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‘The ecology of *Pittosporum undulatum* Vent. (Pittosporaceae) an environmental weed in south east Australia’.

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The ecology of *Pittosporum undulatum* Vent. (Pittosporaceae) 
an environmental weed in south east Australia

by

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Deakin University, Victoria, Australia

December 1999
I certify that the thesis entitled ‘The ecology of *Pittosporum undulatum* Vent. (Pittosporaceae), an environmental weed in south east Australia’ submitted for the degree of Doctor of Philosophy is the result of my own research, except where otherwise acknowledged, and that this thesis in whole or in part has not been submitted for an award, including a higher degree, to any other university or institution.

Trudi Lyn Mullett
May 29, 2000
ABSTRACT

*Pittosporum undulatum* Vent. (Sweet Pittosporum) is a densely foliaged tall shrub or small tree, native to the wet forests of south east Australia. This species now functions as a serious environmental weed in a range of habitats in Australia and on other continents and islands throughout the temperate, sub-tropical and tropical zones. This study investigated some of the ecological causes and consequences of *P. undulatum* invasion across a range of habitat types in south east Australia.

Key aspects of *P. undulatum* biology and ecology investigated in the current study include; patterns of morphological variation across the range of habitats occupied (as a measure of the species’ plasticity), dispersal ecology and seed germinability, population structure and spatial pattern, community relationships and the ecological impacts of invasion.

Phenotypic plasticity is considerable in *P. undulatum*. No clear patterns of geographic variation emerged from a study of leaf morphological attributes across the current range of this species on mainland south east Australia. The pattern of morphological variation is particularly complex in Victoria, where the invasion of this species is most advanced. The species’ adaptability to a range of environments and environmental conditions will likely promote further range expansion.

The abundant winter fruit crop produced by functionally female *P. undulatum* plants attracts a suite of generalist opportunistic frugivores, which feed on *P. undulatum* fruits and seeds at various stages of fruit dehiscence, thereby enhancing dispersal opportunities for this species. *P. undulatum* seed collected from natural and invasive populations, at two stages of fruit maturity and from the scats and pellets of dispersal agents, displayed high germinability. European Blackbirds and Pied Currawongs are implicated as the main avian dispersal agents of *P. undulatum* in south east Australia. The broader ecological implications of developing relationships between invasive fleshy-fruitied bird-dispersed plant species and adaptive frugivores are likely to be considerable.
The distribution of *P. undulatum* seedlings was significantly negatively correlated with adult conspecifics and significantly positively correlated with trees and shrubs of other genera. This pattern reflects the importance of both frugivorous dispersal agents and the species’ germination and establishment requirements, in shaping the contagious distribution pattern typical of this species. These analyses suggest that recruitment opportunities for conspecific seedlings are limited beneath the canopy of adult conspecifics. Densities of *P. undulatum* were on average, 2.7 times higher in invaded populations, compared to the natural populations sampled. A male-bias was evident in all populations and no relationships between reproductive activity and the density of seedlings and juveniles were evident.

Invading populations of *P. undulatum* impose substantial changes on ecosystem-level properties and functions. Mean species richness and cover-abundance declined notably once *P. undulatum* cover-abundance exceeded 20% at the invaded sites and 60% at the natural sites sampled. The natural communities sampled displayed comparatively greater resilience to the competitive effects of *P. undulatum*, but community attributes were affected at high densities and cover-abundance of this species. The cover-abundance of herbs and grasses declined most substantially with increasing *P. undulatum* at invaded sites, whereas, at the natural sites sampled, the species’ structural analogues appeared to be most affected by increasing *P. undulatum* cover-abundance.

This study has demonstrated that the ecological consequences of *P. undulatum* population expansion are substantial and contribute to changes in the composition and successional trajectory of affected communities. These processes ultimately lead to the loss and simplification of biodiversity values and the homogenisation of affected habitats. *P. undulatum* has the potential to emerge as one of south east Australia’s most serious environmental weed species.
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CHAPTER ONE

Introduction

1-1. Introduction

_Pittosporum undulatum_ Vent. (Sweet Pittosporum) is a densely-foliaged tall shrub or small tree native to a diverse range of habitat types in south east Australia (Makinson 1992; Walsh & Albrecht 1996). This species has been widely planted throughout Australia and some locations overseas for ornamental, hedge and windbreak purposes (Cooper 1956). _P. undulatum_ produces abundant winter fruit crops and a suite of generalist avian frugivores facilitate the spread of _P. undulatum_ from these plantings into remnants of native vegetation. These factors, in combination with the species’ inherent plasticity and changes in natural disturbance regimes, have contributed to the dramatic increase in the distribution and local abundance of _P. undulatum_ in south east Australia since European settlement (Gleadow & Ashton 1981; Mullett & Simmons 1995; Rose & Fairweather 1997).

_P. undulatum_ now functions as an environmental weed across a range of habitats outside its natural range in Australia (Gleadow & Ashton 1981; Carr _et al._ 1992; Mullett & Simmons 1995; Mullett 1996, 1999; Keighery 1999) and on other continents and islands throughout the temperate, sub-tropical and tropical zones (Cooper 1956; Richardson & Brink 1985; Kruger _et al._ 1986; Cronk & Fuller 1995; Goodland & Healey 1996, 1997a, 1997b). Some populations of _P. undulatum_ occurring within the species’ natural range are also expanding their distribution and local densities in response to altered ecological conditions (Adamson & Fox 1982; Buchanan 1989a, 1991; Rose 1997a, 1997b; Rose & Fairweather 1997).

Previous investigations indicate that this species may exert considerable impacts on the composition, structure and function of invaded communities (Gleadow & Ashton 1981; Richardson & Brink 1985; Mullett & Simmons 1995; Goodland & Healey 1996, 1997b;
Rose 1997a; Rose & Fairweather 1997; Mullett 1996, 1999), however, many aspects of this species’ invasion ecology remain unclear.

1.1.1. Rationale for research

Environmental weed invasions are widely regarded as a serious threat to the conservation of biodiversity values yet few studies to date, have quantitatively assessed the invasion impacts exerted by environmental weed species on native plant communities. Quantification of the impacts imposed by environmental weeds will assist in determining the threat posed to biodiversity values and guide managers with the prioritisation and targeting of limited resources.

A suite of densely-foliaged, fire-sensitive, fleshy-fruit species are emerging as serious environmental weeds in Australia. This research provides a case study of the processes that facilitate invasion by these species and the impact such species may impose on Australian ecosystems. The invasion of native species into natural ecosystems is also a relatively recent phenomenon in Australia. The native *P. undulatum* has the potential to emerge as one of south east Australia’s most serious environmental weed species.

Little is known about the biology and ecological relationships of *P. undulatum* and the invasion impacts exerted by this species across the range of habitats now occupied. Key aspects of *P. undulatum* biology and ecology targeted for investigation in the current study include; patterns of morphological variation across the range of habitats occupied (as a measure of the species’ plasticity), dispersal ecology and seed germinability, population structure and spatial pattern, community relationships and the ecological impacts of invasion.

To date, control programs for invading populations of *P. undulatum* have had limited success in south east Australia, primarily because the inherent complexities of this species’ invasion ecology have been little understood or appropriately addressed. The findings of the current study will contribute to the more effective management of this
species and have wider application to other suites of environmental weeds including fleshy-fruited woody-weeds with ornamental origins, densely-foliaged fire-sensitive invaders and invasive native species responding to altered ecological conditions.

1-1.2. Aim of this research and thesis structure

The overall aim of this research is to determine the ecological causes and consequences of *P. undulatum* invasion across a range of habitat types in south east Australia.

This thesis consists of eight Chapters. This first Chapter explains the rationale for research and provides an overview of the thesis. Chapters 2 and 3 are background Chapters necessary to put the research on *P. undulatum* into context. The characteristics of invasive species, invasion theory, role of disturbance and landscape factors in facilitating plant invasions and the increasing incidence of native species functioning as environmental weeds are discussed in Chapter 2. Case studies from Australia and overseas are incorporated to illustrate these concepts and provide a theoretical context to the current study of *P. undulatum* invasion ecology.

Chapter 3 describes various aspects of the biology and ecology of *P. undulatum* and discusses previous research on this species. The range of habitats colonised by *P. undulatum* and the factors contributing to the spread of this species since European settlement in Australia are also discussed.

A study of geographic morphological variation in *P. undulatum* leaves measured throughout south east Australia is presented in Chapter 4. This study was initiated by observation of marked variation in *P. undulatum* habit, by habitat type, suggesting considerable phenotypic plasticity is evident in this species. The adaptability of *P. undulatum* to a range of environments and environmental conditions will likely facilitate the further spread of this species.
Aspects of *P. undulatum* dispersal ecology, germination and variation in fruit morphology are reported in Chapter 5. The comparative germinability of seed collected from natural and invaded habitats in Victoria and seeds extracted from the scats and pellets of the principal dispersal agents of *P. undulatum* in south east Australia are also presented. The ecological implications of mutualistic relationships between fleshy-fruitied weeds and adaptive frugivorous dispersal agents are also discussed in this Chapter.

Colonisation patterns and variation in *P. undulatum* population structure within and between various habitat types are described in Chapter 6. The structure of natural and invasive populations were investigated at sites throughout Victoria with particular emphasis on densities, population sex structure, height class assemblages and spatial associations between *P. undulatum* individuals of various developmental stages. Some characteristics of the *P. undulatum* regeneration niche are also discussed.

Chapter 7 reports on the findings of a detailed investigation of the influence of *P. undulatum* on community ecology in natural and invaded sites. Declines in species richness, changes in species composition and the simplification of structural resources are pivotal consequences of *P. undulatum* invasion in south east Australia. Evidence suggests that invading populations of *P. undulatum* contribute to a successional shift, especially in dry sclerophyll forest environments, which favours species adapted to mesic, shaded conditions. The implications of this floristic and structural simplification are discussed.

The main findings of Chapters 4 to 7 and the issues, impediments and opportunities associated with management options for this species are discussed in a broader context in Chapter 8.
CHAPTER TWO

Plant invasions

2-1. Introduction

At the end of the 20th century, ecosystems continue to be destroyed, degraded and ultimately simplified at an extraordinary pace, resulting in massive declines in global biodiversity (Ehrlich 1986, 1993; Soule 1990; Wilson 1993). This simplification of ecosystem composition, structure and function is further compromised by the process of global biotic homogenisation whereby species that are resilient or adaptable to such changes and attractive to humans for utilitarian purposes, emerge as dominants at continental, bioregional and landscape scales (Soule 1990, 1991; Lodge 1993; Vitousek et al. 1996, 1997; Schwartz 1997). Through ecosystem breakdown and via human enterprise, many of these species are proving invasive and constitute a perpetual threat to remaining natural ecosystems (Cronk & Fuller 1995). Invasive species contribute to the simplification process initiated by human-related ecosystem modification (Vitousek et al. 1996, 1997) by displacing indigenous species and further disrupting ecological processes and inter-relationships (Ramakrishnan & Vitousek 1989; Vitousek 1990; Humphries et al. 1991, 1993; Hobbs & Huenneke 1992; Carr 1993; Adair 1995; Walker & Smith 1997).

Invasions by vertebrates and associated impacts such as disruptions to predator-prey relationships, transmission of disease and competitive displacement have been well documented in the literature (for example, Rolls 1969; Kitching 1986; Myers 1986; Brown 1989; Ehrlich 1989a, 1989b; Twyford 1991). The impacts of weeds in agricultural and cultivated environments have received similar attention because of the associated reduction in production and amenity values (Combellack 1989; Fox 1990; Humphries et al. 1991, 1993). In contrast, the invasion of natural ecosystems by plant species has received less attention, partly due to the comparatively recent recognition of the threat posed (Adair 1995) and because the associated ecological and economic impacts are more difficult to quantify (Humphries et al. 1991, 1993).

The study of plant invasions into natural ecosystems in Australia is in its infancy but has emerged as a critical environmental management issue in recent years.

Environmental weed species have the capacity to fundamentally alter the composition, structure and function of an invaded community (Vitousek 1990; Humphries et al. 1991, 1993; Randall 1997). In severe cases, "invasions can convert a healthy, diverse biological community into a barren monoculture" (Center et al. 1995, p. 46).

Thus, the invasion of remaining natural or semi-natural ecosystems by environmental weed species is recognised as a serious threat to the conservation of biodiversity in an Australian (for example, Groves & Burdon 1986; Humphries et al. 1991, 1993; Carr et al. 1992; Carr 1993; Adair 1995; Fox 1995; Panetta & Scott 1995; Adair & Groves 1998) and global context (for example, MacDonald et al. 1986, 1989; Mooney & Drake 1986; Timmins & Williams 1987; Drake et al. 1989; di Castri 1990; Vitousek 1990; Westman 1990; Soule 1991; Center et al. 1995; Luken & Thieret 1997).

2-1.1. Recognition of the environmental weeds issue in Australia

Despite the recent recognition of the ecological consequences associated with environmental weed invasions of natural ecosystems in Australia (Humphries et al. 1991, 1993; Adair 1995; Panetta & Lane 1996), the issue has been heralded in dramatic terms:

"the greatest conservation problem in Australia" (Carr et al. 1986, p. 150),

"an acute and insufficiently appreciated ecological problem" (Humphries et al. 1991, p. 3) and,

"an unprecedented conservation crisis" (Carr 1993, p. 256).
Despite the gravity of these warnings and emerging data about the consequences of plant invasions in Australian ecosystems (for example, Waterhouse 1986; Braithwaite et al. 1989; Griffin et al. 1989; Fensham et al. 1994; Mullett & Simmons 1995), populations of environmental weed species are generally increasing in both their range and local densities (Humphries et al. 1991, 1993). Environmental weed invasions are symptomatic of gross disruptions to ecosystem connectivity, composition, structure and function (Humphries et al. 1991, 1993; Hobbs & Huenneke 1992; Walker & Smith 1997; Woods 1997). These factors and their relationship to environmental weed invasions in terrestrial ecosystems are discussed in this chapter.

2-1.2. Extent of the problem in Australia

Introduced species comprise 10 to 15% of the total Australian vascular plant flora (Michael 1981; Groves 1986a; Humphries et al. 1991, 1993; Saunders et al. 1996; Groves & Hosking 1997). While not excessive by world standards (Kitching 1986), these figures are especially alarming in an Australian context because of the short time scale over which these introductions have occurred (Adamson & Fox 1982). Not all introduced species become invasive and communities vary in their susceptibility to invasion (Williams 1997) although Adair and Groves (1998) warn that, few Australian ecosystems appear to be immune from environmental weed invasions. Humphries et al. (1991) estimate that approximately 50% of Australia’s introduced flora actually invade indigenous vegetation and categorise about a quarter of these species as representing a serious to very serious threat to natural ecosystems.

2-1.3. Patterns of invasions in Australia

The proportional representation of introduced species varies considerably on a State and Territory basis in Australia (Table 2-1). The percentage of introduced species roughly correlates with the intensity of settlement and land use patterns, which is in itself a reflection of rainfall and topographic characteristics (Humphries et al. 1991, 1993).
Table 2-1. Introduced plants as a percentage of the total vascular flora in each Australian State and Territory.

<table>
<thead>
<tr>
<th>Australian State or Territory</th>
<th>Percentage of Introduced Plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tasmania</td>
<td>31%</td>
</tr>
<tr>
<td>Australian Capital Territory</td>
<td>28%</td>
</tr>
<tr>
<td>South Australia</td>
<td>25%</td>
</tr>
<tr>
<td>Victoria</td>
<td>24%</td>
</tr>
<tr>
<td>New South Wales</td>
<td>16%</td>
</tr>
<tr>
<td>Queensland</td>
<td>13%</td>
</tr>
<tr>
<td>Western Australia</td>
<td>11%</td>
</tr>
<tr>
<td>Northern Territory</td>
<td>5%</td>
</tr>
</tbody>
</table>

(Source: Various in Humphries et al. 1991, p. 25.)

The southern states and the Australian Capital Territory have a higher proportion of introduced species than Queensland, Western Australian and the Northern Territory, but this tends to oversimplify the situation on-ground. Invasion patterns are inherently different in these regions. While some exceptions occur, invasions in temperate, southern and eastern Australian ecosystems generally involve a multitude of species in a diverse range of habitats and invasions in the arid and tropical north of the continent tend to be characterised by extensive single-species invasions (Humphries et al. 1991). It is difficult to compare the relative impact of these different invasion patterns. Both modes are destructive and the overall result is the same—loss of biodiversity and fundamental changes to the composition, structure and function of the invaded ecosystems (Humphries et al. 1991).

2-1.4. ‘The ideal weed’

Inventories of demographic, physiological, morphological and genetic characteristics which enhance the invasive potential of plants have been compiled and discussed by numerous authors (for example, Baker 1965, 1986; Barrett & Richardson 1986; Bazzaz 1986; Fox & Adamson 1986; Newsome & Noble 1986; Noble 1989; Roy 1990; Cronk & Fuller 1995).
Plants that are attractive to humans for utilisation and amenity purposes have an increased potential for facilitated range expansion and early favourable management to foster success in the ‘new’ environment. Once access to new environments has been gained, the overall plasticity or adaptability of the invader is an essential component of its invasive potential. Species with a broad ecological amplitude that occupy a range of habitat types in their natural range may have an inherently greater potential to adapt to the conditions of their new environment (Roy 1990; Williamson & Fitter 1996). Pre-adaptation to the conditions of the new environment confers an additional advantage and species originating from climate zones similar to that of the new environments have proved to be particularly invasive (Baker 1986; Groves 1986a, 1986b; Kruger et al. 1986, 1989; Richardson et al. 1992). Plants originating from tropical and some temperate zones are generally more problematic in northern Australia and plants from Mediterranean-type climate regions and other temperate zones have been particularly successful in the southern, temperate regions of Australia (Groves 1986a; Kloot 1987; Fox 1990). Similarly, fire-adapted trees and shrubs tolerant of low-nutrient soils originating from temperate Australia are extremely problematic under similar environmental conditions in South Africa (MacDonald 1985; Kruger et al. 1989; Richardson et al. 1992).

A high level of genetic variation increases the invader’s potential to tolerate, or adapt to, the prevailing conditions of the new environment (Kruger et al. 1986; Roy 1990) but colonising individuals may carry only a limited proportion of the species’ genetic variability and in some cases, the founder population may not establish (Holdgate 1986). Where colonising individuals fail to establish however, “their fate in a new environment may bear little relation to the outcome for genetically different members of the species” (Mack 1996, p. 108). The adaptability of phenotypic expression may be equally important where the genetic diversity of the invader is low (Moran et al. 1981; Lonsdale & Braithwaite 1988; Roy 1990; Wilson & Rapson 1995 and see Chapter 4).

Competitive attributes must normally be expressed at all stages of the invader’s life cycle. A high potential for resource acquisition increases the invader’s ability to commandeer essential resources and contributes to high biomass production (Bazzaz
Plastic, flexible, non-specific growth and reproduction requirements are also important attributes (Baker 1965; Bazzaz 1986; Roy 1990). Plants that are wind-pollinated, use non-specific pollination agents or reproduce by selfing or apomixis are especially successful in attaining a reproductive advantage (Baker 1986; Barrett & Richardson 1986; Bazzaz 1986). Seed dispersal generalists, especially those using physical or non-specific faunal agents, are most effective in dispersing seeds (Kruger et al. 1986). Seed dormancy mechanisms allow for the dispersal of seed through time and provide the invader with a competitive edge if a change in the availability of resources occurs and further germination opportunities arise (Roy 1990). Non-specific germination requirements allow the invader to respond to a range of environmental conditions (Baker 1965, 1986; Roy 1990). A rapid establishment phase and ‘gap-grabbing’ morphology (Grubb 1977) further enables competitive occupation of space and essential resources (Newsome & Noble 1986).

Plants that are quick to reach reproductive maturity and have a high reproductive output can rapidly increase their population base and further sequester resources at the invaded site (Noble 1989; Roy 1990). This provides an ideal foundation for the introduced plant to consolidate and expand its distribution and local abundance. At Woodman Point in Western Australia for example, the introduced climber Asparagus asparagoides (L.) Wight (Bridal Creeper) germinates earlier and more rapidly than its native structural analogue, Clematis microphylla DC. (Small-leaved Clematis) (Fox 1984). Additional demographic factors such as the size of the founder population, stage in life cycle, age and sex structure (where relevant) and the overall health of the colonising population will also influence invasion success (Roy 1990). Resistance to stochastic events at the population level, may also be important (Newsome & Noble 1986).

The possession of advantageous genetic, physiological and reproductive characteristics and non-specific growth requirements will not always result in invasion (Williamson & Fitter 1996). Further, introduced species with specialised ecological requirements may be as equally successful in exploiting new environments as generalist species, if these requirements are fulfilled in the host
community (Holdgate 1986). Timmins and Williams (1987) cite *Ammophila arenaria* (L.) Link (Marram Grass) and *Spartina alterniflora* Loisel. (Cord-grass) invasion of dune and estuarine ecosystems in New Zealand as examples of species with very specific habitat requirements that have become highly successful invaders.

Successful plant invaders in Australian ecosystems represent a diverse range of lifeform groups (Humphries et al. 1991) and this trend is typical of other continents and islands (Randall 1997). Trees and shrubs comprise approximately 60% of the terrestrial introduced plants that Humphries et al. (1991) classify as being capable of broadscale modification or destruction of Australian ecosystems. Vine and creeper species constitute approximately 30% of this ‘very serious’ category and grasses make up the remaining 10% (Humphries et al. 1991).

In the higher rainfall areas of south west, south and south east Australia particularly, it is the cumulative impacts of multi-species invasions representing a range of lifeform groups that is ultimately so problematic and difficult to manage (Humphries et al. 1991). Invaders that occupy a substantially different structural role than indigenous components of the invaded community can impose disproportionate competitive effects (Henderson & Musil 1984; Breytenbach 1986; Vitousek 1986; Woods 1997). The invasion of Queensland Mitchell grassland communities by *Acacia nilotica* (L.) Willd. ex Del. (Prickly Acacia) is a striking Australian example (Brown & Carter 1998). In this case, an entirely novel stratum is added which effectively converts the invaded community from grassland to shrubland (Humphries et al. 1991).

Fortunately, no single invader possesses all the characteristics of ‘the ideal weed’ (Baker 1965) and as Perrins et al. (1992) point out, some species displaying these traits are not obviously invasive and many highly invasive species have only a selection. Introduced plants may only become invasive in certain environments or under certain environmental conditions (Holdgate 1986; Johnstone 1986; Noble 1989; Williams 1997). The identification of weedy attributes has improved considerably over recent decades and weed risk assessment and decision support
systems, while sometimes fallible (Williamson & Fitter 1996), aid in the prediction of potential invasive species (Pheloung 1996; Steinke 1999; Weiss et al. 1999).

Profiles of weedy attributes form an important basis for research and predictive studies, however recent attention has turned to the characteristics of invaded communities and the broader invasion process (Kruger et al. 1986; Crawley 1987; Roy 1990; Hobbs & Humphries 1995; Burke & Grime 1996).

2-2. The invasion process

In the first instance, the potential invader has to gain access to the disturbed habitat by natural or human-mediated dispersal mechanisms. Once this ‘geographic barrier’ (Kruger et al. 1986) has been overcome, the potential invader needs to transcend resistance to colonisation and establishment in the new environment. These ‘habitat’ and ‘biotic barriers’ (Kruger et al. 1986) to invasion are weakened by fundamental changes in ecosystem connectivity and natural disturbance regimes (Roy 1990; Hobbs & Huenneke 1992). The shift in resource availability that accompanies ecological disturbance (Fox & Fox 1986) may serve to open an ‘invasion window’ (Johnstone 1986), which an opportunistic species may exploit. The competitive attributes of the potential invader are paramount if the colonising species is to exploit the invasion opportunity and overcome biotic resistance to establishment (Kruger et al. 1986).

The varying resilience of different communities and the type and severity of disturbance will also influence the nature and extent of invasion. Similarly, the influence of a given introduced species on community dynamics may vary between vegetation types and across environmental gradients (Williams 1997). The successful invasion of natural or semi-natural ecosystems is therefore the result of a complex interaction involving the competitive attributes of the invader and the susceptibility of the natural community to invasion.
2-2.1. Transcending geographic barriers

Changes in the spatial distribution and abundance of plant species occur over time in response to long-term fluctuations in climatic and environmental conditions (Jackson 1997). The movement of plant species across geographic barriers by long distance wind, water and vertebrate dispersal mechanisms has facilitated changes in the distribution of plant species and contributed to species’ expansions and contractions, speciation and extinctions over evolutionary time (Roy 1990). In recent times however, the exchange rate of biotic material within and between previously geographically-remote areas, has risen exponentially as a function of increased human trade and travel (Smith & Waterhouse 1988; Fox 1990; Roy 1990; Humphries et al. 1991; Rejmanek & Randall 1994; Vitousek et al. 1996, 1997; Schwartz 1997).

2-2.1.1. Deliberate introductions

Most of Australia’s current environmental weed flora were intentionally introduced for their apparent ornamental or utilitarian qualities (Humphries et al. 1991; Carr et al. 1992; Panetta & Scott 1995; Groves & Hosking 1997) and have been widely cultivated across the landscape. The origins of Australia’s introduced flora largely reflect our cultural and commercial history. Europe and the British Isles, the Mediterranean Basin, South Africa, Asia and the Americas have been the primary sources of our environmental weed flora (Michael 1981; Kruger et al. 1989; Fox 1990; Carr 1993). The Acclimatisation Societies of the late 1800’s and early 1900’s were responsible for many plant introductions, especially for ornamental purposes (Fox & Adamson 1986). The main agenda of the Acclimatisation Societies was to remodel the unfamiliar Australian environment and as described by Rolls (1969, p. 270), “there was never a body of eminent men so foolishly, so vigorously, and so disastrously wrong”. The legacy of the Acclimatisation Societies and their Euro-centric philosophies continue today. Notorious environmental weed species from all corners of the globe are still commercially available (Carr 1993) and are eagerly pursued by the gardening public.
Large numbers of species have also been, and continue to be introduced for agricultural, horticultural, amenity or other utilitarian purposes (Csurhes & Edwards 1998). While quarantine and screening measures are now more vigorous (Panetta 1993; Pheloung 1996; Steinke 1999) it is still difficult to predict when, where and how introduced species will respond to changes in the availability of resources in their new environments.

2-2.1.2. Accidental introductions

A considerable number of species also gained inadvertent access to Australian environments as contaminants of imported goods, introduced via trade and transport practices from an array of geographic locations (Fox & Adamson 1986; Carr et al. 1992; Parsons & Cuthbertson 1992; Csurhes & Edwards 1998). Inevitably, these same practices have contributed, and continue to contribute to the inter-regional movement of weed species on the Australian continent and associated islands (Fox 1990). Additional opportunities for the inter-regional transfer of weed species arise with further development of domestic trade and travel based industries (Wace 1977; Smith 1985; Adam 1995), including eco-tourism (Kloot 1987). As increasing eco-tourism opportunities entice more people to travel to previously remote natural areas, the inter-regional movement of environmental weed species is likely to increase. Approximately 70% of tourist vehicles entering Kakadu National Park in the dry season of 1989 for example, were inadvertently transporting seeds, most of which were from species not native to the Kakadu region (Lonsdale & Lane 1991).

Similarly, Chaloupka and Domm (1986) implicate human-mediated seed dispersal or ‘anthropochory’ as a major factor in the introduction and subsequent invasion of introduced plants on frequently visited coral cays of the Great Barrier Reef. In both cases, the addition of new weed species is likely to parallel increases in regional tourism.

2-2.2. Transcending habitat barriers

Overcoming habitat barriers to invasion requires some level of preadaptation, or the ability to adapt to, the prevailing conditions of the new environment (Kruger et al. 1986). Hence, many successful species at this level may be quite plastic and
adaptable. Kruger et al. (1986) suggest that historical attempts to match the climates of source and host location enhanced the invasion success of plants introduced for forestry purposes in South Africa. In addition to suitability for forestry, many other factors are now selected for by managers introducing species for various utilisation purposes including rehabilitation of mine-sites and soil stabilisation and increasingly in southern Australia, for the reclamation of saline landscapes (Ryan 1999).

Introducing species suited to a particular set of environmental conditions without the burden of their biotic constraints is a considerable management risk and examples where this strategy has failed are common in the Australian landscape (and folklore). For example, the perennial shrub, *Chrysanthemoides monilifera* ssp. *rotundata* (DC.) T. Norl. (Bitou Bush), was purposefully de-listed as a noxious weed in New South Wales prior to its widespread use in dune stabilisation works by that State’s soil conservation authority throughout the middle decades of this Century (Mort & Hewitt 1953 in Panetta & Scott 1995). *C. monilifera* ssp. *rotundata* is now a notorious invader of these coastal communities and is present along 60%, or over 70,000 hectares, of the New South Wales coastline (Love 1984; Toth et al. 1996). Changes in the geomorphology of beach-dune systems (Wickham & Stanley 1994), competitive displacement of indigenous species (Weiss & Noble 1984) and consequent alteration of habitat opportunities for fauna (French & Zubovic 1997; Vranjic & Groves 1999) are some of the obvious impacts associated with *C. monilifera* ssp. *rotundata* invasion. Invasions at this scale also impact upon recreational opportunities and amenity values and further contribute to the homogenisation of natural and cultural landscapes.

At the habitat or patch scale, barriers to invasion are commonly weakened by modifications to natural disturbance regimes and/or the addition of artificial disruptions (Hobbs & Hueneke 1992); the effects of which are exacerbated by the fragmentation of ecosystems across the landscape (Hobbs & Hopkins 1990; Saunders et al. 1991).
2-2.2.1. The importance of disturbance in shaping vegetation communities

Disturbance, in an ecological sense, entails some level of disruption to resource availability on a given spatial or temporal scale that influences ecosystem composition, structure and function (Fox & Fox 1986; Hobbs 1987). Fundamental to the definition of the term ‘disturbance’ is the recognition that such disruptions occur as part of a regime that has three essential elements; frequency, seasonality and intensity (Godron & Forman 1983; Williams & Gill 1995). Other authors also incorporate the duration (White & Pickett 1985; Grubb & Hopkins 1986; Fox 1988; DeFerrari & Naiman 1994), size (Hobbs 1987) and predictability (Sousa 1984) of disturbance into the definition of ‘disturbance regime’.

The scope for variation in disturbance effects is enormous (Hobbs 1987; Petraitis et al. 1989). Different species have different capacities to respond to disturbance and these responses may vary with population demographics, stage in life history and other inherent factors (Grubb & Hopkins 1986; Rejmanek 1989; Moore & Noble 1990). Equally, different communities vary in their susceptibility to disturbance effects. McIntyre et al. (1988) for example, reported that intermittent wetland communities adapted to drought and flooding regimes may be more resilient to artificial (exogenous) disturbance processes and invasion than communities adapted to less extreme environmental fluctuations. The response to disturbance may be expressed quite differently at a number of hierarchical levels including: 1) the individual, 2) the population, 3) the community, 4) the ecosystem, and 5) the landscape (Pickett et al. 1989). This variable response to disturbance contributes to diversity at the within-habitat or community (alpha diversity), between-habitats (beta diversity) and regional or landscape (gamma diversity) scales (Noss 1983; Hobbs 1992a; Adair and Groves 1998).

Disturbance has long been held as a necessary precursor to invasion (Amor & Piggin 1977; Crawley 1987; Ramakrishnan & Vitousek 1989; Huenekke et al. 1990; Hobbs 1991) and indeed, Fox and Fox (1986, p. 65) contest that “there is no invasion of natural communities without disturbance”. Although as Adair (1995) points out, it is difficult to test the alternative hypothesis given disturbance is such an integral feature of Australian plant communities. Invasion opportunities may be enhanced if
the availability of a limiting resource is increased (Hobbs 1989), amplified or otherwise modified by disturbance factors (Fox & Fox 1986). The combined complexities of variation in response at different hierarchical levels, the frequency, seasonality and intensity of the disturbance event and the subsequent changes in resource availability make the outcomes of disturbance very hard to predict (Fox & Adamson 1986; Hobbs 1987; Petraitis et al. 1989; Rejmanek 1989).

Variations in the approach to, and perspectives on the relationship between disturbance ecology and weed invasions are evident throughout the literature. Mack (1985) suggests that examples exist to demonstrate that invasions can occur without on-going disturbance and cites the spread of Pinus radiata D. Don (Monterey Pine) into eucalypt forest as an example (see Burdon & Chilvers 1977). It is likely that apparently undisturbed communities subject to invasion have undergone some change in disturbance processes, however subtle, even if the introduction of a new species is the only readily identifiable change (Swincer 1986).

### 2-2.2.2. Alterations to natural disturbance regimes

Natural (endogenous) disturbance regimes such as fire, flood and drought are essential to the maintenance and vigour of many Australian ecosystems (Fox & Fox 1986). The ecological relationships and processes that shaped the Australia biota have, however, been fundamentally altered since European settlement (Adamson & Fox 1982; Saunders et al. 1996) and a whole suite of novel disturbances have been imposed on the landscape. Natural disturbances still persist, but in a substantially altered context, so that even ‘natural’ disturbance processes may now be regarded as essentially artificial or exogenous. For example, the extensive Eucalyptus camaldulensis Dehnh. (River Red Gum) flood-plain forests along the Murray River are still subject to flooding, but the seasonality, intensity, frequency, duration and aerial extent of flooding events has been fundamentally altered (Dexter et al. 1986). Bushfires still occur in the dry sclerophyll forests of south east Australia, but again, the regime context has been dramatically modified (Williams & Gill 1995). Disturbance effects are further complicated by substantial changes in the composition, distribution and abundance of species now occupying these
communities and the overriding influences of habitat fragmentation, isolation and land use.

2-2.2.3. Fragmentation and the invasion process

Ecosystem fragmentation disrupts the nature and extent of ecological processes including disturbance regimes (Saunders et al. 1991; Hobbs & Huenneke 1992). Therefore, while fragmentation occurs at the landscape scale, the effects are most apparent at the patch or site scale (Hobbs & Huenneke 1992). The actual fragmentation event may initiate the modification of disturbance processes and contribute to the invasion of a patch (Saunders et al. 1991). In extreme cases, invasive species may become so dominant at the patch scale, that they become a source of fragmentation in themselves (Adair 1995).

The ecological consequences of fragmentation will vary between remnants and need to be considered in context with the time since, and degree of, remnant isolation (Sousa 1984; Saunders et al. 1991). The influence of these factors is further affected by the remnant size, shape and landscape position (Saunders et al. 1991). As a general rule, larger remnants are more resilient to the associated disruptions to ecosystem processes (Janzen 1983; Saunders et al. 1991; Haila et al. 1993) including invasion (Lodge 1993).

2-2.2.3.1. Edge effects

Alterations in wind speed, drainage, humidity, evaporation, temperature and light infiltration are often evident at the remnant-matrix 'edge' compared to the patch interior (Godron & Forman 1983; Saunders et al. 1991; Hester & Hobbs 1992; Scougall et al. 1993). Invasions by plant species are often initiated from the perimeter of the patch as this generally represents the highest source of disturbance and potential for propagule inputs from the surrounding matrix (Hobbs & Huenneke 1992; Tyser & Worley 1992; Center et al. 1995; Rose 1997a, 1997b). The edge environment may also have altered soil characteristics including reduced permeability and different concentrations of essential nutrients compared with the
patch interior (Buchanan 1989a; Hester & Hobbs 1992; Scougal et al. 1993; Morgan 1998a).

Smaller patches may be less able to provide for the full benefit of critical natural disturbance processes because of their physical size or ‘minimum dynamic area’ (Pickett & Thompson 1978). The composition and structural elements of the remnant may be so altered that the full functional response to natural disturbances may be limited (Hobbs & Huenneke 1992). Depending on the configuration of the patch and the penetration of edge effects, small remnants may consist entirely of ‘edge’ habitat (Noss 1983). Species able to exploit these disturbed environments may be favoured to the detriment of less resilient species.

Fragments of remnant vegetation that persist in a matrix of alternate land-use are often referred to as ‘islands’ (Pickett & Thompson 1978; Saunders et al. 1991; Bennett 1999). Oceanic island environments were the traditional focus of invasion ecology and the theories of island biogeography and invasibility now have broader application to the invasion of artificial ‘island’ environments (Fox 1992; D’Antonio 1997). However, remnant islands in the landscape matrix and have a greater potential for physical and biotic interactions from the surrounding landscape matrix (Janzen 1983), which adds “new dimensions to their dynamics” (Hobbs 1987, p. 235).

Oceanic islands are characterised by low species richness and high levels of endemism as a result of isolation pressures (Mauchamp 1997) and have been particularly susceptible to invasions by introduced biota (Looke & Mueller Dombios 1989; Vitousek et al. 1996). Australia’s island environments host a high proportion of introduced species, regardless of settlement patterns and the intensity of land-use practices. Nearly one-third of the total Tasmanian flora (31%) is introduced compared to 24% for the more densely populated Victorian landmass (Humphries et al. 1991). The figures are even more dramatic for smaller islands off the Australian mainland; introduced species comprise 60% of the total flora of Norfolk Island (Gilmour & Helman 1989) and 48.2% of the total flora of Lord Howe Island (Pickard 1984).
2-2-2.3.2. Implications of fragmentation

In an Australian context, the most critical element of fragmentation may be that broadscale ecosystem modifications have been so recent, profound and concentrated that the full biotic response to fragmentation has yet to eventuate (Adamson & Fox 1982; Hobbs & Hopkins 1990; Hobbs 1992b). The short, concentrated period of European-style land management in Australia has left the biota in a state of flux (Hobbs & Hopkins 1990; Fox 1995). An equilibrium has not yet been reached (Adamson & Fox 1982; Hobbs & Hopkins 1990; Hobbs 1992b) and further fluctuations in the distribution and relative abundance of species are predicted (Recher & Lim 1990; Recher 1993; Saunders *et al.* 1996). In this scenario, the invasive potential of introduced species and the susceptibility of natural ecosystems to invasion is even more difficult to predict.

2-2-2.4. Changes to significant disturbance processes in south-east Australia

2-2-2.4.1. Fire regimes

The natural fire regimes of virtually all south east Australian ecosystems have been substantially altered since European settlement (Christensen & Burrows 1986; Williams & Gill 1995). In the drier sclerophyllous vegetation types, particularly those associated with human settlements, natural fires have been vigorously suppressed with the chief intention of protecting lives and property (Adamson & Fox 1982), especially since the 1939 bushfires (Williams & Gill 1995).

Deprived of natural fire regimes, many fire-adapted communities have become less diverse over time and coupled with other disturbance pressures, are more susceptible to invasion by introduced species (Rose 1997a, 1997b). The invasion of fire-adapted communities by the fire-sensitive *Ligustrum* spp. (Privet) in the Sydney region for example, can in time, change the very nature of the community from dry open forest to wet closed forest (Fox & Adamson 1986). Shading associated with the dense *Ligustrum* canopy reduces light infiltration to the groundlayer (Buchanan 1989a) and
leads to changes in the floristic composition of the invaded community as plants able to tolerate increased shading and soil moisture are favoured over the preceding suite of species. The dense shading and increased soil and litter layer moisture accompanying *Ligustrum* invasion further subdues the threat of fire, which at the same time, may reduce regenerative opportunities for some fire-adapted species and facilitate the expansion and local dominance of other mesic species (Adamson & Fox 1982; Buchanan 1989a). Equally, where fire regimes shift to more intense, frequent fires, fire-sensitive native species can be similarly displaced by fire-tolerant introduced species (Christensen & Burrows 1986; Hobbs & Hueneke 1992).

2-2.2.4.2. Grazing regimes

Alterations to natural grazing regimes can have profound ecological consequences (Hobbs & Hueneke 1992). Where grazing or browsing is introduced to an ecosystem previously devoid of herbivores the results have been ‘catastrophic’ (Hobbs & Hueneke 1992). This stress may also apply to ecosystems evolved with grazing pressures where grazing intensity is reduced (Hobbs 1987), amplified (Hobbs & Hueneke 1992) or otherwise modified. In the grasslands and grassy woodlands of temperate Australia, it is the cumulative impacts of declines in some native herbivores, increased abundance of others and the introduction of numerous exotic herbivores that combine to produce fundamental changes in the grazing regime to which a particular community is adapted. These changes may facilitate the invasion of some plant species while generally suppressing the regenerative capacity of many indigenous species.

Introduced herbivores exert considerable pressure on indigenous plant species through selective grazing and browsing and the foraging techniques employed (Twyford 1991). Physical disturbances such as trampling, digging, rooting, pugging and soil compaction, that accompany grazing by introduced herbivores, further disrupt the community ecology and may create gaps for the establishment of opportunistic plant species (Hobbs & Hueneke 1992). Soil disturbance created by the introduced *Bubalus bubalis* (Water Buffalo) for example, has been identified as a major factor facilitating weed invasions in the tropical north of Australia.

2-2.2.4.3. Hydrological regimes

Modification of hydrological systems can occur on many scales. The alteration and diversion of flows from major river systems and the rise of watertable levels in intensively irrigated landscapes are obvious broadscale disruptions. In contrast, Buchanan (1989a) demonstrated that small-scale disruptions, such as the placement of a walking track through bushland, also influence water flow and drainage patterns, soil moisture, nutrient availability and consequentially, vegetation composition. The composition, structure and function of a community can be seriously affected whether disruptions to hydrological systems are subtle or profound. These changes again, may serve to facilitate invasive species, especially when altered nutrient loads (Buchanan 1989a) and soil disturbance (Hobbs & Atkins 1988) accompanies changes to hydrological systems.

2-2.2.4.4. Nutrient regimes

The addition of nutrients, especially phosphorus, to depleted Australian soils can have severe consequences for indigenous communities adapted to low-nutrient soils (Burrell 1981; Hobbs & Atkins 1988; Hester & Hobbs 1992; Hobbs & Huenneke 1992; Morgan 1998a). Introduced species that originated from environments supporting higher soil nutrient loads are advantaged over indigenous species adapted to nutrient-poor soils in such situations (Fox & Adamson 1986). Clements (1983) for example, reported that nutrient levels, especially phosphorus, were higher in soils associated with bushland in suburban areas, than comparable areas outside suburbia in the Sydney region. Introduced mesic species adapted to higher soil nutrient availability were favoured in nutrient-enriched soils over the preceding suite of native species adapted to low-nutrient conditions (Clements 1983). Nutrient cycling and nutrient availability can be further modified by changes in soil temperature, soil fauna and other decomposition agents, that occur in response to habitat
fragmentation and disruptions to endogenous disturbance regimes (Saunders et al. 1991), in some cases, promoting further invasion.

2-2.2.4.5. Climate warming

The effects of anticipated climate warming on plant species assemblages are difficult to predict (Fox 1991, 1995; Adair 1995) but are likely to involve further changes in the distribution and local abundance of some plant species (Westman 1990; Williams 1997). Humphries et al. (1993) suggest weeds of sub-tropical and tropical environments may be further advantaged in present temperate areas of Australia with the anticipated changes in climate patterns. Changes in the distribution and abundance of plant species predicted to accompany global warming are likely to further complicate the objectives of conservation management programs. Issues may range from the philosophic conundrums of actually defining a species’ natural distribution (Schwartz 1997), to changes in the functional roles performed by species (Williams 1997) in the post climate change environment.

2-2.2.5. Cumulative impacts of exogenous disturbance

The disruptions discussed in section 2-2.3.4 are not exhaustive but represent important factors that influence the invasibility of a community and are especially relevant to the south east Australian scenario. These disturbances rarely occur in isolation and in most cases, it is the cumulative effect of different disturbance pressures that ultimately weakens the resilience of plant communities to invasion (Hobbs & Huenneke 1992). For example, an urban bushland remnant, fragmented and isolated from other patches in an otherwise hostile matrix is likely to be subjected to altered fire, drainage, nutrient and grazing regimes (Adamson & Fox 1982). Changes in the composition, distribution and abundance of species performing important functional roles such as decomposition, pollination and dispersal, may also occur as a cause or consequence of altered disturbance regimes and impose further modifications to affected communities.
2-2.2.6. Native plants as environmental weed species

Roy’s (1990, p. 337) definition of invasion emphasises that “the process of invasion brings an organism to an environment in which it did not evolve” and Mack (1985 p. 128) describes invasive species as “any taxon entering a territory in which it has never before occurred”. In south-east Australia however, many examples exist of native species becoming invasive within the environment in which they evolved (Burrell 1981; Kloot 1985; Robinson et al. 1986; Fox 1990; Humphries et al. 1991; Carr et al. 1992; Carr 1993; Keighery 1995, 1999; Mullett & Simmons 1995; Rose & Fairweather 1997; Singer & Burgman 1999). The processes that previously contained such species have been so altered that the environment, from the invasive species’ perspective, is essentially a new one.

Invasion of natural ecosystems by native species is a conservation problem experienced by all States and Territories of Australia (Humphries et al. 1991) and is particularly profound in the most populated parts of the continent. Carr (1993) lists 115 taxa of Australian plants that have naturalised in Victorian environments and at least 51 native species are functioning as environmental weeds in South Australia (Kloot 1985). Sixty-four native species, including 22 Western Australian species, are functioning as environmental weeds in Western Australia (Keighery 1995). In all cases, the majority of these species are trees and shrubs, however, this may be more a reflection of gardening trends than the comparative invasiveness of Australian trees and shrubs over other lifeform guilds. *Sollya heterophylla* Lindl. (Bluebell Creeper), a scrambling vine native to south west Western Australia for example, is a comparatively recent addition to cultivated parks and gardens in the greater Melbourne area. This species has ‘escaped’ from these urban environments and is gradually encroaching on vegetation communities in Victoria, particularly the drier vegetation complexes south of the Great Dividing Range.

