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Anya Lam

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Invasion of indigenous vegetation in south western Australia by

*Leptospermum laevigatum* (Gaertn.) F. Muell. (Myrtaceae)

Anya Lam

A Thesis submitted in the partial fulfilment of the requirements for the award of

Bachelor of Science (Environmental Management) Honours at the School of Natural Sciences, Edith Cowan University, Joondalup.

Date of submission: 20 May 2002

Supervisor: Dr. Eddie van Etten

Cover photograph courtesy of the South African Museum
USE OF THESIS

The Use of Thesis statement is not included in this version of the thesis.
ABSTRACT

The current paradigm of biodiversity conservation requires the assessment of alien plant invaders, and their potential negative impacts on indigenous species and communities. *Leptospermum laevigatum* (Gaertn.) F. Muell. (Victorian tea tree/Coast tea tree) is indigenous to eastern Australia. It has invaded ecosystems within its natural biogeographic range, within new ranges in Australia and overseas. The species is listed as a high priority weed in the Environmental Weed Strategy for Western Australia. However, the basis for its listing has been casual observation rather than focussed research.

This study of *L. laevigatum* is unique in being the first to create a comprehensive synthesis of the ecology and management of *L. laevigatum* in Australia, combining scientific investigation with information from land managers in eastern and Western Australia. The study combined experiments and vegetation sampling with information from researchers, council staff and bush regenerators to provide baseline data about the species' ecology and phytogeography in Western Australia. Sites were chosen where *L. laevigatum* appeared to be invading remnant vegetation; at these sites morphological and life history characteristics of *L. laevigatum* were assessed. Soil and plant litter variables and floristics were examined, comparing invaded areas with the indigenous vegetation. Predation rates and seed viability were also investigated.

The results of the study show that *L. laevigatum* is able to occur on a variety of soil types in the southern part of Western Australia; its distribution is apparently restricted to areas with approximately 400mm average annual rainfall. The species is spreading regionally and locally in Western Australia, with long distance dispersal probably effected by road vehicles. *L. laevigatum* is able to invade bushland in good condition with minimal disturbance and of high conservation value.

Fire is identified as a major factor in enhancing invasion by *L. laevigatum*. Where fire occurs and a seed source is adjacent, resultant recruitment appears to be immense, resulting in high density thickets of *L. laevigatum*. Such thickets are subject to intense intraspecific competition and density dependent mortality. Within thickets, survivorship of indigenous species appears to be low in general, yet some indigenous species are able to co-exist: usually those with a life form substantially different from *L. laevigatum*. 
Through chronosequence analysis, three hypotheses about *L. laevigatum*’s impacts on vegetation have been generated: (1) *L. laevigatum* enhances levels of leaf litter underneath its canopy, leading to differential recruitment by other species and alterations in community composition; (2) increases in litter result in increased soil moisture, thereby favouring mesophyte establishment; and (3) where dense canopies of *L. laevigatum* form, *L. laevigatum* homogenises photosynthetically active radiation over a large area, thereby reducing the variability in microsites with respect to light conditions. Photophilic species are repressed.

Investigations of the biology of the species have allowed recommendations to be made about current and potential control strategies. Tree injection with herbicide leaving the dead plant in place is the least invasive method in sensitive vegetation communities. Despite which method is used, site revisits are required within approximately four years of the first control program, to remove regenerating seedlings.
DECLARATION

I certify that this thesis does not, to the best of my knowledge and belief: incorporate without acknowledgement any material previously submitted for a degree or diploma in any institution of higher education; contain any material previously published or written by another person except where due reference is made in the text; or contain any defamatory material.
ACKNOWLEDGEMENTS

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Thankyou to the people who have supported and inspired me, my dedicated family and friends:

To Keelah for her determination, to Ah-Lek for his quiet wisdom, to Sa for singing, to Gaz for his gentle smiles, to Nin for dancing, to Nik my big brother, and to Dave for his arrows. To the awesome chicks, Kazzie, Amo and Jo. To Karl, Renee and Travis for the barbies, and to Crow and Krusty for the laughs.

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CHAPTER 1: INTRODUCTION

1.1 BIOLOGICAL INVASIONS AND BIODIVERSITY CONSERVATION

The impetus to conserve the Earth's biological diversity (biodiversity) is a pervasive paradigm in political and ecological thought today. The recognition that humans rely on ecosystem services and products for our survival is a common anthropocentric argument for biodiversity conservation. Additionally, there are economic arguments for biodiversity conservation and moral arguments concerning the intrinsic values and rights to existence of all organisms on the planet. The 1993 Convention on Biological Diversity embodies these recognitions; it is the global commitment of over 150 nations to conserve and share biological resources (Glowka et al. 1994).

The various threats to biodiversity stem mainly from the enormous impacts of a single animal species: *Homo sapiens*. The prime threats are habitat loss and fragmentation, overharvesting of resources, pollution, global change and invasion by alien (non-indigenous) species (Heywood and Baste 1995); the latter has been recognised as second only to habitat loss in terms of its potential negative impacts on biodiversity (ISSG 2002). Duly, Article 8(h) of the Convention on Biological diversity requires its signatories to "prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species." The World Conservation Union (IUCN) has established the Invasive Species Specialist Group, to provide information control/eradication methods for invasive alien species, focussing on invasive species which threaten biodiversity (IUCN 2001).

Although biological invasions have occurred for eons in the absence of humans, human behaviour and changing social structures have led to massive increases in the rates and volumes of organisms moving around the globe (Elton 1958). Previously, organisms reached new destinations via ocean currents, winds, hitchhiking on or in other organisms, or active dispersal across barriers that had disappeared or were no longer effective (Vermej 1996). Prior to the era of European colonisation, indigenous people were translocating organisms across the seas in local trade. For instance, tamarind trees (*Tamarindus indica*) have been planted widely in many areas of northern Australia visited by Macassan trepang fishers (Woinarski et al. 2000). Yet during European colonial and post-colonial history there has been a vast and growing number of invasive introduced organisms, which have
deleterious effects on human health, economics and ecological systems (di Castri 1989; D'Antonio 1997; Mack and Lonsdale 2001).

Environmental weeds are a category of these invasive organisms; they are plant invaders which have substantial impacts on natural ecosystems. They can be aliens from overseas, from other habitats in the same country, from adjacent habitats, yet can include ecologically "out of balance" (sensu Carr 1993) indigenous species, where indigenous populations have escalated in response to human disturbance of ecosystems.

Translocations of organisms by people have been both accidental and intentional (Mack et al. 2000). Plantago major (a plant notoriously commensal with agricultural practises) was identified by Native Americans as "Englishman's foot", because of its pervasive presence wherever the colonists had been (Cronon 1983, in Mack and Lonsdale 2001). Intentionally, organisms have been introduced for either utilitarian or aesthetic purposes (Mack and Lonsdale 2001); it is deliberate introductions which have led to the largest number of unwanted plant species (Panetta 1993). Most translocated species do not survive past the first generation without intervention, fewer naturalise (form viable, self-sustaining populations) and even fewer become problem species (Elton 1958; Lodge 1993; Williamson 1996; Mack et al. 2000). Notwithstanding this, so many organisms are now establishing outside of their natural ranges that several researchers have sarcastically coined the term "the Homogocene" to describe the new epoch of homogenised global biota (ISSG 2001; Low 2001).

Despite the recognition of the role of humans in the establishment of unwanted organisms around the globe, and despite attempts to prevent these introductions, it is well accepted that new species will continue to appear in new places because of the current international drive towards freer trade (Elton 1958; Jenkins 1996; Low 1999; Rauber 2000; Campbell 2001; McNeely 2001).

1.2 INVASION THEORY

The study of biological invasions allows insight into how species interact and how ecological communities function (Lodge 1993; Vermeji 1996). Significant ecological theories have been developed through observations of new habitats being colonised, including the Theory of Island Biogeography (Macarthur and Wilson 1967) and the Intermediate Disturbance Hypothesis (Connell 1978). Since Charles Elton's (1958)
milestone book "The Ecology of Invasions by Animals and Plants", ecologists have attempted to find out more about invading species and invaded ecosystems, and why some introductions lead to invasions whilst others do not. The influential notions which have shaped community ecology and invasion biology are summarised here (focussing on plant invaders); more thorough accounts, with suggestions on future directions are available elsewhere (e.g., Rejmanek 1989; Hobbs and Huenneke 1992; Lonsdale 1999; Mack et al. 2000).

1.2.1 Attributes of invaded communities

A common reason for the proliferation of some alien plants is an escape from biotic population constraints present in the natural habitat. Aside from this, three main hypotheses about the attributes of invaded communities are based on the notion of niche overlap and competition (sensu Pianka 1974).

(1) Disturbance and invasion

Fox and Fox (1986) have stated that there is no invasion without disturbance. The notion is based on the idea that species niches are packed tightly into communities, and resources fully exploited. Therefore, the establishment of an invader would only be possible in the event of some disturbance which would create spare resource by either amplifying the resource base (as soil nutrients are increased after fires), or shifting the resource base (for instance, an altered fire regime). There are fewer plant than animal species able to invade habitats undisturbed by humans (Rejmanek 1989). Simberloff (1989) argues that disturbance does not necessarily lead to invasion; the disturbed habitats most likely to be studied are those close to human habitation, which increases their chance of receiving species introductions.

Because all vegetation communities undergo some natural disturbance regime, in more recent years, the question has become focussed on the types of disturbance and the disturbance interval (Hobbs and Huenneke 1992). Despite these confounding factors, novel disturbances or disturbance intensification have promoted some major plant invasions (Mack et al. 2000). As a general rule, disturbance promotes plant invasions.
A key concept in ecology, since it was first proposed by Elton (1958), is that the more species-rich a community, the less susceptible it is to invasion. Large numbers of species are able to fully use all of the available resources and niche spaces, leaving less opportunity for invaders. Support has been in the form of repeated negative correlations between these two factors (e.g., Fox and Fox 1986). However more recently the opposite relationship has been found (Lonsdale 1999). Lonsdale (1999) attributes this to the positive response of both indigenous and invasive plants to greater habitat diversity.

The existence of an empty niche in a community has been suggested to provide opportunities for new species to invade. A possible example is the prevalence of South African cormous and bulbous plant species (Hyacinthaceae and Iridaceae) which are naturalised in Western Australian bushland (Brown et al. 2002), where geophytes such as Orchidaceae and Liliaceae are relatively rare. Blackshall and Bridgewater (1981) have noted different strategies of invading species from that of the Perth flora. Elsewhere (e.g., Shimzu and Tabata 1985; Pheloung 2001) there has been support for this theory, yet unambiguous demonstration has proven difficult (Mack et al. 2000).

There are some plant species which have been introduced repeatedly around the globe, yet have not naturalised or become invasive, whilst others which have almost consistently naturalised and become pests. Such observations have sparked inquiry about whether invading plants can be defined by specific traits which make them invasive (Mack et al. 2000). Baker (1965; 1974) attempted to define the characteristics of an ideal weed. He defined a list of fourteen attributes (e.g., early reproductive maturity, the ability to seed copiously and in a wide range of environmental conditions, germination generalist). Yet the possession of a single one or a mix of these attributes does not necessarily mean that a species will be a successful invader (Baker 1965; Baker 1974; Newsome and Noble 1986).

Since then, other researchers have attempted to identify the common traits of weeds, usually with limited success (Mack et al. 2000). In contrast, some recent attempts have yielded some relatively robust generalisations about the characteristics of woody weeds.
(Rejmanek and Richardson 1996; Reichard and Hamilton 1997). However, the inconsistencies and exceptions to these generalisations about invaders and invaded communities mean that they can only predict the likelihood of invasion; they are not infallible (Lodge 1993).

1.3 DIRECTIONS IN RESEARCH

Researchers have argued that autecological research on invading plants, rather than on the ecosystem as a whole is inadequate to tackle the scale of the problem of environmental weeds (Hobbs and Humphries 1995; Woods 1997). Others have noted that the widespread approach to the study of invasive plants requires experimental work, not just descriptive studies, to provide adequate data to assess cause and effect of the impacts of invading species (Morrison 1997; Edwards 1998). A more holistic approach is emerging, with plant invasions seen in the context of global change (e.g., Lodge 1993; Huenneke 1997; Mooney and Hobbs 2000). Within these accounts, plant invasions are seen as one of the agents of global change, on the same scale as global warming and land cover change (sensu Vitousek 1994).

The different types of invading plants in different ecosystems, the effects of various anthropogenic disturbance types (including altered disturbance regimes) and the various aspects of global change (see Vitousek 1994) create complexities in dealing with plant invasions. It appears that the most constructive approach is to address invaded ecosystems in a site-specific way, considering the intrinsic attributes of the invader and the invaded community, in the context of global change (Hobbs and Humphries 1995; Edwards 1998).

1.4 WEED RISK ASSESSMENT

Weed risk assessment develops frameworks by which invaders and potential invaders can be identified, and their ranges and impacts predicted. The objective is to predict which species are likely to become invasive, therefore allowing invasions to be prevented. The uncertainty of predictions about invading plants and their impacts is a consistent theme in the more recent literature (Lodge 1993; Woods 1997; Mack et al. 2000; Reichard 2001). Despite much effort to find empirical methods of prediction through studying species and communities, the most reliable ways to predict whether or not a species will become invasive is by stochastic and extrapolation approaches (Reichard 2001; Rejmanek 2001). The most robust predictive generalisation has been that the probability of a plant species
becoming naturalised increases with increasing initial populations, numbers of introductions and residence times (Rejmanek 2001). The latter relates to the concept of "sleepers": plants which appear benign for periods of time before their populations explode (Low 2002). Secondly, the knowledge that a species is invasive elsewhere is a good indication that it may become invasive in new places; and data from the invaded region can be used to gather information about its ecological and economic impacts (Rejmanek 2001). A summary of predictive tools emerging from ecological studies is given by Rejmanek (2001).

1.5 WEED MANAGEMENT AND POLICY IN AUSTRALIA

The Australian Quarantine and Inspection Service (AQIS) is the national agency which regulates the entry of non-indigenous species into Australia. The goal is to prevent the entry of potentially invasive plant species, whilst allowing entry of species which pose a minimal threat. The Australian approach to quarantine assessments of invasive plants has changed substantially in the previous 5 years (Walton 2001). The shift has been from a "prohibited" list of plants which had proven invasive, to a "permitted" list of species which have been assessed and are considered safe. The former strategy allows in plants that have not proven invasive; in other words, "innocent until proven guilty". The latter is more precautionary; plants on the permitted list are allowed entry; those that are not are assessed for "weediness", and a decision made to put them on the permitted list or to prohibit entry (Walton 2001). The weed risk assessment system is a question-based scoring system with up to 49 questions, with all plants (whether potential environmental or agricultural weeds) subject to the same evaluation. The score is used to determine three outcomes: accept, reject or further evaluate (Pheloung 2001; AQIS 2002). Testing of the system with known weeds and useful species showed that 100% of major weeds and 84% of minor weeds were rejected, and 74% of useful species were accepted. Reichard advocates the application of a similar permitted plants system for the USA (Reichard 1997; Reichard and Hamilton 1997). This method is more likely to prevent the introduction of invasive alien plants. However, the ability to detect sleepers is questionable.

The National Weeds Program is a Commonwealth Government initiative under the National Heritage Trust to reduce the impact of nationally significant weeds on the sustainability of agriculture and natural ecosystems. Funding is targeted towards the 20 Weeds of National Significance (WONS), which include agricultural and environmental
weeds (Environment Australia 2002). The National Weeds Strategy is a document endorsed by the Commonwealth, State and Territory Ministers for agriculture, forestry and the environment, which seeks to improve the co-ordinated effort on weed control in Australia (Environment Australia 2002).

The Environmental Weed Strategy for Western Australia (EWSWA: CALM 1999) provides an integrated system of management for environmental weeds, combining social, economic and technical approaches. It was funded through the National Weeds Program, and produced by the Western Australian Department of Conservation and Land Management (CALM). Five approaches are outlined, with their suitability dependent on the site or species priorities and the resources available. These include weed led control, site led control (an ecosystem approach), threatened species/community led control, cause led control (e.g., management of disturbance factors rather than the weed) and human resources led control. The latter recognises that volunteer and professional operators are likely to differ in their ability to perform different techniques of weed management. The system ranks weeds as high, moderate, mild or low risk, based on their invasiveness (ability to invade bushland in good condition), distribution and impacts on ecosystems.

1.6 AUSTRALIAN NATIVE PLANTS AS ENVIRONMENTAL WEEDS

In the early 1980s, relatively few Australian weeds were native plants (Groves and Cullen 1981, in Groves 2001). Since this time, the number of Australian plants recognised as environmental weeds has escalated immensely. For instance, in Victoria, there are approximately 200 recognised "native weeds" (Carr 2001); in Western Australia there are at least 60 (Keighery unpublished, in Low 2002).

Australian plants are most commonly invasive in Australian ecosystems when they are translocated substantial distances. Transcontinental invasions of vascular plants are well known between the southern parts of eastern and western Australia (Pigott 2001). For example, *Pittosporum undulata*um (Sweet Pittosporum), and at least seven *Acacia* (Wattle) species are among the eastern Australian plants recognised as invasive in south-western Australia (Keighery 1991; Mullett 2001). Plants indigenous to south-western Australia which are environmental weeds in eastern Australia include *Sollya heterophylla*, *Eucalyptus gomphocephala* (Carr and Yugovic 1989) and *Acacia saligna* (Tozer 1998).
These situations are said to be no different from invasions of exotic species (from overseas), since "Perth and Sydney stand as far apart as Portugal and Russia..." (p. 197, Low 2002). However, Australian plants have become invaders in the biogeographic regions to which they are indigenous also (Groves 2001), for example, Acacia sophorae (McMahon 1994). Leptospermum laevigatum (Victorian tea tree/Coast tea tree) is among this growing number of Australian native environmental weeds, invasive in both its own biogeographic range and new regions in Australia, including southern Western Australia.

1.7 THE STUDY SPECIES: Leptospermum laevigatum

*L. laevigatum* (Gaertn.) F.Muell. is a stout shrub to small tree, indigenous to the coastal dunes of NSW, eastern Victoria and northern Tasmania (Bennett 1994; Wrigley and Fagg 1996). Its profusion of white flowers and tolerance to frost and extended dry periods have made it a popular garden plant in Australia and overseas, where it has been promoted as an excellent windbreak especially against salty coastal winds (e.g. Summit 1980; Wrigley and Fagg 1996). Because of its hardiness, sand binding properties and ability to colonise disturbed habitats, it was commonly used for revegetation after mining or along road verges. However, translocations have frequently resulted in the invasion of non-target habitats. Overseas, it has naturalised in New Zealand (W. Shaw personal communication), California (Calflora 2002), Lana'i (Hawai'i) (Herbarium Pacificum Staff 1999) and South Africa, where it was introduced for dune stabilisation in the early 1800s (Richardson *et al.* 1992; Gordon 1999). In Australia, it has naturalised in South Australia (Kloot 1985), Queensland (Wrigley and Fagg 1996), western and non-coastal Victoria (Carr 1993) and the south of Western Australia (Keighery 1991). As well as naturalising in new biogeographic regions within Australia, in Victoria it has been documented as expanding its range into adjacent grasslands (Calder 1975; Bennett 1994), heathlands (Burrell 1981; Molnar *et al.* 1989) and woodlands (Hazard and Parsons 1977; Bennett 1994), at sites within its natural distribution.
Upon invasion, it commonly dominates areas, producing a thick, species-poor scrub whilst apparently eliminating and excluding indigenous species with its dense canopy (Burrell 1981; Molnar et al. 1989). In Western Australia, the variety of structures this species forms is wide: thickets can form from widely spaced but broad bushy shrubs, from tall, narrow trees spaced densely (Plate 1.1), or as impenetrable, interlocking scrub with horizontal branches.

Plate 1.1: Views of thickets of *L. laevigatum* near Ellensbrook Homestead, near Margaret River, Western Australia.

1.7.1 Current status

*L. laevigatum* has a broad geographic range within Western Australia, occurring in the Carnarvon, Yalgoo, Warren, Jarrah Forest, Swan Coastal Plain, Esperance, Avon Wheatbelt, Geraldton Sandplains and Mallee IBRAs (Interim Biogeographical Regionalisation of Australia) (CALM 1999). It has been recognised (Keighery 2001) as an aggressive coloniser of coastal and non-coastal sandy soils in the south of Western Australia, with the potential to become a major weed in this region. Its current range is expanding and in-filling (Keighery 2001). *L. laevigatum* is listed in EWSWA (CALM 1999) in the highest risk category, because it fulfils all of the three assessment criteria. These include the ability to invade bushland in good to excellent condition, a wide current or potential distribution and the ability to change the structure, composition and function of ecosystems (the ability to form a monoculture in a vegetation community). Its status prioritises funding for control and research for the weed.
1.7.2 Significance

This study is the first formal research on the species in Western Australia. *L. laevigatum* began to be widely recognised as naturalised in the early 1980s (J. Moore personal communication). Since this time, although awareness of and control programs for the species have escalated, there is little baseline data available to assist in decision making for management. For instance, there has been speculation on the longevity of the soil seed bank, on the presence of two subspecies in Western Australia and on the requirement for herbicide application to prevent coppicing when cut. Such information is essential to decide which management options will be most successful and efficient for its control.

Some key studies have addressed the species’ invasion ecology in Victoria (e.g. Hazard and Parsons 1977; Burrell 1981; Molnar *et al.* 1989; Bennett 1994); these studies are valuable for their insights into general biology and invasion requirements. However, considerable differences in climate, soils and vegetation between Victoria and Western Australia mean that this research may not be directly applicable to the situations encountered in the west. Additionally, at separate sites in Victoria *L. laevigatum* displays differences in seed storage strategies: serotiny (storage of a canopy seed bank for greater than one year), versus the lack of it. It is important to establish the variety of traits occurring within populations in Western Australia for management goals.

The basis of this species’ high risk rating in ESWA is the opportunistic observations of G. Keighery (a state weed expert from CALMScience). This study constitutes a verification and expansion of the basis for its listing. Of concern is the presumed threat *L. laevigatum* poses to the internationally renowned South West Botanical Province. The area is notable for its floristic richness and high degree of endemism (Burbidge 1960; Marchant 1973; Hobbs *et al.* 1995); Paczkowska and Chapman (2000) estimated over 5710 species in the Province, 79.2% of which are endemic to Western Australia. The high conservation value of this biologically diverse region warrants its protection. In particular, areas of heathland vegetation are considered to contribute most to both the species richness and high degree of endemism in the province (George *et al.* 1979), and it is these sandy soil communities which appear to be most in danger of invasion by *L. laevigatum*. Infestations are apparently spreading; individuals are often observed along road verges, possibly transported by vehicles (G. Keighery personal communication).
The threat to important indigenous ecosystems posed by this "native weed" has been recognised by both the community and government sectors with local volunteer groups working to control, and its removal from CALM land. There is substantial concern about *L. laevigatum* as an environmental weed in Australia, with initiations of co-operative research (between Victoria and Western Australia) on the potential for biocontrol of the species (Keighery 2001).

