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Comparative ecology of rare and common species in a fire-prone system

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

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by

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Certification

I, Mark Ooi, declare that this thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the School 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

30th May 2007

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Abstract

Due to escalating rates of extinction around the world, it is important to focus research and management on those species most at risk. Factors such as climate change and human population growth are also placing increasing pressure on species that are currently more common and widespread. Understanding the ecology of common species as well as those species that are already threatened is therefore central to conservation biology. In particular, studies targeting species for which little or nothing is currently known can increase our general ecological knowledge and also help to identify species with critical life history traits that could be limiting under future environmental scenarios.

The Ericaceae family in Australia (formerly Epacridaceae) is an example of one such group of species. Our current understanding of the ecology of the Ericaceae in this region is poor, even though species within this family make up a significant proportion of the understorey in temperate, fire-prone plant communities. To address this gap in our knowledge, I selected several obligate-seeding shrub species within the genus *Leucopogon* (Ericaceae) as the focus for this study in south-eastern Australia. Obligate-seeding species such as these, with soil-stored seed banks, have been the subject of far fewer studies than their counterparts that resprout or have canopy-stored seed banks. I used a demographic approach, aimed at providing fundamental ecological data for a rare species, *Leucopogon exolasius*, and some common and more widespread congeneric taxa, in order to explore processes that potentially limit their relative abundance.

Plants of obligate-seeding species are killed by fire, so persistence of populations is dependent primarily on regeneration from stored seed. Fundamental to understanding any aspect of seed ecology is being able to determine whether a seed is viable and dormant or inviable. Taking this primary step in this study was complicated by the fact that the adequacy of the most common method used for checking seed viability, the tetrazolium test, is hard to assess for difficult to germinate species such as *Leucopogon*, and there are no data assessing its applicability for most Australian species. I therefore compared the results of the tetrazolium test with a simple cut test. When estimating the proportion of viable seeds, a strong correlation was found between the two methods for the three species of *Leucopogon* used ($r > 0.9$). The cut test and tetrazolium test both also produced good estimates of viability of seed lots when compared to germination potential of non-dormant seeds retrieved from burial. The results not only supported the use of the less laborious cut test as a reliable method for estimating seed viability throughout this study, but also provided information to assist the accuracy and applicability of the tetrazolium method, previously unavailable for this group of native Australian species.

Dormancy-breaking cues for species within the genus *Leucopogon* are poorly understood and appear to be complex, with laboratory studies often resulting in little or no germination. Due to the difficulties experienced in germinating *Leucopogon* in other studies, I initially established dormancy class in order to identify the mechanisms responsible for controlling dormancy of the three study species. Assessment of seed morphology and preliminary laboratory germination experiments led me to classify the primary dormancy of *L. exolasius*, *L. setiger* and *L. esquamatus* as morphophysiological. Further germination trials revealed that seasonal temperatures overcame primary dormancy and controlled the timing of germination, as has been found for other species with a physiological dormancy component. Despite the fact that the study species display a flush of post-fire seedling emergence in the field, fire cues did not break primary dormancy. Once seasonal temperatures overcame primary dormancy, however, there was a trend for smoke to enhance germination. Knowing if fire is responsible for breaking dormancy, or whether it simply enhances levels of post-fire germination for seeds in which dormancy has been overcome by other factors, is important for a greater understanding of plant population dynamics.

Dormancy had not previously been classified for any species from this fire-prone region, and it was unknown whether physiological dormancy was a common trait, or perhaps a potential cause of rarity. It was also unknown whether a lack of response by *Leucopogon* seeds to fire cues was particular to these species, or a consequence of physiological dormancy mechanisms generally. To investigate this, I estimated the relative proportions of dormancy types for shrub species which occurred in fire-prone habitats in south-eastern Australia. I also assessed the literature for evidence of the effects of fire cues on species with a physiological dormancy component. Representatives of all dormancy classes were found to occur in the region, in proportions similar to that estimated for other fire-prone regions around the world. Over 50% of shrub species had a physiological dormancy component, whilst over 40% had physical dormancy. Additionally, when the assessment was confined to threatened species, the relative proportion of physiologically dormant species represented increased, indicating that dormancy type plays a role in determining rarity. Seasonal temperatures, not fire cues, were the main factors that broke physiologically related dormancy mechanisms. Physiological factors, and therefore seasonal temperatures, are likely to be important in controlling the dormancy and patterns of post-fire germination of many species in fire-prone regions.

Obligate-seeding species are dependent on recruitment from the seed bank for populations to recover after fire. Longevity of seeds stored in the soil is therefore a particularly critical life history trait of the study species. Two points were addressed in this part of the study. Firstly, I estimated the relative seed bank longevities of the *L. exolasius, L. setiger* and *L. esquamatus*. A short-lived seed bank in relation to typical fire return intervals for the region would indicate this as a cause of species rarity. Secondly, I wanted to determine whether primary dormancy was required for seed bank persistence, and whether the distinction between dormancy and persistence affects our understanding of seed bank dynamics in fire-prone regions. Using *in situ* seed burial trials, I found that all three species had persistent seed banks, with estimated half-lives between 3.5 and 5.5 years. Laboratory germination trials and embryo measurements of retrieved seeds showed that primary dormancy was broken during the first year of burial, and I concluded that specific requirements were therefore needed for germination. These results supported the findings from the previous germination Chapter, and supported the conclusion that fire cues that are observed to promote germination *in situ* are not necessarily the ones that break dormancy. Most studies in fire-prone regions have failed to distinguish between these two factors, with attention subsequently diverted away from mechanisms actually controlling dormancy and seed bank dynamics.