Such inter-regional invasions are likely to be on the increase (Fox 1990) and more native species are predicted to become problematic in the future (Humphries et al. 1991; Carr 1993). That some native species, such as *Pittosporum undulatum*, are becoming invasive in the habitats in which they evolved is indicative that biotic barriers—the last line of defense against invasion, are rapidly deteriorating.
2.2.3. Transcending biotic barriers

The biotic resistance of a community will generally be weakened if habitat fragmentation and inappropriate disturbance regimes significantly alter the composition and structure of a community and by association the vital functional processes. In some cases, biotic interference can prevent or delay (Kruger et al. 1986) invasions but reduced pest, pathogen and predation pressures generally provide the invader with a competitive advantage in the new community (MacDonald 1985; Dean et al. 1986; Kruger et al. 1986; Richardson et al. 1992). Successful invaders must be able to overcome biotic resistance to establishment, reproduction and population expansion including seed predation, herbivory, allelopathic inhibition, parasitism and competition in their new environment (Kruger et al. 1986). In some cases, invaders will also need to develop relationships with other components of the invaded community, such as pollination and dispersal agents (Kruger et al. 1986). Invasive species need to be competitive in the overall community ecology and often possess physical, chemical or behavioural defence mechanisms to suppress hostile biotic interactions and dominate essential resources such as space, light, nutrients and moisture.

The concept of introduced species filling vacant or under-utilised niches has received some attention in recent years (Simberloff 1981; Herbold & Moyle 1986; Newsome & Noble 1986). While in a theoretical sense it may be possible to identify apparently vacant niches in a community, this concept may belie the ecological intricacies of niche occupation. What may be perceived as a vacant niche may in fact be a transitory vacancy in time and/or space, or be occupied in ways that are not easily identified or understood, or, in fact be ‘empty’ for any number of reasons (Crawley 1987). Just as not all introduced plants become invasive, it seems reasonable to assume that not all vacant niches will become occupied by invasive species.
2-2.3.1. The time lag phenomena

Many plant species experience a time lag before they become invasive (Humphries et al. 1991) and seemingly “innocuous species...may prove to be biological timebombs awaiting a trigger” (Fox 1995, p. 182). This time lag to invasion or infection pressure (Baker 1986) can be attributed to a combination of many factors although the exact cause of this phenomenon is not clear.

In some cases, the time lag from introduction to invasion may be largely demographic in that the species needs to develop a critical population base from which to expand (Kruger et al. 1986). For some species, the period that elapses between introduction and invasion may relate to the founder effect where time must pass for small populations to develop genetic variation or adapt their phenotypic expression, to meet the conditions of the new habitat (Kruger et al. 1986).

Perhaps the most complex component of the time lag factor, and certainly the most difficult to predict, is that of chance ecological events that serve to alter the resource base in the community and provide an establishment opportunity for a given plant species. Some of Australia’s most dramatic invasions were initiated when environmental fluctuations converged with an opportune stage in a ‘sleeper’ weed’s life cycle (Groves 1999).

A classic Australian example is provided by the recent rapid spread of Tamarix aphylla (L.) Karst. (Salt Cedar) throughout the Finke River system of arid central Australia (Griffin et al. 1989). T. aphylla was planted as an ornamental and windbreak species at homesteads along the Finke River for many years but it was not until a unique set of circumstances converged to provide the ultimate invasion window that this species become invasive. Massive floodwaters swept through the region in 1974, at the same time the scattered populations of T. aphylla had set seed (Griffin et al. 1989). The floodwaters removed much of the native vegetation in its path and T. aphylla seeds were ultimately dispersed throughout the Finke River floodplain and into safe sites created by the removal of indigenous species (Griffin et al. 1989).
T. aphylla was able to exploit such an opportunity because of its inherent weedy attributes and it pre-adaptation to the post-flood conditions. The related discharge of saline water from aquifers and basins further displaced indigenous species while creating ideal conditions for the salt-tolerant T. aphylla (Griffin et al. 1989). The species’ possesses many other physiological attributes favouring population expansion over the preceding assemblage of native species. In addition to tolerance of saline conditions, T. aphylla is poikilohydric, has unpalatable foliage, wind dispersed seeds and, after the 1974 floods, a broad population base from which to spread. T. aphylla invasions reduce the floristic and structural diversity of invaded sites, favour the establishment of other salt-tolerant species, alter habitat opportunities for faunal populations and disrupt flow rates and siltation patterns (Griffin et al. 1989).

Many of the most troublesome invasive species in South Africa were introduced between 1850 and 1900 (Kruger et al. 1986). The authors suggest that this pattern forewarns of future problems given that a large number of species introduced since that interval may be emerging from this adjustment period (Kruger et al. 1986). This theory, when applied to Australia, is especially alarming given the sheer scale of introductions over such a short period. Invasive species are still likely to emerge from the introduced and native flora now present in Australia, even in the absence of further introductions (Short 1987; Humphries et al. 1991, 1993; Hobbs 1995).

Converse to this trend of emerging introduced species, a limited number of examples exist of invasive species that have become less invasive over time, in response to environmental changes (Schwartz 1997). Cooke (1990) suggests that the weeds Anacyclus radiatus and Iva axillaris both previously considered naturalised in South Australia are now presumed extinct in that State, but further field examination would be necessary to clarify this status. Such species are also likely to remain in the minority.
2-3. Impacts and implications of environmental weed invasions

Environmental weed invasions of natural or semi-natural ecosystems are a global phenomenon of immense consequence (Groves & Burdon 1986; MacDonald et al. 1986; Mooney & Drake 1986; Drake et al. 1989; di Castri 1990; Luken & Thieret 1997). Environmental weed invasions occur over infinite temporal and spatial scales and can impose subtle to profound impacts on the composition, structure and function of invaded communities (Vitousek 1990; Walker & Smith 1997). The scope for variation in invasion impacts varies substantially in accordance with the characteristics of the invader, the composition of the invaded community and a range of landscape and disturbance factors (Fox & Fox 1986; Saunders et al. 1991; Hobbs & Huenneke 1992). Key ecosystem modifications imposed by invasive plant species have emerged from the Australian and international literature on this topic. The ecological impacts of environmental weed invasions can be broadly separated into physical and biological categories, but in reality, it is the combination of modifications to the abiotic and biotic environment that is ultimately so problematic.

It is also difficult to separate the ecological causes and consequences of environmental weed invasions (Vitousek 1986, 1990; Ramakrishnan & Vitousek 1989; Humphries et al. 1991; Woods 1997). Plant invasions can be triggered by changes in natural disturbance regimes and in some cases, populations of invading plants can impose further modification to ecosystem processes and disturbance regimes in the invaded communities. The modification of disturbance regimes by environmental weed species “can be the most pervasive impact of all” (Walker & Smith 1997, p. 79), because of the associated impacts on ecosystem composition, structure and function and the difficulties inherent in restoring affected communities.

Just as the invasion of fire-sensitive plants can be facilitated by the suppression of natural fire regimes, so too can fire-sensitive invaders further modify the flammability of the invaded community, further reducing the likelihood of fire and regenerative opportunities for fire-adapted species (Fox & Adamson 1986; Buchanan 1989a; Mullett & Simmons 1995). The converse can also apply. Invasive fire-adapted grasses for example, have induced a shift towards hotter, more frequent
fires in many different vegetation types (Christensen & Burrows 1986; D’Antonio & Vitousek 1992; Milberg & Lamont 1995).

Changes in nutrient availability and aspects of biogeochemical cycling can also occur as a cause or consequence of plant invasions and further influence the floristic composition of the affected community (MacDonald & Richardson 1986; Versfeld & van Wilgen 1986). The addition of nutrients to nutrient-poor soils, especially when coupled with soil disturbance (Hobbs & Atkins 1988), can facilitate the invasion and establishment of species adapted to such conditions (Clements 1983; Hester & Hobbs 1992; Burke & Grime 1996; Morgan 1998a). Invasion by nitrogen-fixing species such as *Myrica faya* Ait. (Faya Tree) in Hawaii (Vitousek & Walker 1989), *Lupinus arboreus* Sims (Bush Lupine) in California (Maron & Connors 1996) and various *Acacia* species in South Africa (Versfeld & van Wilgen 1986) can substantially alter nitrogen accumulation rates and availability with important implications for the invaded community and successional processes. Changes in soil nutrient properties that occur as a cause or consequence of environmental weed invasion are extremely difficult to remediate (Walker & Smith 1997). Fundamental changes in litter accumulation and decomposition rates and biomass production can occur as a cause or consequence of plant invasion and can further induce changes in fuel loads, fire risk and floristic composition (Versfeld & van Wilgen 1986).

Changes in soil chemistry and nutrient availability that result from the accumulation of salts can also profoundly alter the vegetation composition of affected sites. Rising saline groundwater in intensively irrigated landscapes in south western and south eastern Australia for example, has prompted the expansion of salt-tolerant species and in some areas, has contributed to the displacement of indigenous species. Changes in the surface soil salinity can also occur via invasive plants that concentrate salts in shoot and root structures that on abscission and decay or through leaching, can lead to further changes in soil and litter chemistry and induce a shift towards salt-tolerant species (Kloot 1983; Griffin et al. 1989; Walker & Smith 1997).
Substantial changes in hydrological regimes that alter surface run-off and catchment yields can also influence soil erosion and deposition rates (MacDonald & Richardson 1986), providing establishment opportunities for some species while generally reducing the suitability of the substrate for indigenous species (Walker & Smith 1997). Invasive plants can also modify the erodability of invaded patches (Binggeli & Hamilton 1993), the effects of which may vary depending on the invader’s root structure, canopy morphology and water use characteristics (Walker & Smith 1997). Displacement of indigenous riparian species by invasive *Acacia* species in South African fynbos for example, has contributed to substantial soil erosion, as the introduced species are less able to withstand periodic flash flooding (MacDonald & Richardson 1986).

The amplification of resources that accompanies soil erosion and other processes that provide ‘gaps’ are consistently recognised as important factors facilitating plant invasions (Fox & Fox 1986; Newsome & Noble 1986). Introduced species can also substantially alter geomorphological processes (MacDonald et al. 1989) and the local topography of invaded sites during the establishment and colonisation phases. In coastal areas of Australia, *Ammophila arenaria* has been widely planted as a sand stabilising plant, consequently altering the topography of invaded beach-dune systems (Heyligers 1985). Invasion by *Spartina* spp. (Cord-grasses) accelerates accretion of sediments, which can result in a total habitat transformation from mudflats to grasslands (Lane 1992).

The creation of ‘gaps’ in the canopy of sub-tropical and tropical rainforest environments can similarly open invasion windows for invasive vine species and again, occur as a cause or consequence of invasion. Most invasive vine species initially require an opening in the canopy but once established their impact on invaded vegetation is “direct, rapid and total” (Humphries et al. 1991, p. 33). Introduced perennial vines smother invaded vegetation consequentially reducing regeneration opportunities for indigenous species. The increased wind barrier created by vine infestations increases the susceptibility of indigenous host plants to windthrow and may increase the incidence of gap creation in these forests, providing
further establishment opportunities for invasive species of this lifeform (Humphries et al. 1991).

Changes in biotic composition and structure inevitability follow fundamental modifications to ecosystem processes (Vitousek 1990; Walker & Smith 1997). Such changes can facilitate plant invasion, occur as a result of plant invasion and in some cases promote the invasion of other introduced plant species (Binggeli & Hamilton 1993; Rose 1997b). Some indigenous species may be directly out-competed while others may succumb to indirect secondary effects associated with the invasion. Species interactions such as pollination and dispersal syndromes, plant-herbivore relationships and successional processes may be considerably disrupted by the presence of invasive species (Breytenbach 1986), although few studies have attempted to quantify these effects. Declines in species richness, changes in species composition and the simplification of structural resources are pivotal consequences of environmental weed invasions (see Chapter 7).

Changes in habitat opportunities for fauna are an important, but little understood, consequence of environmental weed invasion (Humphries et al. 1991; Loyn & French 1991; French & Zubovic 1997; Adair & Groves 1998; Mullett 1999). Displacement of native vertebrates and invertebrates via weed-induced habitat simplification is further complicated by competitive interactions with introduced vertebrates and invertebrates. The pollination syndromes of indigenous plants for example, may be disrupted by the presence of introduced outcrossing plants and introduced pollination agents such as *Apis mellifera* L. (Honeybees). Similarly, the dispersal potential of indigenous fleshy-fruitied plants may be influenced by competition with introduced plants of the same guild and by changes in the composition and abundance of dispersal agents (Terborgh & Winter 1980; Knight 1986 and see Chapter 5).

Some species may be resistant to changes in habitat opportunities that arise with environmental weed invasion but this resistance is likely to vary over time and space depending the specificity of a given species' habitat requirements, the scale of invasion and the severity of the changes to habitat opportunities. Brown et al. (1991)
for example, reported that dense thickets of *Rubus procerus* Muell. ex Genév. (Blackberry) and *Tetrarrhena juncea* R. Br. (Wire Grass) provide shelter and protection for the rare *Mastacomys fuscus* Thomas (Broad-toothed Rat) in the Dandenong Ranges National Park, Victoria. While Broad-toothed Rats may be advantaged by the increased abundance of *T. juncea*, Carr (1991) reports that at the same location, foraging opportunities for *Menura novaehollandiae* Latham (Superb Lyrebirds) are considerably reduced in areas supporting high densities of *T. juncea*.

Environmental weeds may provide habitat resources for some species, especially where traditional habitat resources have been lost or modified (Braithwaite & Lonsdale 1987; Brown *et al.* 1991). The net effect of environmental weeds on faunal populations is likely to be negative, even if some short-term or species-specific benefits are provided (Abensperg-Traun *et al.* 1998).

The impacts and implications of environmental weed invasions described is far from exhaustive but represents some important intricacies of invasion ecology. As Vermeij (1996, p. 7) concludes, "invasion implies change". A change in disturbance processes can trigger invasion and invasion can then trigger additional changes in disturbance regimes and ecosystem processes that influence the composition, structure and function of the invaded community. Ultimately, the cumulative effects of changed disturbance regimes and environmental weed invasions reduce the diversity and resilience of remaining natural ecosystems. This loss of genetic, species and ecosystem diversity and the modification of ecosystem processes poses incalculable implications (Ehrlich 1986; Recher 1993; Vitousek *et al.* 1996; Adair & Groves 1998), not least of which are to the issues of evolutionary potential, landscape resilience and the provision of ecosystem services (Ehrlich & Mooney 1983; Noss 1983; Wilson 1993; van Wilgen *et al.* 1996; Hobbs & Mooney 1998; Panetta 1999; Panetta & James 1999).

2-4. Summary
The invasion of natural or semi-natural ecosystems by environmental weed species is a serious threat to the conservation of biodiversity on a global scale (Groves &
Burdon 1986; MacDonald et al. 1986; Mooney & Drake 1986; Drake et al. 1989; di Castri 1990; Luken & Thieret 1997). Environmental weed invasions are facilitated by fundamental changes in ecosystem connectivity and disruption to natural disturbance regimes and ecosystem processes (Fox & Fox 1986; Vitousek 1986, 1990; Hobbs 1987; Hobbs & Huenneke 1992). Plant species possessing ‘weedy’ attributes may be best placed to exploit the shifts in resource availability that occur with ecosystem disruption and modification to endogenous disturbance regimes.

The ecological causes and consequences of plant invasions are difficult to isolate (Vitousek 1986, 1990; Woods 1997). Some invasive species respond to changes in disturbance factors through population expansion which in many cases, results in the further modification of the community resource base. Invasive species can reduce the diversity and resilience of natural communities and impose fundamental changes to ecosystem processes.

An understanding of the landscape and disturbance factors that increase the susceptibility of natural communities to invasion is a vital component of environmental weed management strategies (Hobbs & Humphries 1995). An adequate understanding of a targeted weed species’ biology, ecological inter-relationships and invasion patterns and impacts, are equally essential to the development and implementation of effective weed management programs.
CHAPTER THREE

*Pittosporum undulatum* Vent. (Sweet Pittosporum)

3-1. Introduction

*Pittosporum undulatum* is recognised as one of Victoria’s most serious environmental weed species (Carr *et al.* 1992; Mullett & Simmons 1995) and is arguably the most successful ‘native weed’ in south east Australia (Mullett 1999). *P. undulatum* has invaded a range of habitats outside its natural geographic range in Australia (Gleadow & Ashton 1981; Keighery 1995, 1999; Mullett & Simmons 1995), some locations overseas (Cooper 1956; Richardson & Brink 1985; Geldenhuys *et al.* 1986; Kruger *et al.* 1986; Goodland & Healey 1996, 1997a, 1997b; Robertson 1997) and has expanded its distribution and local abundance in some habitats within its natural range (Adamson & Buchanan 1974; Adamson & Fox 1982; Buchanan 1991; Rose 1997a, 1997b; Rose & Fairweather 1997; Mullett 1999). Widespread ornamental plantings, increased dispersal opportunities and changes in natural disturbance regimes have contributed to the dramatic increase in the distribution and abundance of *P. undulatum* this century (Gleadow & Ashton 1981; Mullett 1999).

3-2. Taxonomy

3-2.1. Pittosporaceae

The Family Pittosporaceae is comprised of nine genera and approximately 200 species (Walsh & Albrecht 1996). The Pittosporaceae occurs throughout the temperate, sub-tropical and tropical zones in Australia, the Hawaiian Islands, New Caledonia, New Zealand, south east Asia and Africa (Cooper 1956) suggesting an east Gondwanan origin (Crisp *et al.* 1989). Species from each of the nine Pittosporaceae genera are represented in Australia (Wilkinson 1992) which is regarded as the main developmental centre of this family (Cooper 1956).
3-2.2. *Pittosporum*

*Pittosporum* is the largest and most primitive (Haas 1977) genus in the
Pittosporaceae and includes approximately 160 species, which occur throughout
Nine of the twelve *Pittosporum* species that occur in Australia are endemic (Cooper
1956; Walsh & Albrecht 1996). The Greek derivation of *Pittosporum* is *pitta* (pitch
or resin) and *spora* (seed) in reference to the sticky mucilage that encases the seeds
in most of the species in this genus (Haas 1977; Walsh & Albrecht 1996).

3-2.3. *Pittosporum undulatum* Vent.

Described in 1800 by Ventenat (Maiden 1920), *P. undulatum* is a tall shrub or small
tree reaching an average height of 8-15 metres. Considerable variation is evident in
*P. undulatum* morphology throughout the species’ geographic range (see Chapter 4).
In more exposed sites where soil depth, nutrients and moisture are limited, mature
individuals rarely exceed 10m in height, whereas, in protected environments, *P.
undulatum* can attain heights in excess of 30m (Cooper 1956). In newly colonised
habitats, *P. undulatum* rarely exceeds 15m in height (pers. obs.), although this could
reflect time since invasion and the age of the individuals involved.

*P. undulatum* leaves are generally arranged in whorls or semi-whorls, which tend to
be clustered at the end of branchlets. Adult leaves are entire and ovate to
oblanceolate in shape. The upper leaf surface is a glossy dark green in contrast to the
pale green underneath and reticulate venation is distinct on both leaf surfaces. Leaf
margins are undulate (*undulatum* is from the Latin *undulatus* meaning wavy)
although the number of undulations per leaf varies considerably within and between
populations (see Chapter 4). Leaf buds containing five to ten leaves develop during
autumn and winter and burst in late winter to early spring (Gleadow & Ashton 1981).
Some individuals undergo a second growth flush in early summer (Gleadow 1980).

3-2.3.1. Reproductive biology

*P. undulatum* reaches reproductive maturity in four to five years (Gleadow 1982).
Flowers are arranged in a cyme and flowering occurs first in the terminal flower
(Cooper 1956). The five petals are apically recurved to reveal five stamens in male flowers and five staminodes resembling rudimentary scales in female flowers (Steel 1911). The creamy-white flowers are fragrant and although this species is functionally dioecious, seed-producing flowers are occasionally observed on otherwise male-flowering trees (Steel 1911; Mullett 1996 and see Chapter 5). The non-dehiscent stamens in these 'abnormal' (Steel 1911) flowers are approximately half the length of 'normal' *P. undulatum* stamens but the ovary is very similar in size and shape to those of female flowers. An intermediate form has also been observed but this is apparently an uncommon occurrence (Steel 1911) (Figure 3-1).

Maiden (1920) credits J. C. Bidwill as the first botanist to acknowledge variation in *P. undulatum* flower structure. Bidwill (1847 in Maiden 1920, p. 124) reported that *P. undulatum* plants are "sometimes hermaphrodite, sometimes male and sometimes female". Most of the ensuing discussion on variation in *P. undulatum* flower structure referred to observations of ornamental plantings (Hamilton in Anon. 1894, 1902; Anon. 1900; Steel 1911), but these authors concluded that the species was in a transition phase towards dioecism. Variation in flower structure has never been observed in functionally female flowering trees (Steel 1911) and the incidence of seed-producing flowers on otherwise male flowering trees appears to be restricted to invasive populations and ornamental plantings. Despite considerable field examination throughout south east Australia, these seed-producing flowers have not been observed in natural populations of *P. undulatum* (pers. obs.). In a more global review of *P. undulatum* invasion, Cronk and Fuller (1995, p. 108) reported that "the flowers are usually hermaphrodite, but dimorphic flowers occur in the native area and unisexual individuals have even been found". Additionally, Goodland and Healey (1996) reported that 78.4% of *P. undulatum* trees surveyed (n=60) in invaded Jamaican habitats appeared to have hermaphroditic flowers. Variable dioecism is evident in other *Pittosporum* species (Hamilton 1902; Cooper 1956; Godley 1979; Clarkson & Clarkson 1994) but most Australian *Pittosporum* species have differentiated into a unisexual or bisexual state (Walsh & Albrecht 1996).
Figure 3-1. Variation in *P. undulatum* flower structure.

Key (Steel 1911):
1. Flowering twig, male tree, showing A, normal, not producing seed and B, abnormal flowers which produce seed.
2. Normal male flower showing anthers.
3. Normal male flower, dissected.
4. Abnormal seed-producing flower, male tree, dissected.
5. Normal female flower, dissected.
6. Intermediate flower, male tree, showing two normal and three abortive stamens, corolla removed.
7. Abnormal flower from male tree, showing short abortive stamens, corolla removed.

*Reproduced from Steel 1911*
Introduced Honeybees are likely to be the most important diurnal pollination agents, especially in disturbed habitats (pers. obs.). Native pollinators remain elusive but are likely to include generalist diurnal and nocturnal invertebrates (Hamilton 1902). *P. undulatum* fruit capsules are bivalve or rarely trivalve and fruit development commences immediately after pollination in spring. Development continues over the summer and autumn months and fruits reach maturity in early winter. The orange capsules are obovoid in shape and split on maturity to reveal numerous bright orange to red seeds encased in a sticky mucilage, which attracts a generalist suite of frugivorous vertebrates (see Chapter 5).

### 3-2-3.2. *P. undulatum* hybrids and sub species

Some confusion exists regarding the taxonomic status of *P. undulatum* ssp. *emmettii* and the *P. undulatum* x *P. bicolor* Hook. (Banyalla) hybrid. *P. undulatum* ssp. *emmettii* has been reported as a rare endemic of Tasmania (Stones & Curtis 1978); however, this species is likely to be one and the same as the *P. undulatum* x *P. bicolor* hybrid found at a limited number of sites throughout southern Victoria (D. Albrecht pers. comm.). The *P. undulatum* ssp. *emmettii* type specimen was collected in the Arthur River region of Tasmania in 1874 and was initially considered to be *P. undulatum* (Rodway 1903). *P. undulatum* is not considered indigenous to Tasmania (Carr 1993) but it is possible that the species was introduced to the region as an ornamental planting when tin mining settlements were established in the region in the 1870’s (Blainey 1967).

Isolated occurrences of this putative hybrid have been recorded within the natural and invaded range of *P. undulatum* in Victoria (Robin & Carr 1986; Ashwell 1991; Carr 1993) and New South Wales (Makinson 1992). Individuals display characters intermediate between *P. undulatum* and *P. bicolor*, although morphological attributes are quite variable within and between individuals (pers. obs.). Observation and anecdotal evidence suggests the species is a hybrid. Additionally, *P. undulatum* and *P. bicolor* occupied different habitat types within south east Australia immediately prior to European settlement (D. Albrecht pers. comm.).
Further genetic and molecular studies are needed to determine the taxonomic status of this species as a foundation for sound management prescriptions. If *P. undulatum* ssp. *emmetii* is a rare endemic of Tasmania then appropriate conservation management strategies need to be implemented. Conversely, if the taxon is a hybrid, control programs may be required to prevent swamping of both *P. undulatum* and *P. bicolor* gene pools. Hybridisation between *P. undulatum* and the New Zealand ornamental, *P. tenuifolium* Sol. ex Gaertn. (James Stirling Pittosporum) (Carr 1993), and *P. undulatum* and *P. revolutum* Dryand. (Rough-fruit Pittosporum) (Cooper 1956) have also been reported in the literature.

3-3. Distribution of *P. undulatum*

*P. undulatum* occurs in a diverse range of habitat types across the temperate and subtropical climate zones of south east Australia (Figure 3-2). This pre-adaptation to a range of environments and environmental conditions is considered an important factor in the species’ successful colonisation of previously unavailable habitats (Mullett 1999).

3-3.1. Distribution prior to European settlement in Australia

The natural range of *P. undulatum* is believed to extend seawards of the Great Dividing Range in south east Australia from east of Westernport bay in Victoria to Brisbane, Queensland (Gleadow & Ashton 1981). *P. undulatum* occurs as a natural component of a range of habitats throughout this extensive geographic area but is mainly associated with wet forest (Gleadow & Ashton 1981), rainforest ecotone (Barrett & Ash 1992) and rainforest communities (Beadle et al. 1972; Melick & Ashton 1991; Burgman & Ferguson 1995; Peel 1999).

In Victoria, *P. undulatum* was apparently restricted to warm temperate rainforest, riparian habitats in lowland forests and woodlands, and some coastal sites, prior to European settlement (Walsh & Albrecht 1996). *P. undulatum* is a natural component of the wet sclerophyll forests dominated by *Acmena smithii* (Poir.) Merr. & L. M. Perry (Lilly Pilly), *Eucalyptus muelleriana* A. W. Howitt (Yellow Stringybark), *E.
**Eucalyptus globulus** ssp. *maidenii* (F. Muell.) J. B. Kirkp. (Maiden’s Gum) and *E. elata* Dehnh. (River Peppermint), which extend from Gippsland into southern New South Wales (Gleadow & Ashton 1981). *P. undulatum* is a common component of warm temperate rainforests in this region (Melick 1990; Melick & Ashton 1991; Peel 1999) with the exception of Wilson’s Promontory in west Gippsland (Gleadow & Ashton 1981).

In New South Wales, the species occurs naturally in wet sclerophyll forests and dry rainforest (scrub) communities and extends into sheltered areas in dry forests and woodlands (Makinson 1992). *P. undulatum* is widespread along the coast and associated vegetation communities in New South Wales. Within these broad vegetation types, *P. undulatum* is associated with floristic assemblages characterised by *Eucalyptus pilularis* Sm. (Blackbutt), *E. botryoides* Sm. (Southern Mahogany) and *E. maculata* Hook. (Spotted Gum).

It is generally accepted that the natural distribution of *P. undulatum* is confined to the seaward slopes of the Great Dividing Range in south east Australia and that the natural occurrence of *P. undulatum* on the inland slopes would be restricted to a limited number of suitable locations. Some discrepancies exist in the literature regarding the natural northern and south western range of *P. undulatum* in south east Australia. Cooper (1956) suggested that the natural distribution of *P. undulatum* extended to the MacPherson Ranges, in southern Queensland and Narayan (1993) reported that the natural northern limit of *P. undulatum* could occur as far north as Bundaberg, Queensland. Additionally, an interesting natural outlying population of *P. undulatum* occurs at Carnarvon Gorge, some 720km north west of Brisbane (Queensland Herbarium 1994).

The natural south western extent of *P. undulatum* is equally unclear. Maiden (1889) recorded that the Karnathun people of the Lake Tyers district, Victoria, called *P. undulatum* ‘Bart Bart’, which is a reliable historic reference to the species’ range occupation. The approximate natural south western distribution of *P. undulatum* has been variously described as; the Victorian Alps (Cooper 1956), Gippsland (Maiden 1920), the Mitchell River region (Floyd 1989), the Strzelecki Ranges (Gullan et al.
1981) and Westernport Bay (Bentham 1863). *P. undulatum* was listed in Victorian nursery catalogues before Bentham’s 1863 report (Brookes & Barley 1992), which reduces the reliability of this early account as an indicator of this species’ natural range.

Debates about the exact pre-European range of *P. undulatum* are now largely academic given the broadscale ornamental plantings and documented evidence of the species’ invasion impacts in habitats subject to altered disturbance regimes (Mullett & Simmons 1995). The increased distribution and local abundance of *P. undulatum* at some sites within the species’ apparent natural geographic range does however create a dilemma for managers (Griffiths 1988; Ashwell 1991; Howell 1992). *P. undulatum* is obviously invasive in some dry sclerophyll remnants in the Sydney region for example, but control efforts tend to be directed towards exotic environmental weeds, which have a clearer invasive status (Rose 1997b).

It is likely that isolated populations of *P. undulatum* would have occurred on the Mornington Peninsula and other areas adjacent to the species’ main distribution in recent evolutionary time as a function of natural variation in distribution and abundance that occurs in response to changes in broader environmental fluctuations (Schwartz 1997). Prevailing disturbance regimes and other biotic factors may have contained any transient populations of *P. undulatum* in these areas. The heathy woodland, woodland and forest communities previously common on the Mornington Peninsula for example, would have been exposed to more frequent fires in pre-European times (Bedggood *et al.* 1989), impeding the local persistence and expansion of the fire-sensitive *P. undulatum* (see section 3-4.4).
Figure 3-2. Distribution of *Pittosporum undulatum* on mainland south east Australia.

Green shading indicates the broad natural geographic range of the species. Red shading depicts habitats colonised west of this natural distribution since European settlement. These invaded patches are associated with major human settlements and therefore areas of high ecosystem modification. *P. undulatum* has also increased its range and local densities in some habitats within the indicative natural range, particularly in coastal New South Wales and south east Victoria.
3.3.2. Current distribution of *P. undulatum*

3.3.2.1. Australia

Since the 19th century, *P. undulatum* has colonised a range of previously unexploited habitats in Victoria (Gledow & Ashton 1981; Carr *et al.* 1992; Mullett & Simmons 1995). These include the dry sclerophyll forests, characterised by *Eucalyptus goniocalyx* F. Muell. ex Miq. (Long-leaved Box), *E. macrorhyncha* F. Muell. ex Benth. (Red Stringybark), *E. melliodora* A. Cunn. (Yellow Box), *E. obliqua* L’Her. (Messmate) and *E. cephalocarpa* Blakely (Silver-leaved Stringybark) (Gledow & Ashton 1981; Mullett & Simmons 1995). *P. undulatum* has also invaded the wet *E. globulus* Labill. (Blue Gum) forests along the Otway coast of south west Victoria (Platt 1990) and wet *E. regnans* F. Muell. (Mountain Ash) forests east of Melbourne (Freshwater 1989), especially those associated with human settlements. Heathlands and heathy woodlands, coastal vegetation, grasslands and grassy woodlands and substantial tracts of riparian vegetation have also been invaded by *P. undulatum* in Victoria (Carr *et al.* 1992). *P. undulatum* is now found in most of the broad vegetation types occurring seawards of the Great Dividing Range in Victoria. It is present as an occasional planting in town gardens north of the Great Dividing Range in Victoria (pers. obs.), but the drier climatic conditions limit its spread into remnant vegetation in these areas.

*P. undulatum* is invasive in the Mount Lofty Ranges, South Australia, although populations seem to be kept largely under control due to the vigilance of volunteer groups in the area (pers. obs.). The competitive ability of other woody weeds such as *Olea europaea* L. (Olive) that are better suited to the drier Mediterranean-type climate (van der Sommen 1986) may also restrict the spread of *P. undulatum* in southern South Australia. *P. undulatum* is also expanding its distribution and abundance in invaded habitats in south west Western Australia (Keighery 1995, 1999) and Tasmania (Carr 1993) and is well established on King (Gledow & Ashton 1981), Norfolk (Gilmour & Helman 1989) and Lord Howe Islands (Pickard 1984).
3-3.2.2. Range expansion in habitats within the natural range

Some populations of *P. undulatum* occurring within the species’ natural geographic range are expanding in both distribution and local abundance, in response to altered ecological conditions (Adamson & Buchanan 1974; Adamson & Fox 1982; Buchanan 1989b, 1991; Rose 1997a, 1997b; Rose & Fairweather 1997; Mullett 1999). *P. undulatum* is a natural component of the wetter Gippsland forest types dominated by *Eucalyptus regnans* and *E. cypellocarpa* L. A. S. Johnson (Mountain Grey Gum), and damp sclerophyll forest characterised by *E. radiata* Sieber. ex DC. (Narrow-leaved Peppermint) and *E. viminalis* Labill. (Manna Gum), but many of these forests probably now support higher densities of *P. undulatum* (Griffiths 1988; Ashwell 1991; Howell 1992). Some populations of *P. undulatum* occurring on Sydney sandstone and coastal environments in New South Wales are also considered to be actively expanding (Adamson & Buchanan 1974; Adamson & Fox 1982; Buchanan 1989a, 1991; Rose 1997a, 1997b; Rose & Fairweather 1997; Mullett 1999).

Increasing local densities and movement from sheltered valley and gully environments into adjacent vegetation communities on drier slopes is a common feature of this species’ range expansion in natural habitats (Adamson & Fox 1982; Mullett 1999 and see Chapters 6 & 7).

3-3.2.3. Other Continents and Islands

Early enthusiasm for the ornamental and utilitarian attributes of *P. undulatum* moved the species beyond Australian borders and into an array of locations overseas. Cooper (1956) cites the use of *P. undulatum* as an ornamental, hedge and shelter plant throughout the temperate, sub-tropical and tropical zones in the following locations; the Azores, Bermuda, Bolivia, the Canary Islands, Ceylon (Sri Lanka), China, Chile, Colombia, England, France, Hawaii, India, Israel, Italy, Jamaica, New Zealand and the United States (Florida and California). As with its success in previously unexploited Australian environments, *P. undulatum* has thrived in many of these areas. It is regarded as a serious invader of native vegetation in many of these localities, especially Jamaica (Adair 1995; Goodland & Healey 1996, 1997b),

*P. undulatum* was introduced to Jamaica in 1883, possibly due to the enthusiasm of Jenman (1883 in Goodland & Healey 1996, p. 24), who described the species as “one of the handsomest flowering trees in Australia”. Little over a century later, *P. undulatum* is regarded as one of the most invasive weed species in the Blue Mountains region of Jamaica, and seriously threatens conservation and commercial values in the region (Goodland & Healey 1996, 1997a).

*P. undulatum* was introduced to South Africa as an ornamental and hedge plant in 1901 (Geldenhuys et al. 1986) and existed as a ‘sleeper weed’ for many decades before a rapid expansion phase occurred (Richardson & Brink 1985; Kruger et al. 1986). The time lag from introduction to invasion by *P. undulatum* in this region was related to an adjustment period by frugivorous dispersal agents (Kruger et al. 1986). Populations of *P. undulatum* are now invading riparian forest and scrub communities in the western Cape region (Richardson & Brink 1985; Geldenhuys et al. 1986; Kruger et al. 1986). Ornamental and hedge plantings in the Cape Town and Stellenbosch regions were affected by an unknown leaf blight during the late 1980’s and early 1990’s, although some recovery from this disease and further spread of *P. undulatum* has since been reported (Goodland & Healey 1997a).

*P. undulatum* was introduced to the Azores archipelago in the early 19th century as a windbreak for orange groves (Bean 1976). Now, *P. undulatum* or ‘Incenso’ as it is known locally, is a serious invader of endemic lowland forest environments in the Azores (Robertson 1997) and with other invasive plants, contributes to the homogenisation of native vegetation communities (Ramos 1995, 1996).

*P. undulatum* was introduced to the Hawaiian Islands as a timber crop in 1875 (Cronk & Fuller 1995). The species is naturalised in wet forest communities on several Hawaiian Islands and has the potential to become a serious environmental weed in that region (Haslewood & Motter 1984; Wester 1992).
3-4. Factors contributing to the spread of *P. undulatum*

Widespread ornamental and utilitarian plantings of *P. undulatum* have provided, and continue to provide, abundant *P. undulatum* dispersal foci across the landscape. Vegetation complexes in the urban matrix are particularly vulnerable to *P. undulatum* invasion because of their proximity to planted individuals.

3-4.1. Ornamental plantings

*P. undulatum* has been widely planted as an ornamental specimen for well over a century and early Australian botanists were most enthusiastic about the species’ ornamental attributes (Brookes & Barley 1992; Goodland & Healey 1996; Mullett 1999). Mueller (1876, p. 179) suggested that *P. undulatum* “deserved cultivation for the sake of its fragrant flowers” and these sentiments were echoed by Maiden (1889). *P. undulatum* was known by a variety of common names including ‘Native Daphne’ and ‘Native Laurel’ (Maiden 1889); the Eurocentric association of which may have contributed to the early popularity of this species amongst homesick colonists. As early as 1920, Maiden remarked that *P. undulatum* had been “abundantly cultivated as an ornamental and sweet scented plant in the Sydney district and in various parts of this (New South Wales) and other states” (Maiden 1920, p. 129).

Gardening enthusiasts continued with this support for *P. undulatum* into the latter half of this century. Miller (1964, p. 35) recommended the species as “an ideal tree for specimen, windbreak and avenue planting” and described the foliage as “outstanding” for these purposes. The broad tolerance of *P. undulatum* to a range of environmental conditions was seen as a virtue to those advocating its planting for utilitarian (including ornamental) purposes. Oakman (1964) enthused over the species’ adaptability to a range of soil types and described its dense foliage as ideal for hedges and windbreaks. Similarly, ornamental plantings were encouraged in coastal areas because of the species’ capacity to tolerate sea breezes (Maiden 1920; Oakman 1964).
Enthusiasm for *P. undulatum* as an ornamental species has declined over the last few decades, largely pioneered by the observations of Adamson and Buchanan (1974) and the work of Gleadow and Ashton (1981), who first reported on the range expansion of *P. undulatum* and some of the consequences of invasion. Ironically, the same adaptive and hardy features that so enthused early proponents of this species are now regarded by conservation managers as the very features that make *P. undulatum* so difficult to manage in invaded remnant vegetation (Mullett 1999). Despite growing acknowledgment and acceptance of the ‘weedy’ status of *P. undulatum* by the broader community, the species remains a popular ornamental specimen. For example, the gardening columnist of the ‘Frankston Standard’, a regional weekly newspaper in Victoria, suggested that bird dispersed *P. undulatum* seedlings could be “potted up and given to a friend” (Love 1993, p. 59). This article was published after *P. undulatum* had been identified as a serious environmental weed in that region (City of Frankston, Shire of Hastings & Shire of Mornington c.1992). This example is symbolic of the conflict that can occur when attractive and popular ornamental species also function as environmental weeds.

### 3-4.2. Utilisation purposes

Outdated vernacular names such as ‘engravers wood’ (Maiden 1889; Cooper 1956; Hayes 1964) illustrate early enthusiasm for the potential utilisation of *P. undulatum*. The timber of *P. undulatum* was used for varied purposes including engraving, golf sticks and tool handles (Maiden 1920; Cooper 1956). Maiden (1889) commended further research on the essential oils derived from *P. undulatum* fruit, which was later found by Power and Tutin (1906) to consist primarily of limonene and pinene. Maiden (1889, p. 230) also recounted that the “wound of a dog” healed with “amazing quickness” after application of *P. undulatum* gum resin and the essential oils distilled from *P. undulatum* flowers produce an “exceedingly agreeable, jasmine-like odour” (Bosisto 1862 in Maiden 1920, p. 126). Californian researchers assessed the terpenes in *P. undulatum* fruit as a source of renewable energy (Calvin 1985) and in St Helena, *P. undulatum* is apparently a useful fodder species for goats and cattle (Goodland & Healey 1996), despite the toxicity of the leaves. *P.*
*undulatum* is currently utilised as a source of timber, firewood and charcoal in the Blue Mountains region of Jamaica (Goodland & Healey 1996).

*P. undulatum* is commonly utilised in revegetation programs in south east Victoria and New South Wales because of its adaptability to a range of conditions (pers. obs). The drought tolerance of *P. undulatum* also contributes to its value as a pioneer species for wet sclerophyll forest and warm temperate rainforest communities (Barrett & Ash 1992). Greening Australia (New South Wales) include *P. undulatum* on a list of species suitable for use in revegetation programs in the Clarence, Tweed and Richmond River catchments of north east New South Wales and encourage Nurseries to stock *P. undulatum* and other listed species for this purpose (Nagle 1996a, 1996b). While *P. undulatum* is indigenous to these areas, the ecological conditions and constraints with which the species evolved in these catchments have been so altered that its use in revegetation programs is questionable (Mullert 1999). This is especially true in the context of its documented invasiveness in other habitats (Mullert & Simmons 1995). Revegetation programs are acknowledged as a potential source of spread for invasive species (Humphries *et al.* 1991) and managers should be very cautious about the use of known invasive species in such programs (Woods 1997).

### 3-4.3. Increased dispersal opportunities

Widespread ornamental plantings of *P. undulatum* and other introduced fleshy-fruited species provide an abundant food source for adaptive native and introduced frugivorous species able to exploit these resources (Mullert 1996, 1999). In the greater Melbourne area, *Turdus merula* L. (European Blackbird) has been implicated as the principal dispersal agent of *P. undulatum* (Gleadow 1982). The seeds of *P. undulatum*, which are encased in a sticky mucilage, comprise an extensive proportion of the birds diet over the winter months (see Chapter 5). The abundance of European Blackbirds coupled with high densities of *P. undulatum* plantings across the urban landscape provides a continual source of *P. undulatum* recruitment into vegetation remnants associated with human settlements in Victoria (Gleadow & Ashton 1981; Mullert 1996).
*Strepera gracilina* Shaw (Pied Currawong) assume an important role in *P. undulatum* dispersal outside the suburban Melbourne area in Victoria and have a greater potential for long-distance seed dispersal than the more sedentary European Blackbirds. Pied Currawongs may be the most important dispersal agent of *P. undulatum* in the greater Sydney region, where European Blackbird densities are low (Chapter 5).

Other generalist frugivores, including *Zosterops lateralis* Latham (Silvereye) and the introduced *Pycnonotus jocosus* L. (Red-whiskered Bulbul), have been observed consuming *P. undulatum* seed (Gannon 1935; Cooper 1959; Gleadow 1982; Emison et al. 1987; Buchanan 1989b; Barker & Vestjens 1990). *Ptilonorhynchus violaceus* Vieillot (Satin Bowerbirds) cache and possibly display *P. undulatum* fruit, but their role as a dispersal agent is unclear (see Chapter 5). No additional avian dispersers of *P. undulatum* were recorded in the Australian literature surveyed by Loyn and French (1991) but it is likely that a number of other avian dispersers of *P. undulatum* are yet to be documented.

The role of mammals in the dispersal of environmental weed species is yet to be thoroughly investigated, especially in an Australian context (Bass 1990a). Accounts of mammal species dispersing *P. undulatum* seed again implicate generalist, opportunistic native and introduced species. Hoarding of *P. undulatum* fruits observed at Police Paddocks, Victoria, was attributed to the introduced *Rattus rattus* L. (Black Rat) (D. Wallace, pers. comm.). *P. undulatum* seeds have also been detected in the scats of *Vulpes vulpes* L. (Red Fox) (R. Wallis, pers. comm.), a species known to disperse other environmental weed species such as *Rubus procerus* P. J. Muell. (Blackberry) and *Chrysanthemoides monilifera ssp. rotundata* (Brunner et al. 1976; Dodkin & Gilmore 1984; Meek 1998).

*P. undulatum* seeds have been observed in *Trichosurus vulpecula* Kerr (Common Brushtail Possum) droppings (Brown et al. 1991) and Gleadow (1982) suggested that seeds observed in *Pseudocheirus peregrinus* Boddaert (Common Ringtail Possum) scats were probably those of *P. undulatum*. It is possible that other mammals will
adapt over time, to the abundant food resource provided by the *P. undulatum* winter fruit crop, especially as the abundance of traditional food resources contracts in invaded and otherwise modified environments.

### 3-4.4. Modification of natural fire regimes

Changes in natural fire regimes are recognised as a key factor in the increased distribution and abundance of *P. undulatum* in natural and invaded habitats throughout south east Australia (Gleadow & Ashton 1981; Adamson & Fox 1982; Buchanan 1989a, 1991; Mullett & Simmons 1995; Mullett 1996, 1999; Rose 1997a, 1997b; Rose & Fairweather 1997). *P. undulatum* is fire sensitive, a legacy of its evolution in wet vegetation communities. It has thin resinous bark and fires intense enough to kill the basal buds in the trunk are generally fatal (Gleadow & Ashton 1981; Narayan 1993).