### 1.7.3 Aims

This study will provide information essential for efficient and effective management of *L. laevigatum* as an environmental weed in Western Australia. The project's aims were developed in response to requests for information from CALM, which provided travel support for a broad assessment of the species over its range. Two major objectives were to:

1. Contribute to risk assessment of the species, including its potential for spread and intensification, the likely impacts on indigenous plant communities, and the potential distribution of this environmental weed.

2. Provide insight into vital attributes which may be exploited in developing control strategies for the species.

To achieve this, several methods of inquiry were used. Firstly, sites supporting *L. laevigatum* incursions into bushland in good condition were assessed in detail for floristics, vegetation structure and soil and litter variables. Secondly, manipulative experiments and monitoring were performed to detect the limiting factors in recruitment of *L. laevigatum*. Thirdly, land managers with experience in *L. laevigatum* control were contacted, and their knowledge and observations integrated with the data, and with information from the literature.

Time constraints lead to the main limitations in the research. Assessment of plant invasions ideally requires long-term monitoring over years or decades; time which is unavailable for Honours research. Additionally, as the project is intended to provide baseline data on the species in Western Australia, importance has been assigned to gathering data on the species over as much of its range as possible, rather than to the details of invasion at a specific site.
The thesis is divided into seven Chapters. In Chapter 1, the study is placed in the context of biological invasions, and their threat to biodiversity conservation. Chapter 2 provides information on the climate, soils, vegetation and land use histories of the sites which were assessed in detail in this study. Chapter 3 provides information on the life history of *L. laevigatum*, in the context of the Western Australian landscape and climate. It provides a basis for the understanding of the concepts in the thesis, yet also provides information which will assist in decision making for management of the species. In Chapter 4, the current distribution patterns of *L. laevigatum* at a variety of spatial scales are detailed. Predictions of potential range are included. Chapter 5 examines the interactions of *L. laevigatum* with indigenous vegetation upon invasion, with the objective of providing hypotheses about mechanisms of presumed impacts on vegetation. Chapter 6 assesses current and potential management options for the species, providing recommendations for management decisions. A synthesis of the project is the focus of Chapter 7, in the context of the social aspects of management of invasive species.
CHAPTER 2: STUDY AREAS

The importance of this study lies in the assessment of the ecology of *L. laevigatum* in a wide range of situations in Western Australia. The plant grows in a variety of vegetation structures over a considerable geographic range. Being the first study of the species in Western Australia, determining the variation in the species' ecology over its range was deemed more important than precisely examining its ecological characteristics at a single site.

Sampling, observations and experimental work occurred at sites in the Perth metropolitan area and the south-west of the state (Figure 2.1). Vegetation sampling in native vegetation occurred at Ellensbrook, Shoalwater and Yanchep. Sites chosen carried different structural attributes, different species and varying disturbance regimes, types and intensities (Table 2.1). Sampling to assess management strategies occurred at Ellensbrook and Little Grove. Manipulative experiments to assess predation on reproductive structures of *L. laevigatum* occurred at Catherine Point. These sites and their land use histories are described in this Chapter.

![Figure 2.1: Location of study sites in (A) southern Western Australia and (B) Australia.](image-url)
Casual observations of other infestations were made at Henderson Open Space (Beeliar Regional Park), Woodman Point Regional Park, and several infestations on areas of Crown land along Cockburn Rd; all located south of Fremantle. Various sites in the Albany and Denmark regions were also observed.

Table 2.1: Summary of characteristics of the three main study sites. Vegetation structural classification is consistent with Beard (1990).

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ellensbrook</td>
</tr>
<tr>
<td>Structural classification</td>
<td>Low woodland</td>
</tr>
<tr>
<td>Dominant overstorey</td>
<td>Agonis flexuosa, Dryandra</td>
</tr>
<tr>
<td>species</td>
<td>sessilis var. cordata,</td>
</tr>
<tr>
<td></td>
<td>Spyridium globulosum</td>
</tr>
<tr>
<td>Other common species</td>
<td>Hibbertia hypericoides,</td>
</tr>
<tr>
<td></td>
<td>H. cuneiformis, Macrozania</td>
</tr>
<tr>
<td></td>
<td>riedleri, Olearia axillaris,</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil type</td>
<td>Sand over gneiss</td>
</tr>
<tr>
<td>Rabbits?</td>
<td>Yes</td>
</tr>
<tr>
<td>Kangaroos?</td>
<td>Yes</td>
</tr>
<tr>
<td>Road edge?</td>
<td>No</td>
</tr>
<tr>
<td>Cleared?</td>
<td>No</td>
</tr>
<tr>
<td>Common alien species</td>
<td>Zantedeschia aethiopica,</td>
</tr>
<tr>
<td></td>
<td>Anagallis arvensis, Brita</td>
</tr>
<tr>
<td></td>
<td>maxima, Asparagus</td>
</tr>
<tr>
<td></td>
<td>asparagoideis</td>
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</tbody>
</table>

14
2.1 ELLENSBOOIK

2.1.1 General site description

Ellensbrook Homestead is located in Leeuwin-Naturaliste National Park, near Margaret River, Western Australia (114°59' E, 33°55' S). The climate is Mediterranean, with mean annual rainfall of between 830 and 990mm falling predominantly in winter. Based on data from Cape Naturaliste and Cape Leeuwin, estimated mean monthly temperatures range from 10°C in August to 25°C in February (BOM 2002). The dominant geomorphological feature in the Ellensbrook region is the Leeuwin-Naturaliste Ridge, an undulating surface rising up to 200m above sea level, (CALM 1989). The soils are granite and granitic gneiss overlain by limestone and sand (WASG 2001).

*L. laevigatum* was introduced to the Homestead site in approximately 1951. It has since expanded north of the Homestead, into an area of approximately 1ha which was originally cleared for grazing dairy cattle in 1857 when the Homestead was established (Richards 1992). Richards (1992) notes that this extremely dense *L. laevigatum* thicket (which is now up to 8.5m tall) has become dominant since the late 1970s. The thicket ('Ellensbrook thicket') is one of three sites in which vegetation sampling occurred at Ellensbrook. A comparative study site, from which *L. laevigatum* thicket had been removed by chainsawing, lies to the north of the thicket, in the visitors' carpark ('Ellensbrook chainsawed').

To the north-east, scattered *Dryandra sessilis* var. *cordata*, a P2 taxon\(^1\), begins to appear in the *L. laevigatum* thicket and its density increases with distance away from the Homestead. Approximately 100m north-east of the Homestead, a dune blow-out of approximately 3ha has developed which has been colonised by sparse shrubs of *L. laevigatum* and *D. sessilis* var. *cordata* (Figure 2.2A). The blow-out is defined by a steep north-south dune ridge, which is unvegetated on the western side, but supports a mix of these *L. laevigatum*, *D. sessilis*,

\(^1\) Priority 2 species, as rated by CALM. The classification indicates the priority for undertaking further surveys based on the number of known sites, and the degree of threat to those populations. P2 is the second highest priority.
sessilis var. cordata and Agonis flexuosa. On the eastern side, the ridge flattens to a plateau of approximately 1.5ha. This plateau is the main Ellensbrook study site ('Ellensbrook').

2.1.2 Ellensbrook study site

The vegetation on the plateau is woodland dominated by A. flexuosa and D. sessilis, with an understorey of mainly Hibbertia hypericoides, H. cuneiformes, Macrozamia reidii, Leucopogon parviflorus and Olearia axillaris. In contrast with the degraded vegetation on the western side of the dune blow-out, the vegetation is in good condition. A drainage line runs southwards down-slope in the direction of Ellens Brook, recognised by the presence of mesic species such as Dichondra repens and Zantedeschia aethiopica. L. laevigatum plants occur as scattered trees or small patches of shrubs. No walk trails are present, or other evidence of human presence (such as litter). The major exogenous disturbance appears to be rabbits (presence confirmed by diggings and faeces). Vegetation and soil disturbance by kangaroos was evident. Historical records indicate that the site has never been cleared (Boughton 1980; Richards 1992), and despite the presence of rabbits and L. laevigatum, the vegetation appears in good condition (Plate 2.1B). Dairy cattle were probably confined to paddocks near the homestead because of the requirement for daily milking. Therefore, it is unlikely that the bushland has been subject to cattle grazing, except for the possibility that cattle were occasionally driven through the bushland to other pastoral leases in the Margaret River region (Richards 1992).

A. B.

Plate 2.1: (A). Dune blow-out between Ellensbrook Homestead and study site, looking towards study site. (B). Study site on dune plateau at Ellensbrook, showing L. laevigatum invasion.
2.1.3 Land use history

In contrast, the land to the west of the dune blow-out has been subject to heavy disturbance and degradation since European settlement in 1857. By the 1920s, vegetation cover on the frontal dunes had deteriorated (possibly due to overgrazing), and resultant sand drift rendered paddocks to the north of the homestead no longer useful for grazing (Richards 1992). The property was abandoned (Murphy 2002); presumably cattle were removed, but between 1939 and 1948, a pastoralist running stock in the region grazed cattle on the land around Ellensbrook (Boughton 1980). Rabbits proliferated at this time. Marram grass (*Ammophila arenaria*) was planted on the dunes to the west of the Homestead block in 1940 to counter sand drift. Despite plans to do so (Terry 1997), it is unclear whether cattle were reintroduced to the property upon a change of ownership in 1950. However, a 1973 photograph (Williams 1973) shows several cattle in a fenced area near the homestead. Cattle have been absent from the landscape since at least 1978, when the Homestead and surrounding land became jointly managed by National Trust of Australia (Western Australia) and CALM (previously the National Parks Authority), as Ellensbrook Historical Conservation Zone (CALM 1989).

2.1.4 Fire regimes

Local Nyungars (the Wedandi people) used Mokidup (the Ellensbrook area) as a traditional summer camping ground, and burned the bush in summer (Collard 1994). Burns were sustained by European settlers in the 19th and 20th centuries (Richards 1992); fire frequency is now probably lower than in recent times (Richards 1992) In 1970 a wildfire burned the valley and surrounding hills, and destroyed parts of the homestead (Williams 1973). No records of fires (prescribed or wild) were found since this time.

2.2 SHOALWATER

Shoalwater Foreshore Reserve is a strip of low dunes 100 to 200m wide along Arcadia Drive, Shoalwater, south of Rockingham, Western Australia (115°43' E, 32°18' S). Average annual rainfall is approximately 770mm, mean monthly temperatures range from 10°C in August to 30°C in February (Kwinana data: BOM 2002). The study site lies immediately north of a beach access pathway opposite Coventry Road, which defines the northern boundary of the Mersey Point Reserve. Mersey Point Reserve is designated an A class reserve to complement the adjacent Shoalwater Islands Marine Park. Soils of the
study site are calcareous sands of the Quindalup dune system (calcium analysis; this study). The original high coastal dunes in the area were bulldozed and leveled in 1959 to provide ocean views and access to the sea for housing developments in Shoalwater Bay (Rippey and Dunlop 1999). The resulting structure at the study site is three irregular dunes and swales (of approximately 2m amplitude) which run parallel to the coast. Low open heathland has since re-established, dominated by wind-pruned shrubs of mainly *Alyxia buxifolia*, *Acacia rostellifera*, *Leptomeria preissiana*, *Spyridium globulosum*. The dunes support a large proportion of alien species; a 1988 survey of the adjacent Mersey Point Reserve found 76 species, of which 64.5% were alien (Rippey and Dunlop 1999). Dominant alien species are alien grasses (*Lolium rigidum*, *Avena fatua* and *Lagurus ovatus*) and *Pelargonium capitatum*. The vegetation is degraded.

*L. laevigatum* probably established in the dunes through deliberate plantings or the dumping of garden refuse. Several other garden plants are also naturalised, and garden dumping is identified as a contributing factor to weed problems in the Mersey Point Reserve (Rippey and Dunlop 1999). A single large *L. laevigatum* (up to 14.2m wide, trunk diameter 1.2m) occurs on the southern boundary of the study site and appears to have been a major source of seed, since numerous smaller individuals occur on the leeward side of this tree. Three thickets at the southern end of the study site grade into single individuals whose densities decline northwards away from the infestations.

Human access to the study site is deterred by a steep, uneven embankment adjoining the footpath on Arcadia Drive; no footprints or trails were observed in the reserve, however some rubbish was found underneath the *L. laevigatum* thicket. There was no recent evidence of rabbit presence, however a burrow was discovered (species unknown). Fire has apparently been suppressed in the reserve due to its proximity to residential development.

2.3 **YANCHEP**

The study site is located in Yanchep National Park, on the north-eastern side of Yanchep Beach Road between Wanneroo Road and the entrance to the National Park Recreation Area. The climate is subtropical with a distinctly dry summer and an average annual rainfall of 625mm, with mean monthly temperatures ranging from 10°C in August to 30°C in February (Lancelin data: BOM 2002). Soils are sands of the Spearwood dune system. Dense, spiky vegetation deters human access into the Park from the road edge, and no walk
trails are evident in the bushland. The vegetation is Banksia (B. attenuata and B. menziesii) low woodland, interspersed with tall (up to 3.5m) Xanthorrhoea preissii individuals. Ground layer species are typically Jacksonia sericea, Hibbertia hypericoides and Conosylis aculeata. Dryandra sessilis (to 1.8m tall) is common. Large numbers of dead and dying Acacia pulchella plants occur; presumably these are post-burn recruits reaching maximum age. J. sericea is also dead in patches, due to similar factors.

*L. laevigatum* has invaded the site from the road edge, where a dense thicket has formed, and appears to be spreading into the bushland. Yanchep National Park burned in intense fires which spread north eastwards from the coast from January 30, 1991, under extreme temperatures (45.8°C on 31/01/91) and strong south-westerly winds (Anon. 1991). Several *L. laevigatum* plants were present along the road edge prior to the fire, and *L. laevigatum* numbers increased substantially afterwards (A. Notley personal communication). The source of plants initially present along the road edge was presumably deliberate plantings, or seed spread by vehicles from the Yanchep townsite. Although the road edge is heavily infested by *L. laevigatum*, and alien grasses are common close to the road, vegetation further away from the road is almost completely free from invasion by alien species, and is in good condition.

### 2.4 LITTLE GROVE

Little Grove Foreshore Reserve is located on the south-eastern shore of Princess Royal Harbour, near Albany. The mean average annual rainfall is approximately 930mm, with mean monthly temperatures ranging from 8°C in July to 23°C in February (Albany data: BOM 2002). Soils are sandy, composed of shoreline deposits of Phanerozoic origin (MPR 2002). A dense infestation of *L. laevigatum* on the site burned in 1999, prompting efforts to clear the site of *L. laevigatum* and garbage. In 1999 remaining *L. laevigatum* in the north-western portion of the reserve were chainsawed (H. Kane personal communication).

Regeneration of indigenous species from the soil seed bank has been prolific since the removal of the thicket, including Pimelea ferruginea, Leucopogon puriflorus, L. obovatus, Sollya heterophylla, Anarthria scabra, Lepidosperma gladiatum and Isolepis sp.. Colonisation by alien species such as Sonchus aspa, Pelargonium capitatum and Avena barbata has also been prolific, as has been regeneration of *L. laevigatum*. The site is weeded weekly by volunteers (H. Kane personal communication. A monospecific *L. laevigatum* thicket remains intact in the south-eastern part of the reserve.
2.5 CATHERINE POINT RESERVE

The study site is a 150m wide strip of coastal dunes between the old South Fremantle power station and the coast. Average annual rainfall is approximately 770mm, with mean monthly temperatures ranging from 10°C in July to 28°C in February (Fremantle data; BOM 2002). Soils are sands of the Quindalup dune system. *L. laevigatum* is estimated at 60/ha; the only native species occurring in the reserve is *Spinifex longifolius*. Alien species occurring at low densities on the western side of the infestation include *L. ovatus*, *L. rigidum*, *A. fatua*, *Euphorbia littorea*, *P. capitatum*, *Trachyandra divaricata*, *Tetragonia decumbens* and *Oenothera drummondii*. Extensive paths created by walkers and cyclists are present through the *L. laevigatum*. The area is managed as a dog and horse exercise area, and is highly degraded. The seed source for *L. laevigatum* plants on the study site is likely to be several large individuals within the power station compound.
CHAPTER 3: LIFE HISTORY

3.1 INTRODUCTION

For recruitment to occur in the absence of vegetative reproduction, there must be success at each of the following stages: flowering, pollination, seed set, dispersal, escape from predation, germination, survival and growth (Harper 1977). An understanding of the population biology of an environmental weed is key knowledge for successful management of invasions. In particular, vulnerable aspects may be identified which assist decisions on management strategies (Mack et al. 2000).

3.1.1 Aims

Examination of key life history traits in the context of the Western Australian landscape and climate is detailed in this Chapter. The primary objective is to provide information on the species for management decisions. Additionally, the information forms a basis for the understanding of subsequent Chapters. Aspects chosen for practical examination were: (1) presumed limiting demographic factors; and (2) predation rates because of the suggestion that biocontrol should be considered for the species (Keighery 2001). The risk of death of tree seedlings typically declines with increasing age (Watkinson 1997), therefore survival through the seedling stage often limits recruitment. Thus, seedling survival of \( L. \) laevigatum has been examined. The Discussion section is structured to provide a chronological summary of the life-history attributes of \( L. \) laevigatum, starting from seed germination. It is a synthesis of information about the species from the literature (notably Burrell [1981], who worked on the species for her PhD), supplemented by field and laboratory research conducted on Western Australian populations. The Chapter provides information fundamental to an understanding of subsequent Chapters, as well as the primary objective of serving management goals.
3.2 METHODS

3.2.1 Germination

To determine seed viability rates, germination experiments were performed on seed collected from Ellensbrook, Shoalwater and Yanchep. Six plants at each site were chosen by walking a random number of steps in a random direction, and taking the closest *L. laevigatum* individual with abundant capsules. From each plant, three branches were harvested with secateurs, ensuring that branches were cut lower than the lowest (i.e., the oldest) seed capsule. Harvesting occurred after the most recent season's capsules were fully formed (Ellensbrook: 02/03/02; Shoalwater: 28/02/02; Yanchep: 26/02/02). Capsules were removed from branches, sorted into age classes (up to three years of stored seed was present on plants from Shoalwater), and placed in petrie dishes to dry and release seed. Seed from each site and year class was pooled. Each experimental sample consisted of fifty seeds placed upon filter paper on moist vermiculite, sealed in plastic bags and held at constant temperature (10 °C, 15 °C or 20 °C) to germinate. These temperatures were chosen based on temperatures used in pilot experiments, and on the average maximum and minimum winter temperatures at Perth, Albany and Cape Leeuwin (BOM 2002). Four replicate samples were provided for each age, site and temperature, to test the differences in seed viability rates between sites and at different temperatures (Figure 3.1). The Kruskal-Wallis non-parametric comparison was used, as no transformations yielded equal variance or normal distribution.

One bag = one replicate:

<table>
<thead>
<tr>
<th>Site</th>
<th>Seed Age</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td>1 yr old</td>
<td>10°C</td>
</tr>
<tr>
<td></td>
<td>2 yr old</td>
<td>15°C</td>
</tr>
<tr>
<td></td>
<td>2 yr old</td>
<td>20°C</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>1 yr old</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 yr old</td>
<td></td>
</tr>
<tr>
<td>Yanchep</td>
<td>1 yr old</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 yr old</td>
<td></td>
</tr>
</tbody>
</table>

Figure 3.1: Summary of experimental design for seed viability experiment, testing differences between seed from different sites and age of seeds under different temperature conditions.
3.2.2 Seedling survival

At Ellensbrook and Yanchep, 1-2 year old seedlings were marked using variable plot shapes (dependent on the position of seedlings), and their survival over summer monitored. The position of each seedling was mapped relative to marker stakes and other seedlings, so that the fate of each seedling could be followed. Notes were made of seedling condition, size and estimated age class. Plots were established at the start of summer (14/11/01 at Yanchep; 22/11/01 at Ellensbrook), and final data were gathered at the end of summer (26/01/02 at Yanchep; 02/03/02 at Ellensbrook). No 1-2 year seedlings were observed at Shoalwater.

3.2.3 Insect exclusion

The impacts of external predators on flower and capsule stages were assessed separately. Experiments occurred at Catherine Point, because to work in the main study sites was not approved before flowering commenced.

3.2.3.1 Exclusion of insects from buds

Insects accessing the plant externally were excluded by sealing fine mesh voile bags over samples of ten unopened buds using string. Three treatments were applied to 10 medium sized *L. laevigatum* plants, for the following categories: (1) covered as described; (2) uncovered (mesh bags absent); and (3) procedural control (as for covered, but bags open-ended and with holes cut). The procedural control was intended to account for any effects apart from predator exclusion that mesh bags may have on capsule development. Branches on the eastern sides of plants were chosen. Treatments were applied on 23/08/01, and branches harvested on 26/10/01.

Buds develop terminally; to ensure that the same 10 buds were scored at the commencement and conclusion of the experiment, string was tied around the top and bottom of the row of 10 buds (Figure 3.2). The success rate of buds developing into capsules was scored, and comparisons made between the three treatments. The exclusion of insects was anticipated to exclude insect pollinators. Presuming that flowers cannot be pollinated until open, the only pollen source for covered rows of buds would be from other buds within the bag, that is, self-pollination. It was assumed that differences in the amount of viable seed between covered and uncovered capsules would indicate the potential for self-pollination in *L. laevigatum*, or else for pollination in the absence of insects.
Data were neither homoscedastic, nor normally distributed. Various transformations failed to yield data suitable for parametric methods; therefore the Kruskal-Wallis non-parametric test was applied.

3.2.3.2 Exclusion of insects from capsules

To examine the impact of capsule predation, the same experimental design was applied to rows of ten capsules once flowering concluded, but the procedural control was not applied. New branches were chosen on the same 10 plants used in the previous experiment, and treatments applied on 26/10/01. On 14/03/02 capsules were harvested and checked for feeding scars using a compound microscope.

Various transformations failed to yield a normality of data, or equality of variance between the groups. The Wilcoxon signed ranks test was applied (an non-parametric equivalent to the paired t-test), pairing covered and uncovered branches from each plant. The marked branches extended over the period of covering; stem extension rates were analysed using the Wilcoxon signed ranks test, and average stem extension rates calculated.

