for area of occupancy. The further sub-rules met are:

- (i) Continuing declines – there have been relatively recent (and there are projected future) declines in the extent and quality of habitat and the number of mature individuals.
- (ii) Extreme fluctuations in the number of mature individuals – the species is fire sensitive therefore numbers of mature individuals are likely to vary by an order of magnitude in relation to fire.

Rule C: Total population size – DD

There is insufficient data to estimate the total population size.

Rule D: Total population size and acute restriction – DD

There is insufficient data to estimate the total population size. The type of available habitat is not thought to be acutely restricted.

Rule E: Probability of extinction - DD

There is insufficient data for a quantitative analysis of probability of extinction.

Rule F: Locations containing 90% of total population and conservation – VU (EFN only NB: no Rule F under the IUCN criteria)

90% of all mature individuals are estimated to be contained at five locations (threshold for VU is 10). The further criterion met is:

- (i) No more than two of these locations are free of Class I and II threats (see Table 5.4).

Results from this assessment suggest that the species' listed status of 'vulnerable' under the NSW *Threatened Species Conservation Act* (1995) should be changed. It has a restricted extent of occurrence, well under the threshold for a listing of 'endangered', and the threat caused by encroaching urbanisation and inappropriate fire regimes is continuing.

5.5 Management

Species can become threatened as a result of biological traits, induced changes (Cropper 1993) or a combination of these. A number of threats to *L. exolasius*, including clearing for development, can be classified as induced. Clearing occurs off conservation managed land and is therefore dependant upon the protection provided by the relevant legislation and the sensitivity of the developers. This section of the study, however, concentrates on the management of threats imposed by the species biology. Species dependent on fire, like *L. exolasius*, are often threatened as a result of circumstances related to their fire ecology (Cropper 1993). From the possible limiting factors and threatening processes discussed previously, a number of suggestions can be made regarding the management of *L. exolasius*.

Although not yet specifically determined, the primary juvenile period of *L. exolasius* is thought to be long. Benson (1985) found that some obligate seeders in heaths and forests of the Sydney region take more than 10 years to produce significant levels of flowering. This type of information can help to set precautionary limits for vegetation management guidelines. However, management of vegetation close to urban environments has to incorporate the major principle of protection of life and property (NSW National Parks and Wildlife Service 2001). Increased frequency of hazard

reduction burning is often lobbied for (e.g. New South Wales Farmers Association 2002) as a means to reduce the fuel load and subsequently increase the ability to control wildfire.

This study opportunistically revealed the effect of wildfire on areas burnt by previous hazard reduction fires. One prescribed burn (1999) produced a low intensity fire whilst the other (2001) produced a higher, though still relatively low intensity fire. The upper canopy was not affected in either burn. Ground litter had built up within a few months after each fire, both from the upper canopy and from scorched leaves in the lower canopy. Resprout growth had also recovered significantly, providing more fuel, particularly from resprouters with highly flammable leaves such as *Angophora hispida*. Wildfire subsequently burned through both areas, within 2.3 and 0.7 years of the respective prescribed burns. Although patchier and of a lower intensity than in adjacent areas that had not been burned in recent hazard-reduction fires, 60% and 20% of the *L. exolasius* seedlings respectively, were killed by the wildfire. All *L. esquamatus* seedlings were killed by the wildfire. It is considered that these are significant losses for the regeneration of these plant populations, particularly at such a critical life history stage. Areas burnt twice are completely dependent upon a residual seed bank remaining through both of the earlier fires or, as mentioned previously, surviving adults in fire refugia. The long-term effect of successive fires on the study species requires further research.

Although it is understood that management action should not be based on a single species approach, management considerations for *L. exolasius* should include a minimum inter-fire period. Taking a precautionary approach, it is suggested that the inter-fire interval in habitat containing *L. exolasius* should be greater than 10 years. This interval is also considered as appropriate for a large number of other species within the community.

Prescribed burning is carried out in cooler seasons and in a controlled manner. As a result prescribed fires are of a lower intensity than wildfire. Low intensity, high frequency fire regimes can cause declines in vegetation community types like those studied here (Keith 1996). It is unlikely that increasing the frequency of prescribed

burning would maintain population levels of the obligate seeding study species. A number of studies have shown that other obligate seeding woody shrubs in south-eastern Australia have declined or become locally extinct after increased fire frequency including *Banksia ericifolia*, *Allocasuarina distyla*, *Petrophile pulchella*, *Pomaderris aspera*, *Eucalyptus regnans* and *Hakea teretifolia* (Siddiqi *et al.* 1976, Ashton 1981; Bradstock and O'Connell 1988; Bradstock *et al.* 1997).

It is also considered that, where possible, hazard reduction burning should not be conducted during the late autumn/winter period in these habitats. Burning during this period is likely to cause the longest delay to the onset of seedling emergence. Although the impact of increasing the delay to emergence is unknown, it is quite possible that a longer delay would put the species at a greater competitive disadvantage.

5.6 Future research

The research undertaken here has increased understanding of the ecology of *Leucopogon* species in south-eastern Australia. It has also created a number of additional questions that should be addressed in future research.

(1) How does delayed emergence impact upon subsequent recruitment?

The magnitude of difference in the time till emergence can vary as a result of the season of fire and subsequent lag time to the next germination season. In this study the delay ranged from two to 12 months, and *Leucopogon* emergence was behind that of other species post-fire. However, it is unknown whether or not this delay disadvantages the species. Future research could be conducted on the relative recruitment success of delayed emergents to confirm any disadvantage in this area.

(2) What requirements are necessary to break seed dormancy?

Failure to germinate and/or recruit in sufficient numbers could cause species decline or even local extinction. The post-fire flush of seedling emergence recorded in this study indicated that dormancy breaking cues are related to fire. Further study is required, however, to find out which elements of fire these are. The seasonal emergence patterns found in this study, combined with a post-fire germination

flush, also suggest that dormancy breaking cues in these species are complex. Specific seasonal conditions may be necessary for optimal levels of germination and these may or may not differ with geographical distribution.

Further investigation is also required to ascertain whether seed viability is low. Reports from other studies show that viability varies markedly between different *Leucopogon* species (e.g. Bell *et al.* 1995, Roche *et al.* 1997).

(3) How resilient is the seed bank?

Seed bank resilience is dependent upon a number of variables. In the absence of fire, these include the longevity of seed viability and losses over time to germination. Persistence post-fire is dependent upon fire variables, including intensity, and possibly season. Knowledge of the resilience of a seed bank can help determine the species ability to persist, as well as provide crucial information for species management.

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