### 3-4.5. Reduced biotic resistance to invasion

It is likely that a host of other, more subtle factors also contribute to the increased distribution and abundance of *P. undulatum* across the range of habitats now occupied. Outside Australia for example, *P. undulatum* has invaded relatively undisturbed forest communities in the south west of South Africa (Richardson & Brink 1985). The montane rainforest environments invaded by *P. undulatum* in the Azores are also reportedly, relatively undisturbed (Robertson 1997). The species invades both primary and secondary forest communities in Jamaica, although Goodland and Healey (1996) suggest that considerable *P. undulatum* population expansion was evident in this region, following hurricane-related disturbance.

Adaptive frugivores have facilitated the dispersal of *P. undulatum* from cultivated plantings in all these locations, which parallels the situation in Australia. The lack of natural pests and pathogens is likely to facilitate the range expansion of *P. undulatum* in these invaded habitats.
3-5. Characteristics of *P. undulatum* invasion

3-5.1. Spatial invasion pattern

The establishment of *P. undulatum* individuals from successive generations is generally restricted to the base of mature trees or shrubs as these offer perching sites for frugivorous dispersers that preferentially defecate or regurgitate undigested seeds whilst perching (see Chapter 6). The clumps of *P. undulatum* that develop act as a focus for further avian activity and thus for further seed dispersal (Richardson & Brink 1986; Kruger et al. 1986). The satellite populations or ‘nascent foci’ (Moody & Mack 1988) that establish via this dispersal mechanism increase the species’ potential for range expansion.

Gleadow (1982) suggests that the clumping pattern typical of *P. undulatum* invasion is influenced by seedling response to microclimatic conditions. Seedling survival is higher under shaded conditions (Gleadow 1982) although shading and other competitive effects appear to reach a critical point within *P. undulatum* clumps where the micro-environment is hostile even to conspecific seedlings (Chapter 6).

3-5.2. Physical and biological impacts of *P. undulatum* invasion

Invading populations of *P. undulatum* alter the physical environment of invaded sites in several ways. The deep shade cast by the dense *P. undulatum* canopy can reduce light infiltration to as little as 2% of full daylight (Gleadow & Ashton 1981). The composition and abundance of *P. undulatum* leaf litter further alters the microclimate beneath the *P. undulatum* canopy. *P. undulatum* litter fall in an invaded dry sclerophyll forest remnant sampled in suburban Melbourne, was in the order of 2.6 tonnes per hectare, compared to 0.9 tonnes per hectare produced by mature eucalypts in the same community (Gleadow & Ashton 1981). The nutrient composition of *P. undulatum* leaf litter was also significantly higher (Gleadow & Ashton 1981) in calcium, magnesium and sodium compared to eucalypt litter, while fresh *P. undulatum* leaves contained higher concentrations of potassium.

*P. undulatum* invasion alters species composition and successional processes in affected communities by direct competition and by the changes imposed on
ecosystem-level properties and functions (Chapters 6 & 7). Mullett and Simmons (1995) demonstrated that a decline in indigenous species richness was significantly negatively correlated with increasing cover-abundance of *P. undulatum*. Indigenous species richness declined from an average of 12 species where *P. undulatum* cover-abundance was less than 30%, to 4 species where *P. undulatum* cover-abundance exceeded 70%, in 260 3x3m quadrats sampled in dry sclerophyll vegetation near Melbourne in 1993 (Mullett 1996). The decline in indigenous species richness was largely attributed to the reduction in light infiltration caused by the dense *P. undulatum* canopy.

The potentially inhibiting effects of various saponins, oils and resins present in *P. undulatum* foliage are often alluded to in studies of this species’ invasion impacts (Richardson & Brink 1985; Buchanan 1989a; Mullett & Simmons 1995; Goodland & Healey 1996, 1997a; Rose & Fairweather 1997). Gleadow and Ashton (1981) demonstrated that the germinability of various *Eucalyptus* species watered with *P. undulatum* leaf exudates was significantly lower than untreated seeds, but concluded that no clear inhibiting effects, other than that imposed by shading, were evident in field conditions.

Tunbridge (1997) recorded minor patterns of variation in the germination rates of several native species watered with *P. undulatum* leaf exudates, compared to control seeds. However, no significant differences in germinability were evident between treatments for most species, at the completion of the 27-day experimental period. The suppressive effects of altered light, nutrient, soil moisture and allelopathic properties are difficult to separate (Crawley 1997) and lab-based experiments do not adequately represent natural rates and routes of allelochemical release (Qasem & Hill 1989; Weidenhamer 1996). Future studies of this species’ allelopathic effects are required and should be supported with field-based investigations.

3-6. Summary

*P. undulatum* occurs naturally in a diverse range of habitat types seawards of the Great Dividing Range in south east Australia, but is mainly associated with rainforest
and wet forest communities. The species has been widely planted as an ornamental specimen since the early days of European settlement in Australia. These widespread ornamental and utilitarian plantings, in combination with increased dispersal opportunities and changes in natural disturbance processes (especially fire regimes), have contributed to the invasion of this species in a diverse assemblage of habitat types across a range of climatic zones. *P. undulatum* is now regarded as a serious environmental weed in south east Australia and many locations overseas.
CHAPTER FOUR

Variation in some morphological characters of *P. undulatum*

4-1. Introduction

*P. undulatum* occupies a range of habitat types throughout its extensive geographic distribution and therefore has a broad tolerance to variation in environmental factors. The species’ plastic response to environmental conditions is reflected in the high level of variation in its habit in different habitat types. In sheltered warm temperate rainforest patches in Victoria and New South Wales for example, *P. undulatum* individuals reach heights in excess of 30 metres and have large, spreading canopies. In harsher coastal environments, *P. undulatum* often displays a stunted and sheared habit. Individuals invading dry sclerophyll forest rarely exceed heights of 15m and the canopies are comparatively compact and dense.

The plasticity of *P. undulatum* is regarded as an important factor in this species’ invasion success (Mullett 1996, 1999). Genetic diversity within and between populations of *P. undulatum* is however, “substantially lower than the average for plant taxa” (Orso 1994, p. 18). Most of the genetic variation (97.5%) is contained within populations of *P. undulatum* and no geographic patterns of genetic differentiation are evident (Orso 1994). The influence of specific environmental factors on morphological variation is difficult to quantify, but given most of the genetic variation in this species is contained within populations it is assumed that environmental factors are critical to the morphological expression of *P. undulatum* (Orso 1994).

Phenotypic plasticity allows some modification of the phenotype in response to the demands of the immediate environment and may be reflected in macro- and micromorphological characters, including growth forms (Moran *et al.* 1981; Silvertown & Lovett Doust 1993). While the genotype determines the underlying potential of a character trait, the ultimate phenotypic expression is to some level influenced by environmental conditions (Schlichting 1986; Silvertown & Lovett Doust 1993). Limited genetic variation has been recorded in other invasive plant species, especially those with small founder populations (Moran *et al.* 1981; Lonsdale &
Braithwaite 1988; Wilson & Rapson 1995). Plastic phenotypic expression may compensate for lower levels of genetic diversity in such species and may be a critical factor in the successful colonisation of new environments.

Assessment of morphological characters provides a convenient means of assessing the level of variation in individuals and populations and is the most readily obtainable measure of genetic variation (Silvertown & Lovett Doust 1993). Although, as Chakraborty and Rao (1991) note measuring genetic variation at this level is problematic, as it is difficult to ascertain the extent that observed variation is truly genetic.

The nature of geographic variation in plant species is complex and varies considerably within and between species. Phenotypic and genetic responses to changing and changeable environments can vary over many temporal and spatial scales (Endler 1977; Briggs & Walters 1984). Geographic variation can occur in response to processes such as climate change, sea-level fluctuations, glaciation episodes, land building, sedimentation and erosion cycles and other long term processes (Thorpe 1976). Speciation is the ultimate response to selection pressures over evolutionary time. This process may be enhanced through isolation effects and expansions and contractions in the distribution of species (Thorpe 1976).

Prevailing biotic and physical influences can also induce a plastic response in plant species (Thorpe 1976; Silvertown & Lovett Doust 1993). Patterns of morphological variation may be associated with micro-topographical features such as aspect and slope, edaphic factors such as soil type, depth, nutrient composition and water holding capacity, competition effects and other physical and biotic influences. The influence of these factors, however, is difficult to isolate, especially in heterogenous environments. Most studies of morphological variation in plant species are therefore restricted to using broad climatic and geographic parameters to explain patterns of geographic variation and these parameters are applied in the current study.

Intraspecific variation in response to variable environmental influences and selection pressures can be expressed and measured via genetic and phenotypic characteristics. Continuous or gradational changes in phenotypic expression along environmental
gradients can be quantitatively measured to determine if a cline, or gradient in a given character, is evident (Endler 1977). Variation in morphological expression across a species’ geographic distribution can also be discontinuous, disjunct, conjunct, random, or overlapping; the patterns of which can vary considerably within and between morphological attributes, species and populations (Endler 1977).

4-1.1. Aims of the current study

This study aims to determine the nature and extent of morphological variation in selected leaf attributes within and between populations of *P. undulatum* and to investigate patterns of variation in relation to geographic and climatic parameters as a measure of the species’ phenotypic plasticity. The adaptability of phenotypic expression is recognised as an important trait in invasive species, such as *P. undulatum*, that have limited genetic diversity. This study of morphological variation was instigated by observation of marked variation in *P. undulatum* habit throughout the species’ range in south east Australia (Plate 4-1).

4-1.2. Previous research on phenotypic and genetic variation in *P. undulatum*

No previous studies have been conducted on morphological variation in populations of *P. undulatum* throughout south east Australia. Gleadow (1980) and Gleadow and Rowan (1982) described leaf anatomical characteristics of *P. undulatum* relative to drought tolerance and characteristics of ontogenetic development of *P. undulatum* seedlings. Cooper (1956) and Wilkinson (1992) presented summary data on various anatomical and morphological characters and Orso (1994) and Tabone (1995) have conducted limited genetic analyses of *P. undulatum* populations.

4-2. Methods

4-2.1. Populations sampled

Twenty-six populations of *P. undulatum* (Table 4-1) were sampled across the species geographic range in south east Australia between July 1994 and January 1997. Populations of *P. undulatum* were selected to sample the geographic distribution of the species on mainland south east Australia (Figure 4-1) and to represent the range
of habitats occupied by *P. undulatum*. More populations were sampled in Victoria, compared with New South Wales, South Australia and Queensland, reflecting the pattern of *P. undulatum* distribution and abundance in south east Australia.

### 4-2.2. Characters measured

#### 4-2.2.1. Leaf characters

Five branchlets were collected from each of ten individuals in 26 populations of *P. undulatum* in south east Australia (see Appendix 1 for permit details). Morphological characters were measured on the largest leaf of each branchlet from the previous growth flush to ensure full leaf growth had occurred and to reduce confounding from allometric variation in the data set. Mitutoyo™ 0.05mm callipers were used to measure the following characteristics to the nearest two decimal places; internode interval, petiole length, lamina length, lamina width and the distance from the lamina base to the widest point on the leaf (base to width). The number of undulations on the entire leaf margin was also counted. The morphological characters assessed are summarised in Figure 4-2.

*P. undulatum* leaves are usually arranged in a whorl or semi-whorl comprising an average of four to five leaves. The sampled leaves were invariably part of a whorl, although it is not unusual for a single leaf to be arranged on a stem. If the internode measurement was less than or equal to 1mm, the leaf was considered to be a component of a whorl and the distance to the next leaf or whorl was measured.
Plate 4-1i-ii. *P. undulatum* displays considerable variation in habit, in different habitat types.

4-1i) Typical mature *P. undulatum* in warm temperate rainforest Victoria, displaying broad, spreading canopy (Mitchell River National Park, East Gippsland, Victoria).

4-1ii) Typical mature *P. undulatum* in immediate coastal environment, displaying stunted, sheared habit (Lorne, Great Ocean Road, Victoria).
Table 4-1. Location of *P. undulatum* populations sampled. Five leaves from ten individual trees were sampled from each population.

<table>
<thead>
<tr>
<th>Code</th>
<th>Population</th>
<th>Location</th>
<th>Latitude (°S)</th>
<th>Longitude (°E)</th>
<th>Mean annual rainfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPRG</td>
<td>Springbrook</td>
<td>SE Qld.</td>
<td>27°97'</td>
<td>153°20'</td>
<td>1564.2</td>
</tr>
<tr>
<td>ALST</td>
<td>Alstonville</td>
<td>NE NSW</td>
<td>28°85'</td>
<td>153°46'</td>
<td>1866.6</td>
</tr>
<tr>
<td>SWRK</td>
<td>South West Rocks</td>
<td>NE NSW</td>
<td>30°93'</td>
<td>153°09'</td>
<td>1492</td>
</tr>
<tr>
<td>ELLN</td>
<td>Ellenborough Falls</td>
<td>NE NSW</td>
<td>31°39'</td>
<td>152°25'</td>
<td>1634.2</td>
</tr>
<tr>
<td>CEDB</td>
<td>Cedar Brush</td>
<td>NE NSW</td>
<td>31°50'</td>
<td>150°41'</td>
<td>652.4</td>
</tr>
<tr>
<td>NOWR</td>
<td>Nowra</td>
<td>SE NSW</td>
<td>34°95'</td>
<td>150°54'</td>
<td>1142.1</td>
</tr>
<tr>
<td>BELR</td>
<td>Belair National Park</td>
<td>Mt. Lofty Ranges, SA</td>
<td>35°00'</td>
<td>138°61'</td>
<td>723.2</td>
</tr>
<tr>
<td>STRL</td>
<td>Stirling</td>
<td>Mt. Lofty Ranges, SA</td>
<td>35°03'</td>
<td>138°44'</td>
<td>1188.6</td>
</tr>
<tr>
<td>STCK</td>
<td>Scott Creek</td>
<td>Mt. Lofty Ranges, SA</td>
<td>35°07'</td>
<td>138°86'</td>
<td>769.3</td>
</tr>
<tr>
<td>MYPG</td>
<td>Myponga</td>
<td>Mt. Lofty Ranges, SA</td>
<td>35°39'</td>
<td>138°46'</td>
<td>761.9</td>
</tr>
<tr>
<td>BODL</td>
<td>Bodalla State Forest</td>
<td>SE NSW</td>
<td>36°07'</td>
<td>150°05'</td>
<td>1055.2</td>
</tr>
<tr>
<td>TATH</td>
<td>Tathra</td>
<td>SE NSW</td>
<td>36°44'</td>
<td>149°59'</td>
<td>840.7</td>
</tr>
<tr>
<td>MITR</td>
<td>Mitchell River National Park</td>
<td>East Gippsland, Vic.</td>
<td>37°28'</td>
<td>147°21'</td>
<td>1138.2</td>
</tr>
<tr>
<td>BRUT</td>
<td>Fairy Dell, Bruthen</td>
<td>East Gippsland, Vic.</td>
<td>37°41'</td>
<td>147°46'</td>
<td>876.9</td>
</tr>
<tr>
<td>CROA</td>
<td>Croajingolong National Park</td>
<td>East Gippsland, Vic.</td>
<td>37°80'</td>
<td>149°27'</td>
<td>990.7</td>
</tr>
<tr>
<td>TDRY</td>
<td>Lake Tyers (dry sclerophyll forest)</td>
<td>Gippsland, Vic.</td>
<td>37°87'</td>
<td>148°10'</td>
<td>732.1</td>
</tr>
<tr>
<td>TISL</td>
<td>Lake Tyers (Island – dry rainforest)</td>
<td>Gippsland, Vic.</td>
<td>37°49'</td>
<td>148°03'</td>
<td>732.1</td>
</tr>
<tr>
<td>TWET</td>
<td>Lake Tyers (wet sclerophyll forest)</td>
<td>Gippsland, Vic.</td>
<td>37°72'</td>
<td>147°99'</td>
<td>876.9</td>
</tr>
<tr>
<td>Code</td>
<td>Population</td>
<td>Location</td>
<td>Latitude (°S)</td>
<td>Longitude (°E)</td>
<td>Mean annual rainfall (mm)</td>
</tr>
<tr>
<td>------</td>
<td>--------------------------</td>
<td>-------------------------------</td>
<td>---------------</td>
<td>---------------</td>
<td>--------------------------</td>
</tr>
<tr>
<td>GLEN</td>
<td>Glenmaggie</td>
<td>East Gippsland, Vic.</td>
<td>37°53'</td>
<td>146°44'</td>
<td>1046.4</td>
</tr>
<tr>
<td>MRAY</td>
<td>Mt. Raymond</td>
<td>East Gippsland, Vic.</td>
<td>37°69'</td>
<td>148°46'</td>
<td>853.7</td>
</tr>
<tr>
<td>CANN</td>
<td>Cannibal Hill</td>
<td>West Gippsland, Vic.</td>
<td>38°03'</td>
<td>145°40'</td>
<td>1042.9</td>
</tr>
<tr>
<td>MORW</td>
<td>Morwell National Park</td>
<td>Strezlecki Ranges, Vic.</td>
<td>38°14'</td>
<td>146°23'</td>
<td>895.9</td>
</tr>
<tr>
<td>MORN</td>
<td>Woods Reserve, Mornington</td>
<td>Mornington Peninsula, Vic.</td>
<td>38°24'</td>
<td>145°07'</td>
<td>742.6</td>
</tr>
<tr>
<td>PORT</td>
<td>Portland</td>
<td>SW Vic.</td>
<td>38°39'</td>
<td>141°61'</td>
<td>841.1</td>
</tr>
<tr>
<td>GURD</td>
<td>The Gurdies</td>
<td>Westernport Bay, Vic.</td>
<td>38°22'</td>
<td>145°34'</td>
<td>853.2</td>
</tr>
<tr>
<td>LORN</td>
<td>Angahook-Lorne State Park</td>
<td>SW Vic.</td>
<td>38°53'</td>
<td>143°98'</td>
<td>831.9</td>
</tr>
</tbody>
</table>
Figure 4-1. Distribution of south east Australian populations of *P. undulatum* sampled in this study of morphological variation. See Table 4-1 for explanation of population codes.
Figure 4-2. *P. undulatum* leaf characters assessed in this study.

<table>
<thead>
<tr>
<th>Code</th>
<th>Character</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Internode length (mm)</td>
</tr>
<tr>
<td>2</td>
<td>Petiole length (mm)</td>
</tr>
<tr>
<td>3</td>
<td>Lamina length (mm)</td>
</tr>
<tr>
<td>4</td>
<td>Lamina width (mm)</td>
</tr>
<tr>
<td>5</td>
<td>Distance from lamina base to widest point on leaf margin (base to width) (mm)</td>
</tr>
<tr>
<td>6</td>
<td>Number of undulations (per entire lamina margin)</td>
</tr>
</tbody>
</table>

Adapted from Costermans 1991
4-2.3. Geographic and climatic characteristics of sampled populations

Three geographic and 21 climatic variables were included in the data set to characterise each population sampled (Table 4-2). Long term climatic data were obtained from the Bureau of Meteorology (http://www.bom.gov.au), and averaged to obtain seasonal data. Data from the nearest representative climate station were used if climate data were not available for the sites sampled. Information pertaining to latitude, longitude and altitude was also obtained from the Bureau of Meteorology and, where available, more specific longitude and latitude data were obtained from the Gazetteer of Geographic Place Names (http://www.erin.gov.au/database/html.), and incorporated into this data set (Appendix 2).

Table 4-2. Geographic and climatic variables selected to characterise each population of *P. undulatum* sampled.

<table>
<thead>
<tr>
<th>Geographic variables</th>
<th>Mean rainfall (mm) variables</th>
<th>Mean temperature (°C) variables</th>
<th>Mean Relative Humidity (RH) (%) variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude °S</td>
<td>annual rainfall</td>
<td>summer minimum</td>
<td>summer 9am RH (%)</td>
</tr>
<tr>
<td>Longitude °E</td>
<td>summer rainfall</td>
<td>summer maximum</td>
<td>summer 3pm RH (%)</td>
</tr>
<tr>
<td>Altitude</td>
<td>autumn rainfall</td>
<td>autumn minimum</td>
<td>autumn 9am RH (%)</td>
</tr>
<tr>
<td></td>
<td>winter rainfall</td>
<td>autumn maximum</td>
<td>autumn 3pm RH (%)</td>
</tr>
<tr>
<td></td>
<td>spring rainfall</td>
<td>winter minimum</td>
<td>winter 9am RH (%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>winter maximum</td>
<td>winter 3pm RH (%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>spring minimum</td>
<td>spring 9am RH (%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>spring maximum</td>
<td>spring 3pm RH (%)</td>
</tr>
</tbody>
</table>

4-2.4. Analyses

4-2.4.1. Univariate analyses

Population means and standard errors were calculated for each character measured and an estimate of the variability of the data was obtained by calculating a coefficient of variation for each character (Sokal & Rohlf 1993; Fowler et al. 1998). The distributions of residuals for each character were plotted to assess the normality
of the data and one way analysis of variance (ANOVA) was performed on all leaf characters to assess differences between populations. Fisher’s unrestricted Least Significant Difference (L.S.D.) was used to further investigate significant differences between populations for all characters assessed. All data were entered on an Excel 5 spreadsheet and Genstat 5 version 4.1 was used to perform all univariate analyses.

4-2.4.2. Multivariate analyses

Scatterplots were used to visually assess the relationships between all measured characters and the environmental parameters obtained for each population prior to conducting multivariate analyses. Derived ratio variables that were initially incorporated into the data set were highly correlated with at least one of their constituent components. Subsequent correlation analysis confirmed the highly intercorrelated nature of the ratio variables and these were consequently eliminated from the data set.

A matrix of the mean values of all morphological attributes, geographic parameters and mean climatic data obtained for all populations sampled was constructed and the strength of the relationships between these variables was assessed using Spearman’s Rank Correlation Coefficient (Fowler et al. 1998).

Cluster analysis was used to investigate patterns of similarities between the populations sampled. This technique is commonly employed in studies of geographic variation to investigate relationships between populations. Dendrograms, which display the results of cluster analyses, are valuable to visually assess the classification of the population groups based on their relative similarities and to discern subtleties of interest such as patterns of geographic variation. Dendrograms may have some limitations related to the forced nature of association between objects (Gordon 1981), but when used in association with other multivariate analyses can reveal interesting patterns in the data.

A similarity matrix of mean morphological variables was developed in Genstat 5, version 4.1, using a Euclidean distance measure. The Average-Link associations measure (Sneath & Sokal 1973), which is analogous to the unweighted pair-group
methods using averages (UPGMA) technique, was used to formulate groups based on relative similarities.

Ordination techniques are useful for finding patterns in complex data sets (Quinn & Keough 1996) and have useful application in the study of geographic variation (Thorpe 1976). Ordinations further display the relationships between entities and provide a useful comparison to the groups forced by cluster analysis. Two ordinations were produced in the current study.

The morphological data were subjected to Canonical Variate Analysis (or Multiple Discriminant Function Analysis) and canonical variate means were plotted to investigate the relative position and affinities of the populations sampled. Canonical variates analysis discriminates between groups (populations) by determining the linear combinations of the variates that maximise the ratio of within and between group variation (Sokal & Rohlf 1993; Fowler et al. 1998).

Principal Components Analysis (PCA) was conducted on the independent morphological characters measured (determined as lamina length, petiole, internode and the number of undulations per leaf) to provide a comparison to the relationships portrayed from the canonical variate analysis. Orthogonal linear combinations (principal components) that maximise the information contained in the original data are determined by PCA, which reduces the dimensionality of the data set (Sokal & Rohlf 1993; Fowler et al. 1998). The canonical variates and principal components analyses were conducted using Genstat 5 version 4.1.

The relationships between populations can be obscured in two-dimensional ordination plots (Wright & Ladiges 1997) so the similarity matrix developed for the cluster analysis was also used to construct a Minimum Spanning Tree (MST) to further display population affinities based on morphological attributes.

An estimate of the variability of each population was obtained by calculating the variance of the Euclidean distances of each sample from their respective population centroids in the two dimensional space of the first two discriminant functions.
obtained from the canonical variate analysis (Jordan et al. 1993; Ashburner 1994; Ashburner et al. 1997).

A separate post hoc cluster analysis of population affinities was conducted on ‘natural’ *P. undulatum* populations using the same association and distance measures applied in the cluster analysis of all populations sampled. This analysis was conducted to determine if an ‘underlying’ pattern of morphological variation was evident in the natural populations sampled that may have been obscured in the broader analysis of all populations. The classification of natural populations is necessarily arbitrary given some populations of *P. undulatum* within the species natural range are now invasive (see Chapter 3). For the purposes of this analysis however, populations occurring east of Westernport Bay, Victoria, are classified as natural populations. The GURD population, which occurs on the eastern fringe of Westernport Bay, was excluded from this analysis as it is clearly invasive. No additional, separate analyses of the natural populations were conducted.

4.2.4.3. Minimising confounding from non-geographic influences.

In investigating the morphological affinities of *P. undulatum* populations, it is prudent to prevent non-geographic variation in morphological expression from confounding ‘true’ geographic variation. Non-geographic variation can arise from factors such as ontogenetic variation, temporal variation and sexual dimorphism (Thorpe 1976). The sampling design aimed to avoid these factors although it is acknowledged that some non-geographic variables are difficult to identify, let alone control. *P. undulatum* exhibits sexual dimorphism in flower structure, and consequently, fruit production. It is unknown how the relative reproductive investment provided by the two sexes translates into biomass production and any differences in phenotypic expression of leaf characters. No such differences are recorded in the literature or readily detected on observation and so it is assumed that sexual dimorphism is not displayed in leaf characters.

It was also assumed that the sample size was sufficient to detect any patterns of variation within populations that might be related to the sex of the individuals sampled. Investigation of population structure in *P. undulatum* populations in
Victoria revealed a slight male bias in the six *P. undulatum* populations sampled (see Chapter 6). However, a bi-modal distribution of samples would presumably result if any detectable differences were apparent in male and female leaf morphology and this was not the case. Leaves were collected from mature individuals at all locations to reduce potential confounding associated with variation in the relative age of individuals within and between the populations sampled.

### 4-2.4.4. Lake Tyers samples

Leaf samples were collected from three discrete populations of *P. undulatum* in the vicinity of Lake Tyers, Victoria, to investigate aspects of micro-geographic variation in *P. undulatum* morphology. These three populations occur in distinctly different habitats; wet sclerophyll forest (TWET), dry sclerophyll forest (TDRY) and dry rainforest (TISL). While separate attention is given to the Lake Tyers populations in the discussion, the data obtained from these three populations are included in the larger leaf morphology data set. Cluster analysis was performed on mean leaf measurements obtained from each of the ten individuals sampled from the three Lake Tyers populations using the methods described in section 4-2.4.2. The resultant dendrogram is not displayed in this thesis as the pattern of association between these populations was adequately represented in the other two dendrograms produced.

### 4-3. Results

#### 4-3.1. Univariate analyses

All characters assessed were significantly different (*P* < 0.001) across all populations sampled. Population means, standard errors, least significant differences (L.S.D.), coefficients of variation and grand means obtained for each leaf character are presented in Table 4-3.

The range of the descriptive statistics calculated for each character is indicative of the high level of variation within and between populations of *P. undulatum*. Mean lamina length (mm) was smallest (99.5mm) at CEDB, on the inland slopes of the Great Dividing Range in northern New South Wales. The largest average lamina length was recorded at CROA in East Gippsland, Victoria. Average lamina length
was 148.3mm at this site, nearly one-third larger than the average lamina length recorded at CEDB. Despite the considerable variation evident in the data set for this character, the Coefficient of Variation (CV) of 12.5% obtained for lamina length is the lowest for all characters assessed.

Mean lamina width varied considerably, from 30.1mm at CEDB to 48.7mm at PORT, in south west Victoria. Mean lamina width was not significantly different (L.S.D. = 2.48, \( P > 0.05 \)) between the north east New South Wales populations sampled (ALST, ELLN and SWRK) and SPRG in south east Queensland. These populations however, were also not significantly different (\( P > 0.05 \)) from the geographically-remote populations of STCK (South Australia) and MITR, LORN and MORN (Victoria). The GLEN and CEDB populations were significantly different to all other populations for the lamina width character.

The smallest mean base to width measurement (49.1mm) was recorded at GLEN and the largest mean base to width (75.9mm) was recorded at GURD, Victoria. The CEDB and GLEN populations were significantly different (\( P < 0.05 \)) to all other populations sampled, including each other, for this characteristic.

The highest mean number of undulations per leaf (21.1) was recorded at CROA, where lamina length was also highest on average. The lowest mean number of undulations per leaf was recorded at GLEN (7.8) and CEDB (8.1). Lamina length, width and base to width were also on average, smallest at GLEN and CEDB. No pattern of geographic variation is evident for this characteristic based on examination of least significant differences.

Mean internode length varied from 4.1 to 13.9mm for TWET and NOWR, respectively. The mean internode length recorded for NOWR is over three times that of TWET, indicating the broad spread of averages obtained for this character. The populations sampled in South Australia were not significantly different to each other (L.S.D. = 2.23, \( P > 0.05 \)), but with this exception, no geographic variation in population affinities was evident for the internode character. The Coefficient of Variation for this character was 62.7%, indicating the variability displayed among populations in this character is considerable.
The smallest average petiole length (15.7mm) was recorded at TDRY, while the largest average petiole length (24.9mm) was recorded from MYPG, an invasive population in the southern Mount Lofty Ranges of South Australia. The MYPG population was not significantly different ($P > 0.05$) to the STCK population and all the South Australian populations had an average petiole length higher than the grand mean obtained for this character.

4-3.2. Multivariate analyses

4-3.2.1. Relationships between morphological characters

The leaf dimensional characters; lamina length, width and base to width are highly inter-correlated (See Appendix 3 for full correlation matrix). Lamina length is significantly positively correlated with lamina base to widest point ($r = 0.95, P < 0.001$) and width ($r = 0.80, P < 0.001$). The number of undulations per leaf margin is significantly positively correlated with the distance from lamina base to widest point ($r = 0.47, P < 0.05$), lamina width ($r = 0.41, P < 0.05$) and is significantly negatively correlated with internode ($r = -0.66, P < 0.001$) and petiole ($r = -0.44, P < 0.05$). Petiole length and internode were not significantly correlated with any of the leaf dimensional characters.

4-3.2.2. Relationships between morphological attributes and environmental attributes

4-3.2.2.1. Geographic variables

The leaf dimensional characters (length, width and base to width) were significantly negatively correlated (all $P < 0.05$) with altitude. This indicates a general tendency for leaf size to decrease with increasing altitude. Leaf width was also strongly positively correlated ($r = 0.51, P < 0.01$) with latitude. This trend was reflected with
**Table 4-3.** Population means, coefficient of variation, L.S.D. ($P < 0.05$) and grand mean for selected leaf morphology characters in *P. undulatum* populations sampled throughout south east Australia. All populations differed significantly ($P < 0.001$) across all characters assessed. Standard errors are indicated in sub scripts.

<table>
<thead>
<tr>
<th>Population</th>
<th>Internode (mm)</th>
<th>Petiole (mm)</th>
<th>Width (mm)</th>
<th>Base to width (mm)</th>
<th>Length (mm)</th>
<th>No. of undulations</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALST</td>
<td>13.1 ±1.2</td>
<td>16.0 ±0.4</td>
<td>36.9 ±0.8</td>
<td>55.0 ±0.8</td>
<td>109.8 ±1.8</td>
<td>14.6 ±0.6</td>
</tr>
<tr>
<td>BELR</td>
<td>13.3 ±0.9</td>
<td>21.8 ±0.6</td>
<td>41.8 ±0.7</td>
<td>66.0 ±1.5</td>
<td>134.9 ±2.3</td>
<td>8.6 ±0.8</td>
</tr>
<tr>
<td>BODL</td>
<td>9.2 ±0.7</td>
<td>17.8 ±0.6</td>
<td>39.8 ±0.7</td>
<td>70.4 ±1.1</td>
<td>140.2 ±2.2</td>
<td>15.1 ±0.5</td>
</tr>
<tr>
<td>BRUT</td>
<td>6.8 ±0.4</td>
<td>19.0 ±0.6</td>
<td>45.1 ±0.8</td>
<td>68.6 ±1.2</td>
<td>130.4 ±2.2</td>
<td>17.6 ±0.6</td>
</tr>
<tr>
<td>CANN</td>
<td>8.4 ±1.0</td>
<td>21.4 ±0.9</td>
<td>43.0 ±0.9</td>
<td>63.8 ±1.1</td>
<td>124.9 ±1.9</td>
<td>10.1 ±0.4</td>
</tr>
<tr>
<td>CEDB</td>
<td>7.9 ±0.7</td>
<td>21.2 ±0.7</td>
<td>30.1 ±0.7</td>
<td>50.9 ±0.9</td>
<td>99.5 ±2.4</td>
<td>8.1 ±0.4</td>
</tr>
<tr>
<td>CROA</td>
<td>5.7 ±0.5</td>
<td>19.4 ±0.6</td>
<td>45.7 ±0.8</td>
<td>73.3 ±1.5</td>
<td>148.3 ±2.4</td>
<td>21.1 ±0.7</td>
</tr>
<tr>
<td>ELLN</td>
<td>11.4 ±1.3</td>
<td>17.0 ±0.5</td>
<td>37.4 ±0.7</td>
<td>62.1 ±1.0</td>
<td>102.7 ±1.7</td>
<td>7.8 ±0.4</td>
</tr>
<tr>
<td>GLEN</td>
<td>12.1 ±1.6</td>
<td>18.6 ±0.6</td>
<td>31.1 ±0.7</td>
<td>49.1 ±0.8</td>
<td>138.7 ±2.6</td>
<td>16.7 ±0.6</td>
</tr>
<tr>
<td>GURD</td>
<td>6.8 ±0.6</td>
<td>17.5 ±0.5</td>
<td>44.0 ±0.9</td>
<td>75.9 ±1.5</td>
<td>133.6 ±3.3</td>
<td>11.0 ±0.7</td>
</tr>
<tr>
<td>STRL</td>
<td>11.9 ±0.8</td>
<td>22.1 ±0.6</td>
<td>43.5 ±1.3</td>
<td>71.0 ±1.9</td>
<td>125.6 ±1.9</td>
<td>16.5 ±0.6</td>
</tr>
<tr>
<td>TWET</td>
<td>4.1 ±0.4</td>
<td>18.9 ±0.6</td>
<td>45.3 ±1.0</td>
<td>68.4 ±1.5</td>
<td>126.7 ±1.9</td>
<td>19.9 ±0.7</td>
</tr>
<tr>
<td>TDRY</td>
<td>4.2 ±0.4</td>
<td>15.7 ±0.4</td>
<td>47.8 ±0.9</td>
<td>68.6 ±1.1</td>
<td>107.1 ±2.0</td>
<td>13.2 ±0.6</td>
</tr>
<tr>
<td>TISL</td>
<td>6.1 ±0.4</td>
<td>18.2 ±0.5</td>
<td>40.0 ±1.0</td>
<td>58.7 ±1.3</td>
<td>121.8 ±1.7</td>
<td>14.6 ±0.6</td>
</tr>
<tr>
<td>LORN</td>
<td>7.2 ±0.5</td>
<td>15.8 ±0.5</td>
<td>38.6 ±1.1</td>
<td>60.2 ±1.3</td>
<td>109.8 ±2.0</td>
<td>14.1 ±0.7</td>
</tr>
<tr>
<td>MITR</td>
<td>6.6 ±0.6</td>
<td>16.8 ±0.2</td>
<td>35.9 ±1.0</td>
<td>57.4 ±1.3</td>
<td>128.9 ±2.0</td>
<td>16.1 ±0.7</td>
</tr>
<tr>
<td>MORW</td>
<td>9.3 ±0.6</td>
<td>19.1 ±0.7</td>
<td>42.4 ±0.9</td>
<td>65.7 ±1.4</td>
<td>121.0 ±2.5</td>
<td>11.2 ±0.4</td>
</tr>
<tr>
<td>MYPG</td>
<td>12.7 ±1.2</td>
<td>24.9 ±0.8</td>
<td>40.3 ±0.8</td>
<td>63.5 ±1.6</td>
<td>126.8 ±2.5</td>
<td>9.9 ±0.6</td>
</tr>
<tr>
<td>NOWR</td>
<td>13.9 ±1.1</td>
<td>20.0 ±0.7</td>
<td>41.7 ±1.4</td>
<td>63.4 ±2.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Population</td>
<td>Internode (mm)</td>
<td>Petiole (mm)</td>
<td>Width (mm)</td>
<td>Base to width (mm)</td>
<td>Length (mm)</td>
<td>No. of undulations</td>
</tr>
<tr>
<td>------------</td>
<td>---------------</td>
<td>--------------</td>
<td>------------</td>
<td>-------------------</td>
<td>-------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>PORT</td>
<td>10.6 ±0.7</td>
<td>20.2 ±0.4</td>
<td>48.7 ±0.8</td>
<td>74.0 ±2.0</td>
<td>146.2 ±1.9</td>
<td>12.6 ±0.4</td>
</tr>
<tr>
<td>MRAY</td>
<td>7.4 ±0.5</td>
<td>17.7 ±0.5</td>
<td>39.9 ±0.7</td>
<td>65.5 ±1.1</td>
<td>128.3 ±1.8</td>
<td>16.1 ±0.7</td>
</tr>
<tr>
<td>SPRG</td>
<td>9.6 ±0.5</td>
<td>19.0 ±0.4</td>
<td>37.0 ±0.7</td>
<td>60.0 ±1.3</td>
<td>114.7 ±2.3</td>
<td>16.0 ±0.5</td>
</tr>
<tr>
<td>STCK</td>
<td>13.0 ±0.7</td>
<td>24.0 ±0.5</td>
<td>36.9 ±0.9</td>
<td>59.6 ±1.2</td>
<td>115.4 ±2.5</td>
<td>10.1 ±0.4</td>
</tr>
<tr>
<td>SWRK</td>
<td>10.9 ±0.9</td>
<td>17.6 ±0.6</td>
<td>37.1 ±1.0</td>
<td>63.6 ±1.3</td>
<td>122.3 ±2.3</td>
<td>16.6 ±0.5</td>
</tr>
<tr>
<td>TATH</td>
<td>5.7 ±0.3</td>
<td>22.2 ±1.8</td>
<td>39.4 ±0.9</td>
<td>62.2 ±1.2</td>
<td>118.5 ±2.0</td>
<td>16.2 ±0.7</td>
</tr>
<tr>
<td>MORN</td>
<td>7.4 ±0.4</td>
<td>18.1 ±0.6</td>
<td>37.4 ±0.7</td>
<td>61.0 ±1.1</td>
<td>118.4 ±1.9</td>
<td>14.4 ±0.7</td>
</tr>
</tbody>
</table>

| L.S.D. (P < 0.05) | 2.23 | 1.95 | 2.48 | 3.76 | 6.06 | 1.64 |
| Grand Mean     | 9.1  | 19.2 | 40.3 | 63.8 | 123.52 | 13.9 |
| CV (%)         | 62.7 | 25.9 | 15.7 | 15.0 | 12.5 | 30.1 |
the length \( r = 0.37 \) and base-width \( r = 0.38 \) characters although the strength of these relationships was not significant (both \( P > 0.05 \)).

Internode was significantly negatively correlated with latitude \( r = -0.54, P < 0.01 \) and positively correlated with altitude \( r = 0.59, P < 0.05 \). The number of undulations per leaf was significantly negatively correlated with altitude \( r = -0.59, P < 0.01 \) and petiole length was significantly negatively correlated with longitude \( r = -0.40, P < 0.05 \).

4-3.2.2. Climatic variables

Internode was positively correlated with mean winter rainfall \( r = 0.61, P < 0.01 \) and mean summer maximum temperatures \( r = 0.52, P < 0.01 \). With the exception of these relationships, no other significant interactions between the morphological characters and temperature and rainfall gradients were evident.

All significant relationships between mean relative humidities and the leaf dimensional characters (including the number of undulations per leaf) were positive. Petiole and internode were both negatively correlated with the mean relative humidity variables.

All dimensional characters were significantly positively correlated (all \( P < 0.05 \)) with mean winter 9am relative humidity. Petiole length was significantly negatively correlated with mean 9am and 3pm spring and summer relative humidities and autumn 3pm relative humidities. Internode was significantly negatively correlated with mean autumn and spring 3pm relative humidities.

4-3.2.3. Cluster analysis of \( P. \ undulatum \) populations

Five population clusters are apparent in the dendrogram of mean morphological characters, although at a coarser scale, Clusters A-D are distinct from Cluster E (Figure 4-3). The Clusters identified on the dendrogram are also imposed on the
distribution map of *P. undulatum* populations sampled in this study for ease of interpretation (Figure 4-4).

Cluster A is comprised of the ALST, ELLN, SPRG and SWRK populations. This group represents populations sampled at the highest latitudes and most easterly longitudes. These sites are in a summer rainfall area and have the highest average annual rainfalls of all populations sampled.

Cluster B incorporates the TISL, MITR, LORN and MORN populations. The LORN and MORN populations show the highest affinity of all the populations sampled. These sites are both near coastal environments but have little else obviously in common. TISL and MITR both occur in dry rainforest environments, but other environmental influences are divergent. The TATH population is not closely related to any of the other populations sampled but shares affinities with populations in Clusters A and B.

Cluster C comprises NOWR and all the South Australian populations sampled. These populations all occur at a similar latitude—between 34°95’E (NOWR) and 35°39’E (MYPG). The inclusion of the CANN population in this cluster is curious, as it shares no obvious environmental affinities with other populations in this group.

The GLEN and CEDB populations form their own discrete cluster (Cluster D). Average leaf dimensional characters were consistently smallest for these two populations which may explain some of this separation.

Populations sampled in central and east Gippsland, Victoria; MORW, MRAY, BRUT, TWET, TDRY and CROA combine to form Cluster E. The GURD population, located on the eastern edge of Westernport Bay, Victoria and BODL in south east New South Wales are also grouped into Cluster E. All populations in this group have larger mean lamina width and base to width measurements than the grand mean of all populations sampled. This may explain some of the separation of the Cluster E populations from the other Clusters identified in the dendrogram.
The PORT population joins Cluster E at a higher dissimilarity level and like the TATH population, does not cluster strongly with other populations sampled. The PORT population is comparatively, geographically-remote from other populations sampled in this study which may explain some of this separation.

Geographic affinities based on multivariate analysis of leaf morphology attributes are strongest in the north east New South Wales – south east Queensland complex (Cluster A). The South Australian populations (Cluster C), which are subject to drier climatic conditions than the eastern populations sampled, also show some level of clustering, although the inclusion of the CANN and NOWR populations in this cluster weakens this trend.

The separation of LORN, MORN, MITR and TISL (Cluster B) from the other Victorian populations (Cluster E), is clear but the ecological significance of this separation is difficult to interpret. No obvious pattern of geographic variation is evident across the range of populations sampled in Victoria.

**4.3.2.4. Ordinations of population associations**

**4.3.2.4.1. Canonical variates analysis**

The distribution of canonical variate means represents a continuum related to leaf size (Table 4-4). Canonical variate 1 loads positively on length, base to width, width and undulations and negatively on petiole and internode. Canonical variate 2 loadings are negative for base-width and undulations and positive for all other characters. Canonical variates 1 and 2 account for 49.5% and 25% of the variation, respectively.

The populations are assigned the same symbols used to represent the five clusters identified by cluster analysis in the ordination of canonical variate means (Figure 4-5). Despite different analysis pathways, patterns evident in the cluster analysis are reflected in the ordination of canonical variate means mainly due to the loadings of canonical variate 2, confirming the pattern of population affinities evident in Figure 4-3.
Figure 4-3. Average-link dendrogram of 26 *P. undulatum* populations in south east Australia derived from hierarchical cluster analysis of mean leaf morphology attributes. The similarity matrix was formed using a Euclidean distance measure. Five groups of populations (△ Cluster A; ■ Cluster B; ◆ Cluster C; □ Cluster D; ● Cluster E) are identified.
Figure 4-4. Distribution of south east Australian sampling sites with clustered groups, derived from hierarchical cluster analysis of mean leaf morphology attributes, overlayed.
Clusters A and B identified on the dendrogram are not clearly separated on the ordination of canonical variate means. The South Australian populations again cluster together and incorporate the NOWR and CANN populations. The separation of the GLEN and CEDB populations identified on the dendrogram is also apparent in the ordination of canonical variate means.

The Cluster E populations are less closely related to each other although a core of Gippsland populations; MORW, MRAY, BRUT and TWET form a tighter cluster in this analysis and show greater affinity to some populations in Clusters A and B.

Table 4-4. Loadings of characters on the first two discriminant functions of the canonical variates (CV) analysis. Percentage variation accounted for in each discriminant function is provided in brackets and eigenvalues are indicated in parentheses.