3.2.4 Foliage predation and leaf abscission

The top 50cm of branches harvested for seed collection were scored for rates of foliage predation and leaf abscission. The numbers of intact leaves, missing leaves and leaves with herbivory scars were recorded for each branch (3 branches from each of 6 plants, per site). Phyllotaxis of *L. laevigatum* allows the estimation of the number of missing leaves, as capsules and axillary growth indicate the initial presence of a leaf, and where capsules or branches are absent, leaf scars remain once leaves are dropped. It was anticipated that missing leaves could be attributed to either predation or ordinary abscission.
3.3 RESULTS

3.3.1 Germination

For seeds held at 15°C, germination rates were fast after day 20 (Figure 3.3). Site and temperature had significant effects on germination percentages at 31 days. Germination was significantly greater at 10°C and 15°C than at 20°C. Ellensbrook seeds had the highest germination rates. Overall, no significant effect of seed age was detected (Table 3.1). However, in the 15°C cabinet, seed of different age showed distinct differences, with older seeds consistently germinating at higher rates (Figure 3.3). The only seeds to germinate by 15 days were from Yanchep (e.g., Figure 3.3). The highest final germination was in the 10°C cabinet, with 87.5% (± 0.9 standard error) of seed germinating.

![Germination Graph](image)

Figure 3.3: Germination of seed held at 15°C from Ellensbrook (E), Shoalwater (S) and Yanchep (Y) with comparisons of one (1) and two (2) year old seed.
Table 3.1: Effects of site, temperature and age on final germination percentages of *L. laevigatum*, showing Kruskal-Wallis ranks. *denotes significant difference ($\alpha=0.05$).

<table>
<thead>
<tr>
<th>Site</th>
<th>K-W rank</th>
<th>P, df, $\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td>52.90</td>
<td>$\chi^2=27.582$</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>21.25</td>
<td>df=2</td>
</tr>
<tr>
<td>Yanchep</td>
<td>35.35</td>
<td>P=0.000*</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Temperature</th>
<th>K-W rank</th>
<th>P, df, $\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10°C</td>
<td>48.40</td>
<td>$\chi^2=25.924$</td>
</tr>
<tr>
<td>15°C</td>
<td>41.96</td>
<td>df=2</td>
</tr>
<tr>
<td>20°C</td>
<td>19.15</td>
<td>P=0.000*</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Age</th>
<th>K-W rank</th>
<th>P, df, $\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 year</td>
<td>33.22</td>
<td>$\chi^2=1.768$</td>
</tr>
<tr>
<td>2 years</td>
<td>39.78</td>
<td>df=1</td>
</tr>
</tbody>
</table>

|            |           | P=0.184         |

3.3.2 Seedling survival

At Yanchep, extensive searching revealed only two locations of seedlings. One was within the dense stand of *L. laevigatum* close to the road; despite high plant densities, meagre foliage allowed moderate light penetration to the ground. Seedlings were positioned centrally in the stand, where moderate shading would be available despite changing sun angle. The second location was on the margin of a clump of healthy, foliose *L. laevigatum* among natural vegetation. Despite the presence of some bare ground on every side of the clump, seedlings were only positioned on the southern side of the stand, aggregated in shade cast by other species such as *H. hypericoides*. Surrounding vegetation would provide moderate shade for part but not all of the day. Seedlings were absent from the ground within the clump. All seedlings monitored at Yanchep were considered to be first year recruits based on their small size (approximately 2cm tall), and young looking leaves.

At Ellensbrook, after similar searching effort, seedlings were found in several patches of bare ground underneath *D. sessilis var. cordata* or adjacent to mature *L. laevigatum* trees. Among these seedlings, only two were classed as one year old. The rest were classed as 2 years old or older based on size, degree of establishment and the aged appearance of leaves.
At Yanchep, 93% of seedlings survived in the location with consistent moderate shade, whilst 45% survived in the location where shading was available for part of the day. At Ellensbrook, 92% of seedlings survived over the summer (Table 3.2). The cause of death of most seedlings appeared to be desiccation, since in many cases the dried out seedlings remained in place, free from scars of herbivory or disease.

Table 3.2: Survival rates of seedlings over summer.

<table>
<thead>
<tr>
<th>Site</th>
<th>Pre-summer total</th>
<th>Post-summer total</th>
<th>Proportion surviving</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yanchep, moderate cover</td>
<td>81</td>
<td>75</td>
<td>0.93</td>
</tr>
<tr>
<td>Yanchep low cover</td>
<td>22</td>
<td>10</td>
<td>0.45</td>
</tr>
<tr>
<td>Ellensbrook low cover</td>
<td>37</td>
<td>34</td>
<td>0.92</td>
</tr>
</tbody>
</table>

3.3.3 Insect exclusion

3.3.3.1 Exclusion from buds

Three samples were excluded from data analysis because marked buds were leaf buds rather than flower buds. A fourth sample was excluded because the mesh bag was no longer sealed around the branch and ants were observed inside. Significantly more capsules developed on uncovered branches and the procedural control than on covered branches (means and standard errors: 5.5 ± 0.8; 5.2 ± 1.1; 0.5 ± 0.3 for Ellensbrook, Shoalwater and Yanchep respectively). There was no difference between the uncovered and procedural control treatments (Table 3.3).

Table 3.3: Comparison of capsule development success between covered, uncovered and procedural control treatments of branches.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Kruskal-Wallis rank</th>
<th>Significance, df, $\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Covered</td>
<td>3.90</td>
<td>$\chi^2=11.672$</td>
</tr>
<tr>
<td>Uncovered</td>
<td>12.42</td>
<td>df=2</td>
</tr>
<tr>
<td>Procedural control</td>
<td>12.58</td>
<td>P=0.003</td>
</tr>
</tbody>
</table>
3.3.3.2 Exclusion from capsules

Some capsules had released their seed and detached from the branch by the end of summer. None of the remaining capsules showed herbivory scars. There was no significant difference between covered (rank=3.38) and uncovered (rank=4.83) branches in the numbers of capsules retained closed on the branch (Z=-0.085, p=0.933), so differences attributed to herbivory were discounted, and data were pooled to determine capsule dehiscence (i.e., seed release) rates. Forty-two percent of capsules had released their seed by the end of their first summer.

3.3.3.3 Stem extension

From late 23/08/01 to 26/10/01 (the period of insect exclusion from buds), no stem extension occurred. From 26/10/01 to 14/03/02 (the period of insect exclusion from capsules), stem extension occurred. Of 19 marked stems (covered and uncovered), 15 displayed apical growth of an average 106mm (± 9.64mm standard error). Of four stems which did not display apical growth, two displayed axillary growth. Covered branches sometimes extended far enough to touch the ends of bags, but there was no significant difference (Z=-0.059, p=0.953) between the elongation of covered and uncovered branches so it was considered appropriate to pool the remaining 15 results to calculate average extension.

3.3.4 Foliage predation and leaf abscission

Low proportions of leaves carried herbivory scars on branches (Table 3.4). Scars included leaf mines caused by larvae living and feeding between the epidermal layers, wells, holes or missing leaf margins caused by surface feeding insects. A substantial portion of leaves were no longer attached to the tip 50cm of sampled branches (Table 3.4).

Table 3.4: Percent of missing leaves and leaves with herbivory scars.

<table>
<thead>
<tr>
<th>Site</th>
<th>Percent with herbivory scars (standard error)</th>
<th>Percent missing (standard error)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td>4.25 (±0.72)</td>
<td>27.79 (±2.99)</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>6.12 (±1.37)</td>
<td>26.18 (±3.39)</td>
</tr>
<tr>
<td>Yanchep</td>
<td>4.24 (±0.92)</td>
<td>15.40 (±3.16)</td>
</tr>
</tbody>
</table>
3.4 DISCUSSION

3.4.1 Seed germination

The results show that germination potential of *L. laevigatum* seeds is high at wintertime temperatures (10°C and 15°C), consistent with winter germination (Burrell 1981). At 15°C, germination curves for every category of seed were still increasing at 31 days, suggesting that germination potential had not been reached by this time. The maximum germination rate observed (Ellensbrook: 87.5%, at 10°C) is relatively consistent with Burrell’s (1981) finding that 99% of winged seed was viable.

3.4.2 Seedling survival

3.4.2.1 Light requirements

The lack of seedlings from highly shaded areas suggests that seeds require a minimum light level for germination. Alternatively, if germination is possible under low light levels, light starvation must cause early death of germinating seeds. As seeds are small (approximately 0.25mg, based on 100 seeds from Ellensbrook), it is likely that photosynthesis would be necessary to provide energy almost immediately after germination.

Burrell’s (1981) research supports negligible establishment in highly shaded areas. In her study, standard quantities of *L. laevigatum* seed were sown over undisturbed heathland plots, top-dressed with calcareous sand and compared after two years to plots where the heath canopy had been removed. From a seedling potential of 9000, only five seedlings became established in plots with intact heath canopy, compared with 252 and 249 for two different treatments where the heath canopy had been removed. Similarly, seedling survival rates at Yanchep suggest that consistent shelter from sunlight greatly enhances *L. laevigatum* survival (93% survival in constant moderate shade, compared with 45% in the exposed location). These results could be confounded by proximity to the road edge at Yanchep. However seedlings (and young plants) at Ellensbrook also tended to occur on the margins of other *L. laevigatum* plants or underneath *D. sessilis* var. *cordata*, which has relatively low foliage projective cover. It appears that moderate light can enhance the survival of *L. laevigatum*; too much exposure leads to higher mortality later in establishment, whilst excessively low light levels inhibit germination or initial survival.
3.4.2.2 Moisture requirements

As *L. laevigatum* seedlings in the natural vegetation seemed to have died from dessication, water stress may drive enhanced survival in areas of moderate shade. Of Burrell’s (1981) 149 natural germinants monitored over the first summer underneath a *L. laevigatum* community, only three survived; most died in the hottest month. Seedlings at Yanchep with high survival rates had established on a litter layer up to 40mm thick and seedlings are commonly observed establishing in mulch (B. Goodale personal communication). Mulch (Buchanan 1989) and leaf litter prevent soil moisture loss, so ability to establish in leaf litter suggests a water stress avoidance strategy.

Reasonable summer rainfall occurs within the natural distribution of *L. laevigatum*, yet the species is able to survive and spread despite the hot dry summers of south-western Australia’s Mediterranean climate. Establishment in sheltered microsites, and establishment in leaf litter, may contribute to *L. laevigatum*’s success in south-western Australia.

3.4.2.3 Soil disruption

Many plant species, particularly pioneer species, require soil and/or canopy disturbance to establish. Burrell (1981) established plots where heath canopy was removed by clipping (soil undisturbed) or digging (soil disturbed). All plots were sown with known amounts of *L. laevigatum* seed. A second treatment level was top-dressing (or the lack of it) with calcareous sand. Soil disturbance without top-dressing greatly enhanced establishment of seedlings. Top dressing enhanced survival in plots with disturbed and undisturbed soil, immensely so for undisturbed soil (Table 3.5). A loose surface substrate such as disturbed soil, added sand, leaf litter or mulch probably enhance *L. laevigatum* establishment in south-western Australia also, as it commonly colonises sites with highly disturbed soils such as abandoned quarries.

Table 3.5: Comparison of seedling establishment rates in plots clipped or cleared of vegetation, with or without top dressing with calcareous sand. Estimated seedling potential for each category is 9000 (after Burrell 1981).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Vegetation clipped (soil intact)</th>
<th>Vegetation dug out (soil disrupted)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top-dressed</td>
<td>252</td>
<td>249</td>
</tr>
<tr>
<td>No top-dressing</td>
<td>3</td>
<td>109</td>
</tr>
</tbody>
</table>
3.4.2.4 Nutrients

Burrell (1981) examined the effects of phosphorus fertilisation and mycorrhizal association on the growth of *L. laevigatum* seedlings. Seedlings grown in the absence of mycorrhizae were stunted, but developed normal growth upon either inoculation with mycorrhizal material from underneath an infected stand, or upon treatment with phosphate fertiliser (NaH₂PO₄). In other experiments, *L. laevigatum* seedlings responded to phosphate fertiliser at different concentrations with increased growth. Field monitoring of seedlings of known age showed that the species is capable of persisting in a suppressed condition for at least nine years, with only one of the 292 seedlings monitored for this time period producing capsules (Burrell 1981). Therefore, seedlings monitored at Ellensbrook were possibly older than two years but were suppressed.

3.4.2.5 Disturbance of soil and vegetation

Burrell's (1981) research shows that the disturbance of vegetation cover and the disruption of soil enhance survival of *L. laevigatum*, and that nutrient addition can substitute for lack of mycorrhizal association and subsequent seedling stunting. Several types of disturbance common in bushland can lead to similar conditions. Rabbits remove cover of native vegetation, and are efficient disruptors of soil by digging holes whilst foraging, and establishing burrows in which to live. Their faeces may also create favourable conditions for survival through soil nutrient addition. Evidence of rabbit activity contributing to germination likelihood was found at Yanchep: in the open location, several seedlings were observed germinating in the disturbed ground of a rabbit digging. At Wilsons' Promontory, grazing by rabbits and kangaroos (without fire) has been considered sufficient disturbance to allow the expansion of *L. laevigatum* into areas which were previously grasslands or *Banksia integrifolia* woodland (Bennett 1994). Pathways can also provide disturbed soil and bare ground for establishment; in the Denmark area *L. laevigatum* is observed establishing on the verges of unsealed roads through bushland (personal observation).
The disturbance types discussed so far are anthropogenic. However, even disturbance types indigenous to ecosystems may be sufficient to allow invasion. Kangaroos frequently damage vegetation and disrupt soil as they pass through bushland and falling trees create vacant ground and soil disturbance. Wind and storms may also disturb soil and vegetation. It appears that even small scale indigenous soil and vegetation disturbances potentially provide the characteristics that enhance establishment of *L. laevigatum*.

### 3.4.3 Growth

#### 3.4.3.1 Stem extension

Stem extension occurred in summer rather than spring at Catherine Point. Ability to grow through this period of little or no rainfall suggests that *L. laevigatum* may have a deep root system, able to exploit groundwater. Elsewhere, stem extension rates were considerable: the maximum observed extension rate of a mature plant (at Shoalwater) was 48cm, inferred from differences in stem colour of new growth. There was no increase in seedling height over summer at Ellensbrook or Yanchep; possibly seedling growth occurs in winter when moisture relations are more favourable. Alternatively, seedlings at these sites are suppressed by lack of some other resource, such as soil phosphorus. In mulch adjacent to Naragebup (Rockingham Regional Environment Centre) laid in 2000, foliose, healthy seedlings of *L. laevigatum* approximately 25cm tall and 25cm wide were found (in March 2002) adjacent to an irrigation system. Thus, seedling growth rates can be relatively high under favourable conditions.

#### 3.4.3.2 Leaf abscission and predation

It is possible that low levels of herbivory were recorded because damaged leaves are shed. However, observations of leaf litter collected during the study showed similarly low proportions of fallen leaves with herbivory scars. Leaves do not appear to be retained on the plant for more than three years. They are consistently absent from the portion of the branch closest to the trunk, the age of branches was estimated by noting growth scars on harvested branches. High levels of foliage loss appear to be the norm, rather than instigated by mechanical damage or predation, because a thick level of leaf litter is typical under healthy stands of the species. High levels of litter fall may lead to soil moisture conservation (Section 3.3.2.2).
3.4.3.3 Age at first maturity

Most literature cites Burrell's (1969; 1981) assessment of age at first maturity for *L. laevigatum*, being five years. B. Dixon (personal communication) has suggested three to four years in Western Australia, depending on growth conditions. Field observations suggest that plants growing in native vegetation may take longer than this; there is no obvious reason to expect the onset of maturity to be earlier in Western Australia than Victoria. Limitation of this study to one year meant that determination of age at first maturity was not possible. However, there is potential for monitoring of seedling quadrats established for this study to address the absence of these data in south western Australian populations. Such data are essential for efficient, effective management decisions.

3.4.3.4 Maximum size and age

The maximum height observed for Western Australian *L. laevigatum* plants was 8.5m, from the thicket adjacent to Ellensbrook Homestead. These trees are estimated to be 32 years old, based on time since fire. The widest plant observed was 14.2m wide, and was observed at the start of the transect at Shoalwater. This plant is a maximum of 43 years, and patches of the canopy are senescing, yet it is still producing capsules. The same plant had the maximum stem diameter observed during the study: 1.2m; its height was 3.8m. The maximum height and girth of plants observed in an 80-100 year old stand in Victoria was 12m in height and 1.45m trunk girth, equal to 0.46m stem diameter (Hazard and Parsons 1977). Presumably these measurements come from a dense stand, in which *L. laevigatum* individuals are forced into a taller thinner growth form, similar to specimens in the thicket at Ellensbrook. The maximum age for *L. laevigatum* has been suggested as 150 years (Burrell 1981).

3.4.3.5 Response to mechanical damage

Branches were observed to continue growing well after severe mechanical damage such as complete splitting of the trunk or branch at Ellensbrook and Catherine Point Reserve. Chainsawing of branches did not appear to affect other parts of the plant. There is disagreement about the ability of the plant to coppice when chainsawed at the base. Such methods of control in South African populations have resulted in multi-stemmed resprouting which makes subsequent control efforts more difficult (Gordon 1999), and there have been similar experiences in Albany, Western Australia (J. Moore personal communication). Based on the apparent inability of plants in Perth control programs to
coppice after chainsawing, there has been speculation that Perth and Albany support different subspecies of *L. laevigatum*. However, control programs in the Shire of Serpentine-Jarrahdale, and at Woodman Point (both close to Perth) require herbicide application immediately after chainsawing to prevent coppicing (B. Dunn, S. King personal communication). At both Albany and Woodman Point, it is reported that coppicing does not occur if stems are cut below the lowest adventive shoot. Therefore, it appears that coppicing ability is based on the level at which plants are cut (J. Moore and S. King personal communication) rather genetic differences between populations.

### 3.4.4 Flowering

If flowering is controlled by day length, flowering should occur first in northern-most populations, with southern populations being progressively later in the year. This was not observed: in 2001, flowering was first observed in early July near Margaret River. Flowering in Perth was observed predominantly over late July and August, therefore day length must not control flowering. Elsewhere the species is listed as predominantly spring flowering (August to October or November: Harden 1993; Walsh and Entwisle 1996; Benson and McDougall 1998). In New South Wales, it has been reported to flower in summer (Clarke 1989b). The various reports of flowering times suggest opportunism.

### 3.4.5 Pollination and fertilisation

The most conspicuous insect pollinators observed were introduced honey bees (*Apis mellifera*) and unidentified black ants. Bees were so strongly attracted to the species that they were difficult to avoid during field work in August 2001.

The covering treatment appears to have prevented pollination of *L. laevigatum*, leading to abortion of capsule formation. Prevention could be in three ways: (1) pollination was not possible because insect vectors were excluded; (2) pollination may be possible by wind, but reduced windspeed within bags was not sufficient to allow flowers within the bag to pollinate each other; or (3) wind pollination is possible, and low windspeeds within bags are adequate for this, but *L. laevigatum* is unable to self-pollinate. If the third explanation is true, it is unlikely that single isolated plants will be able to produce viable seed and expand in range.
3.4.6 Capsule and seed development

3.4.6.1 Predation on capsules

None of the capsules from marked branches (covered or uncovered) carried scars from insect damage or otherwise. Casual observations made whilst sorting capsules for viability tests support negligible capsule predation. Some capsules collected from Shoalwater and Ellensbrook had been bitten in half, probably by a parrot or cockatoo (B. Goodale, H. Recher personal communication), yet the remaining unharmed locules were commonly retained green on the plant, and when dissected still contained seed. It seems even severe mechanical damage still allows some seed to remain intact. Therefore, predation that effectively reduces seed production is apparently absent in Western Australia.

3.4.6.2 Pattern of seed release

*L. laevigatum* is an obligate seeder; adult plants are readily killed by fire (Burrell 1981; Clarke 1989b). *L. laevigatum* seed capsules are not woody like many other Myrtaceae. Despite being unremarkable insulators against heat, they are extremely effective at protecting seed from fire (Judd 1993). Serotiny occurs for two to three year at some sites (Hazard and Parsons 1977; Burrell 1981; Clarke 1989a), yet at other sites seed release occurs the summer after spring flowering (S. Coutts personal communication, Molnar *et al.* 1989; Benson and McDougall 1998). All observed Western Australian populations held seed for two years, with three year old capsules occasionally present.

Mass seed release occurs after the passage of fire, or when branches are cut, suggesting that capsule water deficit is a trigger for dehiscence (Burrell 1981). Herbicide applications trigger seed release, even when plants are not killed (J. Moore personal communication). In the absence of plant damage, *L. laevigatum* spontaneously releases some of its stored seed (Bennett 1994), which makes viable seed available even in the absence of fire. At Catherine Point, nearly half of the newly formed capsules had released their seed by the end of the summer they were formed. This release must be supplemented by release of older seed, since capsules older than two years are rare.
Since fire creates conditions that enhance seedling establishment rates (Burrell 1981), a seed store for release upon fire is advantageous. The spontaneous release of half of the seed bank provides for germination opportunities in the absence of fire. This method of seed storage and release may be advantageous, because it provides seed for germination in the presence and absence of fire.

3.4.6.3 Seed abundance

Capsules from Shoalwater contain between nine and twelve locules. As few as six locules have been reported for the species (Harden 1993). Average seed per capsule is 20.4 ± 0.8 (standard error). *L. laevigatum* plants commonly carry copious numbers of capsules (Plate 3.1); considering that each capsule carries approximately twenty seeds, and that seed viability is high, germination potential for the species is extreme.

![Plate 3.1: *L. laevigatum* at Shoalwater, showing large number of capsules](image)

3.4.7 Dispersal

Low seed weight (0.25mg) in combination with winged morphology suggest that seed is able to be transported at least several meters by wind. Separation distances of *L. laevigatum* individuals in the field suggest that dispersal commonly occurs over tens of metres. It is possible that some dispersal at Ellensbrook may be by birds. Branch tips with capsules attached are commonly found on the path through the thicket; the appearance of these is consistent with feeding or damage by a parrot species. *Calyptorhynchus baudinii* (Baudin's Black Cockatoo) is a Schedule 1 species under the Wildlife Conservation (Specially Protected Fauna) Notice 1999, signifying that it is rare or likely to become
extinct. The species was observed in the vicinity of the thicket at Ellensbrook and may be interacting with *L. laevigatum*. As black cockatoos are known to occasionally carry twigs when they fly (H. Recher personal communication), dispersal by these birds cannot be ruled out. However, the size of *L. laevigatum* capsules and seeds indicates that a smaller parrot, possibly *Barnardius zonarius* (Port Lincoln Parrot), is responsible for the damaged branches (H. Recher personal communication).