Realising the potential importance of seasonal germination cues highlighted by previous Chapters, I formulated the hypothesis that seasonal emergence patterns are more likely for species with a physiological dormancy component than their physically dormant counterparts. In regions like south-eastern Australia, which has no distinct rainfall season, seasonal germination could delay post-fire seedling emergence, and subsequently hinder recruitment, depending on the timing of the fire event. I therefore assessed the impact of seasonally delayed emergence and fire season on recruitment success of the three study species, and ascertained how vulnerable they are to changes to fire season. Post-fire seedling survival and growth were measured after the same fire event, comparing the physiologically dormant *Leucopogon* species (displaying seasonal emergence) with physically dormant or “hard-seeded” species (displaying season-independent emergence). I found that *Leucopogon* emergence was delayed compared to physically dormant species and, as a consequence, both survival and growth were significantly reduced. Intra-specific comparisons of *Leucopogon* species after winter and summer fires, indicated that seasonal germination requirements delayed seedling emergence by 12 months after winter fires, in relation to other co-occurring species, and by 3 to 6 months after summer fires. Seedlings emerging after summer fires grew and matured more quickly than those emerging after winter fires. Because species with physically dormant seeds have quick emergence tied closely to fire, whereas the speed of emergence of physiologically dormant species is dependent on fire season, I concluded that fire might not have been the primary force selecting for physiologically dormant species. Season of fire could strongly influence the persistence of the study species, and other seasonally emerging species.

The final aim of this study was to assess any potential causes of rarity In addition to the fundamental ecological data already collected for several key life history traits, data on fecundity, dispersal mechanisms and seedling survival and growth were also analysed and used in a comparative assessment, to establish whether there were any plausible causes of rarity of *L. exolasius*. Compared to the two common congeners, *L. setiger* and *L. esquamatus*, as well as to other obligate-seeding species in the region, *L. exolasius* had a markedly longer primary juvenile period. This raises the likelihood that short inter-fire intervals cause local extinction of populations of this species by killing plants prior to maturation and seed bank replenishment. Seasonal emergence, identified during the analyses of physiological dormancy mechanisms, also had the potential to increase the length of the maturation period. Local extinction of the Emu, a large bird and primary long distance dispersal mechanism for fleshy-fruited species, may have limited opportunities for range expansion and recolonisation.

The investigation of critical life history stages during this study has led to the conclusion that *L. exolasius* persistence appears to be bound to fire frequency. More surprising, however, is the finding that fire season could potentially influence persistence considerably, not only of *L. exolasius*, but of a large proportion of species with physiological dormancy that occur in fire-prone regions. Consequently, the ability of *L. exolasius*, and many other species, to persist in the future would be compromised by changes to the fire regime. The impacts of implemented fires and the effects of climate change are both forecast to promote higher fire frequency and cause changes to peak fire season. These changes could represent significant threats to *L. exolasius* populations, as well as to many other obligate-seeding species in the region with long primary juvenile periods and physiological dormancy. Further research into the effects of seasonal dormancy and germination requirements, particularly in relation to fire season, could help to gain a greater understanding of plant population dynamics and persistence in fire-prone regions. A greater understanding of dormancy mechanisms generally in fire-prone regions could also shed further light onto questions such as the evolution of species in relation to fire.

Acknowledgements

If I were to be completely honest about this PhD, I'd have to say that it has been somewhat of a marathon experience. In fact, in terms of an athletics event, I think a PhD in plant ecology would have to resemble something like the slightly obscure steeplechase, although with less water jumps. It might not be the most popular event on the calendar, but there is a small and passionate support base urging you on from the stands. It can be a lonesome pursuit, with lots of hurdles to negotiate, and it feels like the end is a very, very long way away. But (and I'm determined to take this metaphor all the way to its absolute limit), there's a grand prize at the end which is, hopefully, a trophy cup full of knowledge, as well as fledgling expertise, a couple of publications, new-found friends, a greater understanding of how some parts of this world work, unlimited job prospects, fame, fortune, a new car, smiling people staring at you as you walk down the street, calling out your name and beckoning you into their homes to offer you coffee, cake and a cuddle on the couch. Hopefully. Overall, I think I'm just trying to say that this sometimes difficult experience has felt very worthwhile in the long run. And when I think about the support I've received to get to this point of my education, career and life, I feel very grateful indeed. Tony Auld and Rob Whelan cannot be thanked enough for their ever-helpful encouragement and wisdom. I think that when I first met both of them, I was a much younger, somewhat travel- and surf-addicted person, dressed in boardshorts and a torn t-shirt. How they ever saw potential in me I'll never know, but their supervision has played no small part in helping me along life's path. There has been a lot of intellectual input, in varying shapes and sizes, that has helped brew some of the ideas presented in this study. This input has come in the form of discussions, comments, hallway chats and ponderings over cups of coffee, from many colleagues, friends and ecologists that pass in the night, including Jack Baker, Andrew Denham, David Keith, Belinda Kenny, Todd Minchinton, Charles Morris, John Porter, Mark Tozer, and several folk who remain anonymous in the world of journal referees. Financial support from an Australian Research Council APAI Scholarship made all of this possible. Indispensable practical help was provided in one way or another by Emilie-Jane Ems, Barbara Rice, Mark Robinson, Paul Thomas, Mark Westoby (all who provided access to seed collections), Amelia Martyn from the NSW Seedbank (Mt. Annan Botanic Garden, Botanic Gardens Trust, Sydney), and Natasha

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