<table>
<thead>
<tr>
<th>Character</th>
<th>CV 1</th>
<th>CV 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>[49.5%]</td>
<td>[25%]</td>
</tr>
<tr>
<td></td>
<td>(1.1)</td>
<td>(0.55)</td>
</tr>
<tr>
<td>Base to width</td>
<td>0.01</td>
<td>-0.02</td>
</tr>
<tr>
<td>Internode</td>
<td>-0.05</td>
<td>0.07</td>
</tr>
<tr>
<td>Length</td>
<td>0.01</td>
<td>0.07</td>
</tr>
<tr>
<td>Petiole</td>
<td>-0.08</td>
<td>0.01</td>
</tr>
<tr>
<td>Undulations</td>
<td>0.16</td>
<td>-0.09</td>
</tr>
<tr>
<td>Width</td>
<td>0.06</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Figure 4-5. Ordination of canonical variate means of 26 populations of *P. undulatum* based on leaf morphology attributes. Canonical variates 1 and 2 accounted for 49.5% and 25% of the variation, respectively. The distribution of populations in this ordination reflects the groups determined by classification analysis (Figure 4-3) and have been identified as such; ▲Cluster A; ■ Cluster B; ◆Cluster C; □ Cluster D; ● Cluster E.
4-3.2.4.2. Principal component analysis of independent variables

Principal Components Analysis (PCA) was conducted on the sample data collected for the petiole, internode, undulation and lamina length variables. Lamina length was arbitrarily determined to be representative of the inter-correlated leaf dimensional characters and the lamina width and base to width measurements were eliminated to maximise the explanatory output of the analysis. The first two principal component scores accounted for 79.3% of the variation (Table 4-5).

PC 1 gives a negative weighting to internode and petiole length and a positive weighting to lamina length and the number of undulations per leaf margin. PC 2 gives a negative weighting to all characters. Lamina and petiole lengths have the highest loadings in PC 2. Only PC scores with an eigenvalue greater than one (PC 1 and PC 2) are presented as these explain the greatest amount of variation in the data set.

Table 4-5. Loadings of independent characters on the first two scores of the principal components (PC) analysis. Percentage variation accounted for is provided in brackets and eigenvalues are indicated in parentheses.

<table>
<thead>
<tr>
<th>Character</th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>[52.3%]</td>
<td>[27%]</td>
</tr>
<tr>
<td></td>
<td>(2.09)</td>
<td>(1.08)</td>
</tr>
<tr>
<td>Internode</td>
<td>-0.56</td>
<td>-0.17</td>
</tr>
<tr>
<td>Length</td>
<td>0.26</td>
<td>-0.85</td>
</tr>
<tr>
<td>Petiole</td>
<td>-0.47</td>
<td>-0.47</td>
</tr>
<tr>
<td>Undulations</td>
<td>0.64</td>
<td>-0.14</td>
</tr>
</tbody>
</table>

Clearer separation of populations was achieved through PCA of the independent morphological attributes (Figure 4-6). The South Australian populations again cluster with NOWR and CANN, but the latter two populations are placed closer to the New South Wales and Victorian populations sampled. PORT is also positioned closer to the South Australian populations in this analysis. The PORT population is
geographically-closer to these South Australian sites than the Victorian populations comprising in Cluster E (see Figures 4-1 & 4-4).

The GLEN and CEDB populations again form a discrete cluster but are positioned closer to the north east New South Wales populations in the ordination of PC scores. The TATH population showed greater affinity to populations comprising Clusters A and B in the dendrogram, but was placed between the Cluster A and E populations in the ordination of PC scores. This places TATH between the north east New South Wales and East Gippsland populations, which reflects the geographic position of this population (see Figures 4-1 & 4-4).

The CROA population is placed separately from the other populations in Cluster E in the ordination of PC scores. Lamina length and the number of undulations per leaf are highest in this population. PC 1 loadings were highest for the undulations variable and PC 2 loadings were highest for length, which may explain the relative separation of the CROA population.

4-3.2.5. Minimum spanning tree of population affinities

The separation of populations indicated in the minimum spanning tree (Figure 4-7) contributes to the profile of population affinities developed in the other multivariate analyses. The northern populations sampled (SPRG, ALST, ELLN and SWRK) are linked to the GLEN and CEDB combination. The TATH population is again placed between the New South Wales and Victorian populations. The greater affinity of the PORT population to the South Australian populations indicated in the ordinations is also evident in the minimum spanning tree. TWET and TDRY are linked to the geographically-close BRUT population and are distinct from TISL. The affinity between TISL and MITR held across all analyses and may be related to the similarity of the dry rainforest habitats occupied by these populations.
Figure 4-6. Ordination of the first two principal component scores of independent morphological variables for 26 populations of *P. undulatum* in south east Australia. Principal components 1 and 2 accounted for 52.3% and 27% of the variation among populations, respectively. Symbols represent clusters identified in the dendrogram of population affinities (Figure 4-3); ▲ Cluster A; ■ Cluster B; ◆ Cluster C; □ Cluster D; ● Cluster E.
Figure 4-7. Minimum spanning tree showing relationships between 26 populations of *P. undulatum* in south east Australia based on leaf morphology attributes.
4-3.2.6. Multivariate estimates of within-population variability

Considerable variation is evident in the within-population variance estimates calculated for each population sampled (Table 4-6). The most variable populations are BELR, TATH, STRL, NOWR and MORW. These populations represent natural and invasive sites and divergent environmental influences. The populations with the lowest within-population variance (TDRY, PORT, MORN, TWET and TISL) all occur in southern Victoria and again represent both natural and invasive populations, and populations subject to a range of environmental conditions. The low variability displayed by the three Lake Tyers populations is interesting but difficult to explain. Nearby natural populations including BRUT, MRAY, and CROA, also displayed comparatively low levels of within-population diversity while the Queensland population SPRG, and the invasive Victorian populations PORT and MORN displayed similar levels of within-population variability (all < 0.40).

4-3.2.7. Cluster analysis of ‘natural’ P. undulatum populations

Two broad groups are evident in the dendrogram of 17 natural populations of P. undulatum based on mean leaf morphology attributes (Figure 4-8). With a few exceptions, group one is comprised of the northern populations sampled and group two is comprised of the southern populations sampled (Figure 4-9). The Clusters in this dendrogram have been assigned a different set of symbols to avoid confusion between those used in previous analyses of the entire data set.

Three population clusters are recognised within the two broader groups and two populations (NOWR and TATH) are not strongly aligned with any of the other natural populations sampled. The populations sampled in north east New South Wales (ALST, ELLN, SWRK and SRPG) combine with the Victorian MITR and TISL populations to form Cluster 1.1. The ALST population showed greater dissimilarity to the other populations in this cluster than was evident in the dendrogram of all populations sampled (Figure 4-3). The inclusion of MITR and
Table 4-6. Estimates of within-population variance of *P. undulatum* populations sampled in south east Australia.

<table>
<thead>
<tr>
<th>Population</th>
<th>Multivariate-variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>TDRY</td>
<td>0.26</td>
</tr>
<tr>
<td>PORT</td>
<td>0.30</td>
</tr>
<tr>
<td>MORN</td>
<td>0.31</td>
</tr>
<tr>
<td>TWET</td>
<td>0.34</td>
</tr>
<tr>
<td>TISL</td>
<td>0.35</td>
</tr>
<tr>
<td>SPRG</td>
<td>0.37</td>
</tr>
<tr>
<td>CROA</td>
<td>0.38</td>
</tr>
<tr>
<td>MRAY</td>
<td>0.38</td>
</tr>
<tr>
<td>BRUT</td>
<td>0.39</td>
</tr>
<tr>
<td>ELLN</td>
<td>0.42</td>
</tr>
<tr>
<td>CANN</td>
<td>0.43</td>
</tr>
<tr>
<td>ALST</td>
<td>0.45</td>
</tr>
<tr>
<td>BODL</td>
<td>0.45</td>
</tr>
<tr>
<td>GURD</td>
<td>0.45</td>
</tr>
<tr>
<td>MYPG</td>
<td>0.47</td>
</tr>
<tr>
<td>MITR</td>
<td>0.47</td>
</tr>
<tr>
<td>SWRK</td>
<td>0.48</td>
</tr>
<tr>
<td>STCK</td>
<td>0.50</td>
</tr>
<tr>
<td>LORN</td>
<td>0.51</td>
</tr>
<tr>
<td>CEDB</td>
<td>0.52</td>
</tr>
<tr>
<td>GLEN</td>
<td>0.54</td>
</tr>
<tr>
<td>MORW</td>
<td>0.62</td>
</tr>
<tr>
<td>NOWR</td>
<td>0.73</td>
</tr>
<tr>
<td>STRL</td>
<td>0.96</td>
</tr>
<tr>
<td>TATH</td>
<td>1.08</td>
</tr>
<tr>
<td>BELR</td>
<td>1.17</td>
</tr>
</tbody>
</table>
TISL in Cluster 1.1 may be a reflection of the similar dry rainforest habitats occupied by all populations in this cluster.

The NOWR population (Cluster 1.2) was grouped with the invasive South Australian and CANN populations in the dendrogram of all populations sampled and retains its morphological distinctiveness in this analysis. The CEDB and GLEN association (Cluster 1.3) was again evident in this separate analysis of natural populations. These two populations show greater affinity to the northern *P. undulatum* populations sampled that typify group one, than the southern populations sampled, which typify group two.

Group Two cluster 2.1, is comprised of BODL (south east New South Wales) and the remaining Victorian populations sampled. The geographically-close BRUT, TWET, MORW and MRAY populations, which occupy wet forest environments in East Gippsland are clustered with BODL. The near-coastal populations sampled in East Gippsland, CROA and TDRY are linked to the other East Gippsland populations sampled but at a greater dissimilarity level. The TATH population retained its morphological distinctiveness in this analysis and shows greater affinity to the southern, rather than the northern populations of *P. undulatum* sampled. The three geographically-close Lake Tyers populations show greater morphological affinity to populations sampled from similar habitats, rather than each other.

The cluster analysis of natural populations contributes to the profile of morphological variation in *P. undulatum*. The pattern of geographic variation in this second dendrogram clarifies relationships between some populations, but generally reflects the underlying pattern evident in the dendrogram of all populations sampled.
Figure 4-8. Average-link dendrogram of 17 ‘natural’ *P. undulatum* populations in south east Australia derived from hierarchical cluster analysis of mean leaf morphology attributes. The similarity matrix was formed using a Euclidean distance measure.
Figure 4-9. Distribution of 17 natural *P. undulatum* populations with clustered groups, derived from hierarchical cluster analysis of mean leaf morphology attributes, overlayed.
4-4. Discussion

Populations of *P. undulatum* display considerable variation in leaf morphology attributes throughout south east Australia. No strong patterns of geographic variation were evident when significant differences between populations were further assessed using Fisher’s unrestricted least significant difference.

The leaf dimensional characters—length, width and base to width—were all significantly positively correlated with one another (all $P < 0.001$). The number of undulations per leaf was also significantly positively correlated with these three leaf dimensional characters (all $P < 0.05$). Internode length was strongly negatively correlated with the number of undulations per leaf ($P < 0.001$). This implies that as leaves are more closely arranged on a stem and the interval between leaves decreases, then the number of undulations per leaf increases, or *vice versa*. This relationship may be related to photosynthetic potential. Undulations serve to increase the surface area of a leaf and a higher number of undulations per leaf may be a useful adaptation for greater light inception on more densely foliaged trees. The significant relationship between the internode character and the number of undulations per leaf however, needs to be considered with caution, given the variable distribution of leaves in *P. undulatum*, i.e., in whorls, semi-whorls or singular arrangement.

An interesting pattern emerged in the relationships displayed between *P. undulatum* leaf morphology and the environmental parameters assessed. The leaf dimensional characters, length, width and base to width were all negatively correlated with altitude suggesting *P. undulatum* leaf size decreases with increasing altitude. This pattern has been observed in other species (Pryor 1956; Middleton *et al*. 1996) and at a simple level is an adaptive response to lower temperatures and higher rainfall associated with increasing altitude. The leaf width character was also positively correlated with latitude suggesting that leaf width increases from north to south. Again, this trend is probably related to photosynthetic potential. The southern populations would on average, experience less sunlight hours per day than the northern populations and larger leaf size may be an adaptive compensatory measure.
A relationship between leaf size and geographic position has been observed in other Australian plants. *Acacia melanoxylon* R. Br. (Blackwood) phyllodes for example, are smaller in inland areas (Farrell & Ashton 1978) as an adaptation to water stress in drier environments.

Several mean leaf morphology attributes were significantly correlated with mean seasonal relative humidity variables. The internode character is negatively correlated with mean autumn and spring 3pm relative humidities and positively correlated with mean summer maximum temperatures and mean winter rainfall. The distribution of leaves on a stem is probably again related to photosynthetic potential. Higher summer temperatures may allow greater potential for photosynthesis and so leaves do not need to be as numerous or closely arranged. Seasonal and diurnal variation in factors such as temperature and relative humidities provide a useful picture of the plant’s growing conditions but in reality, the relationships between plant morphology and such climatic variables are likely to be highly complex. The relative humidity experienced by each leaf, whorl, canopy position and individual tree may vary to some extent and these factors may influence the morphological and anatomical structure of a leaf. Variation may also be evident in evaporative demand, which is in itself, related to a complex combination of environmental, morphological and physiological variables. Further research on variation on *P. undulatum* leaf anatomy and physiological response across a range of habitats would be required to determine these relationships.

Studies of anatomical variation in other species have revealed patterns in geographic variation that may not be detected at the ‘coarse’ morphological scale. James and Bell (1995) reported a positive relationship between lamina thickness and aridity in populations of *Eucalyptus camaldulensis*, but relationships between leaf length and width and climatic variables were not significant. Lamina thickness was also higher in coastal compared to hinterland populations of *E. botryoides* (Passioura and Ash (1993) and this is likely to be an adaptation to salt spray. Pryor (1956) also documented a positive correlation between altitude and leaf thickness in *E. pauciflora* Sieber ex Spreng (Snow Gum). Importantly, where no obvious phenotypic response to environmental conditions are evident, this does not imply that the species (or population) lacks the capacity for a plastic response. As
Schlichting (1986) suggests, the relative homogeneity of morphological characters may be compensated for by plasticity of physiological characters.

With the exception of positive correlations between internode and mean winter rainfall and summer maximum temperatures, no relationships between *P. undulatum* leaf morphology and mean temperature and rainfall gradients were evident. Simmons and Flint (1986) also reported a lack of association between morphological variation and environmental conditions in populations of *Chrysanthemoides monilifera* ssp. *monilifera* (L.) Norlindh (Boneseed). *C. monilifera* ssp. *monilifera* also exhibited greater variability than *C. monilifera* ssp. *rotundata*. Simmons and Flint (1986) suggested this might be related to the longer time elapsed since introduction of the former and therefore greater potential for differentiation. *C. monilifera* ssp. *monilifera* may also be inherently more plastic than *C. monilifera* ssp. *rotundata* and able to adapt to a broader range of environments (Simmons & Flint 1986).

Johnstone (1973 in Thorpe 1976) suggested that if characters have the same degree of interdependence, as evidenced by covariation and correlation between geographic locations in which different environmental conditions are experienced, then genetic composition rather than environmental conditions is influencing character variation. As this is clearly not the case in *P. undulatum* populations, especially those that occur in Victoria, environmental influences must be shaping leaf phenology. The pattern of morphological variation within and between the *P. undulatum* populations sampled may reflect a plastic response to other, unknown environmental influences that could not be tested in this analysis. For example, edaphic factors, such as soil type, depth, nutrient availability and water holding capacity may be important factors. Equally, micro-topographical features such as slope and aspect may also influence the morphological expression of *P. undulatum*. Community composition, structure and competition variables may also be important factors.

Duke (1990) found patterns of morphological variation in *Avicennia marina* (Forssk.) Vierh. (Mangrove), especially of leaf characters, were related to quite specific environmental influences such as intertidal location in addition to temperature and rainfall attributes. James and Bell (1995) reported some correlation
between morphological and anatomical characteristics of *Eucalyptus camaldulensis* and climatic conditions but suggested that other factors such as ground water availability and root structure may be more important than climate in shaping leaf structure.

It is also possible that factors inherent in each *P. undulatum* population sampled could be influencing morphological expression. Such variables may include the size and source of the founder population, time since invasion and the genetic diversity within each population. Odum (1971) suggests that it is not uncommon for species with wide geographic ranges to develop locally adapted populations (ecotypes) that have tolerance optima and limits adjusted to the local conditions. Observation of populations of *P. undulatum* occupying different habitat types would seem to support Odum's (1971) assertion. The level of ecotypic variation (and the speed with which it develops) would depend on the intensity of selection pressures and the response of the plants at the individual and population level. Goodland and Healey (1996) suggested that invasive populations of *P. undulatum* in the Blue Mountains region of Jamaica were quite uniform in leaf and capsule morphology and that variation in these traits seemed related to local environmental factors. In addition to the data presented in this study, Gleadow (1982) also reported that *P. undulatum* seedlings display a adaptable root habit in response to different soil types indicating a plastic response to different soil characteristics. *P. undulatum* possesses attributes typical of both sun and shade plants (Gleadow et al. 1983), and the species’ occupation of a range of habitat types may also indicate a plastic response to variation in light regimes.

Ecotypic variation in *P. undulatum* may be the foundation for the groups derived from the multivariate analyses, although the relationship between phenotypic expression and habitat variables are not immediately obvious in all cases. Some aggregations of geographically-close populations were evident in the cluster, canonical variates and principal components analyses and significant relationships emerged between leaf attributes and some environmental parameters. The pattern of variation was clearer to some degree, in the separate cluster analysis of natural populations. The association between the north east New South Wales and south east Queensland populations (ALST, ELLN, SWRK and SPRG) for example, held
across all multivariate analyses. The South Australian populations also displayed affinities but the grouping of the NOWR and CANN populations with this cluster weakens the case for geographic association in this cluster of morphologically similar populations. There was no clear separation of Victorian populations exhibiting similar morphologies based on the geographic and climatic parameters assessed with the possible exception of several wet forest populations sampled in East Gippsland.

The strongest population affinities identified from the cluster analysis of the 26 populations were between LORN and MORN, MITR and TISL, MORW and MRAY, BRUT and TWET, BELR and NOWR and MYPG and STCK. The MORW and MRAY, and BRUT and TWET populations occur in similar wet forest habitats and are subject to a similar set of climatic conditions given their geographic proximity to each other. The LORN and MORN populations however, occur in quite different habitats. LORN occurs in wet sclerophyll forest in the Otway Ranges, Victoria and MORN occurs in heathy woodland on the Mornington Peninsula, Victoria. Both populations are however subject to coastal influences and are in an advanced stage of invasion. The MITR and TISL association may be related to similarities in the dry rainforest habitats occupied by the two populations. The MYPG and STCK populations both occur in the southern Mount Lofty Ranges, South Australia, characterised by a dry climate and low annual (predominantly winter) rainfall. The relationship between BELR and NOWR however is more difficult to explain. The only obvious parameter these two sites have in common is that they occur at a similar latitude. It is possible that invasive populations in this area of the Mount Lofty Ranges were originally sourced from coastal New South Wales or from forests east of Melbourne. The inclusion of the NOWR and CANN populations with the South Australian populations in the cluster analysis may be further evidence of this assumption. Comprehensive analysis of genetic characteristics would be necessary to support this hypothesis.

The PORT and TATH populations have distinct morphologies that prevented strong clustering with morphologically different but geographically-close populations. PORT is grouped with the Victorian populations in the cluster analysis but shows stronger affinity to the geographically-close South Australian populations in the
principal components and canonical variates analyses and was linked to the South Australian populations in the minimum spanning tree. The TATH population was linked to Clusters A and B in the dendrogram and placed as an intermediate between these clusters in the other multivariate analyses.

The three Lake Tyers populations clustered with populations sharing similar habitat conditions. The TISL population was consistently associated with MITR, another dry rainforest population. TWET and TDRY were closely aligned in the principal components and canonical variate analyses and presented as a distinct pair in the minimum spanning tree. TWET was aligned with similar wet sclerophyll forest and warm temperate rainforest populations in the cluster analysis. The same trends were evident in the dendrogram of the 17 natural *P. undulatum* populations sampled.

The GLEN and CEDB populations also formed a distinct pair across all analyses. These two populations exhibited the smallest leaf size, although the climatic conditions experienced by these populations are very different. Annual rainfall at CEDB is the lowest of all populations sampled and mean maximum summer temperature is highest of all populations sampled in this study. Relative humidities are also lowest on average across all seasons at CEDB. By contrast to CEDB, the GLEN population, which occurs in the southern foothills of the Victorian Alps experiences more moderate mean temperatures and relative humidities and considerably higher mean annual rainfall.

Prevailing environmental conditions at these two divergent sites are probably both representative of the limits to *P. undulatum* ecological amplitude or tolerance. At CEDB, low rainfall and relative humidities and high mean seasonal temperatures are likely to be limiting factors. GLEN is probably also on the distributional limits of *P. undulatum*; the limiting factor in this case is probably altitudinal as *P. undulatum* is not able to colonize the higher altitudes and colder climate of the adjacent dry foothill forest. Small leaf size in these two populations may be indicative of environmental constraints. Barrett and Ash (1992) reported an increase in *P. undulatum* leaf area under high nutrient, water and irradiance, but conceded that their glasshouse trials did not exactly reproduce natural environmental gradients. Further sampling of populations at the presumed distributional limits of *P. undulatum* would
be necessary to determine if decreased leaf size is a function of reduced environmental suitability.

No clear geographic patterns are evident in the within-population variability estimates calculated for each population. BELR, for example, is a highly disturbed population in the Mount Lofty Ranges, that is literally surrounded by ornamental plantings of *P. undulatum* that could originate from any part of south east Australia. In this case, the high level of variation evident within samples from this population may be related to the integration of germplasm from a range of provenances. In contrast, the low level of within-population variation evident in the TDRY population may be related to the small size and relative isolation of this population.

Widespread species with large populations generally exhibit more variation within rather than between populations. In contrast, smaller populations with localised distributions express most variability between populations, due to genetic drift (Moran & Hopper 1987). While this assumption holds for some of the *P. undulatum* populations assessed (including BELR and TDRY described above), in most cases there was no obvious association between effective population size and the within-variance estimate calculated for each population sampled.

The pattern of within-population variability in *P. undulatum* is complex and not obviously related to population size, geographic location, the natural or invasive status of each population or prevailing climatic conditions. Many of the populations sampled in Victoria may host individuals from other provenances that have ‘escaped’ horticultural situations or spread via avian dispersal. It is assumed however, that the populations assessed in this study are not functionally connected. Potential exists for seed movement between sites or between intermediate populations via dispersal agents such as Pied Currawongs. *P. undulatum* fruit crop production in late autumn and early winter coincides with Pied Currawong migration to lower altitudes in south east Australia (Readshaw 1968). Theoretically, some movement of seed may occur during Pied Currawong migration and subsequent movement between patches at lower altitudes. Reports of small isolated populations of *P. undulatum* occurring in bushland remote from human settlements for example, are likely to be the result of Pied Currawong dispersal.
The consequent integration of germplasm from other provenances may be an additional factor in the high within and between population variability, although if genetic variation in *P. undulatum* is low as Orso (1994) suggests, this may not be an important influence on phenotypic expression. It is also possible that no clear pattern of morphological variation exists among geographically-close populations in Victoria. Populations sampled in Victoria show some underlying morphological similarities to populations occupying similar habitats, but are inherently variable.

Other studies of variability in plant species have been able to attribute the pattern of within-population variation to environmental or human-mediated influences. Ashburner (1994) found that domesticated populations of *Cocos nucifera* L. (Coconut Palm) sampled in the south Pacific showed higher levels of within-population variability in fruit morphological attributes than natural populations sampled in the same region. Wilson and Rapson (1995) reported that natural populations of *Agrostis capillaris* L. (Brown-top Bent) sampled in Britain were inherently more variable than invasive populations of the same species sampled in New Zealand. Similarly, populations in the *Eucalyptus globulus* complex showed higher levels of within-population variation in the intergradation regions of the various *E. globulus* sub-species compared with populations sampled in the core distribution of each subspecies (Jordan *et al.* 1993).

To some extent, the pattern and extent of the recent range expansion of *P. undulatum* may compromise assessment of the ‘true’ level of geographic variation in this species. As discussed in Chapter 3, *P. undulatum* has been widely planted throughout south-east Australia, the area of interest in this study, and so it is impossible to discern on the basis of morphometric analyses alone, the genetic origin of the individuals sampled. This problem is likely to be more pronounced in habitats outside the species’ natural range, where the parents of any individual *P. undulatum* could have origins literally as diverse as coastal environments in Victoria and warm temperate rainforests in New South Wales. This issue of provenance may also prove important for some populations occurring within the species’ natural range, especially where such populations occur in close proximity to human settlements and the standard suite of *P. undulatum* ornamental plantings. *P. undulatum* is still
incorporated into revegetation programs, particularly in coastal and hinterland New South Wales (Nagle 1996a, 1996b) and south east Victorian environments (pers. obs.). The performance of planted individuals from different provenances compared to known naturally occurring individuals would be interesting to assess.

The importance of conserving the genetic integrity of indigenous provenances, particularly of rare and threatened species, is an important aim of current biodiversity conservation programs (Commonwealth of Australia 1996; Government of Victoria 1997). Considerable between-population genetic variability has been demonstrated in recent studies of some rare Australian plants (McEntree et al. 1994; James & Ashburner 1997). In both cases, conservation of the scattered populations was recommended to conserve between-population genetic diversity.

Conserving the genetic and morphological distinctiveness of indigenous provenances of ‘native weeds’ such as *P. undulatum*, is also important for at least two reasons. First, indigenous populations may be at risk of genetic mixing through breeding with ornamental plantings from other provenances. The genetic integrity of many natural *P. undulatum* populations has perhaps already been compromised in this manner. Second, and perhaps more important from a broader conservation perspective, is the potential introduction of a more aggressive or adaptable genotype that may facilitate *P. undulatum* range expansion in natural and invasive populations. While it is acknowledged that the ultimate invasion potential of a species is linked to numerous factors (see Chapter 2), isolation of *P. undulatum* genotypes may prove prudent. Invading populations of *P. undulatum* have also hybridised successfully with indigenous populations of *P. bicolor* throughout Victoria, thereby compromising the genetic integrity of the latter species (Robin & Carr 1986; Carr 1993; and see Chapter 3).

Measurement of phenotypic or morphological variation is the most readily obtainable measurement of genetic variation (Silvertown & Lovett Doust 1993), but given the potential mixing of genotypes between populations of *P. undulatum*, morphometric analyses alone, cannot provide an accurate representation of genetic variation in this species. Further considerations such as modifications to pollination syndromes may also be important in shaping the pattern of genetic diversity,
particularly within populations of outcrossing species (Playford et al. 1993), such as *P. undulatum*.

Orso (1994) found genetic diversity amongst *P. undulatum* populations was low, but this may not hold true across the geographic distribution of this species. For example, Orso (1994) reported that the genetic constitution of *P. undulatum* sampled at Wingan Inlet was more similar to horticultural plantings sampled in Melbourne than individuals sampled at Point Hicks. Wingan Inlet and Point Hicks are seasonally popular campsites located on the coastal fringe of Croajingolong National Park (CROA) in far east Gippsland, Victoria. These two populations of *P. undulatum* are approximately 20km from each other and 400km from Melbourne. Pied Currawongs are present at both sites within Croajingolong National Park during the autumn-winter migration but due to the abundant food resources available at these two campsites, may be resident temporarily and fairly sedentary spatially and so these populations may not be functionally connected via seed dispersal mechanisms. Further genetic analysis is necessary to further elucidate the pattern of genetic diversity within and between populations of *P. undulatum* and to validate Orso’s (1994) preliminary findings.

Phenotypic plasticity has been reported in other invasive plant species and may compensate for low levels of genetic variability in founder populations (Wilson & Rapson 1995). In the invasive Noogora Burr complex (*Xanthium stumarium* L.) phenotypic plasticity is considered to be the principal mode of adaptation to variable environments and environmental conditions (Moran et al. 1981). *X. chinense*, which is the most widely distributed of the four *X. strumarium* races in Australia (Moran et al. 1981) for example, displays low genetic variation, but this is compensated for by high levels of plasticity (Moran et al. 1981).

In contrast to these examples of phenotypic plasticity other studies have demonstrated that morphological response is dictated by genetic composition, at least in the first few generations. Ramsey et al. (1994) transplanted seedlings derived from coastal and tableland populations of *Blandfordia grandiflora* R. Br. (Christmas Bells) to assess the level of phenotypic response in this species. The phenotypic distinctiveness of natural populations was retained suggesting that the
genetic constitution was more important in determining the morphology of the measured characters than phenotypic plasticity (Ramsey et al. 1994). Wilson and Rapson (1995) compared genetic and morphological characteristics in populations of *Agrostis capillaris* in the species’ native range (Britain) compared to invaded habitats in New Zealand. Variation was higher in populations sampled in Britain compared to New Zealand and the authors attributed this to both the limited gene pool of the New Zealand populations and that insufficient time had elapsed for genotypes to respond to habitats pressures (Wilson & Rapson 1995). Transplant experiments may be necessary to deduce the real environmental effects on phenotypic expression in *P. undulatum*.

4-5. Summary

Significant differences were evident in *P. undulatum* leaf morphologies across the range of populations sampled in this study. An altitudinal cline was evident for the leaf dimensional characters; length, width, base to width and the number of undulations per leaf. Mean leaf width also decreased with increasing latitude. Significant relationships were evident between leaf characters and mean relative humidities but no clear patterns of morphological variation along temperature and rainfall gradients were evident. All significant relationships between leaf dimensional characters and relative humidities were positive, while the significant relationships between petiole and internode and mean relative humidities were negative.

Cluster, principal components and canonical variates analyses revealed a coarse aggregation of populations by geographic region. The north east New South Wales – south east Queensland association held across all multivariate analyses. The South Australian populations also displayed affinities but the grouping of the NOWR and CANN populations with this cluster weakens the case for geographic association in that region. There was no clear separation of Victorian populations exhibiting similar morphologies based on the geographic and climatic parameters assessed with the possible exception of several wet forest populations sampled in East Gippsland.
The pattern of within- and between-population variation in *P. undulatum* is complex and it is only possible to speculate on the factors influencing the observed patterns. The considerable within- and between-population variability evident in the populations of *P. undulatum* sampled may also be related to factors that were not tested or considered in this study. On the other hand, *P. undulatum* may simply be an inherently variable species. The recent disruptions to the natural distribution of *P. undulatum* and the movement of germplasm between populations may also be influencing patterns of variation in this species. In the absence of a comprehensive genetic analysis of *P. undulatum* populations, it is difficult to speculate on the origins and degree of ‘blurring’ in population integrity and the influence of same on the invasive potential of affected populations. This study of morphological variation however, provides an important first step into such an investigation.

Phenotypic variation in this species is considerable and may compensate for low levels of genetic variation (Orso 1994). The degree of variability displayed by *P. undulatum* and the range of environmental conditions experienced by this species across its geographic range, is indicative of high phenotypic plasticity and confirms the species’ potential as a serious environmental weed. For a species thought to have evolved in or near wet forests, it adapts extremely well to invaded coastal and dry forest environments. The successful invasion of a diverse range of vegetation complexes on other continents and islands throughout the temperate, sub-tropical and tropical zones (Cooper 1956) is further evidence of the species’ adaptability and broad ecological amplitude. The phenotypic plasticity and adaptability of *P. undulatum* will facilitate further range expansion of this species across a range of habitats and climate regions.
CHAPTER FIVE

P. undulatum dispersal ecology and seed germination

5-1. Introduction

Ornamental plantings and established populations of P. undulatum produce an abundant fruit crop over the winter months. Limited data and anecdotal evidence implicates several vertebrates as dispersal vectors of P. undulatum in south east Australia (Gannon 1935; Cooper 1959; Rose 1973; Gleadow 1982; Forde 1986; Buchanan 1989b; Barker & Vestjens 1990; Brown et al. 1991). Turdus merula (European Blackbird) and Strepera graculina (Pied Currawong) (Plate 5-Ii-ii) are however, considered to be the principal dispersal agents of P. undulatum in this region (Mullett 1999). European Blackbirds (hereafter Blackbirds) have a small gape and are restricted to feeding on P. undulatum seeds that are exposed when the fruits dehisce on maturity. Blackbirds appear to mainly pursue the sticky mucilage encasing P. undulatum seed, which requires considerable ingestion of seeds. The larger Pied Currawongs consume pre- and post-dehiscent P. undulatum fruits and regurgitate undigested seeds and carpel fragments in pellets of variable cohesion.

Once pollination has been achieved by physical means or mediated by members of the host community in outcrossing species such as *P. undulatum*, successful seed dispersal and germination are the next important phases in the integration of the introduced plant into the host community. Frugivorous dispersal agents assist the movement of seed away from the parent plant which may increase the seeds’ chance of germination, the seedlings chance of survival, and may ultimately serve to increase the species’ distribution and local abundance.

The role of frugivores in the dispersal of *P. undulatum* has received minimal attention in previous studies, yet is likely to be a key factor in the rapid and widespread invasion of this species. Further, it is apparent that pre- and post-dehiscent *P. undulatum* fruits provide food resources to a range of frugivores of various size classes (pers. obs.). As such, understanding the germinability of seeds extracted from pre- and post-dehiscent *P. undulatum* fruits, as well as those eliminated by frugivorous species, is essential if a germination profile for this species is to be established.

The *P. undulatum* dispersal syndrome has been altered in several ways since European settlement. The introduction and subsequent invasion of *P. undulatum* into habitats outside its natural ecological range brings the species into contact with a novel assemblage of frugivores and potential dispersal agents. The addition of introduced frugivorous species, such as Blackbirds (Emison *et al.* 1987), throughout the natural and invasive range of *P. undulatum* in south east Australia also constitutes a change in dispersal opportunities for this species. The increased distribution and abundance of some native dispersal agents, such as Pied Currawongs (Bass 1989, 1996a; Lenz 1990; Recher & Lim 1990), also modifies the *P. undulatum* dispersal regime. Regional declines in the distribution and abundance of some *P. undulatum* seed predators, such as *Alisterus scapularis* Liehenstein (Australian King Parrots) in the Strzelecki Ranges, Victoria (Emison *et al.* 1987), may also represent a change in the dispersal potential of *P. undulatum*. 
5-1.1. Aims of the current study

The aims of the current study were twofold. First, to assess the comparative germinability of *P. undulatum* seed collected from six populations in Victoria and at two stages of fruit maturity; pre- and post-dehiscence (Plate 5-1). The germinability of seeds extracted from pre-dehiscent fruits was tested to obtain a relative measure of the dispersal potential of Pied Currawongs, which tend to preferentially select such fruits for consumption. Secondly, the germinability of *P. undulatum* seeds recovered from Blackbird scats and pellets regurgitated by Pied Currawongs were assessed to determine if seed germinability is influenced by ingestion and subsequent elimination.

Morphological variation in *P. undulatum* fruit collected from the six populations was assessed to complement the larger study of morphological variation in this species (Chapter 4) and to allow some comparison between fruit and seed crop characteristics and germination success.

5-1.2. Previous research on *P. undulatum* seed dispersal and germinability

Previous germination trials on *P. undulatum* seed recovered from the ejecta of Blackbirds and Pied Currawongs have been based on small samples (i.e., Blackbird; Gleadow (1982) 32 seeds, Cooper (1959) 30-62 seeds and Pied Currawong; Buchanan (1989b) 8 seeds). Germination trials were also conducted on seeds produced by a predominantly male flowering *P. undulatum* in the current study as previous germination trials (Steel 1911) had been based on an unspecified sample size.

Gleadow (1982) investigated several aspects of *P. undulatum* germination on seed collected from Kinglake National Park, Victoria. Germination trials were conducted at various temperatures (4, 11, 16, 20 and 25°C) and on seed stored at various humidities (20, 40, 60 and 80% RH) (Gleadow 1982). The optimum temperature range for *P. undulatum* germination was reported to be between 18°C and 21°C (Gleadow 1982) and this temperature regime was used in the current study.
5-2. Methods

5-2.1. Sites selected for sampling

Aspects of *P. undulatum* fruit morphology and seed germinability were assessed from samples collected at six sites in Victoria (Table 5-1). These sites were selected to represent natural and invasive populations of *P. undulatum*. The distribution of these populations is illustrated in Figure 5-1.

Table 5-1. Victorian *P. undulatum* populations sampled in this study of fruit morphology and seed germinability.

<table>
<thead>
<tr>
<th>Natural Range Code</th>
<th>Natural Range Population</th>
<th>Invaded Range Code</th>
<th>Invaded Range Population</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>Croajingolong National Park</td>
<td>MORN</td>
<td>Woods Reserve, Mornington Peninsula</td>
</tr>
<tr>
<td></td>
<td>20 Acre Creek, Glenmaggie</td>
<td>LORN</td>
<td>Angahook-Lorne State Park</td>
</tr>
<tr>
<td>MORW</td>
<td>Morwell National Park</td>
<td>PORT</td>
<td>Goraec Forest, Portland</td>
</tr>
</tbody>
</table>

5-2.2. Fruit morphology

Five pre-dehiscent fruits were randomly collected from each of 10 individuals from the six populations sampled (see Appendix 1 for permit details). Mitutoyo™ 0.05mm callipers were used to measure the pedicel length and fruit length and width to the nearest two decimal places. The number of seeds per fruit was counted and the incidence of abnormal (tri-valved) capsules was also recorded. The characters assessed are summarised in Figure 5-2.

The geographic and mean seasonal climatic data compiled to characterise sampling sites in the leaf morphology study (see Table 4-2) were also utilised in this study. The relationships between fruit morphology attributes and the geographic and climatic parameters obtained for the six sites sampled were assessed using Spearman’s Rank Correlation Coefficient (Fowler et al. 1998).
Plate 5-1 (i-ii). *Strepera graculina* (Pied Currawong) and *Turdus merula* (European Blackbird) are considered to be the main dispersal agents of *P. undulatum* in south east Australia.

*Strepera graculina* (Pied Currawong)

*Turdus merula* (European Blackbird)
Plate 5-2. *P. undulatum* fruits are arranged in clusters at the end of branchlets. The pale orange fruits split on dehiscence to reveal numerous bright red to orange seeds which are set in a sticky mucilage.
Figure 5-1. Distribution of *P. undulatum* populations sampled in this study of fruit morphology and seed germinability. See Table 5-1 for an explanation of site codes and Table 4-1 for further site information.
Figure 5-2. Fruit morphological attributes of *P. undulatum* assessed in this study.

<table>
<thead>
<tr>
<th>Code</th>
<th>Character</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Pedicel length (mm)</td>
</tr>
<tr>
<td>2</td>
<td>Fruit width (mm)</td>
</tr>
<tr>
<td>3</td>
<td>Fruit length (mm)</td>
</tr>
<tr>
<td>4</td>
<td>Number of seeds per fruit</td>
</tr>
</tbody>
</table>

Source: Adapted from Costermans 1991

5-2.2.1. Germination trials on *P. undulatum* seed collected from six populations and at two phases of maturity

*P. undulatum* seeds were extracted from the pre-dehiscent fruits sampled in the fruit morphology component of this study. Equal numbers of seed were also collected at each site from fruits that had recently dehisced. Ten replicates of 25 seeds for each maturity phase, were placed on moistened filter paper and enclosed in 9cm plastic petri dishes. The petri dishes were placed in a Gallenkamp Temperature Control Cabinet at 19.5°C, as this was the mid-point of the optimum germination temperature range (18°C – 21°C) determined by Gleadow (1982). Seeds were watered every two days and cumulative germination was recorded for a period of 61 days. Germination was said to occur when the radicle had extended 2mm from the seed testa (Gleadow 1982). Seeds were not pre-treated to remove mucilage and no anti-fungal agents were used in these trials. Fungal attack was only detected in some samples collected
from PORT. Seeds were collected over 36 days (5/7/96 – 9/8/96) and placement of samples in the Temperature Control Cabinet was necessarily staggered over this period. Seeds were extracted and placed in the Temperature Control Cabinet within 24 hours of collection and the shelf position of all petri dishes was randomly rotated at two day intervals.

5-2.2.2. Seed collection from predominantly male flowering P. undulatum

*P. undulatum* seeds were collected from a predominantly male flowering plant in Blackburn South, Melbourne. This individual had been monitored over numerous flowering and fruiting seasons and was known to produce variable quantities of fruit each year. A total of 250 seeds were collected from this plant and 10 replicates of 25 seeds were subjected to the same germination conditions described in section 2.2.1.

5-2.3. Monitoring fruit selection and seed passage time in Blackbirds and Pied Currawongs

Approval to trap and monitor feeding behaviour in Blackbirds and Pied Currawongs was obtained from the Deakin University Animal Experimentation Ethics Committee. Pied Currawongs were trapped and caged at Croajingolong National Park (CROA) Victoria, under *National Parks Act 1975* and *Wildlife Act 1975* permits (Appendix 1). No approval was required to capture the introduced Blackbirds under current Victorian legislation.

5-2.3.1. Feeding Trials

Two Pied Currawongs were captured near Point Hicks in Croajingolong National Park, south east Victoria. The captured Pied Currawongs were transferred into separate 50x40x30cm cages. *P. undulatum* fruit at various stages of maturity were placed in the cages after a cage-familiarity period of two hours, however neither of the captured individuals attempted to eat the fruit or seeds. Different methods of presenting the *P. undulatum* fruit were trialed, but without success. The birds readily consumed small amounts of chopped apples and bananas (after Levey 1986) placed in the cages at regular intervals and drank water that was available throughout the
trial and did not appear stressed at their capture. The study was abandoned after 36 hours and on release, both Pied Currawongs flew into a nearby *P. undulatum* and immediately started to consume *P. undulatum* fruit.

Dropsheets and tarpaulins were laid underneath *P. undulatum* and *Eucalyptus botryoides* Sm. (Southern Mahogany) trees and regurgitated Pied Currawong pellets were collected over a four-day period. Coherent and semi-coherent pellets found in the immediate area were also collected and the composition of each pellet was examined.

Four Blackbirds were mist-netted at Glen Waverley, Melbourne and transferred into separate 50x40x30cm cages. Blackbird scats observed at the trapping site contained almost exclusively *P. undulatum* seeds, confirming that the seeds are an important component of the winter diet of this species in the Melbourne metropolitan area (Gleadow 1982). The captured birds were fed the same base diet as the Pied Currawongs and *P. undulatum* feeding trials commenced approximately two hours after capture. Despite monitoring the birds for several hours at a time, ingestion of *P. undulatum* seed was not observed. *P. undulatum* seed was present in the scats produced by these birds several hours after the initial capture indicating some seed had been consumed during captivity but gut retention time could not be established. These seeds and seeds recovered from Blackbird scats in the study area were collected for subsequent germination trials. The Blackbird feeding trial was abandoned after 72 hours.

**5-2.3.2. Germination of *P. undulatum* seed collected from vertebrate ejecta**

Twenty replicates of 25 seeds were extracted from the Blackbird scats and the Pied Currawong pellets, transferred into petri dishes and placed in the Temperature Control Cabinet at 19.5°C as described in section 2.2.1. The germinability of equal numbers of fresh seed collected from dehiscent fruits were tested under the same conditions.
5-2.4. Observation of other *P. undulatum* seed dispersal agents and seed predators

Incidental observations of birds and mammals utilising *P. undulatum* as a food resource are described in section 5-3.6.

5-2.5. Analyses

5-2.5.1. Fruit morphology

Population means and standard deviations were calculated for each character assessed. The distributions of residuals were plotted to assess the normality of the data prior to analysis of variance (ANOVA) and were acceptable in all cases. ANOVA was performed on all fruit characters to assess differences between populations (Sokal & Rohlf 1993). Fisher’s unrestricted Least Significant Difference (L.S.D.) was used to further investigate significant differences (*P* < 0.05) between populations. Genstat 5 version 4.1 was used to perform these univariate analyses.

A matrix of the mean fruit attributes, geographic and mean climatic data obtained for the six populations sampled was constructed in SPSS Release 6. The strength of the relationships between these variables was assessed using Spearman’s Rank correlation coefficient (two-tailed test). The correlation matrix constructed for these attributes is provided in Appendix 4.

5-2.5.2. Germination

Mean germination percentages over the length of the study period (61 days) were calculated for each treatment (population and maturity) and plotted on line graphs for visual interpretation. Percentage germination values obtained at four 10-day intervals were arcsine-transformed to improve the normality of the data prior to conducting ANOVA. Germination percentages of zero were increased by 0.05% and germination values of 100% were decreased by 0.05% prior to transformation (Morgan 1998b). Fisher’s unrestricted L.S.D. was used to investigate significant differences between populations (*P* < 0.05), where significant differences across populations were indicated. The germination success of seed collected from the
vertebrate ejecta were compared with the fresh, control seed (as described in section 5-2.2.1) and subjected to the same analyses.

5-3. Results

5-3.1. Fruit morphology

All populations differed significantly ($P < 0.001$) across all fruit morphology characters assessed. The means and standard deviations for these characters are presented in Table 5-2 and populations that are not significantly different (L.S.D., $P < 0.05$) are indicated by the same initialisation. Fruit length varied from an average of 13.5mm at GLEN to 16mm at CROA. The range of means recorded for fruit width was similarly smallest at GLEN (11.3mm) and highest at CROA (14.1mm). The lowest mean number of seeds per fruit (21.2) was also recorded at GLEN and this was significantly different ($P < 0.05$) to all other populations sampled. Fruits obtained from CROA contained the highest mean number of seeds per fruit (30.2). Despite significant differences in fruit length and width ($P < 0.05$) between samples collected from the CROA and PORT populations, the mean number of seeds per fruit was not significantly different ($P > 0.05$) between these two populations. Seed size and weight were not assessed in this study, however seeds collected from PORT appeared to be smaller and more densely arranged than in the other populations sampled. Mean pedicel length varied from 8.9mm to 15.9mm at the PORT and CROA sites respectively.