### 3.4.8 Traits enhancing and limiting recruitment and invasion

The ability of *L. laevigatum* to grow during summer could confer a competitive advantage over other species. Additional field observations suggest that growth rates are indeed higher than indigenous species, as *L. laevigatum* overtops other post-burn indigenous vegetation at Yanchep, such as *Hakea trifurcata*. Therefore, *L. laevigatum* is a good competitor, as it is able to sequester space and other resources before co-occurring species. Variable flowering patterns, the ability to continue growth despite mechanical damage, and the ability to release seed and germinate in the presence and absence of fire also show resilience and opportunism.

*L. laevigatum* possesses traits which probably allow water stress avoidance. In the seedling stage, the ability to establish among leaf litter may allow colonisation of sites with favourable moisture relations in the upper layers of the soil. In contrast, the seedlings of many other species are negatively affected by the presence of leaf litter (Crawley 1997). The ability to grow during summer suggest deep roots and an ability to exploit ground water, where available.

In south-western Australia, *L. laevigatum* recruitment does not appear to be limited by seed abundance or germination viability, as these features were potentially extremely high. Yet at many sites, seedling establishment must be sporadic, with seedlings rarely found despite the presence of seed-bearing plants on-site. These findings strongly suggest that *L. laevigatum* recruitment is microsite limited, with seedlings able to establish and survive mainly where there is disturbed, but soil and moderate levels of light. Parallel with the situation in eastern Australia, predation on leaves and reproductive parts by vertebrates and invertebrates appears to be minimal, with a negligible limiting role in recruitment.
CHAPTER 4: DISTRIBUTION

4.1 INTRODUCTION

4.1.1 Natural distribution

The concept of Australian plants as invaders in Australian ecosystems creates problems in defining natural biogeographic ranges. Some such species are so well integrated in their new ecosystems that they are perceived to be original members of the flora, creating difficulties in conservation decisions (Carr 1993). *L. laevigatum* is a typical example: it occurs naturally in coastal areas of New South Wales, Victoria, Tasmania and the Bass Strait islands (Pidgeon 1938a; Burrell 1981; Carr 1993; Bennett 1994; Wrigley and Fagg 1996). However, there is disagreement over its South Australian distribution, with some authors listing it as indigenous (Curtis 1975; Harden 1993; Wrigley and Fagg 1996), others as introduced (e.g. Kloot 1985; Clarke 1989b) and Walsh and Entwisle (1996) as both. Its western limit in Victoria is also uncertain, being either near Anglesea (Carr 1993; Walsh and Entwisle 1996), or the eastern side of Port Phillip Bay, Victoria (Bennett 1994). Its northern limit is near Nambucca Heads, New South Wales (Harden 1993; NSW DLWC 2001); occurrences in north-eastern New South Wales and south-eastern Queensland are agreed to be non-indigenous (Curtis 1975; Harden 1993; Walsh and Entwisle 1996). There, the species was often planted for revegetation after sand mining (P. Adam personal communication, Wrigley and Fagg 1996).

4.1.2 Soils and vegetation communities

*L. laevigatum* naturally occurs on the well-drained, low nutrient sands of coastal dunes and on other sandy soils overlying a variety of rock types, including sandstone, limestone and granite (Burrell 1981; Clarke 1989b; Benson and McDougall 1998). In New South Wales, it is a typical member of the dune thicket vegetation association of Clarke (1989a), along with *Acacia sophorae*, *Banksia integrifolia* (Clarke 1989a) and *Leucopogon parviflorus* (Benson and McDougall 1998). It is found in *Allocasuarina distyla-Melaleuca nodosa* mixed heath yet also commonly occurs as near monospecific stands (Benson and McDougall 1998). In Victoria, a major association on well drained coastal dunes is *L. laevigatum* thicket with a *L. parviflorus* dominant understorey (Parsons 1966; Molnar et al. 1989). Thus, as well as occurring naturally in mixed species communities, it forms species-poor thickets within its natural range.
4.1.3 Natural role in ecosystems

Differing perceptions of natural distributions of invasive Australian plants are compounded by differing views on their role in ecosystems to which they are indigenous. With current emphasis on vegetation management for biodiversity, it is often perceived that low plant species richness due to one dominant species is an undesirable, anthropogenically induced trait of vegetation, and intervention may be appropriate to restore "lost" species to the community. In many situations, this is true. For example, *Pittosporum undulatum* (sweet pittosporum) plays an important role in the ecology of its natural wet forest habitats. However, a suite of human induced changes have led to within-site population increases, and the invasion of dry sclerophyll and other vegetation types in eastern Australia by this mesic species, causing significant declines in plant diversity (Mullett 2001).

For *L. laevigatum* within its natural habitats, conclusions are less simple. The formation of *L. laevigatum* dominated thickets may be part of its natural role within its range. In gaps created by dune blow-outs, for example, *L. laevigatum* may be among the only species able to tolerate the exposed conditions, and probably plays an important role as a colonising species in dune succession (M. Robinson personal communication). Hazard and Parsons (1977) observed *L. parviflorus* regenerating in canopy gaps produced in a moribund stand of *L. laevigatum*, indicating that thickets of *L. laevigatum* persist for a limited time. In the absence of dune blow-outs, the thickets it forms in exposed locations shelter the salt spray intolerant vegetation immediately inland (Parsons 1966; Robinson 1991). At Wilson's Promontory, Victoria, occurrences of *L. laevigatum* on the richer granitic soils amongst heathland vegetation are restricted to exposed sites receiving salty winds (Parsons 1966).

Therefore, descriptions of the species in its indigenous range suggest that the role *L. laevigatum* in indigenous vegetation is broad and varied. It is possible, however, that the documented role of *L. laevigatum* is not "natural", but a response to environmental change since European settlement. Large expanses of Australia's eastern and south-eastern coastlines are cleared for residential development, and remaining bushland is subject to disturbances of urban patches, such as nutrient rich run-off, altered fire regimes and alien species. It is possible that species-poor thickets of *L. laevigatum* have arisen in response to these factors, as the species appears better adapted to exposure and disturbance (such as salt spray) than are other species.
Regardless of whether low species richness is a natural feature of *L. laevigatum* dune thicket vegetation in eastern Australia, if invasion of new communities by *L. laevigatum* reduces species richness, its impacts are of concern.

### 4.1.4 Fire and other disturbance

Through manipulative experiments, Burrell (1981) identified some factors which enhance seedling establishment of *L. laevigatum*, focusing on its invasion of heathland at Wilson's Promontory. Some experiments were outlined in Chapter 3; in summary, she found that three factors were required for *L. laevigatum* to invade heathland at the observed rates and densities. These include: (1) disturbed vegetation and topsoil, (2) enhanced seed release and (3) a temporary increase in soil phosphorus to compensate for the low phosphorus levels of sand podzols. After considering several different types of disturbance, she postulates that fire is the only one to provide all three requirements at levels which would explain the observed densities.

In support of Burrell's findings, Hazard and Parsons (1977) postulated fire-induced invasion of adjacent vegetation by *L. laevigatum* at Western Port. They noted that in the absence of fire, germination of *L. laevigatum* is rare and only occurs where leaf litter is sparse. The stated implication is that "frequent burning" (p. 196) will encourage landward expansion of dense *L. laevigatum* at the expense of other taxa, yet suppression of fire could lead to its complete elimination. Presumably, by "frequent burning", they refer to fires being common, but with intervals longer than the time taken for *L. laevigatum* to reach maturity (five years: Burrell 1981).

Molnar *et al.* (1989) compared several urban bushland reserves which had recently been burned. Prior to fire, *L. laevigatum* dominated as a near monospecific thicket. After fire, a substantial number of indigenous heath species regenerated, despite being absent from underneath *L. laevigatum* canopy for up to 70 years. Significantly, they challenge the assumption that fire is necessary for invasion of vegetation by *L. laevigatum*, referring to invasions at Portland, Anglesea, Cape Otway and the Mornington Peninsula where fire had been suppressed for several decades. They argue instead that burning kills *L. laevigatum* adults, allowing the regeneration of selected heathland species. However, post-fire hand weeding occurred, including the removal of *L. laevigatum* seedlings. In the absence of
hand weeding, the post-fire succession at their site may have lent more support to the idea that fire promotes invasion by *L. laevigatum*.

Bennett (1994) examined the expansion of *L. laevigatum* at Wilson's Promontory using sequential aerial photographs (1941, 1972 and 1987), and related expansion rates to changes in land management practices. The study shows that fire was neither required, nor the primary cause of expansion of *L. laevigatum* on the Yanakie Isthmus, since expansion continued at a similar rate once fire was excluded. She postulates changes in grazing as the cause for *L. laevigatum* expansion. The suggested mechanism is: (1) the exclusion of cattle (known to graze *L. laevigatum*), and (2) increased bare ground, due to increased grazing pressure by kangaroos (which seldom browse shrubs) and rabbits.

Two of these studies suggest that invasion by *L. laevigatum* at relies on fire; two document invasion in the absence of fire. Most likely, fire frequency is the important factor in whether or not the fire regime leads to increases or declines in *L. laevigatum* (Burrell 1981).

**4.1.5 Aims**

The following aims were established for this component of the research:

1. to ascertain the current geographic range of *L. laevigatum* in Western Australia,
2. based on its current range, to predict the extent of its potential distribution,
3. to determine which habitats are most commonly invaded by *L. laevigatum*, and
4. to elicit patterns of invasion into native vegetation, and to explain these with respect to the literature.
4.2 METHODS

4.2.1 Geographic and habitat distribution

A number of sources were used to ascertain the past and current distribution of *L. laevigatum* in Western Australia. These included requests for information from environmental professionals and community conservation groups, roadside surveys, field notes and herbarium records. These sources were collated to determine the species' geographic and habitat distribution.

4.2.1.1 Roadside surveys

Roadside surveys were undertaken to mark the locations of *L. laevigatum* using a Geographic Positioning System. Major highways between Albany, Mount Barker and Denmark were surveyed in conjunction with J. Moore (Western Australian Department of Agriculture, Albany); locations were also noted *en-route* to Ellensbrook from Albany, recording location and habitat details of *L. laevigatum* individuals and populations (Table 4.1). Field notes focussing on these attributes were made opportunistically for observations around Perth during the course of the study.

Table 4.1: Location attributes recorded in roadside survey.

<table>
<thead>
<tr>
<th>Details recorded</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>- Location type <em>(e.g., roadside/ agricultural land/ bushland)</em></td>
<td></td>
</tr>
<tr>
<td>- Closest town</td>
<td></td>
</tr>
<tr>
<td>- Road name(s)</td>
<td></td>
</tr>
<tr>
<td>- Vegetation structure of invaded habitat <em>(e.g., heathland, woodland, forest)</em></td>
<td></td>
</tr>
<tr>
<td>- Associated plant taxa</td>
<td></td>
</tr>
<tr>
<td>- Plant number/ area, density and life stage <em>(e.g., seedling, shrub, tree)</em></td>
<td></td>
</tr>
</tbody>
</table>
4.2.1.2 Information requests

Government land managers and Bushcare workers (professional and volunteer) were contacted by electronic mail or telephone and asked for details of their knowledge of *L. laevigatum* naturalised in their local areas. Contact details were obtained by requests to local shire councils, and contact lists for community conservation groups. Responses were received from employees of CALM, the Botanic Gardens and Parks Authority, the Western Australian Department of Agriculture, environmental consultants, botanists and local shire councils (Environmental Health Officers and Bushcare Officers), members of urban bushland "Friends" groups and other community volunteers. To ensure that respondents had identified the plant correctly, reference websites were given with clear pictures of the species (for e-mail contacts), or verbal descriptions given.

A request for information was sent to members of the Enviroweeds Listserver, a nationwide mailing list established by the Cooperative Research Centre for Weed Management Systems (Weeds CRC, which is part of the Keith Turnbull Research Institute, Victorian Department of Natural Resources and Environment). Recipients were asked to fill in a survey posted on the World Wide Web (Appendix), requesting the information that was recorded during roadside surveys, plus a question on soil type. Comments on additional information were encouraged.

4.2.1.3 Mapping

The locations for each report of *L. laevigatum* (including data from information requests, roadside surveys, herbarium records and field notes) were recorded as points on a map of Western Australia using ArcView GIS (Geographic Information System) version 3.0a (ESRI 1996). Mapping occurred at large scale for greater accuracy; maps are displayed here at different scales.

4.2.1.4 Habitats at risk

Results of roadside surveys and information requests were tallied to find the locations, vegetation types, soil types and plant species most commonly affected by invasion by *L. laevigatum*. 
4.2.2 Pattern of invasion into native vegetation

4.2.2.1 Field methods

Some invading species (e.g., *Acacia sophorae*: McMahon 1994) display an invasion front, with most plants recruiting close to the invasion source and scattered individuals occurring further into bushland. The spatial distribution *L. laevigatum* in bushland was examined at Ellensbrook, Shoalwater and Yanchep to determine whether *L. laevigatum* also follows this pattern of invasion. Preliminary field observations of *L. laevigatum* in bushland suggested that invasion occurs sequentially, with larger plants close to the invasion source giving rise to progressively smaller plants with distance from the main invasion. This pattern was also investigated.

Three parallel transects (100m x 2m) were established, starting in the main invasion, and running in the direction of the presumed invasion. Morphological features were measured for each *L. laevigatum* along transects (Table 4.2), and notes were made about features and disturbance condition of the microsite.

Table 4.2: Plant and microsite attributes recorded for each *L. laevigatum* along transects.

<table>
<thead>
<tr>
<th>Details recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>- Distance along transect</td>
</tr>
<tr>
<td>- Plant height, width (at widest point) and stem diameter</td>
</tr>
<tr>
<td>- Number of stems at base of plant</td>
</tr>
<tr>
<td>- Competition index</td>
</tr>
<tr>
<td>- Notes (nearby disturbance, proximity of other plants, etc.)</td>
</tr>
</tbody>
</table>

Distance 0m lay closest to and 100m furthest from the source of invasion. Plant height and width was measured using a 10m steel tape measure. A diameter tape was used for stem diameter, measured 5cm above the soil. Where plants were multi-stemmed, stem area was estimated for each stem (based on a circle, $A=\pi r^2$), summed and converted back to a single diameter measurement. Number of stems was defined as the number present 5cm above the soil level. Competition index was estimated as an integer based on the proximity, height and density of surrounding vegetation, with 1 as the lowest and 3 the highest intensity of competition.
4.2.2.2 Calculations and comparisons

Average density over sites was calculated as the number of individuals recorded divided by the area surveyed (600 m$^2$). A search for *L. laevigatum* occurred beyond the ends of transects; average spread rate was calculated by combining each site's date of introduction with the furthest distance a *L. laevigatum* plant was observed away from the main invasion. Date of introduction at Yanchep was unknown, so rate was calculated based on time since fire, and the same calculations applied to Ellensbrook data (fire has not occurred at Shoalwater since introduction).

Plant density was compared between 20 m intervals along transects using graphs and the Kruskal-Wallis non-parametric comparison. Differences in plant shape between sites were explored using linear regressions between plant height and width, which were forced through the origin based on the assumption that when height is nil, width is nil. Although data did not meet all data considerations for linear regression (normality and linear relationship between variables), it was assumed that regression co-efficients should provide some numerical comparison between plant shape at the different sites.

Curve estimation regressions were used to explore the relationships between competition index and morphological features (height, width, stem diameter and number of stems), and to explore relationships of morphological measurements with each other. The fits of data to various models were tested. Models included were linear, cubic, quadratic, inverse, logarithmic, exponential and power. Where significant relationships were found, the $R^2$ value was used to choose the model which fitted data best. Size distributions along transects were investigated using curve estimation regression to explore the relationship between plant size and distance along transect.
4.3 RESULTS

4.3.1 Geographic and habitat distribution

4.3.1.1 Data considerations

A total of 163 reports of *L. laevigatum* occurrence were used in the analysis. These include 55 herbarium records, 45 correspondences and 63 roadside survey reports. *L. laevigatum* is distinct in appearance, and each respondent to information requests was familiar with the species as environmental weed prior to the request. Therefore, error due to misidentification is considered negligible. Reported locations were usually places with which the respondent was extremely familiar, for example reserves in which the respondent had worked, or roads in their locality. Respondents were encouraged to omit information or to indicate if they were unsure of the accuracy of information they provided. Because respondents were either professionals or people with a specific interest in their local bushland, they were assumed proficient at recognising differences between broad vegetation structural classifications such as woodland, forest and heathland. For associated taxa, unless the species reported were distinctive and well known (for instance, Tuart, *Eucalyptus gomphocephala*), records were only collated to genus level. The majority of herbarium specimens were collected by known botanists, who were likely to give reliable site descriptions. Where information was ambiguous, it was omitted from the analysis.

The data are likely to be strongly biased to detect roadside locations because one of the sources was a roadside survey. Additionally, *L. laevigatum* is most likely to be reported from accessible places with which people are familiar, biasing locations to areas influenced by human activity and therefore affected by anthropogenic disturbance. Because of omissions of information, and because respondents commonly detailed more than one location, totals for each category do not sum to the total number of responses.

4.3.1.2 Geographic distribution

Comparisons were made between the geographic distribution of *L. laevigatum* and average annual maximum and minimum temperatures and rainfall for the period 1961-1990 (BOM 2002). Both temperature maps showed a clear north-south temperature gradient, little east-west variation and no correlation with the distribution of *L. laevigatum*. However, there are strong similarities between the distributional boundaries of *L. laevigatum* and the 400mm
rainfall isohyet, with the majority of occurrences lying in the region with more than 400mm average annual rainfall (Figure 4.1A). *L. laevigatum* is not restricted to coastal Western Australia; it was recorded as far inland as Tammin (Figure 4.1B). The species is naturalised throughout the Swan Coastal Plain on each of the five main geomorphological units, including the Quindalup, Spearwood and Bassendean dune systems, the Ridge Hill Shelf and the Pinjarra Plain (after Seddon 1972), and on the Darling Scarp. Of significance is its occurrence along the Albany Highway between Armadale and Albany (Figures 2B, C).
Figure 4.1: Distribution of *L. laevigatum* (green dots) showing (A) 300mm and 400mm rainfall isohyets*; (B) distribution in southern Western Australia and (C) distribution in the Perth region. *data from Bureau of Meteorology (BOM 2002). GIS map data from Geoscience Australia (2001) and Geocommunity (2002)
4.3.1.3 Habitats at risk

Roadside locations were most commonly reported as supporting *L. laevigatum* (Table 4.3). Individuals and populations observed on roadsides were mainly shrubs and seedlings. Railway lines, agricultural land, tips and quarries were also reported as supporting naturalised *L. laevigatum*. The vegetation types most commonly invaded were heathland and woodland, followed by alien grass taxa and lastly open forest (Table 4.3). *L. laevigatum* was commonly found in association with *Eucalyptus* and *Corymbia*, namely *E. marginata* (Jarrah; 8 records), *C. calophylla* (Marri; 8 records) and *E. gomphocephala* (Tuart; 3 records). *Banksia, Acacia* and also *Agonis flexuosa* (Peppermint) were also commonly found at the same sites as *L. laevigatum*. Numerous and various other associated taxa were reported.

Table 4.3: Site characteristics of locations supporting naturalised *L. laevigatum*. Numbers are tallies of reports.

<table>
<thead>
<tr>
<th>Location</th>
<th>Vegetation</th>
<th>Associated taxa</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roadside</td>
<td>Heathland</td>
<td><em>Eucalyptus</em> spp. and <em>Corymbia</em> spp.</td>
<td>49</td>
</tr>
<tr>
<td>Railway line</td>
<td>Woodland</td>
<td><em>Banksia</em> spp.</td>
<td>37</td>
</tr>
<tr>
<td>Agricultural land</td>
<td>Road edge grasess</td>
<td><em>Acacia</em> spp.</td>
<td>22</td>
</tr>
<tr>
<td>Tip/ Quarry</td>
<td>Open forest</td>
<td><em>Agonis flexuosa</em></td>
<td>3</td>
</tr>
</tbody>
</table>

Aside from herbarium records, most records gave no indication of soil type. Amongst herbarium records, *L. laevigatum* was most commonly recorded on sandy soils (39), limestone (6) and loam (4), as well as sandy loam, sandy clay, laterite, clay, clay loam and peaty sand. Herbarium records commonly gave both the soil type and underlying substrate. These included sand (4), laterite (4), granite (3), limestone (2), loam (1) and quartzite (1).
4.3.2 Pattern of invasion

4.3.2.1 Density and spread rate

Densities were 0.045/m² at Ellensbrook, 0.060/m² at Shoalwater and at Yanchep 1.32/m². At Yanchep, there was a distinct boundary between the high density stand and the indigenous vegetation (Figure 4.2). Density calculated for this area alone was 10.51/m². For comparison, density of Ellensbrook thicket was estimated at 3/m². Furthest distance of *L. laevigatum* from the main invasion were approximately 420m at Ellensbrook (distance from Ellensbrook thicket, plus distance along transect), 80.3m at Shoalwater and 134.6m at Yanchep. Calculated linear spread rates based on introduction date are 8.24m/year at Ellensbrook and 1.87m/year at Shoalwater. Based on time since fire, these are 13.13m/year at Ellensbrook and 12.24m/year at Yanchep.

4.3.2.2 Density distribution

At all sites density of *L. laevigatum* was highest within the original invasion than further away from it. There is a gradual pattern of decline over the 100m at Ellensbrook and Shoalwater; at Yanchep an extremely high density in the first 20m is followed by a sharp drop and a steady density over the next 60m. Note that the value shown for the first 20 metres at Yanchep has been reduced by a factor of ten, to allow other values to be visible. Substantial variability between transects is a feature of this trend (Figure 4.2). Despite the clarity and consistency of these trends, the Kruskal-Wallis comparisons detected no significant differences between any of the five densities at any site (P=0.245, 0.151 and 0.078 at Ellensbrook, Shoalwater and Yanchep respectively). However, Kruskal-Wallis rank declined with distance along transect at Ellensbrook and Shoalwater (Figure 4.2). Additionally, comparing the first 20m with the last two 20m, error bars do not overlap at any site.
Figure 4.2: Density distribution of *L. laevigatum* at 20m intervals along transects. Values are the means of three transects. Numbers above standard error bars are Kruskal-Wallis ranks. NB value shown for Yanchep 0-20m has been reduced by a factor of ten.
4.3.2.3 Morphology and competition index

Curve estimation regression yielded no significant relationships between competition level and plant height, width, stem diameter or number of stems, at any site (Appendix). Highly significant positive relationships were found (invariably, \( p=0.000 \)) between height and width, height and stem diameter and width and stem diameter at all sites (Appendix). For this reason, stem diameter only was chosen to investigate relationships between plant size and transect distance.

At Shoalwater, plants were wider than they were tall, that is, short and wide. At Yanchep, plants were almost twice as tall as their height, that is, tall and narrow. Ellensbrook plants were approximately as tall as their width. All of these relationships were highly significant (\( P=0.000 \)), and regression equations fit the data well; the lowest \( R^2 \) value was 0.687 for Yanchep data (Figure 4.3).

Figure 4.3: Linear regression equations of plant shape (relationship between plant width and height) at Ellensbrook, Shoalwater and Yanchep, with significance table.

<table>
<thead>
<tr>
<th>Site</th>
<th>( t )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td>8.522</td>
<td>0.000</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>11.862</td>
<td>0.000</td>
</tr>
<tr>
<td>Yanchep</td>
<td>41.706</td>
<td>0.000</td>
</tr>
</tbody>
</table>
4.3.2.4 Size distribution

There was no significant relationship between stem diameter and distance along transect for Ellensbrook data. At Shoalwater and Yanchep, cubic models gave the best approximations to data; in both cases relationships were highly significant, but low $R^2$ values showed that the models did not fit the data well. At Yanchep, size increased to a maxima at 50m, followed by a decrease. At Shoalwater, the trend was a decline in size, however the pattern was complex (Figure 4.4).

![Graph A. Shoalwater](image)

![Graph B. Yanchep](image)

Figure 4.4: Size distribution of *L. laevigatum* along transects with cubic model curve estimation at (A) Shoalwater and (B) Yanchep. NB a single individual (stem diameter 120cm) has been omitted from Shoalwater data for finer resolution of remaining data points.
4.3.2.5 Microhabitat

A commonly observed pattern was the occurrence of *L. laevigatum* in areas of moderate shade. This included partial shading by other *L. laevigatum* individuals, or by plants of other species. In both cases the shade-provider appeared older than the *L. laevigatum* being shaded. *Banksia* was often the shade-provider at Yanchep (where one *B. menziesii* had five mature *L. laevigatum* growing under its canopy) and at Beeliar Regional Park. At Ellensbrook and Shoalwater, a range of species provided shade (*e.g.*, *Macrozamia reidlei*: Plate 4.1).

Plate 4.1: Two young *L. laevigatum* plants at Ellensbrook establishing in the shelter of foliage of *Macrozamia reidlei*. 
4.4 DISCUSSION

4.4.1 Current and potential geographic distribution

Because of the strong similarities between the distributional limits of *L. laevigatum* and the 400mm rainfall isohyet, it seems that a minimum yearly rainfall of approximately 400mm is limiting the species' geographic distribution. The few occurrences to the north-east of (but close to) this isohyet, indicate that the species is able to survive on slightly less than 400mm annual rainfall, but these locations are marginal for the species. This is consistent with the observation that in this zone of the wheatbelt (near Tammin), *L. laevigatum* is naturalised in some locations, but is barely spreading (M. Ochtman personal communication). In eastern Australia also, *L. laevigatum* has not spread further inland than the 400mm annual rainfall isohyet (BOM 2002). *L. laevigatum* is found on a variety of soil types with various underlying substrates, therefore soil does not appear to restrict its range. Based on the assumption that rainfall limits distribution, the potential geographic range of the species is substantial, extending around the coastline some 1500 kms between Kalbarri on the west coast and beyond Cape Arid on the south coast, and inland beyond Narrogin in the wheat belt.

4.4.2 Invasion and disturbance

4.4.2.1 Extreme disturbance

The importance of low and intermediate levels of soil and vegetation disturbance for seedling establishment have been discussed (Chapter 3). *L. laevigatum* appears to be well adapted also to stronger types of disturbance, such as vegetation clearance or mining. For example, the Mount Brown area of Beeliar Regional Park (south of Perth) was cleared around 1920 for a housing estate but development did not eventuate (Dooley et al. 2001). *L. laevigatum* has subsequently become dominant, forming dense thickets over the western hillside (personal observation). Previous limestone quarry areas in South Fremantle are also heavily infested, with little indigenous vegetation (personal observation). The ability of *L. laevigatum* to colonise extremely disturbed sites is consistent with its ability to establish in exposed coastal locations such as dune blow-outs. *L. laevigatum* is also colonising the dune blow-out behind Ellensbrook Homestead.
4.4.2.2 Roadside disturbance

Despite the bias towards roadside locations in the data, roadside sightings were common in absolute terms. Many roadside populations appear to be naturalised, consisting of seedlings (Plate 4.2) and/or mature plants. Roadside disturbance provides:

(1) Disturbed, bare soil for establishment, caused by road edge grading,

(2) Additional nitrogen, phosphorus and moisture from roadside runoff (Trombulak and Frissel 2000).

The presence of lone seedlings suggests that road vehicles are a significant means of dispersal for the species. Two mechanisms can be suggested. Firstly, localised air currents initiated by passing vehicles are probably responsible for short distance population spread along road verges, by lifting and transporting the winged seed. Secondly, longer range dispersal by vehicles is probably achieved through seed adhering to vehicles. Lonsdale and Lane (1991) sampled seeds carried by vehicles entering Kakadu National Park, by vacuuming the air intakes and outer surfaces of car bodies. Seventy percent of vehicles were carrying seeds, including seeds of environmental weeds. This mode of transport is a realistic possibility for *L. laevigatum*, due to its small seed size. In the Bremer Bay region, a local anecdote tells of a fisherman who frequently parked his vehicle under *L. laevigatum*, and therefore is said to be responsible for the unintentional spread of *L. laevigatum* in nearby coastal areas in the 1970s (Jeffery 1999). Many infestations line the Albany Highway heading south-east away from Perth and north-west away from Albany. These are most likely to be due to vehicles transporting seed from these urban areas, which both support large numbers of *L. laevigatum* either as weeds or in residential gardens.

Plate 4.2: *L. laevigatum* seedlings establishing along a road edge near Albany.
Burrell (1981) postulated that disturbed topsoil, a temporary increase in soil phosphorus level and an abundant seed supply promote the expansion of *L. laevigatum* into heathland, factors which she suggests are best met by fire. Roadside disturbance generally supply these requirements, which is a possible explanation for the prevalence of roadside populations of *L. laevigatum*.

### 4.4.2.3 Fire and invasion density

High density recruitment is expected to occur after fire because favourable conditions for establishment are created: disturbed soil and vegetation, increased soil nutrients and an abundant seed supply due to seed release by the mature population (Chapter 3). At Ellensbrook and Shoalwater, invasion densities are two orders of magnitude lower than at Yanchep and Ellensbrook thicket. Site histories could explain this observation. Fire has been suppressed at Shoalwater since the dunes were created, and Ellensbrook study site was probably too far from the Homestead to be affected by any seed released from Homestead *L. laevigatum* populations during the 1970 fire. Invasion at these sites must have arisen from the spontaneous seed release (Chapter 3) that occurs in the absence of fire. In contrast, the land on which Ellensbrook thicket has grown, and the road edge at Yanchep both had an adjacent seed source when they were burned (Table 4.4). These infestations are probably even-aged, post burn recruits. Additionally, Ellensbrook thicket has grown on land that was once cleared for pasture, and the road edge thicket at Yanchep was probably initially cleared during road construction.

<table>
<thead>
<tr>
<th>Site</th>
<th>Seed source</th>
<th>Fire?</th>
<th>Plants/m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td>350m away</td>
<td>1970</td>
<td>0.045</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>Adjacent</td>
<td>Suppressed</td>
<td>0.060</td>
</tr>
<tr>
<td>Yanchep</td>
<td>Adjacent</td>
<td>1991</td>
<td>1.320</td>
</tr>
<tr>
<td>Ellensbrook thicket</td>
<td>Adjacent</td>
<td>1970</td>
<td>3.000</td>
</tr>
</tbody>
</table>

(Thicket only: 10.515)

Studies in Victoria have noted high densities of *L. laevigatum* after burns (Hazard and Parsons 1977; Molnar et al. 1989). Hazard and Parsons (1977) postulated high densities close to the coast due to an abundant seed supply at the time of fire. Burrell (1981) postulated that an abundant seed supply, along with fire, were important in invasion.

Molnar et al. (1989), and Bennett (1994) have noted that invasion occurs in the absence of
fire. Therefore, invasion by *L. laevigatum* can occur in the presence or absence of fire. However, it appears that the two factors: fire and proximity of seed-bearing plants, control the density at which *L. laevigatum* invades; the combination of fire and an adjacent seed source leads to immense invasion densities. Although the results of each of the Victorian studies support these conclusions, the authors have not emphasised them.

**4.4.3 Pattern of Invasion**

**4.4.3.1 Density distribution**

At the sites examined, *L. laevigatum* distribution conforms to the hypothesis that density is highest close to the main invasion. This reflects *L. laevigatum*’s adaptation for wind dispersal. For any dispersal mode, areas close to the seed source are subject to a denser seed rain than areas further away (Watkinson 1997). Providing there is no large scale gradient of habitat suitability along the transect, it is assumed that lower seed rain further from the seed source will be reflected in lower densities of plant establishment, as was observed. Notably, infestations at Ellensbrook and Yanchep were spreading to the north-east, in the direction of prevailing coastal winds in summer (BOM 2002). At Shoalwater, the narrow east-west width of the sites removed the easterly component of spread, and plants appeared to be spreading to the north. Only a single individual was found to the west of the main stand of *L. laevigatum*.

Fire and an adjacent seed source lead to extreme densities of *L. laevigatum* (Section 4.3.4.3). However, where one or both of these features is absent, as at Ellensbrook, Shoalwater and away from the main invasion at Yanchep, density appears to be controlled strongly by the availability of microsites which provide bare soil and moderate shade (Chapter 3). This pattern accounts for some of the variability associated with density decline along transects. In exposed, post-fire conditions at Yanchep, surviving *Banksia* would provide the only available shelter, creating islands of favourable microsite conditions through providing moderate shade. At Ellensbrook and Shoalwater, existing vegetation provides some shelter on its margins. In these microsites, the survival from a given seed rain density may be enhanced, leading to higher plant densities than would be expected based solely on declining seed rain over a uniform habitat along the transect. Therefore, patchiness in the distribution of mature *L. laevigatum* is probably due to patchiness in suitable microsites for establishment.
4.4.3.2 Size distribution

Problems associated with size-class analysis as a surrogate for age were encountered during this study. The small size of plants in the thicket at Yanchep appears to be an indicator of their condition rather than their age. There is evidence of intense intraspecific competition (stems are commonly less than 100mm apart), leading to suppression of growth and reproduction, and density dependent mortality (some plants are dead). Surviving plants are depauperate of foliage and none are reproductively mature. Other studies support these possibilities: Hazard and Parsons have also postulated density dependent mortality in thickets of *L. laevigatum* (Hazard and Parsons 1977); Burrell (1981) has observed suppression of growth and reproduction for nine years in *L. laevigatum* seedlings. A comparison with Ellensbrook thicket supports self-thinning due to intraspecific competition: Ellensbrook thicket is approximately 20 years older, one quarter less dense and plants are much larger. If the thickets at Ellensbrook and Yanchep arose as post-burn recruits as proposed, the Yanchep thicket may follow the same developmental path, with growth suppression declining as self-thinning operates.

In contrast, the stem diameter of *L. laevigatum* in the indigenous vegetation at Yanchep and at the other two sites is probably a reasonable indicator of plant age. Although plants were commonly clumped (Section 4.3.2.5), clumps were small and plants were healthy, foliose and reproductively mature. At Ellensbrook there was no significant relationship between plant size and transect distance; at Yanchep and Shoalwater the curve regression models did not fit the data well. Larger (presumably older) plants are almost just as likely to be found far away from the main invasion as close to it. Therefore, invasion sequence is not predictable in space or time. Rather, it appears to be controlled by stochastic factors, being mainly the chance of seed falling in a suitable microsite. Consequently, the eradication of *L. laevigatum* from bushland will require careful searching for individuals, considering the irregularity of the pattern and the difficulty to predict locations.

4.4.4 Vegetation communities at risk

Among native vegetation, heathlands and woodlands were most commonly reported as affected by invasion by *L. laevigatum*. These vegetation communities may or may not have a closed understorey, but have canopies absent (heathland) or sparse (woodland). *L. laevigatum* establishes best in moderate light (Chapter 3); woodland trees such as *Banskia*, Tuart (*Eucalyptus gomphocephala*), and Jarrah (*Eucalyptus marginata*) provide moderate
light through having low levels of foliage projective cover. Forest and open forest appear to be less susceptible, probably because the lower levels of light able to enter through canopies of forest or open forest structure allow fewer opportunities for *L. laevigatum* establishment.

A second requirement for *L. laevigatum* establishment is a loose, bare substrate. In either heathland or woodland, this requirement is most likely to be met in conjunction with lowered foliage projective cover of the lower stratum. Additionally, heathlands in urban areas are likely to be subject to anthropogenic disturbance which creates gaps in the heath cover, available for *L. laevigatum* establishment. In both cases, survival will depend on seed falling in a microsite which provides adequate light but moderate shade (Chapter 3).

Therefore, vegetation communities most at risk by *L. laevigatum* include those with open canopies (heathland and woodland). Within these communities, disturbance types which disrupt the vegetation and soil will promote invasion by *L. laevigatum* by increasing the availability of suitable microsites. Disturbance types could include fire, walk trails, rabbits and kangaroos.

4.4.4.1 Morphology and vegetation type

Preliminary field observations indicated that *L. laevigatum* shape was controlled partly by competition factors, with short, multi-stemmed growth occurring where vegetation (*L. laevigatum* and other species) is sparse, and tall, narrow, single stemmed growth occurring where resource competition is greater. At Shoalwater, vegetation is sparse and low, with presumably little competition for light. *L. laevigatum* at that site is short and wide. (Wind pruning may add to this effect). Plants at Yanchep were tall and thin, as they grew amongst relatively dense heath vegetation, 1.8m tall *D. sessilis* and in light competition with each other and with *Banksia*. At Ellensbrook, the relationship was intermediate, reflecting intermediate vegetation density. These observations indicate that *L. laevigatum* is able to etiolate in response to competition. The various growth forms of *L. laevigatum* in response to habitat reflect its opportunistic nature.

Therefore, the absence of significant relationships between competition index and morphological measurements of plants is probably due to: (1) a lack of resolution in the competition index (only three levels were assigned); and (2) the difficulties associated with
assigning competition index when competition level changes in time with growth and death of surrounding plants.

4.4.5 Establishment and distribution

Invasion can proceed in the presence or the absence of fire. However, the presence or absence of fire, along with the proximity of the seed-bearing plants determines the density and rate at which invasion proceeds.

Fire gives rise to an immensely high density of regenerating *L. laevigatum* at and immediately adjacent to the seed source. The resultant high density thicket is subject to intense intraspecific competition, with resultant suppression and density dependent mortality. Invasion after fire is immediate, resulting from post-burn recruitment from seed released upon fire. The high density of the thicket provides protection from exposure in the open landscape after fire; individuals not amongst this thicket survive preferentially in moderately sheltered locations, under fire tolerant species such as *Banksia*.

In the absence of fire, invasion by *L. laevigatum* relies on spontaneous seed release, the chance provision of a suitable seed bed (loose substrate) and site (with moderate shade) for establishment. Therefore, invasion is much slower and occurs at much lower densities than after fire. The sequence of invasion is not easily predictable in space.

The estimated potential geographic range of *L. laevigatum* is large. Within this range, invasion is most likely to occur in human-modified locations such as road verges or cleared land. Within bushland, more open vegetation structures are more likely to be invaded. Small scale disturbances in good condition bushland are sufficient to sustain some level of invasion by *L. laevigatum*. However disturbance which creates additional patches of bare soil will enhance establishment opportunities and are therefore likely to increase invasion densities.
CHAPTER 5: IMPACTS OF INVASION

5.1 INTRODUCTION

5.1.1 Impacts of environmental weeds

The scale of impacts of environmental weeds on ecosystems varies from minor to enormous. Invasion can alter composition, physical structure and/or phenology of the invaded community (Woods 1997). Faunal and microbe populations can be affected directly or through altered vegetation characteristics (Schiffman 1997). At a broader scale, plant invasions can affect primary productivity, ecosystem stability, disturbance types and regimes, rates or pathways of successional recovery from disturbance, and other ecosystem processes. Such changes are brought about by alteration of flows of energy, water and nutrients through the ecosystem (Walker and Smith 1997). These modifications can be summarised as impacts upon species diversity and ecosystem function.

Walker and Smith (1997) summarised the potential effects of an invasive plant species on these ecosystem properties and processes (Figure 5.1). The invader can impact upon, and be impacted by, the disturbance regime, primary productivity, community dynamics and nutrient and water flows within an ecosystem. These four factors also interact with each other, with positive, negative or neutral effects and feedbacks (Walker and Smith 1997). Invasions do not always reduce species richness. The diagram is an effective, concise way to conceptualise the potential impacts upon invasion, and the potential for interactions is depicted. However, it tends to conceal how multifaceted and intricate these interactions can be.
A variety of specific impacts have been documented as the result of plant invasions, each of which can be viewed at different levels. For instance, biotic impacts may result from: (1) direct interaction with the invader (e.g., if the invader is a parasite); (2) from less direct interaction through competition for resources; and (3) from habitat modification by the invader that makes the landscape more or less suitable for various organisms. The distinction between these levels of interaction can be blurry. For example, an invader "winning" competition with an indigenous analogue may allow the invader to dominate, and subsequently alter microhabitat and impact negatively on an additional suite of species.

Plant invasions can have negative or positive effects on indigenous fauna. Expansion of L. laevigatum and A. sophorae into heath vegetation and Wilson's Promontory is believed to threaten populations of Pseudomys novaehollandiae (New Holland Mouse; endangered in Victoria). This species requires understorey vegetation which is apparently suppressed upon L. laevigatum invasion (Atkin and Quin 1996; Quin and Williamson 1996). In Banksia woodlands of south western Australia, ground cover environmental weeds reduce habitat suitability for reptiles which forage between shrubs (How and Dell 1989). In contrast, environmental weed invasion have increased habitat suitability of vegetation for
several bird species, and the acceptance that eradication of these plants would negatively affect bird populations (Schiffman 1997). *Austroassiminia letha* (Cape Leeuwin Freshwater Snail) is known only from Cape Leeuwin and Ellensbrook, Western Australia (CALM 2002). It inhabits *Rorippa nasturtium-aquaticum* (Watercress; an alien species) in Ellens Brook, precluding removal of the watercress, and complicating attempts to control nearby infestations of *Zantedeschia aethiopica* (Arum lilies; K. Ninyett personal communication).

Environmental weeds can alter fire regimes and intensities, with the majority of documented cases increasing fire frequency and intensity (D'Antonio 2000). Invasion of bushland in Kings Park, Western Australia by the African grass *Ehrharta calycina* has been found to increase fire frequency, in a cycle which further enhances invasion by *E. calycina* (B. Dixon personal communication). *Myrica faya* (Fayatree) is an aggressive invader of Hawaiian upland and lowland ecosystems. Dense monospecific stands form with no regeneration of indigenous or alien species. Changes to primary productivity, soil nitrogen, earthworm populations and primary succession after volcanic eruptions have been reported, and the dense forests it forms possibly influence wind dispersal of indigenous species (Walker and Smith 1997). Invaders with such capacity to alter ecosystem structure and function have been termed transformer species.

Reviews of current knowledge on impacts of plant invaders are available elsewhere (e.g., Huenneke 1997; Schiffman 1997; Walker and Smith 1997; Woods 1997; D'Antonio 2000). In general, the potential impacts of plant invaders on natural ecosystems are many and varied. The complex interactions which occur make it difficult to draw generalisations about their effects, and to predict the impacts of invasion by particular species.

### 5.1.2 Cause and effect in assessing impacts

Because plant invasion is often preceded by some novel or altered disturbance regime, it may be difficult to assign causes to changes in community composition. Observed effects may be the ecological effects of invasion, or the consequence of the altered disturbance. Even communities which are apparently unaffected by novel disturbance or a new disturbance regime may have been affected in a subtle way (Woods 1997). The limited resources available for conservation mean that decisions must be made on priority species for control, based on the severity of their impacts on natural systems. It is important that
such decisions are not based on preconceived notions or bias, but rather on sound ecological data (Morrison 1997; Edwards 1998). Unfortunately, there are relatively few studies of the community level consequences of invasion; most studies of invasive species tend to be autecological, focusing on characteristics such as biogeography or life history of the invader (Hobbs and Humphries 1995; Woods 1997). Alternatively, statements about impacts are sometimes made based on descriptive or anecdotal evidence (Mack 1996, in Edwards 1998).

This appears to be true for studies of *L. laevigatum*. Reports of methodical investigation of its impacts on vegetation communities are apparently absent from the literature. Researchers seem to have considered its impacts on species richness great enough and obvious enough not to require quantification, citing mainly Burrell (1981), or papers which cite Burrell (1981), to support statements about the elimination or suppression of other species by the dense canopy. However Burrell’s original statement was based on casual observations rather than structured research: "Apparently, heath species are eliminated after invasion by *L. laevigatum*" (p. 748). However, the confidence in assigning an "impact" to a plant invader increases with the number of times that the impact is observed upon invasion (Morrison 1997). This is probably the case for declines in species richness associated with *L. laevigatum*. Whether or not declines in species richness associated with *L. laevigatum* invasion are caused by invasion, by disturbance which allows its invasion, or by a combination, species richness declines are of concern, justifying research for management.

5.1.3 Approaches to studying impacts

In reviewing the literature, Woods (1997) found three main methods to support claims for impacts of invasive plants. These include field observations ("snapshots"), extended observations of changes occurring during the process of invasion, and experimental manipulations to test hypotheses about the effects of invaders. The tests are arranged in order of their power to provide unambiguous information about the presumed impacts of the invader. Unfortunately they are also arranged in order of increasing difficulty to perform, so more rigorous tests are also rarer in the literature (Woods 1997). Burrell’s (1981) research falls into the third (most rigorous) category. However the hypotheses relate to requirements for establishment of *L. laevigatum* rather than its impacts of invasion.
The development of the sampling methods BACI by Green (1979) and Beyond BACI by Underwood (1991) embodies the recognition that simple sampling methods with no replication in time and or space are unreliable in detecting environmental impacts. These methods require sampling Before and After the impact has taken place, and the use of Control and Impacted sites (BACI) so that any detected changes can be more confidently attributed to the process in question, rather than to natural variability in the system. A major difficulty in applying such experimental designs is that (particularly in the case of environmental weeds) the impact has already occurred before there is the impetus to sample (Morrison 1997). It can be difficult to predict which sites will be invaded, and when. For plant invaders, before-after studies may require many years to complete, but funding, logistical constraints or immediate requirement of data for management may limit the application of such a sampling design.

5.1.4 The importance of assigning cause

If a plant invasion appears to be having a devastating effect on an ecosystem, it is tempting to rapidly implement management for removal of the species, before there is any study of interactions within system. In support of this approach, management costs of environmental weeds can be lower when the problem is immediately addressed. Therefore, this precautionary approach can save time, money and bushland. However, there are incentives behind establishing the causes and impacts of invasion before any management actions are executed.