Fruit size on average, was largest at CROA where the highest mean length (16mm), width (14.1mm) and pedicel (15.9mm) measurements and the highest mean number of seeds per fruit (30.2) were recorded. Mean lamina length (mm) was also greatest at this site (Chapter 4).
Table 5-2. Population means, coefficient of variation, L.S.D \((P < 0.05)\) and grand mean for selected \textit{P. undulatum} fruit morphology characteristics assessed at six populations in Victoria. All characters differed significantly \((P < 0.001)\) across the six sites sampled. Standard errors are indicated in subscripts.

<table>
<thead>
<tr>
<th>Population</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Pedicel (mm)</th>
<th>No. seeds per fruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>16.0±0.2</td>
<td>14.1±0.2</td>
<td>15.9±0.5</td>
<td>30.2±0.9</td>
</tr>
<tr>
<td>GLEN</td>
<td>13.5±0.2</td>
<td>11.3±0.2</td>
<td>10.5±0.5</td>
<td>21.2±0.7</td>
</tr>
<tr>
<td>MORW</td>
<td>14.1±0.2</td>
<td>12.8±0.2</td>
<td>13.8±0.6</td>
<td>25.0±0.7</td>
</tr>
<tr>
<td>MORN</td>
<td>15.1±0.3</td>
<td>13.1±0.2</td>
<td>10.2±0.6</td>
<td>27.8±0.5</td>
</tr>
<tr>
<td>LORN</td>
<td>16.0±0.2</td>
<td>13.9±0.2</td>
<td>9.1±0.7</td>
<td>27.2±0.9</td>
</tr>
<tr>
<td>PORT</td>
<td>13.9±0.2</td>
<td>11.7±0.3</td>
<td>8.9±0.6</td>
<td>29.1±0.9</td>
</tr>
<tr>
<td>\textit{L.S.D.} ((P &lt; 0.05))</td>
<td>0.59</td>
<td>0.53</td>
<td>1.59</td>
<td>2.17</td>
</tr>
<tr>
<td>\textit{Grand Mean}</td>
<td>14.8</td>
<td>12.8</td>
<td>11.4</td>
<td>26.7</td>
</tr>
<tr>
<td>CV (%)</td>
<td>10.1</td>
<td>10.6</td>
<td>35.6</td>
<td>20.7</td>
</tr>
</tbody>
</table>
5-3.1.1. Incidence of tri-valve fruit capsules

Fruits with three carpels as opposed to the usual two carpels were observed in samples collected from each population (Table 5-3). Tri-valved fruits accounted for 12% of fruits sampled at LORN, 8% at each of CROA, MORW and MORN and 2% at GLEN and PORT. The incidence of tri-valved capsules is fairly uniform across the populations sampled and represents a small but important proportion of the *P. undulatum* fruit crop. The maximum number of seeds per fruit recorded at CROA (44), LORN (47) and PORT (39) were extracted from tri-valved fruits. Fruits displaying this tri-valve characteristic did not necessarily contain more seeds than the normal bi-valved fruits across the six sites sampled.

Table 5-3. Percentage of tri-valved *P. undulatum* fruits sampled in each population.

<table>
<thead>
<tr>
<th>Population</th>
<th>Percentage of tri-valve fruits (n=50)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>8%</td>
</tr>
<tr>
<td>GLEN</td>
<td>2%</td>
</tr>
<tr>
<td>MORW</td>
<td>8%</td>
</tr>
<tr>
<td>MORN</td>
<td>8%</td>
</tr>
<tr>
<td>LORN</td>
<td>12%</td>
</tr>
<tr>
<td>PORT</td>
<td>2%</td>
</tr>
</tbody>
</table>

5-3.1.2. Relationships between fruit characters and climatic variables

Fruit length and width were both significantly positively correlated with mean spring, summer and autumn minimum temperatures (all $P < 0.05$) and mean autumn maximum temperatures (both $P < 0.05$) (see Appendix 4 for full correlation matrix). *P. undulatum* fruit development occurs during these months and the significant relationships obtained indicate that fruit size (length and width) is higher at sites with higher minimum temperatures across the fruit development seasons. Peak *P. undulatum* fruit development occurs during autumn and higher mean maximum temperatures in this season are also positively correlated with fruit size. The mean number of seeds per fruit was not significantly correlated with any of the climatic
variables assessed. Mean pedicel length was significantly positively correlated with longitude ($P < 0.001$) indicating a trend for increasing pedicel length from west to east Victoria. The mean pedicel length of fruits sampled at GLEN is an exception to this trend.

5-3.2. Germination of *P. undulatum* seed collected from six sites in Victoria and at two stages of maturity.

Mean germination success after 61 days, was highest in seed collected from dehiscent carpels at CROA (99.6%) and lowest in seed extracted from pre-dehiscent carpels from PORT (28%) (Figure 5-3).

At the completion of the trial, mean percentage germination of seed extracted from pre-dehiscent fruits was marginally higher than that of seeds collected from dehiscent fruits in the GLEN and LORN samples. Fruits were collected from GLEN and LORN later in the fruiting season at which time the difference in the maturity of seeds contained in pre-dehiscent and dehiscent fruits may have been marginal.

Figure 5-3. Mean percentage germination of *P. undulatum* seed extracted from pre-dehiscent and post-dehiscent fruits at six sites in Victoria after 61 days.
5-3.3. **Comparison of cumulative percentage germination in *P. undulatum* seeds collected from six sites in Victoria.**

The earliest germinants (21 days) were recorded in seeds collected from dehiscent fruits at CROA, which ultimately achieved the highest mean percentage germination (99.6%) (Table 5-4). The time elapsed (days) to 50% germination was also considerably shorter in this sample.

In all cases, seeds extracted from dehiscent fruits germinated earlier or on the same day as seeds collected from pre-dehiscent fruits. A shorter lag time (days) to 50% germination was evident in seeds extracted from pre-dehiscent fruits compared to dehiscent fruits in the GLEN, MORW and MORN samples. Both the PORT samples failed to achieve 50% germination in the trial period but this could be more a result of fungal attack than the relative viability of seeds collected from this population.

Table 5-4. Germination attributes of *P. undulatum* seed collected from six populations and at two stages of maturity.

<table>
<thead>
<tr>
<th>Population and fruit maturity</th>
<th>Time elapsed (days) to first germination</th>
<th>Time elapsed (days) to 50% germination</th>
<th>Mean (%) germination after 61 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA (pre-dehiscent)</td>
<td>29</td>
<td>41</td>
<td>72.8</td>
</tr>
<tr>
<td>CROA (dehiscent)</td>
<td>21</td>
<td>29</td>
<td>99.6</td>
</tr>
<tr>
<td>GLEN (pre-dehiscent)</td>
<td>29</td>
<td>47</td>
<td>58.8</td>
</tr>
<tr>
<td>GLEN (dehiscent)</td>
<td>29</td>
<td>53</td>
<td>51.2</td>
</tr>
<tr>
<td>MORW (pre-dehiscent)</td>
<td>23</td>
<td>43</td>
<td>59.6</td>
</tr>
<tr>
<td>MORW (dehiscent)</td>
<td>23</td>
<td>45</td>
<td>62.4</td>
</tr>
<tr>
<td>MORN (pre-dehiscent)</td>
<td>33</td>
<td>49</td>
<td>62.8</td>
</tr>
<tr>
<td>MORN (dehiscent)</td>
<td>33</td>
<td>51</td>
<td>63.6</td>
</tr>
<tr>
<td>LORN (pre-dehiscent)</td>
<td>29</td>
<td>41</td>
<td>89.2</td>
</tr>
<tr>
<td>LORN (dehiscent)</td>
<td>27</td>
<td>39</td>
<td>88.8</td>
</tr>
<tr>
<td>PORT (pre-dehiscent)</td>
<td>35</td>
<td>—</td>
<td>28.0</td>
</tr>
<tr>
<td>PORT (dehiscent)</td>
<td>33</td>
<td>—</td>
<td>39.2</td>
</tr>
</tbody>
</table>
Seeds collected from dehiscent fruits at CROA germinated more rapidly than all other samples (Figure 5-4). A more gradual germination pattern between days 29 to 49 was evident in seeds collected from the other populations. With the exception of the MORN, PORT and to a lesser extent the LORN samples, cumulative germination tapered off after a period of 49 days. Continual accreumnt of late (59-61 day) germinants was evident in the LORN, MORN and PORT samples (Figures 5-4 & 5-5).

Mean arcsine-transformed germination percentages obtained for the seeds collected from dehiscent fruits at CROA were significantly different ($P < 0.05$) to all other treatments across the four, 10-day intervals tested (Figure 5-6). There were no significant differences ($P < 0.05$) based on fruit maturity in the other five populations sampled at each of the four 10-day intervals assessed. The pattern of ranked mean arcsine-transformed germination percentages (see Day 61, Figure 5-6) suggests that fruit maturity is not as important as other, unknown factors operating on seed germinability in each population sampled. Examination of population means reveals no strong pattern of geographic variation in germination success, although the CROA, LORN and MORN populations, which achieved the highest mean percentage germination after 61 days are all subject to coastal influences.

5-3.3.1. Germination of seeds collected from a predominantly male flowering *P. undulatum*

The mean germination success (n=250) of seeds collected from a male flowering plant was 91.6% ($\pm$1.9SE) after 60 days. Germination was first recorded after 28 days had elapsed and 50% germination was achieved by day 36.
Figure 5-4. Cumulative mean percentage germination in *P. undulatum* seeds collected from post-dehiscent fruits.

Figure 5-5. Cumulative mean percentage germination in *P. undulatum* seeds collected from pre-dehiscent fruits.
Figure 5-6. Mean arcsine-transformed percentage germination of *P. undulatum* seed extracted from pre-dehiscent (PRE) and post-dehiscent (POST) fruits differed significantly (*P* < 0.001) at each 10-day interval across all treatments assessed. Treatment codes are arranged from highest to lowest mean arcsine-transformed germination for each of the four 10-day intervals tested. Data are presented for germination after 31, 41, 51, and 61 days. Horizontal lines span populations that are not significantly different from each other (L.S.D., *P* < 0.05).

**Day 31**

<table>
<thead>
<tr>
<th></th>
<th>CROA</th>
<th>Morw</th>
<th>Morw</th>
<th>Glen</th>
<th>Lorn</th>
<th>CROA</th>
<th>Glen</th>
<th>Lorn</th>
<th>Morn</th>
<th>Morn</th>
<th>Port</th>
<th>Port</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>POST</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Day 41**

<table>
<thead>
<tr>
<th></th>
<th>CROA</th>
<th>Lorn</th>
<th>Lorn</th>
<th>CROA</th>
<th>Morw</th>
<th>Glen</th>
<th>Morw</th>
<th>Glen</th>
<th>Morw</th>
<th>Glen</th>
<th>Morw</th>
<th>Morw</th>
<th>Port</th>
<th>Port</th>
</tr>
</thead>
<tbody>
<tr>
<td>POST</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PRE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Day 51**

<table>
<thead>
<tr>
<th></th>
<th>CROA</th>
<th>Lorn</th>
<th>Lorn</th>
<th>CROA</th>
<th>Morw</th>
<th>Morw</th>
<th>Morw</th>
<th>Glen</th>
<th>Morw</th>
<th>Glen</th>
<th>Morw</th>
<th>Glen</th>
<th>Port</th>
<th>Port</th>
</tr>
</thead>
<tbody>
<tr>
<td>POST</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PRE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Day 61**

<table>
<thead>
<tr>
<th></th>
<th>CROA</th>
<th>Lorn</th>
<th>Lorn</th>
<th>CROA</th>
<th>Morw</th>
<th>Morw</th>
<th>Morw</th>
<th>Morw</th>
<th>Morw</th>
<th>GLEN</th>
<th>GLEN</th>
<th>Port</th>
<th>Port</th>
</tr>
</thead>
<tbody>
<tr>
<td>POST</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PRE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
5-3.4. Composition of Pied Currawong pellets

Forty-four pellets regurgitated by Pied Currawongs were collected at CROA (see section 5-2.3.1) for further examination (Table 5-5). *P. undulatum* seeds were present in 55% of all pellets examined. Seeds from *Elaeocarpus reticulatus* Sm. (Blue Olive Berry) and *Eustrephus latifolius* R. Br. (Wombat Berry) were also important components of the pellets examined. Most of the pellets examined (68%) contained seeds from a single species, 23% contained seed and fruit remains from two species and 9% of the pellets contained seeds from each of the three species.

**Table 5-5. Composition of Pied Currawong pellets collected at CROA (n = 44).**

<table>
<thead>
<tr>
<th>No. of species present in each pellet</th>
<th>Species</th>
<th>Average composition</th>
<th>No. of pellets</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>P. undulatum</em></td>
<td>80.6 seeds</td>
<td>12</td>
</tr>
<tr>
<td>1</td>
<td><em>Elaeocarpus reticulatus</em></td>
<td>14.2 seeds</td>
<td>17</td>
</tr>
<tr>
<td>1</td>
<td><em>Eustrephus latifolius</em></td>
<td>15 seeds</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td><em>P. undulatum</em></td>
<td>76%</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><em>Elaeocarpus reticulatus</em></td>
<td>15%</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Eustrephus latifolius</em></td>
<td>9%</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>P. undulatum</em></td>
<td>75%</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td><em>Elaeocarpus reticulatus</em></td>
<td>25%</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>P. undulatum</em></td>
<td>98%</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Eustrephus latifolius</em></td>
<td>2%</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>Elaeocarpus reticulatus</em></td>
<td>66.6%</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><em>Eustrephus latifolius</em></td>
<td>33.3%</td>
<td></td>
</tr>
</tbody>
</table>

5-3.5. Germination of seeds extracted from Pied Currawong pellets and Blackbird scats

Cumulative germination in seeds recovered from Blackbird scats was more gradual than seeds collected from Pied Currawong pellets. At the end of the experiment (60 days), germination in seeds recovered from Blackbird scats was slightly higher.
(95.8%) than that recorded for the Pied Currawong treatment (91.8%) (Figure 5-7). Mean percentage germination after 60 days was highest in fresh seed (97.2%). There were no significant differences in the mean arcsine-transformed germination percentages after 40, 50 and 60 days across the three treatments. Significant differences ($P < 0.001$) were evident across treatments at days 20 and 30. The rapid germination of seeds extracted from Pied Currawongs was significantly different ($P < 0.05$) to the Blackbird and Control treatments at day 20. The comparatively gradual accrument of germinants in the Blackbird treatment was significantly different ($P < 0.05$) to the Pied Currawong and control treatments at day 30.

Germination was first recorded in seeds recovered from Pied Currawong pellets after 16 days (Table 5-6). The first Blackbird and control germinants were noted 18 days after the trial commenced. This is considerably earlier than was recorded in the other trials of this study (Table 5-4). The lag time (days) to 50% germination of the sample was shortest in the Pied Currawong treatment (24 days) and was considerably earlier in the control treatment than in the other dehiscent fruits sampled in this study (section 5-3.3).

Table 5-6. Germination attributes of seed recovered from Pied Currawong pellets, Blackbird scats and fresh (control) *P. undulatum* seed.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Time elapsed (days) to first germination</th>
<th>Time elapsed (days) to 50% germination</th>
<th>Mean (%) germination after 60 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pied Currawong</td>
<td>16</td>
<td>24</td>
<td>91.8%</td>
</tr>
<tr>
<td>Blackbird</td>
<td>18</td>
<td>30</td>
<td>95.8%</td>
</tr>
<tr>
<td>Control</td>
<td>18</td>
<td>26</td>
<td>97.2%</td>
</tr>
</tbody>
</table>
Figure 5-7. Mean percentage germination (± SE) of *P. undulatum* seed recovered from Pied Currawong pellets and Blackbird scats. Seeds were monitored for 60 days but no additional germinants were recorded after 42 days.

![Graph showing germination over time](image)

5-3.6. Observational accounts

5-3.6.1. Satin Bowerbird

A male *Ptilonorhynchus violaceus* Vieillot (Satin Bowerbird) was observed collecting *P. undulatum* fruits at Point Hicks, Croajingolong National Park (CROA) in July 1996. The Bowerbird was collecting *P. undulatum* fruit and transferring these into one of three ‘platforms’ located in the canopy of a mature (approximately 12m) *P. undulatum*. The platforms had the appearance of a dis-used or roughly constructed nest and contained considerable quantities of *P. undulatum* fruit in various stages of maturity and cohesion. The largest of these collections was located approximately 8m off the ground in a fork of the main trunk and was the only one of the three platforms possible to access. The collection contained bundles of *P. undulatum* fruit, individual fruits — both pre-and post-dehiscent, many intact seeds and some masticated seeds (Plate 5-3). This particular collection of *P. undulatum* fruits and seeds was estimated to weigh at least 1.5 kilos.
Whether this collection was intended as a display or as a food cache is unknown. Given the Bowerbird had gone to the considerable effort of collecting fruit in various stages of composition, it seems likely that display was the primary purpose. Satin Bowerbird bowers are normally decorated with natural or artificial blue objects, and almost always occur on the ground (Lindsey 1992). The collections observed at CROA were also comprised entirely of *P. undulatum* fruit, whereas display bowers generally contain a whole range of items.

### 5-3.6.2. Other vertebrates

Large quantities of vertebrate scats containing seeds of *P. undulatum* were observed along and adjacent to the dry stony creekbed of 20 Acre Creek, Glenmaggie, Victoria. It is likely that both *Trichosurus vulpecula* (Common Brushtail Possums) and Satin Bowerbirds were responsible for these scats. *P. undulatum* seeds have been observed in Common Brushtail Possum scats at other locations (Brown *et al.* 1991), although it is probably not an important food resource in or near human settlements given the abundance of other, more palatable fleshy fruits, such as Hawthorn (*Crataegus monogyna* Jacq.) and Plum species (*Prunus* spp.). Common Brushtail Possum scats can be quite variable in size, shape and composition. The scats are usually just single pellets, but may also be attached by fibrous material in groups or strings (Triggs 1996). This variability was reflected in the scats observed at GLEN.

A number of scats containing *P. undulatum* seed smeared in uric acid, which is typical of bird scats (Triggs 1996), were also observed at GLEN. Flocks of adult female and juvenile male Satin Bowerbirds were observed consuming *P. undulatum* seed at this site and are believed responsible for these scats.

A sample of these vertebrate scats was collected from GLEN and the mean germination success (n=500) was high (93%). Data has not been presented in this Chapter however, because of the uncertainty of the vertebrate vectors involved.
Plate 5-3 (composite). A collection of *P. undulatum* fruits and seeds accumulated by a male Satin Bowerbird at Croajingolong National Park, Victoria.

This collection of fruit was one of three collections observed in a mature fruiting *P. undulatum*. It is unknown whether the *P. undulatum* fruits and seeds are for display or cache purposes.
5-3.6.3. *P. undulatum* seed predators

Male and female Australian King Parrots were observed consuming large quantities of *P. undulatum* seed in warm temperate and dry rainforest communities at Mitchell River National Park, Victoria. The Parrots selected single pre-dehiscent *P. undulatum* fruits in their claws and then sliced the fruit in half with their beaks. Seeds were masticated into a pulp and fell from the Parrots beak onto the forest floor. Careful investigation of this seed revealed that the masticated seed had been totally destroyed, although numerous discarded carpels containing presumably viable seed were also observed.

Similar behaviour was observed in *Callocephalon fimbriatum* Grant (Gang Gang Cockatoos) in the Angahook Lorne State Park, Victoria. Large quantities of *P. undulatum* seed were again destroyed through mastication and grinding. *P. undulatum* fruits with cuts and indentations consistent with a beak the size of *Platycercus elegans* Gmelin (Crimson Rosellas) have also been observed at various sites throughout Victoria. Crimson Rosellas also grind and destroy *P. undulatum* seed although the importance of this food resource to the Rosellas is unknown.

These seedeaters apparently avoid the fleshy carpels of the *P. undulatum* fruit, whereas for the frugivorous Pied Currawongs and Blackbirds, the seeds are of little value as a food resource.

5-4. Discussion

Considerable variation was evident in *P. undulatum* fruit morphology attributes across the six populations sampled. Fruit size (length and width) was largest at CROA, which also supported the largest mean lamina length of all populations sampled in the leaf morphology study (Chapter 4).

The mean number of seeds per fruit varied from 21.2 to 30.2 at GLEN and CROA respectively and this variation reflected the relative size of fruits sampled at these
sites. The mean number of seeds per fruit was not necessarily related to fruit size in the other populations sampled. The mean number of seeds per fruit at PORT and CROA was not significantly different ($P > 0.05$) despite significant differences ($P < 0.05$) in fruit length and width between these two populations. Variation from the normal bi-valved capsules was noted in all populations and most pronounced (12% of fruits sampled) at LORN.

Fruit length and width were positively correlated ($P < 0.05$) with mean minimum spring, summer and autumn temperatures and mean maximum autumn temperatures. Fruit development occurs during these seasons suggesting that moderate temperatures may enhance fruit size. There were no significant correlations between the number of seeds and any of the climatic variables assessed. Mean pedicel length was however strongly positively correlated ($P < 0.001$) with longitude, indicating a general trend (with the exception of GLEN) for increasing pedicel length from west to eastern Victoria. Further sampling at intermediate sites would be necessary to determine whether this relationship is indicative of a clinal trend.

Mean arcsine-transformed germination percentages were significantly different ($P < 0.001$) across the six populations and two phases of fruit maturity tested after 61 days. Mean germination was highest in seeds extracted from dehiscent fruits at CROA and lowest in seeds extracted from pre-dehiscent fruits at PORT.

Mean percentage germination after 61 days was higher in seeds extracted from pre-dehiscent fruits collected from GLEN and LORN than dehiscent fruits collected from the same sites.

In this study, site differences proved more important than fruit maturity in the relative germination success of *P. undulatum* seed. With the exception of seeds collected from CROA, no significant differences were recorded within populations, in the germinability of seed extracted from fruits at two stages of maturity at the 31, 41, 51 and 61-day intervals tested.

The lack of significant variation in the germinability of seeds collected from pre-dehiscent and dehiscent fruits satisfies an important aim of this study. The
comparable germination of seeds collected from pre- and post-dehiscent fruits indicates that preferential Pied Currawong foraging on pre-dehiscent fruits can result in the effective dispersal of viable seeds.

No patterns of germinability were evident between the natural (CROA, GLEN and MORW) and invasive (MORN, LORN and PORT) populations sampled. If no clear patterns in the germinability of seeds collected from natural and invasive populations are evident, as this study suggests, then biotic interferences in the establishment phase are likely to be the principal influences on the spatial structure and demographic characteristics of *P. undulatum* populations. The interactions are given further attention in Chapter 6.

Some evidence of a relationship between fruit size and germinability is inferred. With some minor variations, the germinability of seeds (after 61 days) follows the pattern of fruit size (length and width) in the populations sampled. The lowest germinability was recorded in the samples collected at PORT. However, seeds from both PORT treatments were subject to some level of fungal attack, which may have suppressed germination in these two samples.

Seeds collected from a male flowering *P. undulatum* displayed 91.6% germination success at the completion of the trial. This high mean percentage germination was however based on samples collected from only one individual. The incidence of fruit production in predominantly male flowering individuals is low (pers. obs.), but is an interesting facet of this species’ reproductive biology (see Chapter 3).

*P. undulatum* seeds extracted from Pied Currawong and Blackbird ejecta displayed high germinability (91.8% and 95.8 % respectively) and was not significantly different from the germinability of control seed (97.2%) at the completion of the trial. The first germinants occurred by day 16 in the Pied Currawong treatment and day 18 in the Blackbird treatment. The greatest proportion of germination occurred between days 20 and 28 for seeds recovered from Pied Currawong pellets and between days 24 and 34 for seeds recovered from Blackbird scats. Seeds recovered from the Pied Currawong pellets and Blackbird scats did not appear obviously scarified on examination. Bass (1995) also reported that no obvious scarification or
seed damage was evident in over 20,000 seeds of various species extracted from Pied Currawong pellets. The earlier germination and shorter lag time to 50% germination in the *P. undulatum* seeds recovered from the bird ejecta, may be related to the action of digestive acids on expelled seeds more than physical scarification. The nutrient content of other excreted material encompassing the expelled seeds may have also enhanced seed germination. The latter has been found important in some species (Howe 1989).

Gleadow (1982) reported that the germination of *P. undulatum* seed collected from Blackbird droppings was higher than that of fresh seed (91% and 80% respectively) although this result was based on a small sample (32 seeds each treatment). Cooper (1959) also reported over 90% germination success in *P. undulatum* seeds extracted from Blackbird scats. Buchanan (1989b) reported 100% germination of *P. undulatum* seeds extracted from pellets regurgitated by Pied Currawongs although again, this figure was based on a small sample (8 seeds).

Mean percentage germination of *P. undulatum* seed recovered from Blackbird and Pied Currawong scats exceeded 90% in the current study, Cooper (1959), Gleadow (1982) and Buchanan (1989b), confirming that Blackbirds and Pied Currawongs are effective dispersal agents of *P. undulatum* seed.

Silverseyes have also been identified as dispersal agents of *P. undulatum* seed (Gannon 1935; Cooper 1959; Gleadow 1982; Smith et al. 1984; Barker & Vestjens 1990). *P. undulatum* seeds (n=35) collected from Silveryeye scats achieved 82% germinability (Gleadow 1982). Observation of Silveryeye foraging indicates that the mucilage encasing *P. undulatum* seed is the principal target but some ingestion of seed is likely to occur given the stickiness of the mucilage. Silverseyes also vigorously brush *P. undulatum* seeds stuck on their beak or feathers onto bark, leaves or other available surfaces (pers. obs.), which is likely to result in some effective seed dispersal. Silverseyes play an important role in the dispersal of many other environmental weed species (Loyn & French 1991) and have been implicated as a key dispersal agent of *Lantana camara* (Liddy 1985) and *Schinus terebinthifolius* Raddi (Broad-leaved Pepper-tree) (Panetta & McKee 1997) in southern Queensland.
The ultimate profitability of fruits selected by frugivores is the total energy gained by assimilating nutrients contained in the fruits minus pre- and post-ingestional energy expenditure (Martinez del Rio & Restrepo 1993). Pre-ingestional energy expenditure on locating, accessing and handling fruits varies considerably, both within and between frugivorous species, depending on both the characteristics of the frugivore and the characteristics of the fruit crop (Martinez del Rio & Restrepo 1993). Post-ingestional ‘costs’ incurred during digestion, processing and nutrient assimilation are further influenced by the speed with which undigested matter can be eliminated (Martinez del Rio & Restrepo 1993) and similarly varies within and between species.


Ingestion and subsequent elimination of seeds by vertebrates can enhance the overall success and rapidity of germination (Clergeau 1992). Ingested seeds are exposed to mechanical, thermal and chemical action, which can scarify or otherwise damage the seed coat and promote germination (Clergeau 1992). Panetta and McKee (1997) reported that the germinability of *S. terebinthifolius* seeds is enhanced by the removal of the fleshy exocarp that encases seeds, an action that Silveereyes perform upon consumption. In this sense, Silveereyes play a dual role in enhancing the spread of *S. terebinthifolius*; exocarp removal enhances seed germinability and therefore ‘mediates’ germination and transport of seeds away from the parent plant increases *S. terebinthifolius* potential for local population expansion (Panetta & McKee 1997).
Whether ingested seeds are defecated or regurgitated has important consequences for both the dispersal agent and the plant (Janzen 1984). Seed defecation is usually a longer process (15-45 minutes) than regurgitation (5-15 minutes) in most species (Clergeau 1992). Sorensen (1984) suggests that regurgitation is a better option for birds because the rapid removal of undigested 'ballast' from the gut increases the potential for food intake. The burden of undigested ballast in the gut also increases the energy costs of flight (Martinez del Rio & Restrepo 1993). Fruits that are located, ingested and processed easily and quickly are therefore more likely to be eaten and subsequently dispersed (Levey 1986). Seed passage rates depend on a whole range of factors regardless of how seeds are ultimately eliminated. The size and digestion capabilities of the bird, composition of pulp, method of seed attachment, fruit and seed size are some of these factors (Levey 1986).

Sorensen (1984) found that Blackbirds preferentially selected fruits with seeds that are easily detached. These seeds tend to be regurgitated rather than defecated and this hastens the process of nutrient assimilation. While Blackbirds usually defecate *P. undulatum* seed, some individuals also regurgitate *P. undulatum* seed (pers. obs.). Similarly, Pied Currawongs have been observed to defecate undigested *P. undulatum* seeds (pers. obs), although regurgitation is apparently the more common method of seed elimination in this species.

The dispersal potential of seeds spread by frugivorous species varies considerably over temporal and spatial scales. Blackbirds void seed approximately 5 to 15 minutes after ingestion (pers. obs) and tend to preferentially defecate whilst perching (Sorensen 1984). Sorensen (1981) reported an average movement of 48m (84 observations) from food resource to perching site in Blackbirds monitored in a mixed deciduous woodland in England. This distance may be considerably less in areas supporting higher densities of Blackbirds, such as in suburban Melbourne. The sedentary behaviour of Blackbirds in Melbourne would more likely contribute to local populations of fleshy-fruited weeds than to long distance dispersal.

Pied Currawongs observed by Bass (1990c) flew 100 to 300m from the food resource before perching and regurgitating undigested material. The potential for seed dispersal increases considerably if seeds are retained during flight and regurgitated at
nocturnal roosts, which are often located in bushland areas. Bass (1996b) reported that seeds of the environmental weed *Crataegus monogyna* were transported approximately 10-15km from ornamental plantings into bushland areas by this mode of long-distance dispersal. While Pied Currawongs have a higher capacity to disperse more seeds over greater distances than Blackbirds, this potential may not be realised in all situations. It is extremely difficult to predict the spatial dispersal potential of seed dispersal agents. Most studies that attempt to quantitatively assess spatial dispersal potential conclude that seed dispersal is likely to reflect the home range and territorial constraints of the vectors involved (Glyphis *et al.* 1981; Dunlop & Galloway 1984; Bass 1990b, 1990c; French 1996).

Several studies have implicated Pied Currawongs as an important dispersal agent of fleshy-fruitied weed species. Bass (1995) identified seeds from 22 introduced species in Pied Currawong pellets collected near Armidale, New South Wales, and Buchanan (1989b) retrieved seeds from 36 introduced species from pellets collected near Sydney. Fruits from *Ligustrum* spp. and *Pyracantha* spp. (Firethorn), comprise the bulk of the Pied Currawong diet over the autumn and winter months in the Sydney (Buchanan 1989b), Armidale (Bass 1995, 1996a) and Canberra (Mulvaney 1986; Lenz 1990) regions. In the Armidale region, seeds from these genera accounted for over 90% of seeds recovered from Pied Currawong pellets (Bass 1996a).

The composition of Pied Currawong pellets generally reflects the availability of food resources in a particular area. In the current study, Pied Currawong pellets collected from CROA contained remnants of *P. undulatum*, *Elaeocarpus reticulatus* and *Eustrephus latifolius* fruits. These were the only three species in fruit at the time of data collection indicating that the opportunistic Pied Currawongs were exploiting all fruit resources available at the site. Buchanan (1989b), reported that *P. undulatum* was not consumed as often as other available winter fruits in the Sydney region, especially the more palatable fruits of the Oleaceae family including *Ligustrum* spp. and *Olea europaea*.

Blackbirds also feed on and presumably disperse a range of fleshy-fruitied weeds in addition to *P. undulatum* (Cooper 1959, Gleadow & Ashton 1981, Mulvaney 1986, Loyn & French 1991). In south east Australia, such species include:
Chrysanthemoideae monilifera ssp. rotundata DC. (Nor1.) (Bitou bush), C. monilifera ssp. monilifera (Boneseed), Cotoneaster sp. (Cotoneaster), Crataegus monogyna, Hedera helix L. (English Ivy), Ilex aquifolium L. (Holly), Olea europaea, Prunus sp. and Rubus sp. (Blackberry) (Loyn & French 1991).

In the Australian literature surveyed by Loyn and French (1991), 84 bird species were reported feeding on the fruits of 46 introduced plant species. Loyn and French (1991) suggest that the majority of native birds will exploit a new food resource that becomes available in their habitat. Even specialist feeders such as Dicaeum hirundinaceum Shaw (Mistletoe bird) have been recorded eating the fruits of Ligustrum spp., Crataegus monogyna, Lycium feroxissimum Miers (Boxthorn) and Schinus molle L. (Peppercorn) (Loyn & French 1991). In contrast, some frugivorous species experience an adaptation phase as they adjust to the availability of a new food resource in their environment. Kruger et al. (1986) suggested that the time lag from the initial introduction to the subsequent invasion of P. undulatum in South Africa was related to an adjustment period by native and introduced frugivores to this new food resource.


Preliminary and anecdotal evidence suggests that Pied Currawong densities have increased in some areas and that some populations may be altering their normal migration patterns because of the abundant food resources provided by ornamental
fleshy-fruited plants across the landscape (Bass 1989, 1996a; Lenz 1990; Recher & Lim 1990; Buchanan 1992; Major et al. 1996). Resident populations of Pied Currawongs have been reported in Canberra (Lenz 1990) and Armidale (Bass 1996a). Increased nestling predation by the omnivorous Pied Currawongs is reported as an important implication of changed migration patterns and increased local densities in this species (Mulvaney 1986; Lenz 1990; Buchanan 1992; Bass 1996a; Major et al. 1996). In urban areas and rural towns, introduced bird species may form the dominant prey items (Lenz 1990) but native species are also likely to be affected (Major et al. 1996). In addition to nestling predation, altered migration patterns and increased local densities of Pied Currawongs are likely to impact on other native birds through competition for food, nesting and shelter resources (Lenz 1990).

A recent review of Blackbird populations in south east Australia (Kentish et al. 1995) also reported increased local densities of this species. Blackbird incursion into natural habitats has been observed in recent decades (Kentish et al. 1995). The ecological implications of this apparent range expansion may include some displacement of native ground foraging birds and further disruption to dispersal syndromes of native and introduced fleshy-fruited plants over time.

Management of frugivore-dispersed weeds and their adaptive dispersal agents is likely to emerge as a contentious weed management issue in the coming decades. As Bass (1996a) rightly suggests, the solution is more complex than simply controlling the seed source or the dispersal agents. For example, replacement of Pyracantha and Ligustrum species with desirable native species may promote some prey switching in Pied Currawongs and increased nestling predation may be a consequence, at least in the short term (Bass 1996a). The fruits of other introduced plants may assume greater importance in the diet of Pied Currawongs and their invasion may be facilitated by increased dispersal opportunities and reduced competition (Bass 1996a). Similarly, reducing Pied Currawong populations may provide an expansion opportunity for other adaptive frugivores that are able to exploit these resources (Bass 1996a).

It may be politically difficult to devise and deliver a management strategy that addresses birds that disperse popular garden plants, especially when native dispersal
vectors and native plants are involved. Clearly however, this issue needs to be addressed in a pro-active and perhaps radical manner. In the absence of a defined strategy to manage increasing densities of *Corvus corone* (Carrion Crow) and *Pica pica* (European Magpie), these species were persecuted throughout Europe because of the assumed intensity of nestling predation on desirable species (Lenz 1990). Subsequent research demonstrated that the presumed nestling predation by these species was over-estimated (Lenz 1990).

Recent pressure to expand the commercial Olive industry in South Australia has also attracted some controversy as this species functions as a serious environmental weed in the region (Jupp *et al.* 1999). The main dispersal agents of this species are again, adaptive, opportunistic frugivores such as Blackbirds, *Sturnus vulgaris* L. (Common Starling) and *Gymnorhina tibicen* Latham (Australian Magpie), although Starlings accounted for 97% of fruit removal observations (n=1182) (Jupp *et al.* 1999).

Jupp *et al.* (1999) determined that *O. europaea* stones were regurgitated by Starlings at nocturnal roosts, which may be some kilometres from the food source, in addition to the vicinity of the food resource during diurnal feeding activities. A risk management assessment scheme, which incorporates aspects of *O. europaea* dispersal potential, will guide the responsible development of this industry (Jupp *et al.* 1999), but the further spread of *O. europaea* into areas of conservation value is a likely consequence of Olive industry expansion.

Further complexities arise when these adaptive frugivores perform useful ecological roles. Frugivore-assisted movement of seeds from patch to patch contributes to the maintenance of genetic and species diversity in isolated remnants in urban and rural landscapes. The movement of weed species via this and other dispersal mechanisms however, further contributes to the decline of remnant patches and is emerging as a serious and often complex conservation management issue (Panetta & Hopkins 1991).

For example, frugivorous bats play an important role in the dissemination of rainforest species between remnant patches in north east New South Wales (Eby & Palmer 1991). Increasingly, weed species are also being dispersed among patches in
this manner (Eby & Palmer 1991). In the same north east New South Wales landscape, infestations of the invasive *Cinnamomum camphora* (Camphor Laurel) provide critical ‘stepping stones’ (Date et al. 1991) between patches of remnant lowland subtropical rainforest and important winter food resources for at least five frugivorous pigeon species (Date et al. 1991). While the long term replacement of *C. camphora* with suitable native species is recommended, Date et al. (1991) suggest that the short-term conservation of these frugivores in this fragmented landscape depends upon the retention of *C. camphora*.

Changes in the distribution and abundance of fleshy-fruited environmental weeds in the Armidale district have reflected changes in gardening trends and the use of various ornamental species over time (Bass 1996a). Species such as *Pistacia chinensis* (Pistachio), *Crataegus phaenopyrum* (Washington Thorn) and *Nyssa sylvatica* (Tupelo), which are comparatively recent additions to horticultural settings, are already evident in regional remnant vegetation (Bass 1996a). While these species currently occur in low densities in both remnant vegetation and Pied Currawong pellets, they have the potential to emerge as serious weeds in the Armidale district (Bass 1996a).

In contrast to these Australian examples, Burrows (1994) views the role of introduced adaptive frugivores in some New Zealand forests quite differently. Burrows (1994) suggests that introduced Blackbirds and Silvereyes play an important role in seed dispersal and to some extent, compensate for the severe reductions in the distribution and abundance of some native frugivorous birds. The role played by introduced frugivores will however be different, on some scale, to that played by the original frugivorous biota. The composition of the fleshy-fruited flora will also influence the ultimate value of these surrogate seed dispersal agents. Short-term benefits may be off-set if these frugivores facilitate the further spread of fleshy-fruited weeds.

Further research on the ecological implications associated with mutualistic relationships between introduced fleshy-fruited plants and adaptive frugivores are required to form a firm foundation for management strategies. Management options seem limited and are likely to be extremely complex in both development and
implementation (Bass 1996a). Culling of key dispersal vectors may provide a short term solution but adaptive generalists such as Pied Currawongs and Blackbirds may quickly recover their pre-control densities. Management of the seed source seems to be the only practical long term option, even if fluctuations in the dietary behaviour of adaptive frugivore populations is a short term consequence. Such a management program would represent a radical departure from traditional weed management strategies and previous attempts to encourage responsible horticulture indicate that any such program will meet considerable opposition (for example, Fernando 1994; Henderson 1994; Field 1994). Preventing the sale of known or potential fleshy-fruited weeds from Nurseries would seem, by comparison to be a reasonably straightforward option. Recent initiatives between the Cooperative Research Centre for Weed Management Systems (Weeds CRC) and the Nursery Industry Association of Australia (NIIA), to identify and regulate the sale of weedy ornamentals is encouraging (Weeds CRC & NIIA 1999). Replacement of invasive weedy ornamentals in cultivated and bushland settings with suitable native species, may buffer the effects of reduced habitat resources for some species and should be an integral component of any plan to address this issue (Buchanan 1992).

Long term data on the distribution, abundance and dietary behaviour of adaptive frugivores is required to predict which dispersal agents are likely to prove problematic. Disruption to the dispersal syndromes of native fleshy-fruited plants and frugivorous vertebrates may be an additional consequence as relationships between fleshy-fruited weed species, such as *P. undulatum*, and adaptive frugivores develop (Terborgh & Winter 1980; Knight 1986; Debuissche & Isenmann 1990; Buchanan 1992).

In addition to Pied Currawongs, Blackbirds and Silveryeyes, several other dispersal vectors of *P. undulatum* in south east Australia, have been identified (Table 5-7). This list has been compiled from published and anecdotal accounts and personal observations and is not intended to be exhaustive. A common characteristic among the birds and mammals listed is that they are all opportunistic, generalist species.

Fleshy-fruited species represent about 17% of the flora in the forest, woodland and dry rainforest communities occupied by *P. undulatum* in East Gippsland, Victoria
(Willson et al. 1989). *P. undulatum* fruit attributes are not typically consistent with characteristics identified as being attractive to frugivores in these forest types (Willson et al. 1989; French 1991; Buchanan 1992). The pulp to seed ratio is low in *P. undulatum* fruit and most frugivores appear to feed on other fleshy fruits in preference to *P. undulatum*. The sheer abundance of this species, coupled with the species' winter fruiting habit may, however, entice consumption when other resources are limited. Species able to exploit this resource may compensate for the low nutritional rewards by consuming large quantities of *P. undulatum* fruit.

The proportion of the *P. undulatum* fruit crop removed by frugivores is likely to vary substantially within and between populations. Knight (1986) estimated that 6-10% of the *P. undulatum* fruit crop (~5,000 to 10,000 fruits per plant) were removed each week over a three to six month fruiting period in south-western Cape forests in South Africa. Caution is needed in adapting these estimates to south east Australian conditions because of variation in the characteristics of the fruit crops and the dispersal vectors involved. The recent adaptation phase of South African frugivores to this new food resource (Kruger et al. 1986) for example, may also result in different pressures on the *P. undulatum* fruit crop. In addition to variation in frugivore assemblages, the considerable variation in *P. undulatum* habit, by habitat type (Chapter 4), is also likely to influence fruit production across the range of habitats occupied. Some similarities, however, can be drawn between Australian and South African dispersal agents of *P. undulatum*. Species in the *Zosterops* and *Pycnonotus* genera for example, are documented as dispersers of *P. undulatum* seed in both locations (Knight 1986 and see Table 5-7 this Chapter).
Table 5-7. Birds and mammals recorded feeding on *P. undulatum* fruits and seeds in south east Australia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Feeding behaviour</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Strepera graculina</em> (Pied Currawong)</td>
<td>Feeds on pre-dehiscent fruits; seed dispersal</td>
<td>Rose 1973; Forde 1986; Buchanan 1989b; Mullett 1996; Barker &amp; Vestjens 1990</td>
</tr>
<tr>
<td><em>Turdus merula</em> (Blackbird)</td>
<td>Feeds on seeds in dehiscent fruits; seed dispersal</td>
<td>Barker &amp; Vestjens 1990; Cooper 1959; Gleadow 1982; Mullett 1996</td>
</tr>
<tr>
<td><em>Zosterops lateralis</em> (Silvereye)</td>
<td>Ingests minimal quantities of seed; seed dispersal</td>
<td>Barker &amp; Vestjens 1990; Gannon 1935; Cooper 1959; Gleadow 1982; Mullett 1996</td>
</tr>
<tr>
<td><em>Ptilonorhynchus violaceus</em> (Satin Bowerbird)</td>
<td>Caching or display of fruits and seeds; seed dispersal</td>
<td>Emison et al. 1987</td>
</tr>
<tr>
<td><em>Pycnonotus jocosus</em> (Red-whiskered Bulbul)</td>
<td>Feeds on seeds in dehiscent fruits; possible dispersal</td>
<td>Cooper 1959; Barker &amp; Vestjens 1990</td>
</tr>
<tr>
<td><em>Pycnoptilus floccosus</em> (Pilotbird)</td>
<td>Unknown, possible dispersal</td>
<td>Forde 1986</td>
</tr>
<tr>
<td><em>Ptilinopus superbus</em> (Superb Fruit-Dove)</td>
<td>Unknown, possible dispersal</td>
<td>Barker &amp; Vestjens 1989</td>
</tr>
<tr>
<td><em>Vulpes vulpes</em> (Red Fox)</td>
<td>Seeds observed in scats; possible dispersal</td>
<td>R. Wallis (pers. comm.)</td>
</tr>
<tr>
<td><em>Rattus rattus</em> (Black Rat)</td>
<td>Potential caching of fruit; possible dispersal</td>
<td>D. Wallace (pers. comm.)</td>
</tr>
<tr>
<td><em>Trichosurus vulpecula</em> (Brushtail Possum)</td>
<td>Seeds observed in scats; seed dispersal</td>
<td>Brown et al. 1991</td>
</tr>
<tr>
<td><em>Alisterus scapularis</em> (King Parrot)</td>
<td>Feeds on pre-dehiscent fruits, seed predator</td>
<td>Pers. Obs.</td>
</tr>
<tr>
<td><em>Callocephalon fimbriatum</em> (Gang Gang Cockatoo)</td>
<td>Feeds on pre-dehiscent fruits, seed predator</td>
<td>Pers. Obs.</td>
</tr>
<tr>
<td><em>Platycercus elegans</em> (Crimson Rosella)</td>
<td>Attempts to feed on pre-dehiscent fruits, seed predator</td>
<td>Pers. Obs.</td>
</tr>
</tbody>
</table>
The introduced *Pycnonotus jocosus* (Red-whiskered Bulbuls), which are now common in coastal areas near Sydney and other areas on the north coast of New South Wales (Blakers *et al.* 1984) feed on the fruits of native and ornamental fleshy-fruited plants (Barker & Vestjens 1990). The importance of Red-Whiskered Bulbuls as dispersal agents of *P. undulatum* is unclear although Cooper (1959) remarked, “it is a common sight to see Bulbuls feeding on *Pittosporum* seed...they do not appear to eat large quantities, but apparently accept them in lieu of other food”. Bulbuls occupy the same types of disturbed habitats as Blackbirds and may play an important role in *P. undulatum* dispersal in central and north coast New South Wales environments, where Blackbirds are absent or have a patchy distribution (Blakers *et al.* 1984). Barker and Vestjens (1989) report that *Ptilinopus superbis* Temminck (Superb Fruit Dove) feed on *P. undulatum* fruit and other frugivoruous doves and pigeons may also utilise this food resource. Satin Bowerbirds may also be important dispersal agents of *P. undulatum* in south east Australia.

The hoarding of *P. undulatum* fruit observed at CROA is an interesting, but apparently uncommon observation. Mullett (1993) cited anecdotal evidence (D. Wallace, pers. comm.) of a similar cache of *P. undulatum* fruit located 3 to 4m off the ground in a mature *P. undulatum*, observed at the Police Paddocks Reserve east of Melbourne. Mr. Wallace attributed this collection of fruits to hoarding by *Rattus rattus* (Black Rat). Additionally, Goodland and Healey (1996) suggested that piles of several thousand *P. undulatum* seeds and gnawed fruit capsules observed in invaded Jamaican forests, were probably accumulated by Rats.

The role of generalist, adaptive mammals in the dispersal of fleshy-fruited weed species has been largely overlooked in Australia (Bass 1990a). The mammalian species observed feeding on *P. undulatum* are characteristically generalist, opportunistic species but again, the role of these species as dispersal agents is unclear. The viability of *Crataegus monogyna* seeds defecated by Brushtail possums was not affected (Bass 1990a) and seeds of *Rubus procerus* (Brunner *et al.* 1976) and *Chrysanthemoides monilifera* ssp. *monilifera* are similarly unaffected on elimination by *Vulpes vulpes* (Red Fox) (Dodkin & Gilmore 1984; Meek 1998). Seed retention time is vastly higher in mammals than birds, so if seed viability is maintained after defecation, the potential for dispersal is considerable.
The three seed predators observed feeding on *P. undulatum* fruit (Table 5-7) have also been recorded feeding on the fruits of *Pyracantha* sp., *Ligustrum* sp. and *Crataegus monogyna* (Forshaw 1991). These species play an important role in destroying considerable quantities of seed and effectively reducing the dispersal potential of these weed species. Caged King Parrots and Crimson Rosellas destroyed over 10,000 *Pyracantha* and *Cotoneaster* seeds in trials conducted by Mulvaney (1986). In contrast, seeds of these species expelled by Pied Currawongs and Silvereyes displayed the same germinability as fresh seed (Mulvaney 1986).

All of the *P. undulatum* dispersal agents listed in Table 5-7 are generalist, adaptable frugivores. None of the species listed has evolved a specialised seed dispersal mutualism with *P. undulatum*. It appears that the *P. undulatum* fruit crop has evolved to exploit generalist frugivores and attract an opportunistic suite or ‘coterie’ (Janzen 1985) of dispersal agents. *P. undulatum* fruits are attractive to different frugivores over the various stages of fruit maturity and in this sense, dehiscence provides feeding opportunities for a range of species. For example, Pied Currawongs consume pre-dehiscent fruits (which contain viable seeds prior to dehiscence), Blackbirds feed on seeds in dehiscent fruits and Silvereyes ingest some seed while pursuing the sticky mucilage encasing seeds. The mucilage sticks seeds together ensuring birds carry away more seeds than they intended. Some seeds also adhere to beaks and feathers and effective dispersal may also be achieved via this mechanism.

The abundant *P. undulatum* fruit crop can sustain losses to seed predators and the scented fruits may also attract nocturnal mammalian frugivores. The presentation of fruits throughout the canopy may attract frugivores feeding at various horizontal strata; low branches that reach the ground for example may provide a foraging opportunity for foxes and other ground-dwelling mammals.

Some autochorous (van der Pijl 1972) dispersal of the *P. undulatum* fruit crop is also likely to occur. A large proportion of the fruit crop is removed by frugivores, but some seeds persist in the rotten carpels for many months and may persist as a terminal structure for several years. The sticky mucilage adheres the seeds to the carpels until the weathering effects of sun, wind and rain cause the seeds to drop onto
the forest floor. In some cases, abscission of the peduncles or pedicels occurs and the remains of attached fruits are similarly released. The viability of seeds dispersed in this manner may decline over time through desiccation although Gleadow (1982) reported that seeds stored in vials at room temperature maintained their viability for 16 months.

*P. undulatum* seeds possess no true adaptations for wind dispersal so most of the persistent seed crop falls beneath the parent plant over time. *P. undulatum* litter-fall peaks in spring, approximately two months after seed set, offering seed dispersed by frugivorous or autochorous modes some protection from desiccation over the summer months (Gleadow 1982). Late autumn is recognised as the main germination period in this species (Gleadow 1982). Some *P. undulatum* seeds germinate in spring following the winter fruiting period but high temperatures and low relative humidities prevent summer germination in most years (Gleadow 1982).

Avian dispersal agents that eliminate undigested seeds while perching in trees and shrubs initiate the contagious distribution pattern typical of invading populations of *P. undulatum*. Thereafter, the pattern of seedling establishment and subsequent clump development is primarily influenced by the characteristics of the dispersal site. *P. undulatum* germination and seedling establishment are more likely to occur beneath the moderate canopy cover of eucalypts and other trees and shrubs, compared to the dense canopy cover of adult conspecifics (see Chapter 6). Adaptive frugivores, such as those described in this Chapter, play a crucial role in transporting *P. undulatum* seed away from the inhibiting environment of the parent plant where survival and persistence is less likely.

### 5.5. Summary

*P. undulatum* fruit morphology attributes varied significantly across the six populations sampled. No patterns of seed germinability were evident between the natural and invasive populations sampled. With the exception of the CROA samples, no significant differences were recorded in the germinability of seeds extracted from pre- and post-dehiscent fruits. Effective seed dispersal can theoretically occur when seed dispersal agents such as Pied Currawongs feed on pre-dehiscent fruits. Site
differences are apparently more important than fruit maturity in *P. undulatum* seed germinability.

Seeds extracted from Pied Currawong pellets and Blackbird scats achieved greater than 90% germinability. The spatial dispersal potential of Pied Currawongs and Blackbirds is likely to vary considerably. It is most likely that the more sedentary Blackbird contributes to local densities of *P. undulatum*, especially in settled areas including Melbourne, in southern Victoria. Pied Currawongs have a greater potential to disperse *P. undulatum* seed over longer distances and are probably the most important dispersal vector of *P. undulatum* outside the Melbourne metropolitan area, throughout east Gippsland, southern New South Wales and the Sydney Region. Other frugivores recorded feeding on *P. undulatum* are characteristically, generalist or opportunistic species.

The ecological implications of mutualistic relationships between invasive fleshy-fruited plants and their frugivorous dispersal agents is likely to emerge as a serious weed management issue in the coming decades.
CHAPTER SIX

P. undulatum population structure and spatial pattern

6-1. Introduction

P. undulatum has established dense populations in a range of habitat types throughout south east Australia, indicating a capacity for rapid population expansion under a range of environmental conditions. The species’ pollination and dispersal requirements appear to be met through generalist native and introduced agents; especially in invaded habitats (see Chapters 3 & 5). Germinability is high in seeds collected from natural and invaded habitats and in seeds void by the principal dispersal agents of this species in south east Australia (see Chapter 5). These attributes, in combination with the species’ general plasticity, contribute to the successful invasion of a range of habitat types. Little is known, however, about P. undulatum population structure and spatial pattern in natural or invaded habitats in this region.

An understanding of weed population dynamics, including recruitment potential and regeneration patterns, is an essential requirement of effective weed management strategies and has broader applications in weed risk assessment programs (Cronk & Fuller 1995; Luken 1997; Panetta & James 1999). The P. undulatum population structure and spatial association data collected in this study will provide some indication of prior establishment patterns and a basis for predicting long-term population trends in this species. Variation in population attributes within and between natural and invaded habitats may provide further insights into establishment constraints and expansion opportunities acting on this species. An understanding of population dynamics and conspecific inter-relationships will assist in the identification of critical developmental stages in this species’ lifecycle, which may be exploited in management programs. To this end, the sex structure and proportional representation of ‘reproductively active’ (see section 6-2.3.1) individuals were also assessed in this study to determine if a relationship exists between these attributes and the relative invasion success of a given population.
6-1.1. Aims of the current study

This study aims to investigate aspects of *P. undulatum* population structure and spatial pattern in natural and invaded habitats in south east Australia and to resolve some of the uncertainties regarding the *P. undulatum* regeneration niche. An understanding of *P. undulatum* population dynamics, regeneration patterns and recruitment constraints and opportunities, will contribute to the profile of this species’ invasion ecology and the effective management of this species across a range of natural and invaded habitats.

6-1.2. Previous research on *P. undulatum* population structure and spatial pattern

No studies have been conducted on *P. undulatum* population structure in south east Australia, but aspects of spatial pattern within *P. undulatum* populations, particularly between adult plants and seedlings, have been reported in various studies. Gleadow (1982) investigated *P. undulatum* establishment requirements in a transplant experiment at Langwarrin, Victoria during 1978-79. *P. undulatum* seedlings grown under glasshouse conditions were transplanted in a split plot design underneath mature *P. undulatum*, *Eucalyptus* trees and in open areas without canopy cover. Seedling survival was monitored over a 16-month period and survival was highest in seedlings planted beneath mature *P. undulatum* (Gleadow 1982). At the completion of the trial, there was no significant difference between the low survival of seedlings planted in open conditions and those planted beneath mature *Eucalyptus* trees (Gleadow 1982). The significantly higher survival rate of *P. undulatum* seedlings planted beneath conspecific adults led Gleadow to suggest that “it is essential…that *P. undulatum* forms a regeneration niche under its own canopy to ensure survival of succeeding generations” (Gleadow 1982, p. 197).

No evidence in support of this regeneration niche theory was found in later studies (Richardson & Brink 1985; Buchanan 1989a; Mullett & Simmons 1995). *P. undulatum* seedlings were not observed beneath mature *P. undulatum* in South African tall scrub and riparian forest communities surveyed by Richardson and Brink (1985). Mullett and Simmons (1995) also reported very little association between mature *P. undulatum* and conspecific seedlings in invaded dry sclerophyll forest
environments in Victoria. These findings were consistent with those of Buchanan (1989a) in dry sclerophyll forest remnants in the Sydney region.

6-2. Methods

6-2.1. Populations sampled
Aspects of _P. undulatum_ population structure and spatial pattern were investigated at six sites in Victoria (Table 6-1). These sites were selected to represent natural and invasive populations and a range of habitat types occupied by this species. The distribution of these Victorian populations is indicated in Figure 6-1 (see Table 4-1 and Appendix 2 for further site information).

<table>
<thead>
<tr>
<th>Code</th>
<th>Population</th>
<th>Habitat type</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>Croajingolong National Park</td>
<td>Dry coastal woodland</td>
<td>Natural</td>
</tr>
<tr>
<td>GLEN</td>
<td>20 Acre Creek, Glenmaggie</td>
<td>Dry rainforest</td>
<td>Natural</td>
</tr>
<tr>
<td>MORW</td>
<td>Morwell National Park</td>
<td>Wet sclerophyll forest</td>
<td>Natural</td>
</tr>
<tr>
<td>MORN</td>
<td>Woods Reserve, Mornington Peninsula</td>
<td>Dry sclerophyll forest</td>
<td>Invasive</td>
</tr>
<tr>
<td>LORN</td>
<td>Angahook-Lorne State Park</td>
<td>Wet sclerophyll forest</td>
<td>Invasive</td>
</tr>
<tr>
<td>PORT</td>
<td>Gorae Forest, Portland</td>
<td>Dry sclerophyll forest</td>
<td>Invasive</td>
</tr>
</tbody>
</table>

6-2.2. Sampling technique

_P. undulatum_ population structure was surveyed in five 10 x 30m belt transects at each of the six sites sampled. Each transect was divided into 30 2 x 5 m quadrats and the distribution of _P. undulatum_ individuals in each quadrat was recorded. _P. undulatum_ individuals were assigned to one of nine height classes representative of various developmental stages, as annual growth rings are not obvious in this species (Meir 1991 in Goodland and Healey 1996). _P. undulatum_ individuals greater than
Figure 6-1. Distribution of *P. undulatum* populations sampled in this study of population structure and spatial pattern. See Table 6-1 for an explanation of site codes and Table 4-1 for further site information.
1m in height were considered adults in the current study based on previous observation of the minimum average height of reproductively mature individuals across a range of habitats (pers. obs.). Plants less than 0.5m and between 0.5-1m in height, were classified as seedlings and juveniles, respectively. Adult individuals (>1m) were assigned to one of seven additional height classes; 1-2m, 2-4m, 4-6m, 6-8m, 8-10m, 10-12m, 12m+.

Functionally male and female plants were distinguished by flower structure (see Figure 3-1), as no obvious differences in vegetative characteristics or habit are evident between male and female plants. The incidence of ‘abnormal’ (Steel 1911) seed-producing flowers or fruit remnants on otherwise male flowering plants were noted during data collection and the small number of individuals displaying these traits were classified as male plants. A count of trees and shrubs >2m in height occurring in each quadrat was also recorded to allow further investigation of *P. undulatum* densities and dispersion patterns, relative to the distribution of trees and shrubs. Sampling was conducted during the spring 1995 flowering season (permit details are provided in Appendix 1).

6-2.3. Analyses

6-2.3.1. Population structure

Mean *P. undulatum* densities were determined on a grid (300m²) and quadrat (10m²) basis to provide an overall comparison of *P. undulatum* densities across the six populations sampled. The mean (±SE) height class structure of each population sampled is displayed in histograms. These height class data were also converted to percentages and graphed to illustrate variation in the proportional representation of each developmental stage across the six populations sampled. A generalised linear model, assuming a Poisson distribution, was applied on log-transformed data to test for significant differences in the mean densities of seedlings and juveniles between the six populations. Least significant differences between populations were determined on the log-transformed means, however the back-transformed means are presented. Genstat 5 version 4.1 was used to perform these analyses.
The sex of a high percentage of presumably adult (>1m) individuals could not be determined because individuals were not flowering, or in the case of a few taller individuals, the flowers were too high in the canopy to be accurately assessed, even with the aid of binoculars. The number of individuals whose sex could not be determined were calculated and presented as percentages of all plants >1m, to allow comparisons across the populations. These individuals were excluded from further sex structure analyses although it is assumed that the sex ratios obtained from the data are representative of the true sex ratios in each population sampled. The total number of known males and females were summed for each population and expressed as a proportion of all individuals >1m recorded in each population, to gain a measure of 'reproductive activity' across the six populations sampled (Falinski 1980; Shapcott et al. 1995).

Ratios of known males to females were determined using the raw data obtained from the five 300m² grids sampled at the six sites and a chi square test (χ²) was applied to determine any significant departures from the expected 1:1 sex ratio. The sex ratio data were also pooled into three height class categories (1-4m, 4-8m, 8-12m+) to investigate whether the ratio of males to females varied over successive height classes. The significance of these patterns was not tested because of the sparse nature of the data in the 8-12m+ height class. These attributes are however presented in graphs to allow some comparison of the patterns within and between the populations sampled.

6-2.3.2. Spatial relationships

The association between P. undulatum seedlings, juveniles and mature trees (conspecific adults >2m, and other trees and shrubs >2m), was identified as the spatial pattern of interest in this study. The probability that P. undulatum seeds will be dispersed in clumps is high, through either autochorous or frugivorous modes of dispersal. Further, the probability that seeds will be dispersed to a shaded micro-environment is also high, whether this is beneath an adult conspecific or beneath other mature trees and shrubs.
The associations between *P. undulatum* seedlings, juveniles, adults (>2m) and other trees and shrubs were tested by correlation analyses (Spearman’s Rank Correlation Coefficient). *P. undulatum* individuals in the 1-2m height class were also incorporated into these analyses, to determine if the patterns evident in seedling and juvenile associations were characteristic of a consistent pattern through the early developmental stages. These four *P. undulatum* developmental stages were considered appropriate for representing the spatial pattern of interest in this study as no patterns of association between mature female or male *P. undulatum* with seedlings and juveniles were detected in preliminary analyses. The quadrat data collected from each site (n=900) were assessed to gain an overall picture of association between these population attributes. Separate correlation analyses were then performed on the quadrat data from each site (n=150). Significant correlations between the variables assessed are presented in constellation diagrams. The correlation matrices constructed for each site and the pooled data are included in Appendix 5.

6-3. Results

6-3.1. Population structure

6-3.1.1. Mean densities of *P. undulatum* at six sites in Victoria

Considerable variation in mean *P. undulatum* densities were recorded across the six populations sampled (Table 6-2). *P. undulatum* densities were on average, 2.7 times higher in the invaded populations, compared to the natural populations sampled. The natural population CROA, which supported higher densities of *P. undulatum* than the invasive LORN population, was the only exception to this trend. The highest mean densities per grid (300m$^2$) and quadrat (10m$^2$) were recorded in the invasive PORT population. Mean *P. undulatum* densities at this site, were over three times that of any other natural or invaded population sampled. *P. undulatum* densities were lowest in the natural MORW population.
6-3.1.2. Comparison of mean *P. undulatum* population profiles

The most ‘even’ representations of individuals across the height classes or developmental stages were evident in the natural GLEN and MORW populations (Figure 2i-vi). Population profiles are skewed towards the early developmental stages in the invasive populations and the natural CROA population. An overall decline in density with each successive developmental stage is displayed across the six populations sampled and is most obvious in the PORT population profile. Minor exceptions to this trend are evident in the CROA, GLEN and MORN profiles. Mean densities of 1-2m individuals, were higher than those of juveniles, in both the CROA and GLEN populations. Similarly at MORN, the mean number of juveniles recorded exceeded that of seedlings, at the time of sampling.

6-3.1.3. Differences in seedling and juvenile densities within and between the populations sampled.

Mean seedling and juvenile densities were significantly higher (*P* < 0.05) at PORT and significantly lower (*P* < 0.05) at MORW, compared to the other four populations sampled (Table 6-3). No significant differences in seedling densities were detected between CROA, GLEN, MORN and LORN. Significant differences in juvenile densities were however, evident between these populations with the exception of CROA and GLEN.

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean density /300m²</th>
<th>Mean density /10m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>172.8</td>
<td>5.8</td>
</tr>
<tr>
<td>GLEN</td>
<td>127.6</td>
<td>4.3</td>
</tr>
<tr>
<td>MORW</td>
<td>49.8</td>
<td>1.7</td>
</tr>
<tr>
<td><strong>Natural populations</strong></td>
<td><strong>116.9</strong></td>
<td><strong>3.9</strong></td>
</tr>
<tr>
<td>MORN</td>
<td>197.8</td>
<td>6.6</td>
</tr>
<tr>
<td>LORN</td>
<td>140.8</td>
<td>4.7</td>
</tr>
<tr>
<td>PORT</td>
<td>616.6</td>
<td>20.6</td>
</tr>
<tr>
<td><strong>Invaded populations</strong></td>
<td><strong>318.4</strong></td>
<td><strong>10.6</strong></td>
</tr>
</tbody>
</table>
Table 6-3. Differences in mean seedling and juvenile densities (10m³) between six populations of *P. undulatum* in Victoria. Means (back-transformed) with the same initialisation in each column are not significantly different (L.S.D, *P* < 0.05).

<table>
<thead>
<tr>
<th>Population</th>
<th>Seedlings</th>
<th>Juveniles</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>1.4ᵇ</td>
<td>1.2ᶜ</td>
</tr>
<tr>
<td>GLEN</td>
<td>1.6ᵇ</td>
<td>0.5ᵈ</td>
</tr>
<tr>
<td>MORW</td>
<td>0.9ᶜ</td>
<td>0.03ᵉ</td>
</tr>
<tr>
<td>MORN</td>
<td>1.5ᵇ</td>
<td>2.2ᵇ</td>
</tr>
<tr>
<td>LORN</td>
<td>1.4ᵇ</td>
<td>1.1ᶜ</td>
</tr>
<tr>
<td>PORT</td>
<td>9.5ᵃ</td>
<td>7.1ᵃ</td>
</tr>
</tbody>
</table>

6-3.1.4. Mean proportion of population in each height class interval.

Seedlings and juveniles accounted for 81% of the *P. undulatum* population sampled at PORT and approximately half of all individuals sampled in the other populations (Figure 6-3). The proportional representation of seedlings and juveniles is reasonably consistent between populations despite considerable differences in the overall profiles (Figure 6-2). The natural MORW population, which supported the lowest *P. undulatum* densities of the six populations sampled, has the highest proportion of seedlings and the lowest proportion of juveniles. The most ‘even’ proportional distribution of individuals across the height class categories is evident in the natural MORW and GLEN populations.
Figure 6-2(i-vi). Height classes profiles for six populations of *P. undulatum* in Victoria

**6-2i. CROA**

**6-2ii. GLEN**

**6-2iii. MORW**

**6-2iv. MORN**

**6-2v. LORN**

**6-2vi. PORT**

Height class: 1. <0.5m (seedlings), 2. 0.5-1m (juveniles), 3. 1-2m, 4. 2-4m, 5. 4-6m, 6. 6-8m, 7. 8-10m, 8. 10-12m, 9. 12m+.
6-3.1.5. Variation in adult (>1m) sex structure

A male bias was evident in each population sampled (Table 6-4). The mean ratio of males to females, pooled over the six populations, differed significantly ($\chi^2 = 6.97$, $P < 0.01$) from the expected 1:1 ratio. The ratio of males to females was highest at PORT (1:0.7) and departure from the expected 1:1 ratio was significant only in this rapidly invading population ($\chi^2 = 5.16$, $P < 0.01$). The sex structure was closest to unity in the GLEN, MORN and LORN populations (all 1:0.9). Overall, no pattern of variation in sex structure is evident between the natural and invasive populations sampled.
Table 6-4. Total number of known males to females, sex ratios and significance of departure from expected 1:1 ratio in Victorian *P. undulatum* populations (sum of 5 300m² grids).

<table>
<thead>
<tr>
<th>Population</th>
<th>Male</th>
<th>Female</th>
<th>$X^2$</th>
<th>Male:Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>64</td>
<td>54</td>
<td>0.84 NS</td>
<td>1:0.8</td>
</tr>
<tr>
<td>GLEN</td>
<td>55</td>
<td>50</td>
<td>0.24 NS</td>
<td>1:0.9</td>
</tr>
<tr>
<td>MORW</td>
<td>50</td>
<td>45</td>
<td>0.26 NS</td>
<td>1:0.8</td>
</tr>
<tr>
<td>MORN</td>
<td>171</td>
<td>148</td>
<td>0.83 NS</td>
<td>1:0.9</td>
</tr>
<tr>
<td>LORN</td>
<td>98</td>
<td>85</td>
<td>0.92 NS</td>
<td>1:0.9</td>
</tr>
<tr>
<td>PORT</td>
<td>73</td>
<td>48</td>
<td>5.16*</td>
<td>1:0.7</td>
</tr>
<tr>
<td>Total</td>
<td>511</td>
<td>430</td>
<td>6.97**</td>
<td>1:0.84</td>
</tr>
</tbody>
</table>

Significant departures from the expected 1:1 sex ratio ($X^2$) are indicated

(* $P < 0.05$, ** $P < 0.01$, NS Not Significant $P > 0.05$).

The sex ratio data were pooled into three broader height class categories (1-4m, 4-8m, 8-12m+) to investigate if the ratio of males to females varied over successive height class categories (Figure 6-4). Increases in the ratio of males to females were recorded in the CROA, MORW and MORN populations over the 1-4m, 4-8m and 8-12m+ categories. The ratio of males to females declined through the successive height classes in the GLEN population, from a male dominance in individuals 1-4m, even sex ratios in the 4-8m intervals and female dominance in the 8-12m+ height class interval. A female bias is evident only in the LORN (4-8m) and GLEN (8-12m+) categories. Insufficient data were obtained in the LORN and PORT populations to establish if a trend was evident in sex structure over successive height classes. Overall, the invasive populations supported a comparatively higher number of reproductively mature individuals in the 1-4m height category compared to the natural populations sampled. The reverse is apparent in the 8-12m+ height class category and is most likely due to the comparatively recent naturalisation of *P. undulatum* at these sites.

6-3.1.6. Incidence of ‘abnormal’ males in *P. undulatum* populations

Functionally female flowers or remnants of fruit, on otherwise predominantly male flowering trees, were observed only at MORN and LORN. Fourteen of these ‘abnormal’ males (Steel 1911 and see Chapter 3) were recorded at MORN and four
Figure 6-4. Variation in *P. undulatum* sex structure through progressive, pooled height classes (sum of 5 300m² grids) at six sites in Victoria.

6-4i) Male:Female 1-4m height class

6-4ii) Male:Female 4-8m height class

6-4iii) Male:Female 8-12m+ height class
were recorded at LORN. This represents 8% and 4% of the total known males recorded at MORN and LORN, respectively. These individuals were often clustered together in the same or adjacent quadrats in the MORN population, but this trend was not evident at LORN. The characteristics of the remnant fruit crop (where present), varied considerably between such individuals at both locations. In most cases, fruit crops were very small, with only one to two fruits per branchlet. A small number of the seed-producing male plants at MORN had, however, produced a large fruit crop in the winter prior to sampling (pers. obs.).

6-3.1.7. Relationship between ‘reproductive activity’ and densities of seedlings and juveniles

The overall mean percentage of ‘reproductively active’ (>1m) plants (see section 6-3.2.1) was high across the six populations (49.7%), but considerable variation in this attribute was evident between the six populations sampled (Table 6-5). There appears to be no relationship between the proportional representation of reproductively active plants and the density of seedlings and juveniles across the populations sampled, or between natural and invaded habitats. The proportion of reproductively mature plants in the PORT population (20.4%) was low in comparison to the other populations sampled yet this population supported the highest densities of seedlings and juveniles (2490 in total). The opposite applies to the MORW population, which supported the highest proportion of reproductively mature plants (89.6%) and the lowest densities of seedlings and juveniles (143 in total). Non-flowering plants accounted for 79% of the 1-2m individuals sampled across the six populations. This percentage dropped to 26% for the 2-4m height class.
Table 6-5. Relationship between seedling and juvenile density and proportion of known males and females (‘reproductive activity’) at each site (sum of 5 300m² grids).

<table>
<thead>
<tr>
<th>Population</th>
<th>Total seedlings and juveniles</th>
<th>*Reproductive activity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CROA</td>
<td>390</td>
<td>24.8%</td>
</tr>
<tr>
<td>GLEN</td>
<td>320</td>
<td>33%</td>
</tr>
<tr>
<td>MORW</td>
<td>143</td>
<td>89.6%</td>
</tr>
<tr>
<td>MORN</td>
<td>555</td>
<td>73.5%</td>
</tr>
<tr>
<td>LORN</td>
<td>383</td>
<td>57%</td>
</tr>
<tr>
<td>PORT</td>
<td>2490</td>
<td>20.4%</td>
</tr>
</tbody>
</table>

*Reproductive activity: known males and females expressed as a percentage of the total number of individuals >1m sampled at each site (see section 6-2.3.1).

6-3.2. Spatial pattern

6-3.2.1. Spatial pattern of association between P. undulatum and other trees and shrubs

A clear pattern of association is evident in the constellation diagram of significant correlations constructed from the pooled population data (Figure 6-5). P. undulatum seedlings and juveniles are positively correlated with trees and shrubs of other genera >2m, and negatively correlated with P. undulatum >2m. Positive correlations between P. undulatum seedlings, juveniles and 1-2m individuals may be an artefact of dispersal, that is, there is a strong possibility that seeds from successive generations may be dispersed to the same locations because of the availability of suitable perches. This analysis suggests this is more likely to be beneath other trees and shrubs than beneath adult >2m P. undulatum. The observation that seedlings and juveniles are positively correlated with P. undulatum 1-2m, and negatively correlated with P. undulatum >2m, is further evidence of this association. Germination and establishment may be possible beneath P. undulatum 1-2m, but is apparently reduced or prevented beneath P. undulatum individuals >2m in height.
Figure 6-5. Constellation diagram of significant interactions between trees and shrubs of various genera (overstorey >2m), P. undulatum seedlings, juveniles, 1-2m and >2m individuals at six sites in Victoria (900 10m² quadrats).

All relationships are significant at $P < 0.001$ (Spearman’s Rank Correlation Coefficient, two-tailed test). Solid lines (——) indicate positive correlations and dashed lines (*** ) indicate negative correlations.
6-3.2.2. Site-based analyses of spatial association

Despite some minor differences, the association patterns indicated in Figure 6-5 are reinforced in the separate analyses of spatial associations conducted for each population (Figure 6-6i-vi). Different patterns of association evident between the sites are most probably related to habitat-based variation in establishment pressures. These are further discussed in section 6-4.

Significant negative correlations were evident between *P. undulatum* >2m and trees and shrubs >2m at the three natural sites. This may be indicative of inter-specific competition between *P. undulatum* >2m and structural analogues. This trend is also apparent from analyses of *P. undulatum* vegetation relationships and invasion impacts (see Chapter 7).

Seedlings are negatively correlated with *P. undulatum* 1-2m at CROA (Figure 6-6i). This relationship was not evident in the other five populations and may be related to site factors specific to CROA. The *P. undulatum* population at CROA for example, occurs on sandy, nutrient-poor soils, which may limit growth conditions. The density of 1-2m individuals at this site was high and in places, achieved a closed canopy similar to that imposed by individuals >2m at the other sites sampled.

The pattern of association at GLEN (Figure 6-6ii) is the same as that presented for all populations in Figure 6-5, however some differences in the significance of the relationships between variables are evident. The negative correlation between *P. undulatum* >2m and juveniles was significant at a higher level (*P* < 0.001) than that between *P. undulatum* >2m and seedlings (*P* < 0.05). This suggests that the chance of seedling survival declines as development of the individual and the clump progresses. The negative correlation between seedlings and *P. undulatum* >2m evident at GLEN, is also apparent at MORW (Figure 6-6iii), LORN (Figure 6-6v) and PORT (Figure 6-6vi).

In contrast to the other sites sampled, overstorey was not correlated with any other variable at MORN (Figure 6-6iv). A significant relationship (*P* < 0.001) between the
Figure 6-6(i-vi). Constellation diagrams of significant interactions between various *P. undulatum* developmental stages and overstorey at six sites in Victoria.

Significant relationships determined by Spearman’s Rank Correlation Coefficient, two-tailed test; positive correlations: —— *P* < 0.05, ——*P* < 0.01, ———*P* < 0.001; negative correlations: ——*P* < 0.05, ———*P* < 0.01, ————*P* < 0.001.
*P. undulatum* 1-2 and >2m variables was also apparent only at MORN. These relationships could be related to the long-term invasion of *P. undulatum* at this site. Some displacement of overstorey species by *P. undulatum* is indicated in the vegetation relationships analyses conducted for this site (see Chapter 7). The *P. undulatum* population at MORN appears to be in a phase of clump coalescence or gap-infilling (pers. obs).

**6-3.3. Mean densities of trees and shrubs >2m and *P. undulatum* >2m at six sites in Victoria**

The significant negative correlations evident between *P. undulatum* >2m and trees and shrubs of other genera >2m, indicated in the constellation diagrams constructed for natural populations is reflected in Figure 6-7. The mean density (10m$^3$) of *P. undulatum* was lower than that of other trees and shrubs at the three natural sites and the PORT population. Mean densities of *P. undulatum* >2m exceeded that of other trees and shrubs in the invasive populations MORN and LORN. Differences in the mean densities of trees and shrubs and *P. undulatum* >2m at PORT, compared to the other invaded sites, may reflect the relatively recent invasion of *P. undulatum* at this site.

**Figure 6-7. Relative densities of *P. undulatum* >2m and other trees and shrubs >2m at six sites in Victoria (10m$^3$).**
6-4. Discussion

This study has demonstrated considerable variation in *P. undulatum* population attributes within and between the natural and invaded populations sampled. It is difficult to ascertain from this ‘snap-shot’ population data, whether the within-population variation in seedling and juvenile densities is due to density-dependent factors, density-independent factors, or some combination of both. *P. undulatum* seedlings that germinate from clusters of seed eliminated by frugivores, or which fall from dehiscent carpels beneath parent plants, would experience intense intra-specific competition pressures. Seedling survival is influenced by a range of environmental factors including spatial and temporal fluctuations in macro- and micro-climatic conditions, the nature and extent of intra- and inter-specific competition, interactions with other biota and disturbance history and a range of other factors (Grubb 1977; Howe 1989).

*P. undulatum* seedlings are well adapted for survival in a range of habitat types and under various and varying environmental conditions. Seedlings develop taproots or diffuse root structures in response to edaphic conditions, enabling establishment and persistence on a range of soil types (Gleadow 1982). Seedlings are reasonably drought tolerant, especially in shaded conditions (Gleadow & Rowan 1982) and respond to browsing or other forms of leaf damage with vigorous coppicing (Gleadow 1982; Goodland & Healey 1997b). Bud burst can occur up to five times in the seedlings’ first year enabling rapid growth and competitive utilisation of resources (Gleadow 1982).

Despite these adaptations for survival, the general pattern of declining abundance from the seedling to juvenile phase suggests considerable seedling mortality is evident in the *P. undulatum* populations sampled. Competition factors and light regimes at the dispersal location are likely to be the critical factors influencing seedling survival. *P. undulatum* seedlings are rarely observed in open, exposed sites or beneath dense *P. undulatum* canopies, but occur frequently beneath the canopies of eucalypts and other mature trees and shrubs suggesting that these sites provide the most appropriate micro-climatic conditions for germination and establishment. The
association patterns displayed in the constellation diagrams indicate that the chance of *P. undulatum* survival through successive developmental stages is higher beneath other trees and shrubs than beneath *P. undulatum* >2m.

The findings of the present study are in agreement with those of Richardson and Brink (1985), Buchanan (1989a) and Mullett and Simmons (1995), but clearly conflict with Gleadow’s (1982, p. 197) assertion that “it is essential...that *P. undulatum* forms a regeneration niche under its own canopy to ensure survival of succeeding generations”. The discrepancy between Gleadow’s (1982) findings and those of the more recent studies, may be attributed to a number of possible factors.

In the first instance, Gleadow’s (1982) regeneration niche theory was based on results obtained from one site (Langwarrin, Victoria). The establishment conditions and competition variables experienced during the course of the experiment may have been sufficiently different to influence the pattern of *P. undulatum* recruitment observed at this site. Importantly, the establishment experiment conducted by Gleadow (1982) did not adequately mimic aspects of *P. undulatum* dispersal ecology. Seedlings of *P. undulatum* that germinate from both frugivorous or autochorous modes of dispersal face intense intraspecific competition that seedlings transplanted by Gleadow (1982) did not experience. It is further possible that the transplanted seedlings, grown from seed collected at other locations, performed differently to those that germinate at the study site and under field conditions. Additionally, in the initial phase of Gleadow’s experiment, seedlings were watered to buffer the effects of transplanting (Gleadow 1982), thereby reducing competition for this resource.

No significant differences were reported in light infiltration through eucalypt and *P. undulatum* canopies sampled at the Langwarrin site (Gleadow 1982). This suggests that the *P. undulatum* canopies measured at this site were not well developed, may have been <2m in height or more sparsely distributed than individuals sampled in the current study. *P. undulatum* seedling growth rates reach a compensation point at 1.6% light infiltration, although growth rates increase commensurate with photon flux densities (Gleadow et al. 1983; Barrett & Ash 1992). Light infiltration through the *P. undulatum* canopy may be reduced to between 2-11% of full daylight
(Gleadow & Ashton 1981) and this shading may be an important factor limiting recruitment opportunities for conspecific seedlings. Shading, soil moisture and leaf litter, are likely to increase as a function of P. undulatum canopy development (Gleadow & Ashton 1981). Changes in the nutrient composition of soils beneath the P. undulatum canopy (Gleadow & Ashton 1981) and allelopathic inhibitors (Richardson & Brink 1985) may also reduce recruitment opportunities for conspecific seedlings.

The comparatively moderate shade cast by eucalypts typical of the vegetation communities sampled in the current study, provides a more suitable light-environment for seedling growth, compared to that beneath the developed P. undulatum canopy (Rose 1997a). The distribution pattern initiated by frugivorous dispersal agents is therefore compatible with the species’ germination and establishment requirements (Gleadow 1982 and see Chapter 5). Previous studies of feeding behaviour in frugivorous species indicate that most species forage for short (<5 minutes) periods (Wheelwright 1991; Green 1993) and that seed passage rates generally range from 15-45 minutes in seeds that are defecated and 5-15 minutes in seeds that are regurgitated (Clergeau 1992). This regurgitation passage rate is typical of Pied Currawongs (Bass 1990c), an important dispersal agent of P. undulatum.

In observations of Pied Currawong feeding behaviour in south east Queensland, Green (1993) reported that Pied Currawongs rarely remained at feeding sites long enough to eliminate undigested seeds (Green 1993). Similar patterns of Pied Currawong feeding behaviour have been observed in north east New South Wales (Bass 1990c, 1995). Following these short feeding events, Pied Currawongs consistently move to perching sites remote from the feeding tree to rest and regurgitate undigested material (Bass 1990c). Seeds dispersed in this manner germinate to form clumps around the bases of perching sites. Frugivores are attracted to the food resources provided by the developing clump (Richardson & Brink 1985; Kruger et al. 1986) and clumps expand as individuals are added to the clump perimeter by frugivorous and autochorous modes of dispersal. Some recruitment of P. undulatum seedlings occurs within the clump, particularly at the clump margin where competition factors are reduced, but in most cases, successful
recruitment and persistence through developmental stages occurs at the base of trees and shrubs of other species.

This pattern of recruitment is typical of fleshy-fruited frugivore-dispersed species (Bass 1990a, 1990b; Buchanan 1992; Rose 1997a, 1997b; Jupp et al. 1999). As frugivorous vertebrates adapt to the abundance of this food resource (Geldenhuys et al. 1986; Knight 1986; Kruger et al. 1986), the volume of seeds transported away from the parent plant may increase, leaving a reduced number of seeds to fall beneath the parent plant. This strategy may promote further regeneration opportunities for *P. undulatum* and contribute to the local expansion of populations.

*P. undulatum* leaf-fall peaks about two months after seed set and while this leaf litter provides fallen seeds with some protection from desiccation (Gleadow 1982). The benefits conferred may potentially be offset by auto-allelopathic inhibition although there is little quantitative evidence in support of this relationship for *P. undulatum* (Tunbridge 1997). *P. undulatum* seeds rarely germinate from a burial depth greater than 4cm (Gleadow 1982), so it is further possible that the dense leaf litter beneath the *P. undulatum* canopy is another important factor restricting conspecific seedling germination. *P. undulatum* generally produces more leaf litter than eucalypt species in dry forest environments (Gleadow & Ashton 1981). Presumably, *P. undulatum* seed dispersed beneath the canopy of eucalypts and other suitable trees and shrubs, may be less likely to be buried amongst the leaf litter.

Considerable variation in the nature and extent of biotic and abiotic factors operating on the populations sampled may also explain some of the between-site differences evident in population structure and spatial pattern. Higher *P. undulatum* densities were, on average, evident at the invaded sites compared to natural habitats sampled. This trend is consistent with findings in other studies of weed population dynamics in natural and invaded environments (Weiss & Milton 1984; Dean et al. 1986; Scott 1996; Rees & Paynter 1997; Paynter et al. 1998). The ‘ecological release’ from predators, pathogens and other biotic constraints, may enable rapid population growth in invaded, compared to natural habitats for some species (MacDonald 1985; Kruger et al 1986).
The CROA population was an interesting exception to this general trend. The population profile constructed for CROA was skewed toward the early developmental stages, and in this sense, more closely resembled the profiles of the invasive populations, than the other natural populations sampled. The CROA population occurs on sandy, nutrient-poor soils, which are likely to reduce growth rates. Such habitat-based variation in growth conditions may influence the distribution of ages in a given height class (Hutchings 1997). Individuals in the 1-2m height class accounted for approximately 40% of the CROA population, but may in fact represent a broader range of ages or older individuals, compared to 1-2m individuals sampled at other sites. Notwithstanding these factors, the mean density of the CROA population was considerably higher than the other natural populations and it is possible that this population is in an expansion phase.

The CROA population also displayed significantly higher germinability than the other populations sampled (Chapter 5). Additionally, the CROA population is relatively free of galls, blights and other leaf diseases common to many indigenous populations of this species (pers. obs.). Dispersal opportunities for *P. undulatum* have probably increased at this site with the recent encroachment of Blackbirds and increased seasonal abundance of Pied Currawongs (pers. obs.).

The greatest proportional change in densities, from the seedling to juvenile phases, was recorded at MORW. This may indicate that considerable recruitment constraints are operating on this natural population. The significant negative correlation (*P < 0.05*) between seedlings and *P. undulatum* adults (>2m) supports the assumption that the germination of seeds would be largely prevented beneath the dense canopy of conspecific adults. Seedling establishment at MORW may also be contained by the foraging activities of Superb Lyrebirds, which are very common in Morwell National Park (MORW). Lyrebirds scratch and rake through topsoil and leaf litter in their search for invertebrate prey and in doing so, may dislodge small *P. undulatum* seedlings (pers. obs.). The considerable soil and litter disturbance caused by Lyrebird foraging (Ashton & Bassett 1997) may also result in some burial of *P. undulatum* seed beyond the maximum emergence depth of 4cm (Gleadow 1982). Lyrebirds foraging may therefore provide a small but important constraint to *P. undulatum* recruitment at sites where Lyrebirds are present.
The most even proportional representation of individuals across the adult height classes was evident at MORW and GLEN. Like CROA however, these two natural populations are also showing early signs of population expansion. *P. undulatum* encroachment from indigenous riparian and gully environments onto drier associated slopes is evident at both these sites (pers. obs). The main factors in these expansions are most probably changes in natural fire regimes and changes in the composition and abundance of dispersal agents. Fires would have naturally occurred more frequently on these drier slopes than is currently the case (Griffiths 1988; Howell 1992). Frugivore-assisted movement of *P. undulatum* seed from the gully and riparian environments to the drier associated slopes may not be a new trend in these areas, but more frequent fires may have previously contained these nascent foci.

Introduced Blackbirds are now common in MORW (pers. obs.) and as mentioned in Chapter 5, populations of King Parrots, a potentially important *P. undulatum* seed predator, have declined considerably throughout the Strezlecki Ranges, where this MORW site is located (Emison et al. 1987). Large flocks of Satin Bowerbirds were observed feeding on considerable quantities of *P. undulatum* fruits and seeds at GLEN. Pied Currawongs are also seasonally common at this site, but it is unknown whether dispersal opportunities for *P. undulatum* at GLEN have changed appreciably in recent decades. Reduced fire frequency may be a critical factor in the observed local population expansion.

Negative correlations between *P. undulatum* >2m and trees and shrubs >2m, were evident at the three natural populations, suggesting some inter-specific competition between *P. undulatum* >2m and its structural analogues. Indigenous shrubs and trees common to these sites may be better adapted to mesic, shaded conditions and therefore more resilient to the competitive effects imposed by *P. undulatum*, than the trees and shrubs sampled in the invaded dry forest communities. The mean density of trees and shrubs >2m was also higher on average, in the natural habitats compared to the invaded habitats sampled. It is difficult to speculate from these data whether some displacement of structural analogues may have already occurred at the invaded sites, particularly the long-invaded MORN and LORN. Mean densities of trees and
shrubs at the relatively recently invaded PORT site were also more similar to those at
the natural sites compared to MORN and LORN.

Deviations from the expected pattern of attrition with each developmental stage
(Luken 1990) were apparent at GLEN and CROA where densities of *P. undulatum*
individuals in the 1-2m height class, exceeded that of juveniles. These population
profile ‘humps’ may indicate previously favourable seed production, dispersal,
germination and/or establishment conditions for some *P. undulatum* generations.
Establishment pressures operating on the individual and the population are likely to
vary considerably on any number of spatial and temporal scales (Watkinson 1997).
Long-term patterns of germination and establishment may be influenced by broader
fluctuations in climatic conditions and the influence of other disturbance factors.

Intra-generational establishment opportunities may be enhanced by the seasonal
separation of germination events described by Gleadow (1982) as less direct
competition may occur between seedlings that germinate in spring and those that
germinate in autumn (see Chapter 5). However, *P. undulatum* seeds dispersed by
frugivores may initially experience additional inter-specific germination competition
pressures, if the frugivore scats or pellets contain seeds of other species (Loiselle
1990).

Rose (1997a) suggested that rapid *P. undulatum* population expansion might occur
after site conditions become more suited to the species’ requirements. In the dry
sclerophyll forests sampled by Rose (1997), these site conditions include the absence
of fire for a crucial period, changes in soil nutrient composition and increase in
reproductive potential as the population develops. In the tall scrub and riparian
forests invaded by *P. undulatum* in South Africa, the time lag in *P. undulatum*
population expansion was attributed to an adaptation period by frugivores (Kruger et
al. 1986), the critical condition in this case being dispersal opportunities.