Direct management such as weeding or herbicide application may be useless or even counterproductive, if community change and invasion are the parallel results of anthropogenic disturbance rather that the former being caused by the latter (Woods 1997). Where the management approach attacks the effect of environmental degradation rather than the cause, the door is open for complications such as reinvasion by successive alien plants each time one alien is removed (Edwards 1998). In this way, adequate study of an environmental weed prior to management decisions may save time, money and ecosystems over the long term.

Simple correlations between classes of facts may be useful in managing environmental weeds, without being sure of cause and effect. However, differences between the biotas and landscapes at different sites can make observed relationships invalid, and may lead to
inefficient or inappropriate management decisions. If causality can be established, there can be more confidence in wider application of the ecological information, and the chances of management mishaps are reduced.

5.1.5 Ideal versus real: difficulties of proving impacts

Faced with logistical difficulties of accounting for every source of variability in the system, many assessments of the impacts of plant invasions are not unambiguously supported. Instead, the results of a snapshot study can be combined with other sources of knowledge to make deductions about what the impacts probably are. For instance, chronosequence analysis can be used to infer the impacts of invasive species on ecosystems. Comparisons are made between areas with high abundance of the invader and areas free from the invader, and the assumption made that the two areas were similar prior to invasion (Woods 1997). In applying this method, the possibility that the two areas may not have been similar must be considered. Site records and aerial photographs and field evidence (such as charcoal for fire) can be useful in confirming similarities. Ideally, this approach should be used as a way to form testable hypotheses about invasion impacts.

5.1.6 Aims

Because the current study is the first on the species in Western Australia, an approach which generates hypotheses to guide further research is deemed appropriate. Chronosequence methods have been used, because time limitations did not allow monitoring of before and after effects of invasion. Additionally, the literature reviewed suggested only light reductions by *L. laevigatum* as a limiting the survival and recruitment of other species. Field observations suggested that invasion by *L. laevigatum* might alter other important factors. The objective is to highlight potential mechanisms by which *L. laevigatum* could effect alteration of plant communities, in relation to soil and litter variables.
5.2 METHODS

5.2.1 Community composition and ecosystem variables

5.2.1.1 Sampling design

Along each transect established for *L. laevigatum* sampling (Chapter 4), three 5 × 5m quadrats were set up, lying at 0-5m, 45-50m and 95-100m along the transect line. Distance was planned to correspond with invasion level, so that invasion zone, ecotone and indigenous vegetation would be sampled. Notes were taken on floristics, disturbance evidence and vegetation structure, and samples of vegetation litter and soil were taken (Table 5.1). Where possible, the taxa of dead plants were noted.

Table 5.1: Summary of field notes and soil and litter samples taken for each quadrat.

<table>
<thead>
<tr>
<th>Field notes and samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>- Crown cover of each vascular plant species (percent of the quadrat covered by each species)</td>
</tr>
<tr>
<td>- Plant condition (per species or individual; where applicable)</td>
</tr>
<tr>
<td>- Foliage projective cover (foliage density rather than total area covered; provides an indication of light penetrating the canopy)</td>
</tr>
<tr>
<td>- Evidence of disturbance (e.g., rabbit diggings/faeces, dead vegetation, ants nests)</td>
</tr>
<tr>
<td>- Vegetation litter samples</td>
</tr>
<tr>
<td>- Topsoil samples</td>
</tr>
</tbody>
</table>

5.2.1.2 Plant identification

Specimens of unrecognised plant species were collected. These were identified by consulting relevant floras (Marchant *et al*. 1987; Bennett and Dundas 1988; Rippey and Rowland 1995; Corrick and Fuhrer 1997; Hussey *et al*. 1997; Western Australian Herbarium 1998; Paczkowska and Chapman 2000), the Western Australian Herbarium public collection and plant experts (J. Stevens, A. Bellman and G. Keighery).
5.2.1.3 Vegetation litter collection and processing

Within each 5x5m quadrat, four vegetation litter samples were collected from randomly placed 250x250mm quadrats, and stored in paper bags. In the laboratory, samples were sieved (2mm) to remove soil inadvertently collected, then dried in paper bags to a constant weight in a drying oven (80°C for at least 48 hours). Litter weight was calculated as gross dry weight (including paper bag), minus the average weight (n=10) of an oven dried paper bag.

5.2.1.4 Soil collection and processing

Four topsoil samples (0-5cm depth) were collected from the same random points as vegetation litter, using a trowel marked to 5cm. Four soil samples from each quadrat were pooled and stored in a sealed plastic snap lock bag. These were weighed using a portable electronic balance within 24 hours of collection to determine gross wet weight (including bag), and stored with bags open to allow drying to discourage growth of organisms which may have promoted changes to soil pH. In the laboratory, soil samples were transferred to paper bags, dried to constant weight under the same conditions as vegetation litter, then weighed.

**Soil moisture**

Net soil wet weight was calculated as the gross wet weight (including bag) minus the weight of each empty plastic bag after soil was transferred. Net soil dry weight was calculated as gross post-drying weight (including bag), minus the average weight (n=10) of an oven dried paper bag. Soil moisture content was determined as the loss of mass upon drying, divided by net wet weight. Oven dry soil was homogenised and sieved to remove particles greater than 2mm and subsequent analysis was performed on this fraction.

**Content of organic matter and calcium carbonate**

Soil samples of known weight (approximately 20g; accurate to 3 decimal places) were placed in crucibles of known weight and heated to 500°C for 3 hours in a muffle furnace. Crucibles were transferred to a dessicator for cooling, then reweighed. Samples were returned to the furnace and heated to 950°C for 1 hour, cooled again in the dessicator and reweighed. For both treatments, timing began when the furnace reached the desired temperature. Content of organic matter or calcium was calculated as:
Percent organic matter or calcium = \( \frac{\text{initial weight} - \text{post-ignition weight}}{\text{initial weight}} \)

where weight after 500°C ignition was used for organic matter determination and weight after 950°C was used for calcium carbonate determination.

To evaluate the accuracy of these methods, and to ensure that position in the furnace had no effect on loss of mass during the heating period, three replicates of three soil samples were placed at varying positions in the furnace for each batch, and the results compared.

**Soil pH and salinity**

For each sample, 50mL of deionised water was added to 10g of oven dry soil in a 75mL sample jar, shaken ten times and placed on an inverting machine for 10 minutes. Samples were then removed, shaken again and allowed to settle for 10 minutes. Soil pH and conductivity were measured simultaneously using a WTW multiline pH and conductivity meter with dual probes. The first pH reading to remain stable for 20 seconds was recorded (in all cases conductivity stabilised immediately). To ensure that measurements were accurate, the first two samples in each of the four batches were measured again after all samples had been processed, and the results compared with the initial measurements.

**Soil water repellence**

The Molarity of Ethanol Droplet (MED) test (King 1981; Moore and Blackwell 1998) was used to rate the water repellence of soil samples. Three replicate droplets of ethanol solutions of varying concentrations (0M to 4M, with gradations of 0.5M) were placed onto soil samples of 1cm depth. The lowest molar concentration for which all replicates were absorbed by the soil in 10 seconds was recorded.

5.2.2 Photosynthetically active radiation

A Li-Cor Integrating Photometer (LI-188B) was used to measure Photosynthetically Active Radiation (PAR) at ground level. All readings used a 10-second integration time (average PAR over 10 seconds), and were taken between 10am and 2pm to reduce any impact of sun angle. Sunny days were chosen to minimise the effects of cloud cover on measurements. Ellensbrook was the only site where clouds appeared; when cloud covered the sun, readings were postponed several minutes until clouds had passed.
To compare PAR levels in invaded areas with those in the indigenous vegetation community, twenty readings were taken in each area. These were alternated (10 "invaded" then 10 "unaffected" readings, repeated) to minimise effects of changes in light levels with time of day. Points for readings were chosen by taking a random number of steps in a random compass direction. For "invaded" readings, if this method returned a point which was outside of the infested area, the method was repeated until a suitable point was returned.

To compare the PAR attenuating properties of different plant species, six common species at each site were chosen, and six light readings taken at different points underneath a typical individual. Where the life form of a species was small (e.g., *Olearia axillaris* individuals were smaller than *Acacia rostellifera* individuals at Shoalwater), three readings were taken underneath each of two individuals.

5.2.3 Data analysis

5.2.3.1 Soil, litter, floristics and foliage projective cover

Data collected from quadrats were intended to be analysed using one way Analyses of Variance (ANOVAs) with distance along transect as treatment (surrogate for invasion level), and each transect as a replicate. *L. laevigatum* density generally decreases with distance from invasion source (Chapter 4), however this pattern occurs at a broader scale than the quadrat scale, and is extremely variable. The surrogate did not function as planned. No quadrats at 50m contained *L. laevigatum* cover at any site. Yanchep was the only site where all three quadrats at 0m lay within high *L. laevigatum* cover; at Shoalwater only two quadrats had high cover, and at Ellensbrook only one did. As an alternative for data analysis, quadrats with 0-15% *L. laevigatum* cover were classed as "unaffected" and those with 65-100% cover were classed as "invaded". (No quadrats had *L. laevigatum* cover between 16 and 64%.) Comparisons were made between unaffected and invaded quadrats within sites. Consequently, there were twice as many replicates of unaffected quadrats as invaded quadrats at Yanchep, at Shoalwater only two quadrats were invaded compared with seven unaffected and at Ellensbrook there was no replication of unaffected quadrats.

Therefore, no data conformed to the assumptions of parametric statistics. The non-parametric Mann-Whitney U test was applied for paired comparisons between invaded and
unaffected quadrats within sites. Low statistical power due to low replication was a feature of all comparisons, so the chance of detecting differences was low. Therefore, graphical representations are also presented, showing standard error to indicate trends in addition to significant differences. Additionally, the chance of detecting a difference was considered more important than the risk of making a type I error (rejecting a null hypothesis when it is true). This is because interpretation of results and postulating impacts has been strictly subject to other evidence that is supportive of impacts. Therefore, \( \alpha \) has been set at 0.10.

5.2.3.2 Community composition

Cluster analysis, a classification technique, was used to group quadrats with similar species composition. Multi-dimensional scaling, an ordination technique, was used to represent community similarity between quadrats in two-dimensional space. These methods were chosen (over techniques such as SIMPER) because they treat each quadrat separately, without having to assign a factor (i.e., cover) to define groups of observations. Assignment of factors was avoided because of the failure of distance along transect to be an adequate surrogate for cover of \( L. \) laevigatum, and the accompanying problems of uneven replicate number. Species recorded as dead were excluded from the analysis.

5.2.3.3 Photosynthetically active radiation

Various methods of transformations were unsuccessful to overcome unequal variances between infested and natural PAR readings. Data comparing PAR levels underneath common species were not normally distributed, despite transformations attempted. The Mann-Whitney U test was applied for paired comparisons between invaded and natural PAR readings, and between \( L. \) laevigatum and common species.
5.3 RESULTS

5.3.1 Community composition and ecosystem variables

5.3.1.1 Species abundance and richness

Cover of indigenous species was significantly lower in infested quadrats compared to unaffected ones at Shoalwater and Yanchep. The same pattern was true at Ellensbrook. Indigenous species richness was marginally significantly lower in invaded quadrats at Yanchep and lower at Ellensbrook. There was no apparent difference at Shoalwater. Alien species cover and richness was lower in invaded quadrats at Ellensbrook and Shoalwater, the difference was significant for richness at Shoalwater. The opposite pattern occurred at Yanchep, with invaded quadrats supporting higher abundance and variety of alien species (Table 5.2, Figure 5.2). The Simpson and the Shannon-Weiner diversity indices were applied to data in the same way, with results uninformative due to the low number of species recorded from each quadrat (Appendix).

At Yanchep, *Petrophile serruriae, Acanthocarpus preissii, Acacia saligna, Jacksonia sericea* and *Banksia attenuata* were found dead or moribund within invaded quadrats. Other indigenous species, including *Conostylis aculeata, Mesomelaena pseudostygia,* and *Trachymene pilosa* appeared in good condition in invaded quadrats. At Shoalwater, several shrub skeletons were observed. These were possibly *L. laevigatum,* however the state of decay made identification unreliable.

**Table 5.2: Paired comparisons between invaded and unaffected quadrats with respect to crown cover and richness of indigenous and alien species.** * denotes significant difference ($\alpha=0.10$).

<table>
<thead>
<tr>
<th>Site</th>
<th>Indigenous species</th>
<th></th>
<th>Alien species</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cover</td>
<td>Richness</td>
<td>Cover</td>
<td>Richness</td>
</tr>
<tr>
<td></td>
<td>U</td>
<td>p</td>
<td>U</td>
<td>p</td>
</tr>
<tr>
<td>Ellensbrook</td>
<td>0.000</td>
<td>0.121</td>
<td>2.000</td>
<td>0.429</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>0.000</td>
<td>0.040*</td>
<td>6.5</td>
<td>0.876</td>
</tr>
<tr>
<td></td>
<td>0.000</td>
<td>0.019*</td>
<td>1.5</td>
<td>0.051*</td>
</tr>
</tbody>
</table>

73
Figure 5.2: Paired comparison between invaded and unaffected quadrats with respect to cover of (A) indigenous and (C) alien species, and species richness of (B) indigenous and (D) alien species. inv.=invaded, unaff.=unaffected. * denotes significant difference.

5.3.1.2 Community composition

Community composition of indigenous species in invaded quadrats was distinctly different compared with unaffected quadrats at Yanchep. At Shoalwater, the same effect was apparent but less distinct, and at Ellensbrook the invaded quadrat was grouped with unaffected quadrats, albeit on the margin. At Yanchep and Shoalwater, invaded quadrats were similar in composition to each other (Figure 5.3).
5.3.1.3 Foliage projective cover

Foliage projective cover was significantly greater in invaded quadrats compared with unaffected quadrats at all sites. Mean foliage projective cover was highest at Ellensbrook and lowest at Yanchep (Table 5.3).
Table 5.3: Paired comparisons of foliage projective cover between invaded and unaffected quadrats. All canopy species are included.

<table>
<thead>
<tr>
<th>Site and L. laevigatum cover</th>
<th>Mean foliage projective cover</th>
<th>Standard error</th>
<th>Mann-Whitney U and associated p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Invaded</td>
<td>80</td>
<td>-</td>
<td>U=0.000</td>
</tr>
<tr>
<td>Unaffected</td>
<td>40</td>
<td>4.5</td>
<td>p=0.106</td>
</tr>
<tr>
<td>Shoalwater</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Invaded</td>
<td>70</td>
<td>0</td>
<td>U=0.000</td>
</tr>
<tr>
<td>Unaffected</td>
<td>0</td>
<td>0</td>
<td>p=0.005</td>
</tr>
<tr>
<td>Yanchep</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Invaded</td>
<td>61.6</td>
<td>13.64</td>
<td>U=0.000</td>
</tr>
<tr>
<td>Unaffected</td>
<td>5.8</td>
<td>2.51</td>
<td>p=0.020</td>
</tr>
</tbody>
</table>

5.3.1.4 Soil and litter

In soil organic matter and calcium carbonate determinations, replicates of samples in all four batches returned similar results (±0.03%), so the central result was retained and non-replicated measurements were assumed to be satisfactorily accurate. In pH determinations, all repeated measurements returned readings within 5$\mu$S and 0.1 pH units of the initial measurements, so results were considered acceptably accurate.

Litter weight was significantly higher in invaded than in unaffected quadrats at Shoalwater and Yanchep. The same pattern was observed at Ellensbrook. Visual examination of leaf litter samples used in the analysis confirmed that the bulk of leaves collected from invaded quadrats were L. laevigatum leaves. Soil moisture was significantly higher at Yanchep, higher at Shoalwater, but lower at Ellensbrook in invaded quadrats than unaffected ones. Invaded quadrats had significantly higher soil pH at Shoalwater and Yanchep than unaffected quadrats; there appeared to be no difference (significant or otherwise) at Ellensbrook (Figure 5.4).

Soil organic matter was significantly higher in invaded quadrats at Yanchep, significantly lower at Shoalwater and apparently unchanged at Ellensbrook. Soil water repellency was significantly higher in invaded quadrats at Shoalwater, appeared to be higher at Ellensbrook and similar at Yanchep (Figure 5.4). Soil calcium and salinity were significantly higher in invaded quadrats than unaffected ones at Yanchep (both variables: U=0.00; p=0.020); there was no significant difference at other sites.
5.3.2 Photosynthetically active radiation

At all sites invaded readings were significantly lower and much less variable compared with readings taken at random points in the indigenous vegetation (Figure 5.5; Table 5.4). Pairwise comparisons between *L. laevigatum* and other species showed that *L. laevigatum* gave significantly lower PAR readings than *Agonis flexuosa* and *Hibbertia cuneiformis* at Ellensbrook, and than all species except *Acacia rostellifera* at Shoalwater. However, it gave significantly higher readings than *Adenantheros sericeus* at Little Grove (Appendix; Figure 5.5). Thus, although the mean PAR values underneath *L. laevigatum* at each site are among the lowest, they are not consistently the lowest.
Table 5.4: Paired comparisons of PAR between invaded areas and indigenous vegetation.

<table>
<thead>
<tr>
<th>Site</th>
<th>U</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td>3.50</td>
<td>0.000</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>61.0</td>
<td>0.000</td>
</tr>
<tr>
<td>Yanchep</td>
<td>74.0</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Figure 5.5: Comparison of photosynthetically active radiation (PAR) levels underneath (A) invaded (inv.) areas and indigenous vegetation (unaff.), and underneath common species at (B) Ellensbrook, (C) Shoalwater and (D) Little Grove. PPFD stands for photosynthetic photon flux density. * denotes significant difference (α=0.05).
DISCUSSION

5.3.3 Community composition and structure

The results support casual observations that *L. laevigatum* has a negative impact on indigenous species. Low cover of indigenous species was a feature of each invaded quadrat. Changes to species richness are less clear. Low cover alone can affect species richness, since less cover generally means fewer propagules are produced. Indigenous shrubs found in invaded quadrats were small or moribund. Because of a reduced ability to regenerate (reduced fitness), declines in species richness could be seen in the next generation of indigenous plants. That is, reductions in species richness may occur in future, but have not been detected yet.

Growth of alien species also appeared to be affected negatively, with lower cover and richness in invaded quadrats. The notable exception was at Yanchep, where these features were higher in invaded quadrats. Two observations could explain this result. At Ellensbrook and Shoalwater, there should be no gradient of disturbance level or alien species propagules along transects (Chapter 2). At Yanchep invaded quadrats were next to the road edge while unaffected quadrats lay at least 45m away. The dual effects of roadside disturbance and availability of alien plant propagules close to the road edge are often responsible for invasion of alien species into roadside habitats (Trombulak and Frissel 2000); at Yanchep these factors are likely to have enhanced colonisation by alien species in the invaded quadrats. The comparatively low foliage projective cover values of invaded quadrats at Yanchep could have allowed invasion by photophilic (light-loving) species such as *Briza maxima* and *Ehrharta calycina*. In summary, higher light levels, roadside disturbance and propagule availability have promoted establishment of alien herbs in the stand of *L. laevigatum* at Yanchep, whilst under alternative conditions *L. laevigatum* may exclude them.

Invasion by *Spartina* spp. in estuaries in western USA has been shown to differentially affect the diversity of different life forms (Daehler and Strong 1996). Among indigenous and alien species remaining in infested quadrats at Yanchep, indigenous shrub species were in poor condition (although no alien shrubs were recorded) whilst species with ground cover habits appeared in good condition. Competition for soil resources is presumably strongest between shrub species (including *L. laevigatum*), whilst the
shallower roots of ground cover species are exploiting soil resources at a shallower depth and therefore are not in direct competition with *L. laevigatum*. Alternatively, the ground cover species may be more shade tolerant. The result of differential effects of *L. laevigatum* on given plant species is likely to result in community composition change, as shrub species and photophilic species succumb to competition.

Differences in vegetation communities between invaded and unaffected quadrats are reflected in multivariate analyses. The degrees of difference in plant communities can be related to the densities of *L. laevigatum* occurring at each site. Among invaded quadrats, *L. laevigatum* densities were extremely high at Yanchep (see densities at start of transects; Chapter 4), followed by Shoalwater and only a single (large) plant occurred in the invaded quadrat at Ellensbrook. Correspondingly, Yanchep invaded quadrats were grouped as distinctly dissimilar to unaffected quadrats, at Shoalwater the division was discernible but less distinct and at Ellensbrook there was little distinction. Additionally, the community similarity between invaded quadrats at Yanchep and Shoalwater suggests that *L. laevigatum* invasion has the ability to homogenise the indigenous communities it invades, presumably because only a small suite of (probably shallow rooted and shade tolerant) species are able to co-exist.

### 5.3.4 Impacts on soil and litter

Because of the relatively high probability of incorrectly detecting significant differences (α set at 0.10), significant differences required support from other evidence to be considered potential impacts. Because manipulative experimentation is not the basis for these suggestions, none can be considered unequivocally as impacts. However, supporting evidence for some of them is strong, as is discussed.

#### 5.3.4.1 Increased litter

Where *L. laevigatum* invades, litter cover is increased. This impact is not contentious; the leaf litter samples collected from invaded quadrats were almost fully composed of *L. laevigatum* leaves. Plant litter can have considerable negative impacts on seedling establishment through shading, crushing, allelopathy, increasing dessication, creating a barrier to seedling roots (Crawley 1997) and harbouring herbivores (Facelli 1994). The magnitude of these impacts is variable (Xiong and Nilsson 1999). Plant diversity in productive habitats can be suppressed directly by litter accumulation (Tilman 1993).
frequently, litter has positive impacts on vegetation development, for instance by buffering frosts, protecting seed from predation, adding nutrients and conserving water during dry conditions (Xiong and Nilsson 1999). Allelopathic chemicals from a plant's roots may be buffered by its own leaves (Tolliver et al. 1995). Importantly, leaf litter can have differential effects on species within the same community. For example, Facelli (1994) found that leaf litter and competition with herbs both had a negative effect on a woody alien species. However, leaf litter addition had a stronger negative effect on herb seedlings, therefore improved the growth of woody seedlings (Facelli 1994). Because of the differential effects of leaf litter on plant species, leaf litter plays a potential major role in structuring plant communities (Xiong and Nilsson 1999). Consequently, increase in leaf litter accumulation upon invasion by *L. laevigatum* has the potential to alter community composition, and therefore the structure and function of vegetation.