Rapid *P. undulatum* population expansion in the Blue Mountains region of Jamaica
was related to hurricane-related disturbance and the species’ competitive occupation
of consequent gaps (Goodland & Healey 1996, 1997b). Hurricane-related gap
creation is however intensified in areas dominated by *P. undulatum* because the
species’ comparatively shallow root system makes it more susceptible to wind throw during hurricane conditions than comparable native species in the region. Goodland and Healey (1996, 1997b) predict that future hurricane activity may promote further expansion opportunities for *P. undulatum* in Jamaica.

The ecosystem-level changes imposed by *P. undulatum* generally allow for further population expansion. At the clump level, these changes include increased shading and soil moisture, increased leaf litter, alteration to soil nutrient loads and the potential influence of allelopathic inhibitors (Gleadow & Ashton 1981). Displacement of indigenous species with increasing *P. undulatum* cover-abundance occurs through direct competition and through changes in the availability of resources in the invaded environment (see Chapter 7). Associated changes at the site or patch level, will influence broader ecosystem processes and functions including fire, nutrient cycling and hydrological regimes and inevitably alter the rate and direction of successional processes (Luken 1990, 1997). High densities of *P. undulatum* may also encourage some change in the distribution and abundance of pollination and dispersal agents (see Chapter 5), which again, facilitate further range expansion of this species.

Once established, the process of *P. undulatum* population expansion is self-perpetuating. In the absence of management intervention, the process of *P. undulatum* clump enlargement and population expansion is likely to continue until complete patch dominance is achieved. Ultimately however, *P. undulatum* population expansion will be regulated by the availability of resources. Recruitment opportunities may decline over time as the relative proportion of adults increases and the clumps start to coalesce. As populations approach a more stable seral stage, which for *P. undulatum* would be a low closed forest structure, the distribution of adult plants would be expected to approach a more regular distribution as a result of competition.

There is some evidence to suggest that the *P. undulatum* population at MORN may be approaching this stage. Two association patterns unique to MORN of the six populations, were the strong positive correlation between the 1-2m and >2m *P. undulatum* variables and the lack of interaction between trees and shrubs >2m, and
any other variable. It is possible that *P. undulatum* invasion is so advanced at MORN that the clumps of *P. undulatum* are starting to coalesce. MORN was the only population sampled in which juvenile densities exceeded seedling densities; this may indicate that ‘safe sites’ for *P. undulatum* seedling establishment may be increasingly limited as the clumps coalesce. This pattern has also been observed in dense *Cytisus scoparius* (L.) Link. (Broom) infestations in open forest and woodland communities in New South Wales (Smith & Waterhouse 1988).

It is difficult to determine why the sex structure of the six *P. undulatum* populations sampled were male biased and further, if sex ratios in this species are genetically determined or influenced by ecological selection pressures (Willson 1979; Bawa 1980; Givnish 1982; Baker 1984). Male biased sex ratios are common in dioecious plant populations and are usually attributed to differential reproductive effort between the sexes (Lovett Doust et al. 1987; Allen & Antos 1988; Armstrong & Irvine 1989; Korapelainen 1992; Gibson & Menges 1994), which may in some cases, contribute to disproportionate female mortality (Meagher 1980; Allen & Antos 1993). Observed male biased ratios in some species may also be a function of earlier male maturation (Falinski 1980; Allen & Antos 1993; Osunkoya 1999).

Differential resource allocation to reproduction can result in some degree of niche partitioning between sexes of the same species although the level of spatial sex segregation may vary substantially within and between species (Cox 1981; Sakai & Oden 1983; Bierzychuden & Eckhart 1988; Gibson & Menges 1994). Some degree of sexual dimorphism in vegetative structures may also be a function of between-sex habitat division (Wallace & Rundell 1979; Korapelainen 1992). No patterns of spatial sex segregation were noted in the *P. undulatum* populations sampled in the current study although this pattern, if it occurs, may only be detectable on a larger spatial scale than that used in the current study.

Niche division between sexes of the same species can occur temporally as well as spatially. In many species, male plants flower earlier and over different periods than female plants, implying different temporal resource requirements between the sexes. (Cox 1981; Armstrong & Irvine 1989). Functionally male *P. undulatum* often flower earlier than female plants (Steel 1911), but this temporal separation is difficult to
discern in most cases, especially against broader influences on flowering patterns such as climatic and habitat factors.

Reduced reproductive potential may be a consequence of uneven sex ratios in some species (Osunkoya 1999). For example, uneven sex ratios are considered a major impediment in the conservation management of the rare *Pittosporum obcordatum* Raoul. (Heart-leaved Kohuhu) in New Zealand (Clarkson & Clarkson 1994). Obviously, uneven sex ratios do not restrict the invasive potential of *P. undulatum*. It is interesting to note however, that of the six populations sampled in the current study, the invasive PORT population supported the most uneven sex structure, the lowest proportion of reproductively mature plants and the lowest seed germinability (see Chapter 5). Despite these apparent (and possibly inter-related) constraints to fecundity, seedling and juvenile densities were significantly ($P < 0.05$) higher at PORT, compared to the other populations sampled. Harper and White’s (1974) contention that age structure is unreliable predictor of a population’s reproductive activity is highly relevant to *P. undulatum*.

Managers are encouraged to control weed populations in the early invasion stages when the ecological impacts exerted are minimal and the chance of successful control is high (Humphries *et al.* 1991; Hobbs & Humphries 1995; Panetta & James 1999). This study has demonstrated that the impacts exerted by *P. undulatum* tend to amplify as the invasion progresses, and additionally, that the ecosystem-level changes imposed by *P. undulatum* invasion, facilitate further population expansion of this species to the detriment of the host community (see Chapter 7).

Data on population structure and regeneration patterns contribute valuable information to weed management strategies but should not be considered in isolation when designing and implementing control programs. For example, the *P. undulatum* population at PORT could feasibly be contained by an appropriate control burn given most of the population at this invaded dry forest site consists of seedlings and juveniles. The weeds *Genista monspessulana* (L.) L. A. S. Johnson (Montpellier Broom) and *Acacia longifolia* var. *longifolia* Willd. (Sallow Wattle) are however, also present at this site in low densities, but may be increasing their local population base in terms of above ground biomass and soil stored seed reserves. The
implementation of a control burn to reduce *P. undulatum* densities and create regenerative opportunities for some indigenous species at this site may also stimulate mass germination of *G. monspessulana* and *A. longifolia*. In this scenario, the long-term weed problem at this PORT site may shift from *P. undulatum* to these leguminous invaders.

Studies on population dynamics and recruitment patterns and processes contribute valuable information regarding the invasion potential of environmental weed species. An understanding of how these factors operate in a broader community context is essential to the development and implementation of effective weed management programs (Kluge *et al.* 1986; Groves 1989, 1991). These factors are considered, in detail, in Chapter 7.

6-5. Summary

Mean densities of *P. undulatum* individuals were higher in invaded populations than the natural populations sampled in this study. Proportionally, seedlings and juveniles accounted for approximately 50% of individuals in all populations, with the exception of the PORT population, where 81% of individuals sampled were seedlings or juveniles. A male bias was evident in all populations sampled and the average male to female ratio across the six populations was 1:0.84, representing a significant departure from the expected 1:1 sex ratio.

*P. undulatum* seeds are mainly dispersed in clumps through both autochorous and frugivorous dispersal mechanisms and seed deposition generally occurs beneath the canopy of mature trees and shrubs, including conspecific adults. The moderate canopy cover of eucalypts, some other trees and shrubs, and at the *P. undulatum* clump margin, provide appropriate conditions for *P. undulatum* establishment. Reduced light infiltration and other competition factors are likely to limit recruitment opportunities beneath the dense adult canopy. Gleadow’s (1982) *P. undulatum* regeneration niche theory was not applicable at the sites sampled in this study.
Current management activities, especially the suppression of natural fire regimes, may be just as important as the biological factors described, in facilitating further *P. undulatum* clump development and population expansion.
CHAPTER SEVEN

_P. undulatum_ community relationships and invasion impacts

7-1. Introduction

Environmental weed invasions are widely regarded as a major threat to biodiversity values (see Chapter 2). To date, however, few studies have quantitatively assessed the ecological impacts of environmental weed invasions on invaded ecosystems (Adair & Groves 1998). In the absence of empirical evidence, the impacts of environmental weed invasions are largely assumed and management priorities may be misdirected (Adair & Groves 1998). Quantitative data on environmental weed impacts are required for the assessment of risks posed by environmental weed species and to guide the targeting of limited resources to ensure their efficient and effective allocation (Hobbs & Humphries 1995; Adair & Groves 1998; Panetta & James 1999). Policy and management decisions regarding funding allocations to environmental weed control will increasingly depend upon the ability to compare, and ultimately prioritise, between the impacts imposed by invasive species (Adair & Groves 1998; Panetta & James 1999). This is especially apparent in an era where funding for environmental management programs is limited and competition for public sector funding is high across natural resource management sectors in Australia.

A thorough understanding of disturbance and other landscape factors that facilitate invasion are also critical to the design and implementation of effective, targeted weed management strategies (Humphries _et al._ 1991; Hobbs & Humphries 1995; Panetta & Lane 1996). Identification of the invader’s ecological role, community inter-relationships and influence on the rate and direction of succession, will further assist managers in selecting the control techniques and approach most likely to promote the desired species composition (Luken 1997; Woods 1997).
7-1.1. Aims of the current study

This study aims to quantify the impact of increasing *P. undulatum* cover-abundance on community composition and structure and to investigate the community relationships of *P. undulatum* in natural and invaded habitats.

The results obtained from this study also provide an opportunity to address some key questions posed by Adair and Groves (1998) regarding the impacts of environmental weed invasions on biodiversity values.

1. *What is the impact on plant and animal richness and diversity?*
2. *Is the impact affecting ecosystem-level functions and if so how?*
3. *What interactions occur between vegetation succession and invasion?*
4. *What are the threshold points for declines in biodiversity as a result of invasion?*

*Adair & Groves (1998, p. 32)*

7-1.2. Previous research on *P. undulatum* invasion impacts Australia.

Gleadow and Ashton (1981) reported on changes in the floristic composition associated with *P. undulatum* invasion in an open *Eucalyptus* forest remnant in suburban Ringwood, east of Melbourne. Mullett and Simmons (1995) investigated the impacts of *P. undulatum* invasion on floristic attributes at four dry sclerophyll forest remnants in the greater Melbourne region. Rose (1997a) and Rose and Fairweather (1997) examined the relationship between suburb age and increasing density of *P. undulatum* on the floristic composition of woodland and forest communities in the Sydney region. In all cases, *P. undulatum* invasion was demonstrated to impose considerable impacts on species richness and community composition. Declines in sclerophyllous species diversity with invasion by *P. undulatum* have also been reported in other botanical studies conducted in the Sydney region (Adamson & Fox 1982; Buchanan 1991). Richardson and Brink (1985) described some characteristics of *P. undulatum* invasion ecology in South Africa and Goodland and Healey (1996, 1997b) investigated some ecological impacts of *P. undulatum* invasion in a broader study of control prospects for this species in the Blue Mountains region of Jamaica.
These studies have utilised different sampling strategies to investigate various aspects of *P. undulatum* invasion impacts and together contribute to the profile of this species’ invasion ecology. None of these studies has examined the ecological role and community relationships of *P. undulatum* in natural and invaded habitats. Similarly, none of the previous studies has attempted to quantify changes in community attributes with incremental increases in *P. undulatum* cover-abundance or investigated the applicability of weed damage thresholds to *P. undulatum* invasions.

7-2. Methods

7-2.1. Sites selected for sampling

Four sites were selected for sampling in the current study (Table 7-1). The MORN and PORT sites were selected to represent invasive populations of *P. undulatum*. CROA and BODL were sampled to represent natural populations of *P. undulatum* although it is acknowledged that local densities of *P. undulatum* may be increasing in response to altered fire regimes and other disturbance factors at these ‘natural’ sites. The distribution of these sites in south east Australia is illustrated in Figure 7-1.

Table 7-1. Sites selected for sampling in this study of *P. undulatum* community relationships and invasion impacts.

<table>
<thead>
<tr>
<th>Natural Range</th>
<th>Invaded Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Code</td>
<td>Location</td>
</tr>
<tr>
<td>CROA</td>
<td>Point Hicks,</td>
</tr>
<tr>
<td></td>
<td>Croajingolong National Park, Victoria</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>BODL</td>
<td>Brou Lake, Bodalla State Park, New South Wales</td>
</tr>
</tbody>
</table>

It was impossible to strictly match the environmental characteristics of the sites selected for sampling, but the four sites are broadly characterised by dry sclerophyllous vegetation subject to coastal influences. These four sites are also located away from major human settlements, are part of relatively large vegetation
remnants and contain minimal populations of other weed species. Every effort was made to sample homogenous vegetation assemblages within the larger remnant to better elucidate the influence of increasing *P. undulatum* cover-abundance on floristic attributes. Clumps were sampled on gentle (~5°) slopes with south-westerly aspects at MORN, PORT and CROA and on similar slopes but with a predominantly western aspect at BODL. The latitude, longitude, elevation and mean seasonal climate data for each site are included in Appendix 2.

7-2.2. **Sampling the floristic composition associated with a *P. undulatum* clump**

The sampling strategy employed in the current study was designed to measure changes in floristic attributes associated with the clumped distribution pattern typical of *P. undulatum* (see Chapter 6). Two 33m transects, orientated north to south and west to east, were located through the approximate centre of five *P. undulatum* clumps at each site (Figure 7-2). Ten 3x3m (9m²) quadrats were sampled along each transect and a 3x3m quadrat was sampled at the junction of the two transects at the approximate centre of the clump. This quadrat size was determined appropriate for sampling in dry sclerophyll forest environments (Mullett 1993) from species/area curve analyses (Kershaw & Looney 1985) and was repeated across the four sites sampled in the current study.

All vascular plant species occurring in, or projecting into, each quadrat were recorded and assigned a cover-abundance value in accordance with a modified Domin-Krajina cover-abundance scale (Mueller-Dombois & Ellenberg 1974). This scoring system (Table 7-2) allows for quantitative assessment of changes in species composition and cover-abundance with incremental increases in *P. undulatum* cover-abundance.
Table 7-2. Modified Domin-Krajina cover-abundance scale used to score cover-abundance in the current study.

<table>
<thead>
<tr>
<th>Code</th>
<th>Cover-abundance</th>
<th>Code</th>
<th>Cover-abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>+</td>
<td>0 - 9%</td>
<td>5</td>
<td>50 - 59%</td>
</tr>
<tr>
<td>1</td>
<td>10 - 19%</td>
<td>6</td>
<td>60 - 69%</td>
</tr>
<tr>
<td>2</td>
<td>20 - 29%</td>
<td>7</td>
<td>70 - 79%</td>
</tr>
<tr>
<td>3</td>
<td>30 - 39%</td>
<td>8</td>
<td>80 - 89%</td>
</tr>
<tr>
<td>4</td>
<td>40 - 49%</td>
<td>9</td>
<td>90% - 100%</td>
</tr>
</tbody>
</table>

The codes used to represent each cover-abundance interval (Table 7-2) are used throughout the results section. Total quadrat cover-abundance exceeds 100% in some cases, for example, when mean cover-abundance scores per quadrat are displayed. These attributes are termed ‘community cover-abundance’ throughout the Chapter. Mean community cover-abundance refers to the average cover-abundance of all vascular plant species recorded in each 3 x 3m quadrat (with the exception of *P. undulatum*) at each transect position, or, at each 10% increment in *P. undulatum* cover-abundance. The codes used to represent *P. undulatum* and community cover-abundance increase in 10% increments and as such, are consistent with those indicated in Table 7-2. A mean community cover-abundance of 100-110% for example, is represented by the code ‘10’.

Approval to conduct sampling in National Parks and other areas of public land in Victoria and New South Wales was obtained from appropriate government agencies (See Appendix One for permit details). Introduced species are preceded by an asterisk (*) in the text and two-way tables. Nomenclature follows Ross (1996) and Harden (1992) and a list of species recorded at each site is provided in Appendix 6.
Figure 7-1. Distribution of south east Australian sites sampled in this study of *P. undulatum* community relationships and invasion impacts. See Table 7-1 for an explanation of site codes and Table 4-1 for further site information.
Figure 7-2. Sampling design for assessing changes in floristic attributes across the *P. undulatum* clump profile.

Key:
- Approximate centre of the radiating *P. undulatum* clump
- 3x3m quadrat

33m
7-2.3. Analyses

7-2.3.1. Influence of *P. undulatum* on community composition

The floristic data obtained from the four sites were entered into Excel v.5 spreadsheets and descriptive statistics were calculated to summarise and describe the data collected. Relationships between *P. undulatum* cover-abundance, species richness and cover-abundance were initially assessed by Spearman’s Rank Correlation Coefficient (two-tailed test). The quadrat data obtained for each site were then sorted to reflect increasing increments of *P. undulatum* cover-abundance. Changes in mean species richness and community cover-abundance with each 10% increase in *P. undulatum* cover-abundance were calculated (with standard errors) and plotted on separate graphs for each of the four sites sampled. For the purposes of these and subsequent analyses, a cover-abundance score of “+” was assigned a nominal value of 0.10 (Adams & Simmons 1996).

Mean values and standard errors were calculated for *P. undulatum* cover-abundance, species richness and community cover-abundance at each transect position, to explore the relationships between *P. undulatum* cover-abundance and these floristic attributes, across the north-south and east-west clump profiles. Weed species richness and cover-abundance were not excluded from the analyses described, however, relationships between *P. undulatum* and weed species’ cover-abundance were investigated in separate correlation analyses. Weed species accounted for 14.5% of the 62 species recorded at MORN, 19% of the 72 species recorded at PORT and 3% of the 75 species recorded at BODL. No weed species were recorded in the quadrats sampled at CROA.

The CSIRO pattern analysis program, PATN (Belbin 1993), was used to further investigate patterns in the data set. The robust Bray-Curtis association measure and the intensively clustering Ward’s sums of squares fusion strategy (Belbin 1993) were used to generate similarity measures between the 105 quadrats sampled at each site. The results of these hierarchical cluster analyses are displayed as dendrograms. *P. undulatum* cover-abundance values recorded for each quadrat are included in the dendrogram display to assist in the interpretation of the resultant quadrant.
assemblages. Mullett (1993) masked *P. undulatum* cover-abundance values to determine that quadrat groups were not unduly influenced by the comparatively high *P. undulatum* cover-abundance values. As the same patterns emerged (Mullett 1993) this procedure was not repeated in the current study.

Two-way tables, which illustrate patterns of species’ associations within the quadrat assemblages, were created by transposing the row (quadrat) and column (species) attributes and subjecting these matrices to the same association and fusion strategies described. Vertical lines in the two-way tables delineate groups of quadrats with similar floristic compositions and these reflect the groupings displayed in the dendrograms of quadrat associations. These groups were arbitrarily classified on the basis of the predominant *P. undulatum* cover-abundance scores in the quadrats comprising the groups. The quadrat groups were then re-ordered to reflect increasing *P. undulatum* cover-abundance to improve the clarity of the two-way tables, although the integrity of each group and the quadrat associations therein were maintained. Cover-abundance values obtained for each species recorded in the 105 quadrats sampled at each site were incorporated back into the two-way tables to further enhance the visual interpretation of these results as the TWAY option in PATN, does not display the original data values in these tables (Belbin 1993). Labels assigned to each quadrat in the dendrograms and two-way tables represent the site, clump and transect position sampled. A quadrat code of ‘P2WE8’ for example, represents quadrat number eight, sampled along the west-east transect in clump two at PORT.

Multi-dimensional scaling using a semi-strong hybrid technique (Belbin 1993) was performed on the quadrat data to provide an alternative display of quadrat associations. The vectors obtained from these analyses were plotted as two-dimensional ordinations. These ordinations confirmed the patterns evident in the dendrograms and two-way tables and as they did not contribute further information regarding *P. undulatum* community relationships and invasion impacts they were not included in this chapter.
7-2.3.2. Influence of *P. undulatum* on various structural guilds at four sites in south east Australia

The vascular plants censused at each site were pooled into several structural guilds to investigate the influence of increasing *P. undulatum* cover-abundance on the structural composition of the natural and invaded communities. The structural classifications used in the current study are an amalgamation of various schemes (Mueller-Dombois & Ellenberg 1974; Kershaw & Looney 1985; Holmes & Cowling 1997) and are based predominantly on groups of species that are similar in structure.

7-2.3.2.1. Classification

The vascular plants recorded at the four sites were categorised into one of seven broad structural guilds (Table 7-3). This is a coarse representation of structural complexity, however, in combination with the other analyses described, these guild analyses further contribute to the analysis of *P. undulatum* community relationships and invasion impacts.

All grasses of the family Poaceae were classified as ‘graminoids’ and non-woody vascular plants were classified as ‘herbs’; the latter category accounting for a large proportion of species sampled at the four sites. Herbaceous twiners including *Comesperma volubile* Labill. (Love Creeper), *Thysanotus patersonii* R. Br. (Twining Fringe-lily), woody twiners such as *Billarderia scandens* Sm. (Common Appleberry) and trailing herbs such as *Kennedia prostrata* R. Br. (Running Postman) were incorporated into a separate guild, ‘twiners, trailers, creepers and climbers’. Shrub species were assigned to one of three shrub categories based on the average height of mature individuals; ‘low-shrubs’ (<2m), ‘shrubs’ (~2-6m) and ‘tall shrubs/small trees’ (~6m+). All *Eucalyptus* species, some *Acacia* species and other overstorey species were classified as ‘trees’.

Several species sampled did not obviously fall into any of these coarse groupings. The fern, *Pteridium esculentum* (G. Forst.) Cockayne (Austral Bracken) was a common component of the vegetation at all sites sampled and its relationship with *P. undulatum* was subject to a separate analyses. The gymnosperm, *Macrozamia communis* L. Johnson (Cycad) was recorded in 53% of quadrats sampled at BODL
and was also subjected to a separate analysis. The fern, *Adiantum aethiopicum* L. (Maidenhair Fern) was recorded in only 13% of quadrats sampled at PORT. Due to the comparatively low representation of this species, it was excluded from these analyses. The structural guild into which all species sampled were categorised are indicated in the list of species sampled at each site (Appendix 6).

### 7-2.3.2.2. Analyses

No tests for homogeneity in the relative cover-abundance of each structural guild across the four sites were conducted because of the confounding influence of *P. undulatum* on these attributes. The proportional representation of species in each structural guild was however, reasonably even across the four sites sampled in the current study (Table 7-3).

**Table 7-3. Representation of species in each structural guild at four sites in south east Australia. The number of species in each guild is listed and the representation of each guild, as a proportion of the plants sampled at each site, is indicated in parentheses.**

<table>
<thead>
<tr>
<th>Structural guild</th>
<th>MORN</th>
<th>PORT</th>
<th>CROA</th>
<th>BODL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Graminoids</td>
<td>11 (15%)</td>
<td>9 (13%)</td>
<td>5 (10%)</td>
<td>5 (7%)</td>
</tr>
<tr>
<td>Herbs</td>
<td>36 (51%)</td>
<td>30 (42%)</td>
<td>22 (43%)</td>
<td>35 (47%)</td>
</tr>
<tr>
<td>Trailers, twiners, creepers and climbers</td>
<td>4 (6%)</td>
<td>5 (7%)</td>
<td>7 (14%)</td>
<td>9 (12%)</td>
</tr>
<tr>
<td>Low shrubs</td>
<td>4 (6%)</td>
<td>4 (6%)</td>
<td>0 (0%)</td>
<td>5 (7%)</td>
</tr>
<tr>
<td>Shrub</td>
<td>7 (10%)</td>
<td>11 (15%)</td>
<td>3 (6%)</td>
<td>9 (12%)</td>
</tr>
<tr>
<td>Tall shrubs/small trees</td>
<td>4 (6%)</td>
<td>4 (6%)</td>
<td>9 (18%)</td>
<td>5 (7%)</td>
</tr>
<tr>
<td>Trees</td>
<td>4 (6%)</td>
<td>7 (10%)</td>
<td>4 (8%)</td>
<td>5 (7%)</td>
</tr>
<tr>
<td>Other (ferns and gymnosperms)</td>
<td>1 (1%)</td>
<td>2 (3%)</td>
<td>*1 (2%)</td>
<td>2 (2%)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>71 (100%)</strong></td>
<td><strong>72 (100%)</strong></td>
<td><strong>51 (100%)</strong></td>
<td><strong>75 (100%)</strong></td>
</tr>
</tbody>
</table>

*The gymnosperm *Callitris rhomboidea* R. Br. ex Rich. (Oyster Bay Pine) was recorded in two quadrats sampled at CROA and was included in the tree guild for the purposes of these analyses*

The floristic data set for each site were pooled into the structural guilds described and the cover-abundance of each guild was summed for each quadrat sampled.
Correlation analyses were conducted to test the significance of the relationships between these variables and that of the *P. undulatum* cover-abundance value recorded for the relevant quadrats.

7-3. Results

7-3.1. Relationship between *P. undulatum* cover-abundance and species richness

Species richness was highly significantly negatively correlated with *P. undulatum* cover-abundance at the invaded sites, MORN (r = -0.49, *P* < 0.001) and PORT (r = -0.64, *P* < 0.001) and the natural site, CROA (r = -0.43, *P* < 0.001). In contrast, the cover-abundance of *P. undulatum* was not significantly correlated (r = 0.18, *P* > 0.05) with species richness at the natural site, BODL.

The relationship between species richness and *Monotoca elliptica* Sm. (Tree Broom-heath), a dominant native tall tree/small shrub recorded in 96 quadrats at CROA, was assessed by correlation analysis to determine if this species also exerts an influence on species richness. The cover-abundance of *M. elliptica* and species richness were negatively correlated but not at a significant level (r = -0.14, *P* > 0.05).

7-3.2. Influence of increasing *P. undulatum* cover-abundance on mean species richness

Considerable variation is evident in the influence of increasing *P. undulatum* cover-abundance on mean species richness across the four sites sampled (Figure 7-3i-iv). The impact of increasing cover-abundance of *P. undulatum* on mean species richness was most pronounced at the invaded sites sampled.

7-3.2.1. MORN

Incremental increases in *P. undulatum* cover-abundance had a dramatic impact on mean species richness at MORN (Figure 7-3i). Species richness declined from a mean of 14 and 16 species per 3x3m (9m²) quadrat where *P. undulatum* cover-abundance was less than 10% and between 10 and 19% respectively, to an average of
four species per quadrat where *P. undulatum* cover-abundance exceeded 90%. Mean species richness was slightly higher in quadrats where *P. undulatum* cover-abundance was between 10 to 19%, compared to quadrats where *P. undulatum* cover-abundance was less than 10% at MORN. This suggests that species richness is not suppressed at low levels (10-19%) of *P. undulatum* cover-abundance. The micro-climatic conditions provided by low *P. undulatum* cover-abundance may even enhance the diversity of micro-sites available for other species. With this exception, the overall pattern at MORN is for declining species richness with increasing cover-abundance of *P. undulatum*. Where *P. undulatum* cover-abundance levels exceed 20%, the competition and shading effects imposed on associated species are critical and exert a negative influence on some species. Mean species richness declines notably after *P. undulatum* cover-abundance exceeds 20%, but remains relatively stable where *P. undulatum* cover-abundance is between 30 to 49%. A linear decrease in mean species richness is evident with each subsequent 10% increase in *P. undulatum* cover-abundance after *P. undulatum* cover-abundance exceeds 60% at MORN.

**7-3.2.2. PORT**

Mean species richness also declined substantially with incremental increases in *P. undulatum* cover-abundance at PORT (Figure 7-3ii). Mean species richness declined from a mean of 15 species per quadrat where *P. undulatum* cover-abundance is between 10-19% to an average of four species per quadrat where *P. undulatum* cover-abundance exceeded 90%. Species richness was highest (18 species) in the only quadrat sampled at this site where *P. undulatum* was not recorded. The decline in mean species richness with incremental increases in *P. undulatum* cover-abundance at PORT follows the same pattern evident at MORN. Mean species richness declines when *P. undulatum* cover-abundance exceeds 20%, but a more considerable decline in this attribute is evident where *P. undulatum* cover-abundance exceeds 60%
Figure 7-3(i-iv). Influence of incremental increases in *P. undulatum* cover-abundance on mean species richness (±SE) at four sites in south east Australia.
7-3.2.3. CROA

The pattern of declining species richness with increasing cover-abundance of *P. undulatum* at CROA (Figure 7-3iii) is similar to the pattern evident at the invaded sites MORN and PORT, although the overall decline in mean species richness is not as substantial. Mean species richness declines from a mean maximum of 13 species per quadrat where *P. undulatum* cover-abundance is between 10-19%, to an average of six species per quadrat where *P. undulatum* cover-abundance is greater than 80%.

Mean species richness is highest in quadrats supporting minimal (10-19%) cover-abundance of *P. undulatum* at CROA; an average of four more species than in quadrats where *P. undulatum* was absent. Mean species richness is however similar in quadrats where *P. undulatum* is absent to quadrats supporting considerably higher levels of *P. undulatum* (70-79%) at this site.

7-3.2.4. BODL

In contrast to the other three sites sampled, mean species richness is maintained (between 10 to 14 species per quadrat) regardless of *P. undulatum* cover-abundance at BODL (Figure 7-3iv). Mean species richness is higher in quadrats supporting greater than 60% *P. undulatum* cover-abundance, compared to quadrats supporting less than 30% *P. undulatum* cover-abundance, at this site. The highest mean species richness at BODL was recorded in quadrats supporting 50-59% *P. undulatum* cover-abundance and the lowest mean species richness was recorded in quadrats where *P. undulatum* was absent.

7-3.3. Influence of *P. undulatum* on community cover-abundance

The cover-abundance of *P. undulatum* was significantly negatively correlated with total community cover-abundance at each of the four sites sampled. The strongest negative relationships between *P. undulatum* cover-abundance and community cover-abundance were apparent at the invaded sites, MORN (*r* = -0.68, *P* < 0.001) and PORT (*r* = -0.66, *P* < 0.001).
Despite the lack of association between *P. undulatum* cover-abundance and species richness at BODL, *P. undulatum* cover-abundance was significantly negatively correlated (*r* = -0.32, *P* < 0.01) with community cover-abundance at this site.

*P. undulatum* cover-abundance was significantly negatively correlated (*r* = -0.41, *P* < 0.001) with community cover-abundance at CROA, but this relationship was influenced to some extent by the dominance of *Monotoca elliptica* at this site. When the cover-abundance values of *M. elliptica* were masked in a subsequent analysis, the relationship between *P. undulatum* and community cover-abundance remained significant (*r* = -0.22, *P* < 0.05), but at a reduced level. While the cover-abundance of *M. elliptica* was not significantly correlated with species richness at CROA, a significant negative relationship was evident between *M. elliptica* cover-abundance and community cover-abundance (excluding *P. undulatum*) (*r* = -0.22, *P* < 0.05). The cover-abundance of *M. elliptica* and *P. undulatum* was also significantly negatively correlated (*r* = -0.30, *P* < 0.01) indicating some competitive interaction between these two species.

### 7-3.4. Influence of increasing *P. undulatum* cover-abundance on mean community cover-abundance

Declines in mean community cover-abundance with incremental increases in *P. undulatum* cover-abundance were recorded at all four sites (Figure 7-4i-iv), although loss of community cover-abundance was more substantial and occurred at lower *P. undulatum* cover-abundance levels at the invaded sites sampled.

### 7-3.4.1. MORN

A linear decline in mean community cover-abundance with incremental increases beyond 20% *P. undulatum* cover-abundance is evident at MORN (Figure 7-4i). This decline in community cover-abundance reflects the same pattern evident in declining mean species richness at this site.
7-3.4.2. PORT

Mean community cover-abundance also declines dramatically with incremental increases in *P. undulatum* cover-abundance at PORT (Figure 7-4ii). Mean community cover-abundance drops sharply where *P. undulatum* cover-abundance exceeds 20%, but reaches an obvious plateau between 30-59% *P. undulatum* cover-abundance. Mean cover-abundance declines after this critical level and plateaus again between 60-89% *P. undulatum* cover-abundance. The overall reduction in mean community cover-abundance from quadrats with minimal (<20%) cover-abundance of *P. undulatum*, compared to quadrats where *P. undulatum* cover-abundance exceeded 90%, is substantial.

7-3.4.3. CROA

Considerable variation in mean community cover-abundance is evident across the *P. undulatum* cover-abundance categories at CROA (Figure 7-4iii). Mean community cover-abundance declines most notably where *P. undulatum* cover-abundance exceeds 60% at this site. The overall decline in community cover-abundance at comparable levels of *P. undulatum* cover-abundance is not as substantial at this site compared to MORN and PORT.

7-3.4.4. BODL

As at CROA, the decline in mean community cover-abundance with increasing *P. undulatum* cover-abundance, was not as substantial at BODL (Figure 7-4iv) in comparison to the invaded sites sampled. Mean community cover-abundance fluctuates at the lower *P. undulatum* cover-abundance levels and remains relatively stable across the 20 to 59% *P. undulatum* cover-abundance intervals. As at CROA, mean community cover-abundance declines most notably where *P. undulatum* cover-abundance exceeds 60%.
Figure 7-4(i-iv). Influence of incremental increases in *P. undulatum* cover-abundance on mean community cover-abundance at four sites in south east Australia.
7-3.5. Variation in floristic attributes across the *P. undulatum* clump profile

The cover-abundance of *P. undulatum* was generally highest in the clump centres and adjacent quadrats at all sites sampled (Figure 7-5i-viii). In most cases, mean community cover-abundance mirrors increases and decreases in mean *P. undulatum* cover-abundance.

7-3.5.1. MORN

Variations in *P. undulatum* cover-abundance are reflected in the mean community cover-abundance across the north-south (Figure 7-5i) and the west-east (Figure 7-5ii) clump profiles sampled at MORN. Mean species richness is lowest in the clump centres and adjacent quadrats. Shading and other competition variables may reduce the availability of micro-sites for the establishment and persistence of indigenous species, especially in the clump centre and in the quadrats immediately south of the clump, where high *P. undulatum* cover-abundance values are evident.

7-3.5.2. PORT

Greater variation in mean community cover-abundance and *P. undulatum* cover-abundance are evident across the clump profiles sampled at PORT (Figures 7-5iii and 7-5iv) compared to MORN. Variation in the patterns evident along both transects sampled at PORT may be related to the nature of the invasion impacts exerted by the comparatively ‘young’ *P. undulatum* population at this site (see Chapter Six).

7-3.5.3. CROA

The effects of high *P. undulatum* cover-abundance on mean community cover-abundance are most pronounced in the centres of the clump profiles sampled at CROA (Figures 7-5v and 7-5vi). Greater variation in mean *P. undulatum* cover-abundance was evident across the west-east compared to the north-south transects sampled. An additional analysis of changes in floristic attributes across the
Figure 7-5(i-viii). Variation in mean (±SE) *P. undulatum* and community cover-abundance across the north-south and east–west clump profiles at four sites in south east Australia. Closed boxes (■) represent mean *P. undulatum* cover-abundance and open boxes (□) represent mean community cover-abundance.
P. undulatum clump profile were undertaken with M. elliptica cover-abundance values excluded, but as the same pattern was evident, these results were not included.

7-3.5.4. BODL

The pattern of association between mean P. undulatum and community cover-abundance across the clump profile at BODL (Figures 7-5vii and 7-5viii) is similar to that recorded at the other sites sampled. Mean community cover-abundance is again, lowest in the centre of the P. undulatum clump and adjacent quadrats supporting high P. undulatum cover-abundance.

7-3.6. Hierarchical cluster analyses of the influence of P. undulatum on vegetation composition

The hierarchical cluster analyses performed on the quadrat data obtained from the four sites confirm the important influence of P. undulatum on community composition (Figure 7-6i-iv). At each site, quadrat groups with similar P. undulatum cover-abundance scores are generally clustered together. Sub-clusters or groupings within these broad groups represent variation in species composition relative to local environmental factors and are best interpreted by examination of the two-way tables of quadrat and species associations (Figure 7-7i-iv).

7-3.6.1. MORN

At a coarse level, a broad division of quadrats supporting low-medium (division A) and medium-high (division B) P. undulatum cover-abundance values are evident in the dendrogram of quadrat associations produced for MORN (Figure 7-6i). Within these broad divisions, five clusters or groups are identified, and assigned an arbitrary descriptive classification based on the predominant P. undulatum cover-abundance scores in each group.

Quadrats in group 1 support low to medium cover-abundance of P. undulatum. This low to medium group is linked to the two groups that support low densities of P.
undulatum (groups 2a and 2b). Within-group variation is higher in groups 2a and 2b compared to group 1, reflecting the greater floristic diversity in quadrats where P. undulatum cover-abundance is comparatively low.

Groups 1, 2a and 2b are distinct from groups 3 and 4, which include quadrats where high P. undulatum cover-abundance scores were recorded. Within-group variability is comparatively lower in the group 3 quadrat assemblage where P. undulatum cover-abundance values are medium-high. The quadrats in group 4 supporting high P. undulatum cover-abundance show the least within-group variation reflecting the comparatively low floristic diversity in these quadrats. These quadrats were generally sampled in the middle regions of the transects although some exceptions to this trend are evident. P. undulatum cover-abundance estimates of greater than 90% for example, were recorded in the M2WE1 and M2WE10 quadrats, which occur at the western and eastern ends of the Clump 2 west to east transect, respectively. Due to the nature of the P. undulatum invasion at this site, it was not possible to sample a discrete clump in every case. The P. undulatum invasion at MORN is so advanced that some clumps are starting to merge (see Chapter Six). Hence, quadrats M2WE1 and M2WE10, represent the approximate centres of adjacent clumps.

7-3.6.2. PORT

P. undulatum exerts a clear influence on the quadrat associations formed from the hierarchical cluster analysis of floristic attributes at PORT (Figure 7-6ii). A broad division between quadrats supporting low to medium (division A) and high (division B) P. undulatum cover-abundance is also evident at this site. Six quadrat groups within these broader divisions are identified on the dendrogram of quadrat associations constructed for PORT. The lowest within-group variation is evident in quadrats where P. undulatum cover-abundance values are highest (division B/group 6). Quadrats assembled into this group show greater dissimilarity to, and lower within-group variation than, the groups of quadrats supporting low to medium P. undulatum cover-abundance. Within-group variation is slightly higher in the two low-medium (groups 1 and 3) quadrat groups, compared to the groups supporting medium-high (group 2) and medium (group 4), P. undulatum cover-abundance.
Figure 7-6i. Dendrogram of quadrat assemblages sampled at MORN derived from hierarchical cluster analysis of floristic attributes.

Quadrat codes indicate the clump number and position of the quadrats sampled along the transects (see section 7.2.3.1). *P. undulatum* cover-abundance values recorded in each quadrat are provided in parentheses and coarse groupings of quadrats reflecting *P. undulatum* cover-abundance values and are indicated.
Figure 7-61. Dendrogram of quadrat assemblages sampled at PORT derived from hierarchical cluster analysis of floristic attributes.

Quadrat codes indicate the clump number and position of the quadrats sampled along the transects (see section 7-2.3.1). *P. undulatum* cover-abundance values recorded in each quadrat are provided in parentheses and coarse groupings of quadrats reflecting *P. undulatum* cover-abundance values and are indicated.

```
0.0267  1.3334  2.6400  3.9467  5.2533  6.5600

Group 1
Low-medium
P.u. c-a

P1NS1  (P.u.2)  
P1NS3  (P.u.1)  
P1NS4  (P.u.1)  
P1WE10  (P.u.+)  
P2NS10  (P.u.+)  
P1NS2  (P.u.3)  
P2NS8  (P.u.3)  
P1NS5  (P.u.5)  
P1WE4  (P.u.3)  
P5WE6  (P.u.4)  
P5WE7  (P.u.3)  
P1WE3  (P.u.5)  
P5NS5  (P.u.5)  
P1WE5  (P.u.4)  
P1NS6  (P.u.4)  
P1WE6  (P.u.4)  
P4NS5  (P.u.5)  
P4WE2  (P.u.7)  
P3NS1  (P.u.6)  
P5WE2  (P.u.5)  
P5WE3  (P.u.4)  
P3WE6  (P.u.4)  
P5NS7  (P.u.4)  
P4WE1  (P.u.4)  
P3NS2  (P.u.4)  
P5WE10  (P.u.4)  
P4WE6  (P.u.6)  
P5NS1  (P.u.5)  
P5NS9  (P.u.6)  
P5WE9  (P.u.4)  
P1NS7  (P.u.2)  
P1NS10  (P.u.2)  
P4NS9  (P.u.3)  
P3NS9  (P.u.3)  
P4NS4  (P.u.2)  
P4WE4  (P.u.2)  
P4WE10  (P.u.2)  
P5NS2  (P.u.2)  
P2NS1  (P.u.3)  
P2NS4  (P.u.2)  
P2NS5  (P.u.4)  
P2WE3  (P.u.2)  
P1NS9  (P.u.2)  
P1WE1  (P.u.2)  
P1WE2  (P.u.2)  
P1WE7  (P.u.2)  
P1WE8  (P.u.2)  
P3NS1  (P.u.+)  
P3NS0  (P.u.1)  
P5NS3  (P.u.2)  
P3NS10  (P.u.2)  
P5WE8  (P.u.2)  
P3WE5  (P.u.4)  
P3WE8  (P.u.3)  
P5NS4  (P.u.2)  
P3WE7  (P.u.3)  
P3WE9  (P.u.2)  
P3WE10  (P.u.5)  
P4NS3  (P.u.2)  
```

Division A

Group 3
Low-medium
P.u. c-a
7-3.6.3. CROA

Two broad divisions based on predominant *P. undulatum* cover-abundance values are identified in the dendrogram of quadrat associations produced for CROA (Figure 7-6iii). Division A is comprised of two quadrat groups supporting medium-high (group 1) and low-medium (group 2) *P. undulatum* cover-abundance. No obvious differences in within-group variability are evident between these two groups, or the division B/group 3 quadrat assemblage, in which *P. undulatum* cover-abundance values were predominantly low.

7-3.6.4. BODL

Quadrats with similar *P. undulatum* cover-abundance values have again been grouped together in the dendrogram of quadrat affinities produced for BODL (Figure 7-6iv). At a coarse level again, a broad division between quadrats supporting high (division A) and low-medium (division B) *P. undulatum* cover-abundance is evident.

Group 1/division A quadrats, which support the highest *P. undulatum* cover-abundance values, show the least within-group variation, especially in the sub-grouping of quadrats where *P. undulatum* cover exceeds 70%. The quadrat assemblages with low-medium (group 2) and low (groups 3a, 3b, 3c) *P. undulatum* cover-abundance display similar levels of within-group variation. The separation of groups 4 and 5 from quadrat groups in which similar *P. undulatum* cover-abundance levels were recorded, is indicative of floristic variation at the site, which was the least homogenous of the four sites sampled. These patterns are best explored with reference to the two-way table constructed for this site (Figure 7-7iv).
Figure 7-6iii. Dendrogram of quadrat assemblages sampled at CROA derived from hierarchical cluster analysis of floristic attributes.

Quadrat codes indicate the clump number and position of the quadrats sampled along the transects (see section 7-2.3.1). *P. undulatum* cover-abundance values recorded in each quadrat are indicated in parentheses and coarse groupings of quadrats reflecting *P. undulatum* cover-abundance values and are indicated.
Figure 7-6iv. Dendrogram of quadrat assemblages sampled at BODL derived from hierarchical cluster analysis of floristic attributes.

Quadrat codes indicate the clump number and position of the quadrats sampled along the transects (see section 2.3.1). *P. undulatum* cover-abundance values recorded in each quadrat are indicated in parentheses and coarse groupings of quadrats reflecting *P. undulatum* cover-abundance values and are indicated.
7-3.7. Two-way table of species and quadrat assemblages

The quadrat groups depicted in the two-way tables (Figure 7-7i-vi) reflect the groups indicated in the dendrograms, but have been re-ordered to reflect increasing cover-abundance of *P. undulatum*, to enhance the clarity of the patterns displayed.

7-3.7.1. MORN

Several species commonly recorded in quadrats assembled into low and low-medium *P. undulatum* cover-abundance groups (groups 1, 2a, 2b and 3) are absent in the quadrat assemblage supporting high *P. undulatum* cover-abundance (group 4) (Figure 7-7i). These species include *Acrotriche serrulata* (Labill.) R. Br. (Honey Pots), *Pimelea humilis* R. Br. (Small Rice-flower) and *Hydrocotyle hirta* R. Br. ex A. Rich. (Hairy Pennywort). The occurrence and cover-abundance of many other commonly recorded species declined notably with increasing cover-abundance of *P. undulatum*. These species include *Hibbertia riparia* (R. Br. ex DC.) Hoogland (Erect Guinea-flower), *Epacris impressa* Labill. (Common Heath), *Burchardia umbellata* R. Br. (Milkmaids), *Orcularia varia* Hook. f. (Variable Stinkweed), *Euchiton involucratus* (G. Forst.) Anderb. (Common Cudweed), *Hypericum gramineum* G. Forst. (Small St. Johns Wort), *Leptospermum continentale* Joy Thomps. (Prickly Tea-tree), *Goodenia geniculata* R. Br. (Bent Goodenia), *Austrostipa rudis* ssp. *australis* S. W. L. Jacobs & J. Everett (Veined Spear-grass), *Poa morrissii* Vickery (Velvet Tussock-grass), *P. sieberiana* Spreng. (Tussock-grass), *Themeda triandra* Forrs. (Kangaroo Grass), *Oxalis exilis* A. Cunn. (Wood Sorrel), *Xanthorrhoea minor* R. Br. (Small Grass-tree), *Acrotriche prostrata* F. Muell. (Trailing Ground-berry), *Microleana stipoides* (Labill.) R. Br. (Weeping Grass) and the weeds *Hypochoris radicata* L. (Cat’s Ear) and *H. glabra* L. (Smooth Cat’s Ear).