Among the documented impacts of litter on vegetation, most operate on seeds, germination and seedlings. *L. laevigatum* is able to establish amongst its own leaf litter and in mulch; establishment and survival may even be enhanced by these conditions (Chapter 3). If indigenous species are inhibited by thick layers of litter, or even if they do not establish as well under those conditions as does *L. laevigatum*, regeneration will favour *L. laevigatum*, and invasions would be perpetuated. Additionally, some indigenous species may be favoured: seedlings of *D. sessilis* occurred in the leaf litter of the *L. laevigatum* thicket at Yanchep, whilst seedlings of other species were not observed. Increased litter accumulation and soil moisture facilitates germination and establishment of some species (including *L. laevigatum*) and not others, with subsequent changes to the composition of vegetation communities.

5.3.4.2 Increased soil moisture

Plant mulch retards soil moisture loss (Buchanan 1989) and litter has the same effect. Higher soil moisture in infested quadrats at Shoalwater and Yanchep is likely to be caused by associated high levels of leaf litter. (Presumably, a drainage line through the unaffected quadrats has influenced soil moisture at Ellensbrook to produced the opposite result. The drainage line was recognised by the presence of moss and a proliferation of the mesophyte *Zantedeschia aethiopica.*) Different plant species have different soil moisture requirements (*i.e.*, the continuum between mesophytes and xerophytes). Increases in soil moisture upon invasion by *L. laevigatum* have the potential to enhance the growth of more mesic species,
and therefore to change community composition. This occurs in New South Wales, where rainforest taxa are observed on the margins of *L. laevigatum* thicket close to the coast (M. Robinson personal communication). Among mesic species, those with roots gathering resources at a different depth to *L. laevigatum* would be favoured (Section 5.3.3).

5.3.4.3 Soil pH

Reductions in soil pH at Shoalwater and Yanchep may be caused by invasion by *L. laevigatum*. Substances in the litter of *L. laevigatum* may be causing these changes. However, increases in soil pH at Yanchep could be due to imported road building material. Calcium and salinity levels of this soil were significantly different from soil further into the site, in contrast with the other two sites. Additionally, upon sieving for soil analysis, soil samples from 0m quadrats at Yanchep were the only samples containing particles larger than 2mm.

5.3.4.4 Other soil variables

The possible impacts of *L. laevigatum* invasion on other soil organic matter and water repellency are inconclusive. The absence of similar patterns in these variables between sites, without an obvious alternative explanation suggests that where significant differences occur, they are probably controlled by factors other than direct or indirect impacts on *L. laevigatum*. Alternatively, replication was not extensive enough to detect differences.

5.3.5 Homogenisation of PAR

*L. laevigatum* is able to reduce PAR levels and their variability underneath its canopy, compared with the indigenous vegetation as a whole. However, this impact is likely to be true of most species. Although *L. laevigatum* has among the highest light attenuating properties of plant species tested, it was not consistently the highest. Therefore, where *L. laevigatum* establishes as single plants within a mix of other species, its impacts on PAR should be negligible. Different species have different light requirements for germination (Rees 1997) and establishment; therefore heterogeneity in light levels within a vegetation community will promote species richness. If *L. laevigatum* invasions impact substantially on species composition by altering light characteristics, it is not due to an extraordinary ability to attenuate light. Rather, its tendency to form monospecific stands, homogenising light levels over a large area, would reduce the variety of microsites offering different light conditions. Therefore, variety of species able to establish will be lowered. Few indigenous
species have the same tendency to form monospecific stands with dense canopies (c.f. Acacia rostellifera in coastal dunes: Rippey and Rowland 1995). Elsewhere also, it has been suggested that the level of impact of a plant invader may be related to the ability to form a closed canopy (Woods 1997; Bennett et al. 1999).

5.3.6 Other impacts

There have been suggestions (e.g., K. Ninyett personal communication) that *L. laevigatum* may have allelopathic substances in its leaves which suppress germination of other species, and its own seedlings. C-methyl flavonoids have been isolated from the leaf wax of *L. laevigatum* (Wollenweber et al. 1996). Some flavonoids are known allelochemicals which appear to act primarily as cell growth and germination inhibitors, and may be released from leaf litter (Berhow and Vaughn 1999). However, plant phenolics (such as flavonoids) have a number of known ecological functions. These include herbivory defence, pollination attraction and hormone interactions as well as allelopathy (Harborne 1993). Allelochemicals produced by *L. laevigatum* may be affecting the germination of other species. However, the presence of *L. laevigatum* and *D. sessilis* seedlings underneath the thicket at Yanchep suggests that allelopathy is either not occurring, or not affecting all indigenous species.

*L. laevigatum* invasion may alter fire intensity and frequency. Difficulty has been encountered in igniting dense *L. laevigatum* stands for its control on the Mornington Peninsula because of the lack of elevated fuel. However, these thickets are tall and dense, with negligible horizontal growth and little fuel at a low level (S. Coutts personal communication). Additionally, eastern Australia receives rain during summer, which could reduce the likelihood of ignition. In contrast, it has been suggested (B. Dixon, D. Pike personal communication) that *L. laevigatum* in south-western Australia could increase fire frequency or intensity. Unlike thickets at Ellensbrook and Yanchep, many Western Australian populations consist of bushy shrubs, with horizontal branches low to the ground. Marked summer drought on the south-western coast should allow branches and foliage to dry, increasing the probability of ignition.
5.3.7 Hypotheses

The research indicates that *L. laevigatum* is able to change the community composition of the vegetation it invades. Alternatively, invasion by *L. laevigatum* may be secondary to the cause of the observed differences between invaded and unaffected quadrats. For example, deaths of indigenous species in the thicket at Yanchep could be attributed to the effects of road edge disturbance rather than competition by *L. laevigatum*. Despite the possibility that *L. laevigatum* invasion and observed community changes are the result of a common factor, rather than the former causing the latter, the research has provided some evidence that *L. laevigatum* may have the following effects:

1. Increased accumulation of leaf litter. This impact is not contentious; leaf litter from invaded quadrats was composed of *L. laevigatum* foliage.

2. Increased soil moisture, due to litter layer reducing evaporation.

3. Creation of uniformly low light levels over relatively large areas, yet only in places where invasion is as a stand or a thicket.

4. Resultant changes in species composition, due to differential responses of species to changes in soil, litter and light conditions.

5. Lowered cover of indigenous shrub species resulting from competition for soil resources, leading to decreased species richness in the long term.

In synergy, these potential impacts may result in alterations to ecosystem structure and function.
6.1 INTRODUCTION

The weed control method with the most predictable impacts on non-target organisms is hand weeding. It can preclude the requirement for commonly used herbicides; some of which can remain residual in substantial quantities for up to five years (e.g., tebuthiuron in Graslan, Department of Agriculture 2001). In removing roots from the soil, however, the possibilities of soil disturbance leading to further weed invasion, or damage to the roots of indigenous plants must be considered. The other drawback is that hand weeding is labour intensive, and may only be applied to smaller plants. Where larger plants are removed, soil disturbance is high, and if the plant material is left in the soil, it may resprout (Brooks 2001).

Chemical control of environmental weeds in the form of herbicide sprays is fast, but the possibility of non-target damage can be high, and may be dependent on the skill of the operator. Herbicides are developed primarily for agricultural use and testing for toxicology on animal species occurs in laboratories on a limited number of species. Only two published articles addressing the impacts of herbicides on invertebrates in natural ecosystems were found (Dewey 1986; Linz et al. 1999). The former detailed a negative effect on invertebrates, attributed to the direct effects of the herbicide. The latter detailed a positive response to habitat change because of the impact of the herbicide on vegetation. The dearth of research concerning the non-target impacts of herbicides on vegetation communities underlines the need for caution in its use in sensitive indigenous ecosystems, consistent with the precautionary principle. A number of systemic herbicides (those which act through vascular absorption) are registered for use on woody weeds in Western Australia, including glyphosate, picloram and triclopyr based products (Brooks 2001).

The application of herbicide directly to vascular tissue (rather than surface sprays) can be a safe and efficient compromise. Techniques such as cut and paint (herbicide applied directly to the cut stem), or tree injection (for woody plants: herbicide applied into a drilled hole in the stem) can be more time efficient and cause less soil disturbance than hand weeding, yet use less herbicide and reduce the non-target herbicide damage of herbicide sprays. A
second advantage is the greater effectiveness of low-toxicity glyphosate\(^2\) (the active ingredient of Roundup\textregistered) when used in this way.

Biological control can be an appropriate technique for managing extensive infestations which are not prioritised for rapid techniques such as herbicide application (Bruzzese and Faithfull 2001). Cost-benefit analysis for *Chondrilla juncea* and *Echium plantagineum* in Australia have been extremely favourable (Groves 1992), and the perception of high economic, health and environmental costs of chemical control elevate its level of support (Louda *et al.* 1997). Whilst some biological control "mistakes" occurred in the early days of the practice, some problems have been more recent (Simberloff and Stilling 1996). Whilst host specificity testing is a requirement for biological control in Australia (Environment Australia 2001), the outcomes of controlled experiments may not be directly applicable to field situations, because it cannot incorporate testing of the trophic interactions or indirect effects of the introduction (McEvoy 1996). Nevertheless, where environmental weeds have devastating impacts on the ecosystem they are invading, the potential risks of biological control may be outweighed (Simberloff and Stilling 1996).

In Western Australia, volunteers play an instrumental role in managing environmental weeds (CALM 1999). In coastal areas of the state, volunteer groups have been the driving force behind control programs of *L. laevigatum*, with operations near Dunsborough, Cowaramup Bay, Walpole, Denmark, Albany (including Cosy Corner and Little Grove), Bremer Bay, Esperence and at numerous Perth sites.

This Chapter details the results of vegetation surveys conducted at sites where *L. laevigatum* had been removed by chainsaw. It also provides an evaluation of the success of control strategies applied to *L. laevigatum* in Western Australia and the potential for the

\(^2\) Glyphosate has low toxicity in comparison with other herbicides, and appears to become inactive upon contact with clay particles (Department of Agriculture 2001). (No references were found detailing its activity in sand; this may be relevant to its use in vegetation on sandy soils). However, its water solubility means that penetration of this chemical when applied to the surface of woody plants can be low because of plant mechanisms to prevent moisture exchange with the atmosphere. Herbicides which dissolve in non-polar substances like diesel are more effective if externally treating woody weeds, since penetration through bark layers is more effective (J. Moore personal communication). However, these chemicals have higher toxicities (Department of Agriculture 2001).
use of biological control. This information was gathered by communicating with those 
with practical experience managing infestations, whose input is gratefully acknowledged. Recommendations are made for control.
6.2 METHODS

6.2.1 Removal by chainsawing

At Little Grove, four 5x5m plots were placed randomly (by walking a random number of steps in a random direction) within the zone of regeneration after chainsaw removal of *L. laevigatum*. At Ellensbrook, there were three irregularly shaped plots within the carpark (Figure 6.1a) from which *L. laevigatum* had been removed. Dimensions of plots were measured and area estimated. For comparison, three 5x5m plots were positioned in the thicket adjacent to Ellensbrook Homestead. Within plots vegetation sampling occurred as outlined in Chapter 5.

Statistical tests were not applied to these data. Because the area being sampled will affect the number of species recorded (Macarthur and Wilson 1967), different sized plots were not comparable. Little Grove chainsawed plots had no comparative data; sampling was attempted in the thicket that remained at the site, but was abandoned because dense, horizontal scrub made progress too time consuming. Data have been presented as totals for all plots within each category.
6.3 RESULTS

6.3.1 Removal by chainsawing

6.3.1.1 Ellensbrook

Indigenous and alien species richness and cover were higher in plots from which *L. laevigatum* had been removed compared to invaded plots; total area was similar (Table 6.1A). Cover of indigenous species in chainsawed plots was composed of seedlings and older plants. For instance, two plots contained a single *Acacia cyclops* which had apparently survived amongst the thicket of *L. laevigatum*; one of these plants was strongly etiolated (Plate 6.1B). One of the three chainsawed plots was almost devoid of growth, and did not support any indigenous species. Soil from carpark construction had apparently been pushed into this plot (recognised from dark gravel). A single *L. laevigatum* seedling was observed in each plot (less than 5cm tall).

In addition to these islands, larger blocks of *L. laevigatum* are gradually being removed by chainsawing a strip one to two meters into the thicket per year. There is some regeneration from seed of coastal species (e.g., *Acacia littorea*, *Rhagodia baccata*) in these strips.

Table 6.1: Species richness and mean cover of chainsawed plots at Ellensbrook and Little Grove, and invaded plots at Ellensbrook. Values in brackets are standard error.

<table>
<thead>
<tr>
<th>Site</th>
<th>Area</th>
<th>Indigenous species</th>
<th>Alien species</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Richness</td>
<td>Cover</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean±SE</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ellensbrook invaded</td>
<td>75m²</td>
<td>3</td>
<td>21.833±20.335</td>
<td>0.500±0.285</td>
</tr>
<tr>
<td>Ellensbrook chainsawed</td>
<td>79.6m²</td>
<td>10</td>
<td>37.5±22.250</td>
<td>4.667±2.682</td>
</tr>
<tr>
<td>Little Grove chainsawed</td>
<td>100m²</td>
<td>18</td>
<td>21.125±5.85</td>
<td>15.750±7.273</td>
</tr>
</tbody>
</table>

6.3.1.2 Little Grove

Large numbers and considerable cover of indigenous species have apparently regenerated from seed at Little Grove. This is accompanied by high species richness and cover of alien species (Table 6.1). Over the majority of the control area, indigenous and alien species are regenerating in close proximity (Plate 6.1B). Some areas of the site have been overrun by *Avena barbata* since removal of *L. laevigatum* thicket (Plate 6.1C). Along a pathway (present before the removal of *L. laevigatum*), there has been a "wheat field" regeneration.
of *L. laevigatum* seedlings, to a density of 301/m² (n=5, quadrat size=0.0625m²; standard error=38: Plate 6.1D).
6.4 DISCUSSION

6.4.1 Physical removal

The results show that at some sites, there can be high potential for regeneration of indigenous species from soil seed banks upon removal of *L. laevigatum*. Because of the high potential for regeneration of alien species, including *L. laevigatum* seedlings, removal of *L. laevigatum* should only be undertaken on scale for which there are available resources for follow up monitoring, and weed and erosion control. Otherwise, reinvasion by alien species could pose threats to regenerating seedlings. Gradual removal of stands, that is, the Bradley method (Bradley 1988) may be more practical and efficient. This method reduces the requirement for erosion and weed control, instead allowing indigenous plants to establish and perform these roles. Additionally, plants that have survived in thickets are able to acclimatise to exposed conditions more slowly with protection from the remaining portion of the thicket, and their chance of survival is increased (K. Ninyett personal communication). Where plants are etiolated underneath the *L. laevigatum* canopy, such an approach may be important as their modified shape may make them more susceptible to damage from strong coastal winds.

Chainsaw removal was among the most commonly reported control method for *L. laevigatum* in Western Australia. It is preferred in areas where the aesthetics is of concern, such as in urban areas where standing dead trees are considered unsightly. Additionally, removal of dead plant material forming a fire hazard may be a priority. Several community bushcare groups reported the use of dead plant material as brush matting to stabilise soil post-removal, resulting in extensive regeneration of *L. laevigatum* seedlings. Presumably, the dead branches provide the moderate shade that enhances seedlings establishment and survival (Chapter 3). Land managers should be wary of this.

At sites where *L. laevigatum* is smaller, cutting stems with secateurs or hand saws can be efficient and cause only low levels of disturbance to vegetation and soils. Because of the ability of *L. laevigatum* to coppice when cut (Chapter 3), to prevent the requirement for follow up treatment, herbicide applications to cut stems are recommended for every chainsawed or cut plant. Herbicide must be applied immediately that plants are cut. Otherwise, the wound seals and uptake does not occur (Brooks 2001).
6.4.2 Herbicide spray

Applications of Access™ (triclopyr and pictoram) as a basal spray and Roundup™ (glyphosate) as a foliar spray have been trialled by J. Moore at a roadside location (Parry's Beach Road, near Albany). Some plants sprayed with Roundup™ were still alive (albeit sick), had reddened leaves and bunchy growth. Plants sprayed with Access were mostly dead. An advantage of herbicide over physical removal of plants is that light levels underneath the plant increase slowly as the plant dies. This provides more opportunity for indigenous species to establish in the newly vacant area rather than favouring alien photophytes, such as faster growing African grasses (J. Moore personal communication). Both foliar and trunk sprays are risky to surrounding plants because of the possibility of overspraying, more so for foliar sprays. Therefore, this method is only appropriate in areas with few indigenous plants. Herbicides which remain residual should be strongly avoided in situations where an indigenous soil seed bank may persist.

6.4.3 Herbicide wicks and tree injection

These wicks were initially developed for control programs at Cosy Corner, near Albany. Herbicide soaked sponges are clamped around the base of plant stems using wire and left in place for approximately one week. This method has been applied in Esperence for two seasons, using Garlon 600™ (triclopyr) in diesel at a rate of 1:10 (herbicide:solvent). Each 30mL dose provided two wicks. Where plants were not killed, they were at least set back (C. Turley personal communication). A drawback is that clamps can be labour intensive to produce and attach, because of the requirement to directly access each stem. Larger and multi-stemmed trees required more than the standard dose (C. Turley personal communication).

Tree injection is a widely used method to control woody weeds. Holes are drilled in the stem of the plant to access vascular tissue, and herbicide applied into the hole immediately. This method has been applied in *L. laevigatum* control relatively recently, with success; in 2001, tree injection trials began in Esperence. Cordless drills were used to bore 10mm holes into the trunk, which were filled with Roundup™ at a ratio of 1:2 (herbicide:water) (S. Wheeler personal communication). An advantage of this method (and of others that leave tree skeletons in place) is that the site is marked for follow up monitoring of seedlings. Commercial tree injector guns are also available.
At an extensive infestation near Esperence, the Esperence Weed Action Group performed a comparison of herbicide wicks and tree injection, applying different treatments on adjacent plants. Tree injection gave higher success rates; plants died more quickly without requiring re-treatment, whilst some plants treated with wicks did not die without re-treatment. A further advantage of tree injection was comparatively greater herbicide efficiency (C. Turley personal communication).

6.4.4 Fire

In Victoria, prescribed burns have been used to regulate populations of *L. laevigatum*. On the Mornington Peninsula *L. laevigatum* is not serotinous; it releases seed in early summer directly after capsules are formed. Spring burns have been most effective since there is negligible viable seed remaining in the soil from the previous year's seed release, and the new seed is not yet mature (Coutts 2001). In implementing such a program, the natural fire season to which indigenous plants are adapted must be considered (Coutts 2001).

In other areas where *L. laevigatum* is serotinous, two successive burns, with an interval shorter than the time taken for *L. laevigatum* to reach maturity, have been applied to *L. laevigatum* populations at Wonthaggi Heathlands. For safety reasons, it is preferable to perform burns when fires can be more easily controlled (outside of summer). At this site, the likelihood of achieving adequate fuel to ignite under these conditions within the timeframe required is low, which limits the application of this method (D. Drummond personal communication). In implementing such strategies, the impacts of fire more frequent than five years on indigenous flora must be considered, as well as the appropriate fire season.

In Victoria, difficulties in burning *L. laevigatum* stands have been reported, because plants grow tall and straight with few low branches to ignite (S. Coutts personal communication). In contrast, wider growth forms with horizontal branches may dry sufficiently over summer in southern Western Australia for live plants to become a fuel source during fire (B. Dixon and D. Pike personal communication).

6.4.5 Bulldozers

Heavy infestations have occasionally been removed using bulldozers. In Craigie Bushland north of Perth, a bobcat was used to remove a thicket of 30-40 *L. laevigatum*, and
subsequently to remove topsoil and the seed that it was assumed to contain (K. Armstrong personal communication). Ideally this method should be used only at sites which are already severely disturbed and devoid of indigenous plants, where the soil is unlikely to contain a seed bank of indigenous species. Follow up will be required in the form of labour intensive and relatively expensive planting. Alternatively, direct seeding may be undertaken, depending on the timespan available to revegetate the site. Either way, machinery and erosion mitigation costs must be considered. The method will be preferred if rapid removal is required, and where resources are available for adequate post-removal management.

6.4.6 Regeneration of *L. laevigatum* from seed

*L. laevigatum* is soft-seeded, and soil seed bank viability is generally agreed to be less than one year. All viable seed can be expected to germinate the winter after it is shed (Burrell 1981). Therefore, where *L. laevigatum* is killed, a single visit within 3-4 years of the initial effort should allow identification and removal of any plants which have regenerated, before they begin to produce seed. Increased efficiency can be achieved by delaying the first visit because (1) plants will be larger and easier to find, (2) and demographic processes will mean that fewer plants require treatment. The method applied will depend on the size of the immature plants, and disturbance considerations.

Research and most reports indicate that no further seedlings will emerge after the first cohort. However, seedlings are reportedly still emerging at a Bremer Bay site seven years after the original plants were chainsawed and used on-site as brush matting. An alternative seed source is apparently absent (M. Jeffery personal communication). Possibly, conditions within the brush matting have prevented simultaneous germination of all seed. For instance, if brush matting is not physically disturbed, seed may remain within open capsules or amongst the dead foliage, where they are prevented from receiving the moisture required for germination. Because the factors leading to longer-term survival of *L. laevigatum* seeds is unknown, it is recommended that sites subject to *L. laevigatum* control should be checked for seedlings every 3-4 years, twice or three times. If survival for longer than a year is in future discounted, or the conditions which allow it are identified, single visit monitoring of sites will be adequate.
Where *L. laevigatum* is removed by bulldozer or chainsaw, the successful removal of branches from sites before seed release may be logistically difficult, since capsules can begin to open within hours of being cut (Burrell 1981). Additionally, there is likely to be some seed remaining in the soil. It will usually be practical to leave removed material at a single location on-site, so that most seedling establishment will be confined near the pile of branches, and can be easily monitored. The potential consequences of transporting *L. laevigatum* material was observed in the Albany region, where branches removed in a roadside control program had fallen out of the truck, onto an uninvaded road verge.

At sites where low density infestations are removed from sensitive natural areas, immediate removal of plant material should occur to reduce the amount of seed available for regeneration. The site of removal should be marked to allow for monitoring.

6.4.7 Biological control

*Parectopa thalassias* Meyrick (Gracillariidae), a leaf-mining moth from the natural range of *L. laevigatum* was first introduced to combat South African populations in 1996 (Gordon 1999), but does not appear to be having a major impact on the weed (T. Gordon personal communication). A gall midge, *Dasineura* sp. (Cecidomyiidae) also from eastern Australia appears to have escaped from quarantine between 1984 and 1994. It stunts seedlings by galling the vegetative buds; its effectiveness as a biological control agent is being evaluated. (T. Gordon personal communication).

The development of biological control for *L. laevigatum* is not recommended for several reasons, aside from its inherent risks:

6.4.7.1 Efficacy

When seed production is high and recruitment is microsite limited, even large reductions in seed density resulting from predation are unlikely to have any impact on mature plant density (Crawley 1997). Examination of invasion patterns strongly suggests that recruitment of *L. laevigatum* is microsite limited (Chapter 4), and seed production is copious (Chapter 3). Therefore, any biological control agent which targets reproductive parts is unlikely to be effective in the control of *L. laevigatum*. Agents which target reproduction rather than vegetative stages are generally thought to be more promising (S. Neser personal communication, in Goodland *et al.* 1998).
If a species is common or weedy in its native range, as is *L. laevigatum*, classical biological control (where natural predators are introduced) may be of little value (Scott and Panetta 1993). Additionally, insect agents may not be as effective against plants scattered in bushland (such as at Ellensbrook) because of difficulties in survival and dispersal (Goodland *et al.* 1998).

6.4.7.2 Practicability

Current technologies for management of *L. laevigatum* are successful. Slow spread rates, even after fire mean that manual control can be highly effective. Where plants are scattered in bushland, they are most likely to be within 100m of other individuals (Chapter 4), which will aid in locating individuals for control. If current methods are continued, by the time that a suitable agent has been selected, tested for host specificity, released and dispersed, the strategy may be of little value. If current management funds are diverted to the development of biocontrol, populations could be allowed to expand, which would hinder control attempts regardless of control method chosen.

6.4.7.3 Specific risks

Two priority flora species of *Leptospermum* occur within and near the predicted range of *L. laevigatum*. *L. confertum* (P2) is known only from a coastal site between Albany and Esperence, two regions suffering from widespread infestation of *L. laevigatum*. *L. exsertum* (P1) occurs only east of Geraldton, close to predicted the eastern limit of *L. laevigatum*. At least 10 other *Leptospermum* species occur within its predicted range. Insect biological control agents, including those subject to host specificity testing, have been known to switch hosts, particularly within a genus. For example, *Rhinocyllus concicus*, the Eurasian weevil is attacking five indigenous thistle species within conservation areas (Louda *et al.* 1997; Strong 1997).

6.4.7.4 Cost

Although cost-benefit analysis of biological control agents has been favourable in some cases in Australia (Groves 1992), costs must be weighed against the probability of success of the program. A recent estimate of worldwide success (partial or complete control) is 47% (Julien 1992, in Goodland *et al.* 1998).

There are a number of arguments against biological control in general. A main weakness are the inability of host specificity tests to address complex field interactions with species
other than the host organism, and the possibility of a time lag between release and negative effects. Summaries of the issues are available elsewhere (McEvoy 1996; Simberloff and Stilling 1996; Louda et al. 1997; Strong 1997).

6.4.8 Conclusions

Where *L. laevigatum* is invading bushland sites, preferred control methods are tree injection for larger plants, cut and paint for smaller plants and hand weeding of small seedlings. These methods will be effective, whilst causing minimal off target damage. Attempts to remove seed bearing branches from bushland sites may result in capsules breaking from branches in transport. Therefore, in most cases *L. laevigatum* material should be left in-situ, since monitoring for seedlings will need to occur regardless of whether additional seed is removed. Sites should be revisited within 3-4 years of the first operation, and at least once more 3-4 years afterwards. A search radius of 100m should be sufficient to detect recruits, but search should continue further away if possible. If the plant skeleton is not left in place, the site of must be marked by an alternative method.

For large stands, chainsawing is recommended with immediate application of herbicide to the cut stump. Subsequently, control of *L. laevigatum* and other aliens, and erosion must be considered when removing large areas. Regeneration can be from soil seed bank where possible, otherwise through direct seeding or planting. Extreme infestations can be removed quickly with a bulldozer or bobcat, with similar considerations as for chainsawing. Biological control is not the most effective option.
CHAPTER 7: SYNTHESIS

This study has shown that *L. laevigatum* can invade bushland in excellent condition and of high conservation value, in addition to highly disturbed sites. The species has limited ability to form extensive stands within healthy vegetation in the absence of fire. However, fire is of major importance in Australian plant communities (Gillet et al. 1981), and can be considered inevitable in many ecosystems of the south-west. There is strong evidence that increased invasion densities result from the combination of fire and adjacent seed bearing plants (Chapter 4). Consequently, where *L. laevigatum* exists at low densities within a site, a fire event can greatly increase invasion density even where communities remain relatively undisturbed by human activities. Therefore, if no intervention occurs, *L. laevigatum* can be expected to spread extensively into bushland, invading gradually and at low densities until fire occurs, and subsequently establishing *en-masse* after fire.

Management to limit anthropogenic disturbance, or a return to natural disturbance regimes (where known), has been suggested as a way to alleviate plant invasions (Woods 1997). Since current research suggests fire often promotes invasion (Milberg and Lamont 1995; D'Antonio 2000), fire suppression may be an option in some ecosystems. Whilst reducing anthropogenic disturbance which creates soil disturbance may reduce the availability of suitable establishment microsites for *L. laevigatum*, attempts to suppress fire in south-western Australia are unlikely to be successful. Additionally, fire suppression would have detrimental effects on the fire-adapted indigenous flora.

7.1.1 Invasion Impacts

The study found that high levels of leaf litter were associated with invasion by *L. laevigatum*. The conventional focus on competition and predation as the major factors shaping communities has been questioned by some researchers (Facelli 1994; Xiong and Nilsson 1999), who have argued that plant litter plays an equally important role in influencing vegetation composition. Alterations in litter characteristics were found to have major impacts on community structure, due to the differential abilities of species to establish under different litter conditions. That *L. laevigatum* increases litter fall is not contentious in this study; litter collected from invaded plots was mainly *laevigatum* foliage. The ability of the species to alter litter levels in this way is believed to be an
important causal factor in the alterations to vegetation structure and composition observed upon invasion by *L. laevigatum*.

Other possible impacts of *L. laevigatum* which could lead to effects on community composition and structure include increases in soil moisture (associated with increased level of litter) and the homogenisation of PAR levels over a large area. The latter is hypothesised to reduce the variability of PAR properties of microsites, thereby enhancing establishment of a small suite of shade tolerant species. Similarly, increases in soil moisture may preferentially enhance the establishment of mesophytes. Within Ellensbrook thicket, as within thickets at Wilson's Promontory, little else survives within the stand but hardy, shade tolerant *Lepidosperma gladiatum* (*Lepidosperma concavum* at Wilson's Promontory: Bennett et al. 1999). It is highly conceivable that the three proposed impacts: increases in litter and soil moisture, and homogenisation of PAR over a large area, individually and in synergy can effect large scale changes to ecosystem structure and function.

This study indicates that increasing impacts of *L. laevigatum* on vegetation structure is positively correlated with invasion density. Therefore, where high densities of seedlings establish after fire, attempts should be made to remove them before competition from *L. laevigatum* seedlings impacts greatly on regenerating indigenous species.

### 7.1.2 Dispersal vectors: management implications

Despite the high potential of *L. laevigatum* to reduce the biodiversity values of southwestern Australian ecosystems, its control or eradication is achievable. The species spreads slowly in the absence of fire (less than 10m per year as individual plants: Chapter 4). It can be expected to establish within a predictable range of the main invasion due to wind dispersal, therefore removal efforts are likely to succeed. In searching for recruits in bushland, the high variability in establishment pattern away from the main invasion must be considered. Because older, seed bearing recruits may occur quite far from the main invasion, the possibility that those plants have produced recruits even further away from the main invasion must be accounted for. If fire occurs when seed bearing plants are present, conservative estimates of age at first maturity still allow several years for sites to be cleared of post-burn recruits before they begin to produce seed. Therefore, its eradication from invaded sites will generally be achievable with adequate follow-up.
Ant dispersal is a possibility for *L. laevigatum* seeds. However, the seeds lack an elaiosome. Therefore dispersal could only be by harvester ants, rather than by true myrmecochory, which means that seeds are mostly consumed. The large number of seed stored in the canopy away from ants suggests that ant predation probably has negligible impact on seed abundance. Additionally, ants are known to carry seed a maximum of 70m (Sernander 1906, in Berg 1981). In comparison with wind dispersal, the influence of dispersal by ants is considered to be small.

The only long distance dispersal vector clearly identified in this study was road vehicles. The resultant road edge populations are relatively conspicuous and easy to target, before plants begin to spread into adjacent land. However, the possibility of bird dispersal creates a problem, as such a vector would allow *L. laevigatum* to penetrate conservation reserves and escape detection. The relationship between *C. baudinii* (and other parrot taxa) and *L. laevigatum* at Ellensbrook requires investigation for this reason. More importantly, the possible mutualism should be addressed because of the potential for *L. laevigatum* control strategies to negatively affect populations of this rare fauna species.

### 7.1.3 Mutualisms

The formation of novel mutualisms upon invasion is a common factor which allows plant invaders to naturalise in their new habitats. Cockatoos are known to disperse *Pinus* spp. which are originally adapted to wind dispersal (Richardson and Higgins 1998, in Richardson *et al.* 2000). *L. laevigatum* in Victoria is known to associate with an ectomycorrhiza (Bascidiomycetes), and that this association can normalise the growth of stunted seedlings (Burrell 1981). Some species of ectomycorrhizae have low levels of host specificity and a widespread distribution (Richardson *et al.* 2000). Therefore, *L. laevigatum* in south western Australia is probably able to form associations with a similar or substitute ectomycorrhiza. Richardson *et al.* (2000) note the importance of generalist pollinators such as *A. mellifera* (honey bees), which are implicated in increasing the seed set of *Centaurea solstitialis* (Yellow Starthistle), an environmental weed of Californian ecosystems. In Western Australia, *A. mellifera* also appears to be a major pollinator of *L. laevigatum* (Chapter 3).

The ability to form novel mutualisms, and several features of the species' life history suggest plasticity in ecological requirements. The species possesses a seed storage and
release strategy that allows recruitment in the presence or the absence of fire. It is able to successfully invade in regions which have lower average annual rainfall than its natural range (BOM 2002). It is able to colonise a large variety of soil types, and is able to invade after extreme or minor disturbance. Ability to germinate in some proportion at a range of temperatures (10°C to 20°C) may also indicate plasticity. In contrast, \textit{L. laevigatum} is not unusual in requiring small scale soil disturbance for establishment (Hobbs and Huenneke 1992; Crawley 1997).

7.2 ENVIRONMENTAL WEEDS AND HORTICULTURE

7.2.1 \textit{L. laevigatum}

A major hurdle in combating the spread of \textit{L. laevigatum} is its continued popularity as an ornamental plant. It is extremely common in Perth gardens on the coast and inland; ironically, it often is cultivated several hundred metres from bushland sites from where volunteers are working to remove it. Its ease of cultivation and its long history of promotion in Australia have enhanced its popularity; Victoria's government botanist, Baron Ferdinand von Mueller advocated its planting in the publication, "Industrial plants deserving culture in the colony of Victoria" (1876). Apparently, in the 1960s branches of \textit{L. laevigatum} were often placed on the roofs of nursery shade houses to protect potted seedlings. Seed was released into the pots below, which were transported to new locations for planting resulting in spread of the species over the Perth metropolitan area (A. Notley personal communication). Based on the date of introduction to South Australia (pre-1892: Kloot 1985), it was probably introduced in Western Australia towards the end of the 19th century or just after. As with many "garden escape" plants (\textit{sensu} Keighery 1988), the features which have made the \textit{L. laevigatum} desirable for horticulture are the same ones which contribute to its invasive capacity. These include its hardiness, profusion of flowers, its drought tolerance, and its dense growth which makes it suitable for a hedge. In Western Australia it was still commonly being used in reclamation of mine sites and for dune stabilisation until several years ago (M. Ochtman personal communication).

The recognition that the majority of pest plants are intentionally introduced (Panetta 1993) has sparked attempts to address plant invasions at their source, rather than manage them once they are naturalised. The term "garden thugs" has arisen to describe environmental
weeds which originate from garden plants (Randall 2001). The nursery industry has been identified as a source of environmental weeds.

7.2.2 Are the solutions really solutions?

The Nursery and Garden Industry of Australia (NGIA) acknowledges that nurseries contribute to the introduction and dissemination of environmental weeds (Burnett 2001). Flora for Fauna is an initiative of the NGIA, funded by the federal government through the National Heritage Trust scheme. The aim is to encourage gardeners to plant native species, to create faunal habitat, and to discourage the use of potential environmental weeds (Burnett 2001). The initiative is a positive step, dividing Australia into "growing zones" and recommending suitable plants for these zones. Species which have proven invasive within south-western Australia such as *L. laevigatum* and *Acacia longifolia* are notably absent from the list of plants for the "Mediterranean growing zone". However, other eastern Australian plants are recommended for planting in Western Australia, and *vice versa*, including the commonly invasive genus *Acacia* (see NGIA 2001). Therefore, whilst the program attempts to address the issue of native Australian plants as environmental weeds, it may be creating future environmental weeds. Some Australian plants that have been popular in gardens for over a century, yet invasions have only begun to be noticed within the last decade (e.g., Carr 1993). Although proven invasive plant species are left off the Flora for Fauna list, they have been replaced by a suite of other Australian plants which could become pests given adequate time and introduction frequency.

7.2.3 The future of invading species

"The sheer volume of international commerce virtually guarantees that species known to be weeds will arrive in new ranges. This same international traffic will also transport an increasing array of seemingly innocuous species to ranges in which they will become pests".

-Mack and Lonsdale (2001)

It is well recognised (e.g., Low 1999; Campbell 2001; McNeely 2001) that increases in the volume of trade will increase biological invasions by intentionally translocated species, and accidental introductions. These processes will continue to occur despite quarantine controls and other measures. Mack and Lonsdale (2001) give a thought-provoking, if
cynical account of some aspects of human nature and ignorance which have led to species translocations. In the case of intentional introductions, it is not the species themselves that are the problem, but rather the attitudes that lead to their translocation. Invasion biologists are now aware that it is impossible to completely stem the tide of introduced organisms in a world of travel and international trade. They have resigned themselves to some "acceptable" homogenisation of the Earth's biota, and have set about the task of deciding which invaders they would prefer to have. The emphasis is on keeping out the worst of them. As long as the economic importance of trade is placed higher on the agenda than environmental protection, invasions can be expected to increase at an alarming rate. They are already considered an agent of global change, along with global warming, land use change and alterations to nitrogen cycling (Vitousek 1994; Mack and Lonsdale 2001).

In Australia, the growing problem of Australian native plants as weeds will be difficult to address. It will require a re-education of the public's ideas of "native" and "exotic," (Low 2001). The Flora for Fauna initiative is a positive step towards changing gardener behaviour, but the approach appears to be misguided in its encouragement of further plantings of species which are, by the definition of the IUCN, alien plants (plants outside of their natural range). Awareness of the potential for garden escape plants such as *L. laevigatum* is likely to result in their avoidance by well-meaning gardeners. However, whilst attitudes like those displayed by the Flora for Fauna initiative persist, we can expect to observe *L. laevigatum* 's replacement by different species from elsewhere in Australia. Therefore, problem of *L. laevigatum* must not be viewed in isolation as a problem plant, but rather in the context of other potential garden escapes. The experience with *L. laevigatum* should be made to provide an example so that the mistakes are not repeated.

*L. laevigatum* has the potential to threaten a large proportion of the South West Botanical Province, if allowed to invade. However, control and eradication is possible. The information within this thesis provides baseline data and recommendations for control of the species. There are many people in Western Australia who are familiar with the species and its presumed impacts. However, this research is unique in that for the first time in Western Australia, and possibly Australia, it provides a comprehensive synthesis of scientific investigation and the valuable knowledge and observations of experienced land managers from both eastern and western Australia.
REFERENCES


CALM (1999). 'Environmental weed strategy for Western Australia'. (Department of Conservation and Land Management, Como).


Clarke, P. J. (1989a). Coastal dune vegetation of New South Wales. Chatswood, University of Sydney Coastal Studies Unit, Soil Conservation Service of NSW.

Clarke, P. J. (1989b). Coastal dune plants of New South Wales. Chatswood, University of Sydney Coastal Studies Unit, Soil Conservation Service of NSW.


Department of Agriculture (2001). Herbiguide 2001 Western Australian Department of Agriculture, Albany. 12/12/01.


Environment Australia (2002). National weeds program Environment Australia. 12/02/02.


Hussey, B. M. J., G. J. Keighery, et al. (1997). 'Western Weeds: A guide to the weeds of Western Australia'. (The Plant Protection Society of Western Australia (Inc.), Victoria Park).


IUCN. 15/03/02.


MPR (2002). GeoView: interactive GIS Western Australian Department of Mineral and Petroleum Resources. 11/05/02.


WASG (2001). Geology and geomorphology: south-west of Western Australia. 
http://wasg.iinet.net.au/, 05/12/01.


## APPENDIX

Table A.1: Curve estimation regression relationships between morphological variables at the three sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Comparison</th>
<th>Model</th>
<th>R squared</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellensbrook</td>
<td>Height-Width</td>
<td>Cubic</td>
<td>0.941</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.571</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Height-S. diam.</td>
<td>Cubic</td>
<td>0.855</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.496</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Width-S. diam.</td>
<td>Cubic</td>
<td>0.940</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.929</td>
<td>0.000</td>
</tr>
<tr>
<td>Shoalwater</td>
<td>Height-Width</td>
<td>Power</td>
<td>0.766</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.550</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Height-S. diam.</td>
<td>Power</td>
<td>0.503</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.195</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Width-S. diam.</td>
<td>Cubic</td>
<td>0.689</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.667</td>
<td>0.000</td>
</tr>
<tr>
<td>Yanchep</td>
<td>Height-Width</td>
<td>S</td>
<td>0.820</td>
<td>0.000</td>
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<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.499</td>
<td>0.000</td>
</tr>
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<td>Height-S. diam.</td>
<td>Power</td>
<td>0.850</td>
<td>0.000</td>
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<td></td>
<td></td>
<td>Linear</td>
<td>0.575</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Width-S. diam.</td>
<td>Cubic</td>
<td>0.865</td>
<td>0.000</td>
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<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>0.856</td>
<td>0.000</td>
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Table A.2: Pairwise Mann-Whitney comparisons between L. laevigatum and other species at Ellensbrook.

<table>
<thead>
<tr>
<th></th>
<th>LL v dryand</th>
<th>LL v aeguis</th>
<th>LL v spyrid</th>
<th>LL v hibhyp</th>
<th>LL v hibcun</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL</td>
<td>17.94</td>
<td>9.56</td>
<td>20.5</td>
<td>17.56</td>
<td>13.03</td>
</tr>
<tr>
<td>Other</td>
<td>19.06</td>
<td>27.44</td>
<td>16.5</td>
<td>19.44</td>
<td>23.97</td>
</tr>
<tr>
<td>U</td>
<td>152</td>
<td>1</td>
<td>126</td>
<td>145</td>
<td>63.5</td>
</tr>
<tr>
<td>Asympt sig</td>
<td>0.752</td>
<td>0.000</td>
<td>0.255</td>
<td>0.591</td>
<td>0.002</td>
</tr>
<tr>
<td>Exact sig</td>
<td>0.767</td>
<td>0.000</td>
<td>0.265</td>
<td>0.606</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Table A.3: Pairwise Mann-Whitney comparisons between L. laevigatum and other species at Shoalwater.

<table>
<thead>
<tr>
<th></th>
<th>LL v olearia</th>
<th>LL v a.cycls</th>
<th>LL v a.roset</th>
<th>LL v lmeria</th>
<th>LL v alyxia</th>
<th>LL v spyrid</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL</td>
<td>3.5</td>
<td>3.67</td>
<td>5.17</td>
<td>4.33</td>
<td>3.5</td>
<td>3.5</td>
</tr>
<tr>
<td>Other</td>
<td>9.5</td>
<td>9.33</td>
<td>7.83</td>
<td>8.67</td>
<td>9.5</td>
<td>9.5</td>
</tr>
<tr>
<td>U</td>
<td>0</td>
<td>1</td>
<td>10</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Asympt sig</td>
<td>0.004</td>
<td>0.006</td>
<td>0.2</td>
<td>0.037</td>
<td>0.004</td>
<td>0.004</td>
</tr>
<tr>
<td>Exact sig</td>
<td>0.002</td>
<td>0.004</td>
<td>0.24</td>
<td>0.041</td>
<td>0.002</td>
<td>0.002</td>
</tr>
</tbody>
</table>
Table A.4: Pairwise Mann-Whitney comparisons between *L. laevigatum* and other species at Little Grove.

<table>
<thead>
<tr>
<th></th>
<th>LL v agonis</th>
<th>LL v allocas</th>
<th>LL v adenan</th>
<th>LL v leucop</th>
<th>LL v ac.lit</th>
</tr>
</thead>
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### CONTRIBUTORS

Table A.5: Personal communications mentioned in-text.

<table>
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<tr>
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<tbody>
<tr>
<td>Adam, Paul</td>
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</tr>
<tr>
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<td>Heather Adamson</td>
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<tr>
<td>Peter Attiwill</td>
<td>Department of Botany, University of Melbourne</td>
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<tr>
<td>Brian Bainbridge (VIC)</td>
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<tr>
<td>Karin Baker</td>
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<tr>
<td>Jan Bant</td>
<td>Mirrabooka Primary School Bushland (?)</td>
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<tr>
<td>Kathryn Batchelor</td>
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<tr>
<td>Robyn Benken</td>
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<td>Graham Blacklock</td>
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<td>Kate Blood</td>
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<tr>
<td>Julia Boniface</td>
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<td>Wendy Bradshaw</td>
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<td>Dave Bright</td>
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<td>Lorna Charlton</td>
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<td>Mike Clarke</td>
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3 Victorian Department of Natural Resources and Environment
4 Environmental Weeds Action Network
5 Keith Turnbull Institute
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<td>Hazel Dempster</td>
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<td>Jenny Dewing</td>
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<tr>
<td>Bob Dixon</td>
<td>BGPA&lt;sup&gt;6&lt;/sup&gt;</td>
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<td>Jane Flower</td>
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<tr>
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<td>Tony Gordon (South Africa)</td>
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<tr>
<td>Mark Jeffery</td>
<td>FTTEG&lt;sup&gt;7&lt;/sup&gt;, Bremer Bay</td>
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<td>Don Jewell (VIC)</td>
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<sup>6</sup> Botanic Gardens and Parks Authority
<sup>7</sup> Feral Tea Tree Eradication Group, Bremer Bay.
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<td>Peter Jolly</td>
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<td>Sean Kenwery</td>
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<tr>
<td>Stephen King</td>
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<td>Linda Kirchner</td>
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<td>Robyn McElroy</td>
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<td>Ro McFarlane</td>
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<td>Clayton Stokoe (QLD)</td>
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² United States Department of Agriculture
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