In contrast, a small number of commonly recorded species more typical of shaded micro-environments, did not appear to be affected by increasing cover-abundance of *P. undulatum*. These species include *Viola hederacea* Labill. (Ivy-leaf Violet), *Drosera peltata* ssp. *auriculata* (Backh ex Planch.) B. J. Conn (Tall Sundew).
whittakeri Planch. (Scented Sundew), Lomandra filiformis (Thunb.) Britten (Wattle Mat-rush), Lagenifera stipitata (Labill.) Druce (Blue Bottle Daisy) and Gonocarpus tetracynus Labill. (Common Raspwort). The cover-abundance of the dominant eucalypt at this site, Eucalyptus obliqua L’Her (Messmate), is also not obviously affected by *P. undulatum* based on these results although little evidence of eucalypt regeneration was observed at the study site. A considerable number of species sampled at MORN occurred too infrequently to conduct any meaningful analysis of their relationship with *P. undulatum*. No species appear to be obviously favoured by increasing cover-abundance of *P. undulatum*.

*Gahnia radula* (R. Br.) Benth. (Thatch Saw-sedge) and *Pteridium esculentum*, both common species at MORN, persisted in quadrats supporting high cover-abundance of *P. undulatum*. The cover-abundance of both these species declined however, as *P. undulatum* became more dominant. *P. undulatum* cover-abundance is significantly negatively correlated with *G. radula* cover-abundance (*r* = -0.33, *P* < 0.01) and *P. esculentum* cover-abundance (*r* = -0.34, *P* < 0.01) at this site.

Minor variations evident within the quadrat groups supporting similar *P. undulatum* cover-abundance scores are related to subtle variations in floristic composition. For example, slight variations are evident in the characteristic species composition of groups 2a and 2b; the *P. undulatum* ‘low’ quadrats. Group 2a is comparatively less diverse than group 2b and supports higher densities of low shrubs, herbs, grasses and sedges than the quadrats assembled into group 2b.
7.3.7.2. PORT

Declines in several commonly recorded species with increasing cover-abundance of *P. undulatum* are evident in the two-way table of quadrat and species assemblages constructed for PORT (Figure 7-7ii). Species showing obvious declines with increasing *P. undulatum* include *Hibbertia fasciculata var. prostrata* (Hook.) Hook. f. (Bundled Guinea-flower), *Themeda triandra, Bursaria spinosa* Cav. (Sweet Bursaria), *Pteridium esculentum, Clematis aristata* DC. (Old Man’s Beard) and *Hydrocotyle laxiflora* DC (Stinking Pennywort).

*Viola hederacea, Acacia melanoxyylon* R. Br. (Blackwood), *Lomandra filiformis* and *Acaena novae-zelandiae* Kirk. (Bidgee-widgee), were amongst some of the common species recorded at PORT that were not obviously affected by increasing *P. undulatum* cover-abundance. No species appear to be favoured by higher densities of *P. undulatum*, with the possible exception of *Rubus* sp., which was only recorded in quadrats supporting high *P. undulatum* cover-abundance values. *Indigofera australis* Willd. (Austral Indigo) was only recorded in quadrats where *P. undulatum* cover-abundance was low but given all records of this species are limited to clump two west-east transects, this is probably more indicative of contagious distribution in *I. australis*, than an association with *P. undulatum*.

The separation of quadrat groups supporting similar cover-abundance of *P. undulatum* (groups 1 and 3 – both low-medium) is again related to subtle variations in species composition. A principal difference between these groups appears to be in the relative cover-abundance of *Bursaria spinosa*, which is a dominant species in the group 1 quadrats and a comparatively minor component of the group 3 quadrats.
<table>
<thead>
<tr>
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<th>Column 2</th>
<th>Column 3</th>
<th>Column 4</th>
<th>Column 5</th>
<th>Column 6</th>
</tr>
</thead>
<tbody>
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<td>Data 4</td>
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<td>Data 14</td>
<td>Data 15</td>
<td>Data 16</td>
<td>Data 17</td>
<td>Data 18</td>
</tr>
</tbody>
</table>

Note: The table continues with similar data entries.
7.3.7.3. CROA

Most of the plants sampled at CROA were recorded very infrequently and as such it is more difficult to assess the influence of increasing *P. undulatum* cover-abundance on community composition (Figure 7-7iii). Some interesting patterns are however evident amongst the more commonly recorded species at this site.

The negative correlation between *P. undulatum* and *Monotoca elliptica* is clear in the two-way table of quadrat and species assemblages produced for the CROA data set. It is difficult to determine from this analysis alone, whether either of these species has a competitive advantage over the other and no clear differences are evident in the assemblages of species associated with *M. elliptica* or *P. undulatum*.

Species obviously suppressed by increasing cover-abundance of *P. undulatum* include *Banksia serrata* L. f. (Saw Banksia), *Bursaria spinosa*, *Pteridium esculentum* and *Clematis aristata*. Many of the commonly recorded species at CROA were not obviously affected by increasing *P. undulatum*. These species include *Banksia integrifolia* L. f. (Coast Banksia), *Lomandra longifolia* Labill. (Spiny-headed Mat-rush), *Viola hederacea*, *Dichondra repens* J. R. & G. Forst. (Kidney Weed), *Dianella tasmanica* Hook f. (Tasman Flax-lily), *Elaeocarpus reticulatus*, *Eucalyptus botryoides, Comprosma quadridifida* (Labill.) B. L. Rob (Prickly Currant Bush) and *Eustrephus latifolius* R. Br. (Wombat Berry). No species appear to be obviously favoured by increasing cover-abundance of *P. undulatum* at CROA.
7-3.7.4. BODL

Some separation of two reasonably distinct vegetation communities is evident in the BODL two way table (Figure 7-7iv). Quadrats supporting similar *P. undulatum* cover-abundance were clustered in both of these vegetation types indicating the important influence this species exerts on species composition in both communities. The species composition of quadrats assembled into groups 1, 2 and 3 are typical of an open *Eucalyptus botryoides* woodland and quadrats in groups 4 and 5 are more characteristic of a *Eucalyptus maculata-Macrozamia communis* forest community.

Species typical of the *E. botryoides* woodland appear to be more affected by increasing cover-abundance of *P. undulatum* than species typical of the *C. maculata-M. communis* forest, which generally supports a denser canopy cover. Declines are most obvious in *Hibbertia fasciculata* var. *prostrata*, *Clematis aristata*, *Senecio quadridentatus* Labill. (Cotton Fireweed) and *Banksia serrata*. *Macrozamia communis* also declines with increasing *P. undulatum* cover-abundance, however this relationship was not significant (*r* = -0.13, *P* > 0.05).

Species not obviously affected by increasing *P. undulatum* include *Gahnia sieberiana* Kunth. (Red-fruit Saw-sedge), *Dichondra repens*, *Oplismenus hirtellus* (L.) P. Beauv. (Australian Basket-grass), *Clematis microphylla* DC. (Small-leaved Clematis), *Desmodium brachypodum* A. Gray (Large Tick-trefoil), *Schelhammera undulata* R. Br. (Lilac Lily) and *Indigofera australis*. Clumps of the fleshy-fruited shrub, *Elaeocarpus reticulatus*, occur in quadrats supporting high densities of *P. undulatum*. Pied Currawongs feed on the fruits and seeds of both these species (see Chapter 5) and this association may be indicative of previous bird dispersal patterns.
7-3.8. Influence of *P. undulatum* on structural guilds

Matrices of the cumulative cover-abundance of each structural guild and the corresponding *P. undulatum* cover-abundance for each quadrat sampled were assembled for the four sites. The significance of the interactions between all variables were tested by correlation analyses but only the interactions between *P. undulatum* and the structural guilds are presented in Table 7-4. The full correlation matrices constructed for each site are included in Appendix 7.

7-3.8.1. MORN

*P. undulatum* cover-abundance was significantly negatively correlated with the cover-abundance of graminoids (*r* = -0.46, *P* < 0.001), herbs (*r* = -0.46, *P* < 0.001), low shrubs (*r* = -0.27, *P* < 0.01) and shrubs (*r* = -0.29, *P* < 0.01) at MORN. No significant correlations were evident between *P. undulatum* cover-abundance and the cover-abundance of the trailers, twiners, creepers and climbers, tall shrubs/small trees and trees guilds.

7-3.8.2. PORT

The cover-abundance of *P. undulatum* was significantly negatively correlated with all guilds assessed at PORT with the exception of the low shrub and shrub guilds. *P. undulatum* was significantly negatively correlated with the graminoid (*r* = -0.48, *P* < 0.001) and herb (*r* = -0.45, *P* < 0.001) guilds at this site. The strength of the negative correlations between *P. undulatum* and the tall shrub/small trees (*r* = -0.21), trees (*r* = -0.20) and twiners, trailers, creepers and climbers (*r* = -0.21) guilds were weaker, but still significant (all *P* < 0.05).

7-3.8.3. CROA

In contrast to the relationships evident at the invaded sites MORN and PORT, *P. undulatum* was not significantly correlated with the cover-abundance of herbs or graminoids at CROA (both *P* > 0.05). There were also no significant correlations
between \textit{P. undulatum} cover-abundance and that of the trees, shrubs, and trailers, twiners, creepers and climbers guilds (all \( P > 0.05 \)).

\textit{P. undulatum} cover-abundance was however, highly significantly negatively correlated (\( r = -0.42, \ P < 0.001 \)) with the cover-abundance of the tall shrubs/small trees guild at CROA. This suggests that the competitive effects exerted by \textit{P. undulatum} at this site are most evident on species occupying a similar structural niche. When the cover-abundance of \textit{Monotoca elliptica} was excluded from a re-analysis of the relationship between \textit{P. undulatum} and the tall shrubs/small trees guild, the relationship between these variables remained significant (\( r = -0.33, \ P < 0.01 \)), but at a reduced level.

\textbf{7-3.8.4. BDL}

\textit{P. undulatum} cover-abundance was not significantly correlated with the cover-abundance of the graminoid, herb, low shrub, shrub or tree guilds sampled at BDL (all \( P > 0.05 \)). A significant positive correlation (\( r = 0.26, \ P < 0.01 \)) was evident between \textit{P. undulatum} cover-abundance and the cover-abundance of the trailers, twiners, creepers and climbers guilds—this is the only positive association between \textit{P. undulatum} and any lifeform guild recorded in the study.

The cover-abundance of \textit{P. undulatum} was again, significantly negatively correlated (\( r = -0.24, \ P < 0.05 \)) with the cover-abundance of the tall shrubs/small trees guild at BDL. As at CROA, the principal negative impact of increasing \textit{P. undulatum} cover-abundance at BDL, appears to be exerted on the species' structural analogues.

\textbf{7-3.9. Association between \textit{P. undulatum} and the cover-abundance of other introduced plants}

Cumulative weed cover-abundance was not significantly correlated with \textit{P. undulatum} cover-abundance at PORT (\( r = -0.17, \ P > 0.05 \)) or BDL (\( r = 0.04, \ P > 0.05 \)). Weed cover-abundance was however significantly negatively correlated with \textit{P. undulatum} cover-abundance at MORN (\( r = -0.30, \ P < 0.01 \)), indicating that other
weedy species are suppressed by increasing *P. undulatum*. No weed species were recorded in the quadrats sampled at CROA.

Table 7-4. Correlations between *P. undulatum* and the cover-abundance of seven structural guilds at four sites in south east Australia.

<table>
<thead>
<tr>
<th>Structural guild</th>
<th>MORN</th>
<th>PORT</th>
<th>CROA</th>
<th>BODL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Graminoids</td>
<td>-0.46***</td>
<td>-0.48***</td>
<td>-0.07NS</td>
<td>0.03NS</td>
</tr>
<tr>
<td>Herbs</td>
<td>-0.46***</td>
<td>-0.45***</td>
<td>-0.18NS</td>
<td>-0.08NS</td>
</tr>
<tr>
<td>Trailers, twiners,</td>
<td>-0.12NS</td>
<td>-0.21*</td>
<td>0.02NS</td>
<td>0.26**</td>
</tr>
<tr>
<td>creepers, climbers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low Shrubs</td>
<td>-0.27**</td>
<td>-0.02NS</td>
<td>n/a</td>
<td>0.05NS</td>
</tr>
<tr>
<td>Shrubs</td>
<td>-0.29**</td>
<td>-0.14NS</td>
<td>-0.17NS</td>
<td>0.19NS</td>
</tr>
<tr>
<td>Tall shrubs/small trees</td>
<td>0.14NS</td>
<td>-0.21*</td>
<td>-0.42***</td>
<td>-0.24*</td>
</tr>
<tr>
<td>Trees</td>
<td>-0.04NS</td>
<td>-0.20*</td>
<td>0.08NS</td>
<td>0.08NS</td>
</tr>
</tbody>
</table>

Significant relationships (Spearman Rank Correlation Coefficient - two-tailed test) are indicated (* P < 0.05, ** P < 0.01, *** P < 0.001, NS Not Significant P > 0.05).

7-4. Discussion

This study has demonstrated that species richness, community cover-abundance and structural complexity decline with incremental increases in *P. undulatum* cover-abundance. Variation in response to increasing *P. undulatum* cover-abundance is however evident at the site, guild and species level. At the broadest level, this study has demonstrated that high cover-abundance of *P. undulatum* imposes considerable impacts on invaded communities, compared to the natural communities sampled. Species richness was significantly negatively correlated with *P. undulatum* cover-abundance at the invaded sites MORN and PORT and the natural site CROA. Considerable differences in the pattern of attrition in mean species richness were evident between the natural and invaded sites sampled.

At both invaded sites, mean species richness declined notably once *P. undulatum* cover-abundance exceeded 20%. In contrast to the invaded sites, mean species
richness at CROA only declined notably when *P. undulatum* cover-abundance exceeded 60%. Species richness was not significantly correlated with *P. undulatum* cover-abundance at the natural BODL site, where mean species richness was maintained between 10-14 species per quadrat, regardless of *P. undulatum* cover-abundance. Mean species richness at this natural site was higher in quadrats supporting >50% *P. undulatum* cover-abundance, than in quadrats supporting <30% *P. undulatum* cover-abundance.

Community cover-abundance was significantly negatively correlated with *P. undulatum* cover-abundance at all sites but again, the decline in community cover-abundance was most pronounced at the invaded sites sampled. Mean community cover-abundance at PORT for example, was highest (~140%) in the single quadrat where *P. undulatum* was absent and lowest (~5%) in quadrats where *P. undulatum* cover-abundance exceeded 90%. Various ‘plateaus’ were evident within the overall pattern of declining mean community cover-abundance with increasing *P. undulatum* cover-abundance at PORT. These plateaus may represent critical invasion threshold levels for some species or groups of species.

A consistent decline in mean community cover-abundance was evident with each incremental increase beyond the 10-19% *P. undulatum* cover-abundance interval at MORN. Differences in the pattern of declining community cover-abundance with increasing *P. undulatum* between PORT and MORN, may be related to the relative age or invasion stage, of the two populations. Seedling and juvenile densities were significantly higher at PORT compared to MORN, while the density of adult (>1m) *P. undulatum* was higher at MORN (see Chapter 6). A dense cluster of *P. undulatum* seedlings and juveniles may be allocated a similar cover-abundance score as one densely-foliaged adult tree, although the impacts exerted by these progressive developmental stages of *P. undulatum* may be expressed differently and impose different impacts on community attributes.

Community cover-abundance was significantly negatively correlated with *P. undulatum* cover-abundance at CROA and BODL but again, the loss of community cover-abundance was not as substantial at these natural sites, compared to the invaded sites sampled. A marked decline in mean community cover-abundance
occurred at approximately 60% *P. undulatum* cover-abundance at the natural sites, whereas community cover-abundance declined notably from about 20% *P. undulatum* cover-abundance at the invaded sites. At all sites, declines in mean community cover-abundance were most pronounced in the centres of the radiating clumps where shading and other competitive effects are most concentrated.

The mosaic of microclimates provided by *P. undulatum* canopies at various stages of development may contribute to the diversity of microsites available within the community for other species. A slight rise in mean species richness from the <10% to 10-19% *P. undulatum* cover-abundance interval at MORN, and fluctuation in mean species richness across the progressive *P. undulatum* cover-abundance intervals at CROA and BODL, may be evidence of community response to ‘intermediate disturbance’ (Grubb 1977; Petraitis et al. 1989). More species present in the natural communities would be expected to be better adapted to the microclimatic conditions imposed by *P. undulatum*, than species in the invaded communities. Shading and other competitive effects contribute to a decline in mean community cover-abundance at these natural sites however, when *P. undulatum* cover-abundance exceeds 60%.

The analyses of association between *P. undulatum* and the various structural guilds at the natural and invaded sites sampled indicate some clear trends. The herb and graminoid guilds were significantly negatively correlated with increasing cover-abundance of *P. undulatum* at the invaded sites. By contrast, no significant correlations between these guilds and *P. undulatum* cover-abundance were evident at the natural sites sampled. Negative correlations between *P. undulatum* and its structural analogues – the tall shrubs/small trees guild were evident at both natural sites.

Competitive displacement of structural analogues by *P. undulatum* effectively reduces the diversity and complexity of resources provided by this guild, even if the volume of tall shrubs/large trees is increased by *P. undulatum* population expansion. *P. undulatum* is not simply replacing its less competitive structural analogues at these sites. The sheer density of *P. undulatum* imposes a substantial change in the distribution, abundance and biomass of the tall shrubs/small trees layer in these
communities. A range of ecosystem-level changes are likely to be induced by the imposition of a fundamentally novel structural layer (Vitousek 1986).

All structural guilds represented at PORT, with the exception of the low shrub and shrub guilds, were significantly negatively correlated with *P. undulatum* cover-abundance. Low shrubs and shrubs were significantly negatively correlated with *P. undulatum* at MORN, but no significant interactions were evident between *P. undulatum* and species comprising the tall shrubs/small tree and tree guilds at this site. Differences in significant interactions between *P. undulatum* and the various structural guilds demonstrated for PORT and MORN may again, be a function of the relative age and stage of the *P. undulatum* invasion at these sites. Alternatively, these differences may reflect minor site variation in the relative representation of each guild (see Table 7-3).

It is also possible that some guilds assessed have already been displaced to some extent by *P. undulatum* and other disturbance factors. Regenerative opportunities for fire-adapted shrubs and trees have been minimal at MORN for example, with the long-term absence of fire and concurrent invasion of *P. undulatum* (Bedggoed et al. 1990). While regeneration was not quantitatively assessed in this study, evidence of tree and shrub regeneration appeared low at MORN and PORT, compared to similar vegetation assemblages where *P. undulatum* is absent (pers. obs.). Additionally, eucalypts encompassed by *P. undulatum* clumps at the invaded sites were invariably in poor health or dead (pers. obs.). Whether this is directly related to competitive interactions with *P. undulatum* or other site factors is unknown. Eucalypt dieback is a serious issue in woodland and forest remnants across the Australian landscape and has been attributed to a range of causal factors (Heatwole & Lowman 1986; Landsberg et al. 1990). Whatever the impetus for decline in these species is, the situation is compounded by a lack of effective regeneration at the invaded sites sampled (pers. obs.).

The hierarchical cluster analyses confirmed the important influence of *P. undulatum* on the floristic composition of the natural and invaded sites sampled. Quadrats supporting similar *P. undulatum* cover-abundance were consistently grouped together based on their inherent floristic similarities. Quadrat groups supporting high
P. undulatum cover-abundance values displayed the lowest within-group variation in all cases.

The two-way table presentations provide an opportunity to explore the impacts of increasing P. undulatum cover-abundance on a species-specific basis. It is acknowledged that natural variation in floristic patterns including contagious distributions in some species may confound the assessment of P. undulatum impacts at this level. Some commonly recorded species however, obviously declined in occurrence or cover-abundance with increasing P. undulatum. A common theme emerged across all sites, in the type of species displaced by high P. undulatum cover-abundance. In most cases, the declines involved sclerophyllous shrubs and other grasses and herbs typical of open, dry forest environments including Bursaria spinosa, Leptospermum continentale, Banksia serrata, Xanthorrhoea minor, Acrotriche serrulata, Epacris impressa, Burchardia umbellata and various species in the family Poaceae.

Declines in sclerophyllous species richness with P. undulatum invasion of dry sclerophyll forests in the greater Melbourne and Sydney regions, have been reported in previous studies and appear to be a key invasion impact imposed by P. undulatum (Gleadow & Ashton 1981; Buchanan 1989b; 1991; Mullett & Simmons 1995; Rose 1997a, Rose & Fairweather 1997).

It is not possible to deduce from these data whether infrequently recorded species, which characteristically occur at low frequencies in the communities sampled, are affected by P. undulatum. Controlled competition experiments may provide some insight into these relationships, but the intricacies of the ecological relationships within and between these species would not be adequately represented. The seasonal and clump-specific sampling constraints of this study necessarily precluded determination of any local extinction in the indigenous plant populations sampled. Nevertheless, substantial declines in cover-abundance were documented for many species, representative of most structural guilds, with increasing P. undulatum. Loss of genetic diversity within and between populations may be a consequence of the local declines in affected species (Ehrlich 1986; Hobbs & Mooney 1998). Declines in the local abundance of plant populations may lead to local extinction and in
extreme cases, species extinction (Ehrlich 1986; Hobbs & Mooney 1998). As such the declines in local abundance documented for some species in the current study, are of conservation significance.

Some species sampled in the current study were not obviously affected by high _P. undulatum_ cover-abundance. Such species are typical of shaded, mesic micro-environments and include _Viola hederacea, Drosera whittakeri, D. peltata_ ssp. _auriculata_ and various species in the _Lomandra_ and _Lepidosperma_ genera. These species may be better able to tolerate conditions beneath the _P. undulatum_ canopy than species more typical of open, drier sites. There is no evidence from the current study to suggest that populations of any of these characteristically mesic species are increasing in response to _P. undulatum_ invasion. The displacement of sclerophyllous species described, however, may provide expansion opportunities for species able to tolerate the changed conditions. Such changes may have already occurred in some dry forest remnants in the Sydney region, where altered fire regimes and long-term invasion by _P. undulatum_ have promoted a shift towards mesic, fire-sensitive, shade-tolerant species that are adapted to moist, nutrient-rich soil conditions, to the detriment of the original sclerophyllous, fire-adapted flora (Rose 1997a, Rose & Fairweather 1997).

Significant positive correlations between _P. undulatum_ and weed species richness and cover were reported by Rose and Fairweather (1997), however this trend was not apparent in the current study or reported by Mullett and Simmons (1995). _P. undulatum_ and weed species cover-abundance was significantly negatively correlated at MORN, but this was the only significant association determined between these attributes in the current study. Key differences in sampling design and site selection between the two studies may explain some of this variation. Rose and Fairweather (1997) deliberately sampled remnants within the Sydney urban matrix, where high weed frequencies would be expected, to satisfy the broader objectives of assessing the impact of suburb age on vegetation composition. Sites with low weed densities outside the urban matrix were purposefully sampled in the current study to better elucidate the influence of _P. undulatum_ on community composition.
Rose and Fairweather (1997) proposed two possible explanations for the consistent change observed in species composition with increasing suburb age and importance of *P. undulatum* in Sydney. First, that *P. undulatum* exerts a 'direct influence' on community composition and second, that *P. undulatum* and the associated suite of species with each suburb age were 'passively associated' (Rose & Fairweather 1997). In this second scenario, floristic composition is more determined by the prevailing environmental conditions especially changes in disturbance regimes, than the influence of *P. undulatum*.

The clump sampling strategy employed in this current study enables some separation of the influence of *P. undulatum* impacts on community composition, from those of changed disturbance regimes. At the clump scale sampled, the vegetation was reasonably homogenous and subject to the same disturbance pressures, including changed fire regimes. Tolerance to such factors varies appreciably within and between species and over various temporal and spatial scales. The impacts of *P. undulatum* invasion on community composition are undoubtedly confounded to some extent by changes in disturbance regimes, however, at the clump level sampled, the prevailing environmental conditions are likely to be reasonably constant. Changes in the community composition measured across the clump profile and with increasing *P. undulatum* cover-abundance in the current study can be attributed to changes in ecosystem properties and function imposed by increasing cover-abundance of *P. undulatum* with some confidence.

The ecosystem-level changes imposed by increasing cover-abundance of *P. undulatum* operate in a complex and often synergistic manner. The deep shade cast by the dense *P. undulatum* canopy is perhaps the critical invasion effect contributing to changes in microclimatic conditions and the displacement of some plant species (Gleadow & Ashton 1981; Mullett & Simmons 1995). The sampled communities are already subject to altered fire regimes but the composition and moisture content of fuels are further altered by the increased shading and leaf litter associated with high densities of *P. undulatum*. A higher concentration of nutrients and allelopathic compounds present in *P. undulatum* foliage (Gleadow & Ashton 1981) are likely to further modify ecosystem properties and aspects of ecosystem functioning. The impacts of these factors are likely to vary considerably over temporal and spatial
scales, depending on the stage and scale of the *P. undulatum* invasion, the characteristics of the invaded or host community and the nature and extent of various disturbance factors.

It is likely that the substantial reduction in light infiltration—reduced to 2% of full daylight in severe cases (Gleadow & Ashton 1981) is of itself, enough to displace many species. Mullett and Simmons (1995) demonstrated that light infiltration was significantly negatively correlated with *P. undulatum* cover-abundance and native species richness at four dry sclerophyll remnants in Victoria. The modification of community light regimes by invasive plants is recognised as an important factor contributing to the displacement of indigenous species (Hobbs & Mooney 1986; Waterhouse 1986; Braithwaite et al. 1989; Simberloff 1993; Woods 1997). The effects are especially dramatic in communities where dense shading is a novel condition (Woods 1997), such as in the invaded dry open eucalypt forests sampled in the current study. Goodland and Healey (1996, 1997b) reported that the growth and survival of even shade-tolerant species were affected by shading from dense *P. undulatum* infestations in the Blue Mountains region of Jamaica.

At high densities, fundamental ecosystem functions such as nutrient cycling may also be affected by *P. undulatum*. Increased moisture retention in the soil and litter layer is an effect of the shaded microclimate and comparatively high leaf litter input beneath the *P. undulatum* canopy (Gleadow & Ashton 1981). *P. undulatum* leaf litter also contains high concentrations of some essential nutrients (Gleadow & Ashton 1981), however little is known about *P. undulatum* decomposition rates. Changes in soil micro-fauna have not been investigated in relation to *P. undulatum* invasion, but have been reported as a consequence of other environmental weed invasions (Aplet 1990; Bingelli & Hamilton 1993).

Considerable alteration of habitat opportunities is a further consequence of the floristic and structural simplification imposed by *P. undulatum* invasion (Mullett & Simmons 1995, Goodland & Healey 1996, 1997b; Rose 1997b; Mullett 1999). Habitat resources at the ground layer are simplified by the significant decline in herb and graminoid cover reported in this study. The increased canopy cover provided by high densities of mature *P. undulatum* and concurrent displacement of indigenous
trees and shrubs, also changes the quality and quantity of canopy foraging, shelter, nesting and roosting opportunities at affected sites. Shifts in the composition, distribution and abundance of faunal assemblages may occur, or have already occurred, in response to these changes in habitat resources. Brown et al. (1991) for example, noted that basking opportunities for some heliothermic poikilotherms were reduced beneath the *P. undulatum* canopy at invaded sites.

Changes in faunal composition may further affect ecosystem properties and functions including pollination and dispersal regimes (see Chapter 5). Such disruptions may include the attraction of higher densities and/or a different composition of seed dispersal agents that may alter the dispersal potential of both *P. undulatum* and other indigenous fleshy-fruited species. As Schiffman (1997) warns, novel relationships between fauna and invasive plants may have unexpected ecosystem-level consequences. This critical aspect of environmental weed invasion ecology requires further investigation (Adair & Groves 1998).

Changes in species composition, shading, soil and litter moisture, nutrient availability, allelopathic properties and other ecosystem effects associated with *P. undulatum* invasion, fundamentally affect the community resource base and aspects of ecosystem functioning. Substantial changes of this nature “can alter the conditions of life for all of the organisms in an ecosystem” (Ramakrishnan & Vitousek 1989, p. 281) and inevitably influence the successional trajectory of affected communities (Luken 1997). Species or suites of species better able to tolerate the changed conditions may be selected for over the previous assemblage of established species (Luken 1997).

Luken (1997) suggests a pattern of ‘long-term dominance’ may be likely in species such as *P. undulatum*, that modify disturbance regimes to suit their own requirements, especially when such changes are accompanied by the displacement of other species. The pre-adaptation and adaptability of *P. undulatum* to a range of environments and environmental conditions (see Chapter 4) and the ability to cope with drought stress (Gleadow & Rowan 1982) and other perturbations, increases the likelihood that this species will maintain its dominance through successional phases.
An association between *P. undulatum* and other fleshy-fruited species including *Elaeocarpus reticulatus*, *Eustrephus latifolius* and *Comprosma quadrifida* was noted at both CROA and BODL. These patterns are probably artifacts of previous bird dispersal patterns and this spatial pattern has also been observed elsewhere. In South Africa for example, *P. undulatum* generally occurs in clumps with other fleshy-fruited species (Richardson & Brink 1985; Kruger *et al.* 1986). Food resources provided by the developing clumps of fleshy-fruited species attract further frugivore activity and thus provide further opportunities for seed dispersal and clump enlargement (Richardson & Brink 1986; Kruger *et al.* 1986, Geldenhuys *et al.* 1986 and see Chapters 5 & 6). Increases in the distribution and abundance of adaptive frugivores may also contribute to the incursion of fleshy-fruited species into remnant vegetation, especially when ornamental plantings are in close proximity (see Chapter 5).

The relative importance of other bird dispersed, fleshy-fruited trees and shrubs increased with suburb age and *P. undulatum* density in the Sydney remnants sampled by Rose and Fairweather (1997). These species included *Elaeocarpus reticulatus*, *Cinnamomum camphora*, *Ligustrum sinense*, *Ochna serrulata* (Hochst.) Walp. (Bird’s Eye Bush) and *Lantana camara*. All of these species are dispersed by Pied Currawongs, which are common in the greater metropolitan region of Sydney (Buchanan 1989b; Rose & Fairweather 1997). The multiple-invasion of fleshy-fruited weeds observed by Rose and Fairweather (1997) may be indicative of a future successional trend in dry forest remnants invaded by *P. undulatum* in Victoria.

Fleshy-fruited weed species were not prevalent in the invaded dry forest environments sampled in Victoria in the current study or by Mullett (1993). As the microclimate of such invaded sites becomes more mesic and shaded however, it is possible that conditions will become more suitable for a suite of fleshy-fruited weeds, including those listed above. Such invasions are already evident in some wet sclerophyll forest remnants in the greater Melbourne area. Twelve of the 14 weeds nominated for priority control in Sherbrooke Forest (Freshwater 1989) for example, are fleshy-fruited, bird-dispersed species.
Given that limited resources are allocated to environmental weed management programs, some authors have suggested that that the efficacy of weed management in natural ecosystems could be improved by managing weeds below a threshold level where native plant declines and other ecosystem-level effects are evident (Adair & Groves 1998; Henry 1994 in Panetta & James 1999). This concept does have ‘intuitive appeal’ (Panetta & James 1999), but the identification of damage thresholds is greatly complicated by the choice of ecological indicators employed. Additionally, an evaluation of the benefits provided by the natural area is required before management objectives and damage thresholds can be determined (Panetta & James 1999). Natural ecosystems provide an array of direct and indirect benefits that may or may not have quantifiable values. The perception of ‘value’ may vary considerably and in this sense, any assessment of weed damage thresholds in natural systems, would be further complicated by social, political and economic considerations. It is beyond the scope of this thesis to fully explore the intricacies of these social, political and economic issues and their ramifications for environmental weed management. It is acknowledged however, that these concerns influence the effectiveness of current environmental weed management programs (Hobbs & Humphries 1995; Humphries 1995; Adair & Groves 1998) and these issues are discussed further in Chapter 8.

These factors aside, weed damage thresholds are still immensely difficult to identify in an ecological sense. At a simple level, the results from this study indicate that mean species richness declines once P. undulatum exceeds 20% at invaded sites. However, this may not be the case at all invaded sites and across the range of vegetation types subject to P. undulatum invasion. No clear threshold for this attribute was evident at the natural sites sampled either.

Community cover-abundance declined once P. undulatum exceeded 60% at the natural sites, but ecosystem properties and some functional processes including succession, may be substantially modified at this level of dominance. The ‘snap shot’ nature of the impacts quantified in this study should also be taken into account in the determination of damage thresholds. The various plateaus evident in declining community cover-abundance at PORT for example, may reflect the rapid and relatively recent invasion of P. undulatum at this site. The long-term invasion at
PORT may resemble the current situation at MORN, where a continued and relatively consistent decline in community cover-abundance was evident with each 10% increase in *P. undulatum* cover-abundance.

Damage thresholds are also likely to vary considerably between weed species and in accordance with the characteristics of the invaded communities. Morgan (1998a) reported a significant decline in grassland species richness and cover when the cover of non-native species exceeded 40%. Herb species richness and cover declined when *Lonicera tatarica* L. (Tatarian Honeysuckle) cover exceeded 30% in drier communities, but these invasion effects were not evident in mesic communities sampled (Woods 1993). Richardson *et al.* (1989) reported considerable declines in fynbos species richness when the cover of introduced species (mainly *Hakea*, *Acacia* and *Pinus* spp.) exceeded 50%. Loss of species richness was also equated with time since invasion in the latter study. Species richness and cover-abundance are therefore not likely to be reliable indicators of weed damage thresholds, especially if considered in isolation from other ecosystem-level effects.

From a broader conservation perspective, the influence of weed invasion on the composition of affected communities may be of greater importance in terms of defining thresholds and providing a more useful indicator of changes in functional processes, including succession. The issue with this approach is in determining the appropriate compositional elements to monitor (Lamont 1995). Disparate impacts were demonstrated for the various structural guilds assessed in this study, but the impact of *P. undulatum* on other ecological guilds remains unknown.

Environmental weed management is to some degree, conducted around the concept of a damage threshold, intuitive or subjective as these thresholds may be in the absence of quantitative data. Some objective criteria against which weed managers can prioritise resource allocation may be beneficial given the severe resources constraints that impede environmental weed management in Australia. This study has demonstrated that *P. undulatum* exerts significant impacts on the population status of some native species. Ecosystem-level properties and functions are further disrupted and the rate and direction of successional pathways are modified with high
levels of *P. undulatum*. The continued invasion of *P. undulatum* will contribute to the further attrition of biodiversity values at affected sites.

### 7-5. Summary

*P. undulatum* exerts a considerable influence on the composition, structure and function of natural and invaded plant communities. Species richness and community cover-abundance were significantly negatively correlated with *P. undulatum* cover-abundance at the invaded sites sampled. Notable declines in these attributes were evident when the cover-abundance of *P. undulatum* exceeded 20%. The natural communities sampled were more resilient to higher cover-abundance of *P. undulatum* compared to the invaded sites sampled. Community cover-abundance was however, significantly negatively correlated with *P. undulatum* at these sites and notable declines in this attribute were evident where *P. undulatum* cover-abundance exceeded 60%.

Sclerophyllous species appear to be most affected by *P. undulatum* invasion and disparate impacts are exerted on various structural guilds. High *P. undulatum* cover-abundance disrupts a range of ecosystem-level properties and functions, including ultimately, the rate and direction of community succession. *P. undulatum* shading and related effects modify the microclimate beneath the clump canopy and contribute to the further alteration of fire regimes at invaded sites. These changes may select for fire-sensitive species adapted to shaded, mesic environments, over the preceding suite of species. *P. undulatum* invasions may also impact upon faunal populations through the simplification of habitat resources.
CHAPTER EIGHT

General discussion and conclusions

8-1. Review of main findings

The distribution and local abundance of *P. undulatum* has increased dramatically since European settlement in south east Australia. The species has been widely planted for its ornamental qualities and a range of other utilitarian purposes. From these widespread and abundant dispersal foci, a suite of generalist, opportunistic frugivores facilitate the movement of *P. undulatum* into native vegetation communities. The species’ inherent adaptability to a range of climatic and edaphic conditions, in combination with changes in natural fire regimes, have contributed to the establishment and expansion of *P. undulatum* populations in a diverse range of habitat types.

Phenotypic plasticity is considerable in *P. undulatum* and no clear patterns of geographic variation emerged from the study of leaf morphological attributes across the current range of this species on mainland south east Australia (Chapter 4). The pattern of morphological variation is particularly complex in Victoria, where the invasion of this species is most advanced. The species’ considerable phenotypic plasticity and adaptability to a range of environments and environmental conditions will likely promote further range expansion.

*P. undulatum* reaches reproductive maturity in four to five years. Pollination requirements appear to be met by generalist species and the introduced honeybee may an important pollination agent, especially in invasive populations and ornamental settings (Chapter 3). Functionally female plants produce a large annual fruit crop and the incidence of fruit production in predominantly male flowering plants is low. Seed collected from natural and invaded populations displayed high germinability and no significant differences were evident, within sites, in the germinability of seeds extracted from pre- and post-dehiscent fruits, with the exception of CROA (Chapter 5).

*P. undulatum* has not evolved a specialist dispersal mutualism with any one species; a suite of generalist, opportunistic frugivores feed on *P. undulatum* fruits and seeds at various stages of fruit dehiscence, thereby enhancing dispersal opportunities for this
species (Chapter 5). European Blackbirds and Pied Currawongs are implicated as the main avian dispersal agents of *P. undulatum* in south east Australia (Gleadow 1982; Mullett 1999). The germinability of *P. undulatum* seeds extracted from scats and pellets voided by these frugivores was greater than 90% and not significantly different to fresh *P. undulatum* seed (Chapter 5). The broader ecological implications emerging from relationships between fleshy-fruited environmental weeds and adaptive frugivorous dispersal agents are likely to be considerable (Chapter 5).

The contagious distribution pattern typical of *P. undulatum* is initiated by frugivorous dispersal agents, which preferentially eliminate undigested seeds while perching, and to a lesser extent, by autochorous dispersal. Conspecific germination pressures are presumably substantial and intra-specific competition pressures are likely to continue throughout all stages of this species’ life history given its clumped spatial distribution. Conspecific recruitment opportunities are limited beneath the densely-foliaged canopy of adult *P. undulatum* (Chapter 6). Dense shading, deep leaf litter and other competitive effects are probably the main factors preventing recruitment. Allelopathic inhibitors may also be important (Richardson & Brink 1985), although further research is required to resolve aspects of this relationship (Tunbridge 1997). Recruitment of successive generations is most likely to occur beneath the moderate canopy cover of eucalypts, other trees and shrubs and at the *P. undulatum* clump margin (Chapter 6). In this sense, the contagious distribution pattern instigated by frugivorous dispersal agents is reinforced by the species’ micro-climatic establishment requirements (Gleadow 1982 and see Chapter 6).

Densities of *P. undulatum* were on average, 2.7 times higher in invaded populations, compared to the natural populations sampled (Chapter 6). A male-bias was evident in all populations and no relationships between reproductive activity and the density of seedlings and juveniles were evident in the populations sampled (Chapter 6). The *P. undulatum* population profiles at the invaded sites and the natural population CROA were biased towards the early developmental stages and the most even proportional representation of individuals across the height class categories were evident at the natural populations MORW and GLEN. The continued expansion and local consolidation of *P. undulatum* populations is likely at all sites sampled in the absence of management intervention.
Invading populations of *P. undulatum* impose substantial changes on ecosystem-level properties and functions. Reduced light infiltration, increased leaf litter, changed nutrient composition, greater retention of soil and leaf litter moisture and the possible influence of allelochemicals are the principal impacts exerted by *P. undulatum* (Gleadow & Ashton 1981). These factors and other competitive effects are likely to intensify and compound with increasing *P. undulatum* density and cover-abundance. The ecosystem-level changes imposed by *P. undulatum* contribute to the displacement of indigenous species and alter the rate and direction of community succession (Chapters 6 & 7).

Mean species richness and cover-abundance both declined notably once *P. undulatum* cover-abundance exceeded 20% at the invaded sites and 60% at the natural sites sampled (Chapter 7). The natural communities sampled displayed comparatively greater resilience to the competitive effects of *P. undulatum*, but community attributes were affected at high densities or cover-abundance of this species.

Different impacts were exerted with increasing *P. undulatum* on the cover-abundance of the various structural guilds assessed (Chapter 7). The cover-abundance of herbs and grasses declined most substantially with increasing *P. undulatum* at the invaded sites whereas, at the natural sites sampled, the species’ structural analogues appeared to be most affected by increasing *P. undulatum* cover-abundance. *P. undulatum* exerts a considerable influence on community composition and declines in the cover-abundance of sclerophyllous species were evident across the four sites (Chapter 7). Broader changes in faunal assemblages are a likely consequence of the associated simplification of habitat resources. The process of *P. undulatum* invasion and some of the ecosystem-level impacts exerted by this species are summarised in Figure 8.1.
Figure 8-1. Diagrammatic representation of some of the processes and ecosystem-level effects of *P. undulatum* invasion in south east Australia.
8-2. Management of *P. undulatum* in south east Australia: Issues, impediments and opportunities

It is beyond the scope of this thesis to provide specific management prescriptions for invasive populations of *P. undulatum* as these would necessarily vary considerably between sites and in accordance with the characteristics of the host community and other landscape and land-use factors. Management considerations pertinent to the implementation of commonly employed control techniques are discussed below using examples of their application in south east Australia.

A number of physical, chemical and ecological control options are available to manage invasive populations of *P. undulatum*. To date however, control programs for *P. undulatum* have had limited success because inappropriate techniques have been implemented or, as is often the case in environmental weed management, the symptom and not the cause of the problem is addressed. These inefficiencies in *P. undulatum* management have been largely due to an inadequate understanding of the species’ biology, ecology and community inter-relationships and fundamentally, to insufficient resource allocation. Weed management programs are consistently under-funded and managers are effectively forced into implementing ineffectual weed management programs. Whether control programs are devised and implemented by government agencies or community groups, it is vital that the relatively few opportunities available for *P. undulatum* control are maximised.

Management objectives need to be clearly established prior to the implementation of control programs. If the overall objective for management is to maintain or enhance biodiversity values, then it should first be established if *P. undulatum* imposes a negative impact on these values. This is clearly the case at the invaded sites sampled in this study and may also be a consequence at sites within the natural range of this species, when densities or cover-abundance of *P. undulatum* exceed a critical level. *P. undulatum* plays an important role in the community composition of natural and invaded sites (Chapter 7). Managers therefore need to anticipate the community response to reduced densities of *P. undulatum* and determine the appropriate control technique(s) to promote the desired species composition.
Weed damage thresholds can theoretically, be determined by any of the measures used in this study, or by use of many other indicators, including faunal composition (Noss 1990). The key problem with each of these approaches is that when measured in isolation, an accurate representation of the damage inflicted by weeds on biodiversity values may not be provided. Other indicators of ecosystem function such as those advanced for agricultural systems (Lefroy & Hobbs 1992) and bush regeneration practices (Buchanan 1991) may have useful application in the identification of weed damage thresholds. Complex, specific ecological indicators, particularly those proposed by Buchanan (1991), are valuable tools for monitoring the effects of environmental weed invasions and restoration programs on ecosystem properties and function. However, weed managers are not likely to adopt complex, multi-faceted damage threshold assessment schemes, even though these may provide the most accurate representation of weed impacts. This is especially apparent given most environmental weed management in Australia is conducted by volunteers (AACM International 1997).

Even if critical *P. undulatum* damage thresholds could be identified as a means of directing intervention, there is no guarantee that populations could be maintained below this level given the unpredictable nature of resource allocation (Hall 1999). As for most environmental weed species, control of *P. undulatum* is likely to be most effective in the early invasion stages. Delaying control will reduce the potential for community restoration and increase the demand for management resources. *P. undulatum* is emerging as a serious weed in some parts of south west Western Australia (Keighery 1995, 1999) and there is a considerable risk in delaying control of emergent invasive populations in this region. Conservation managers in south west Australia have access to information regarding the threat posed by *P. undulatum* in the south east of the continent and the cost:benefit of controlling these emerging populations of *P. undulatum* should be obvious. It remains to be seen if early intervention will occur in this region, against the ‘opportunity costs’ (Panetta 1999) of spending resources in their (perceived) next best alternate use.

The development and implementation of management prescriptions for *P. undulatum* are likely to be more complex at sites within the natural range of this species. This may be especially apparent where the status of the population is uncertain (Rose 1997b) and
where beneficial interactions with other species are evident. A short case study outlined below exemplifies some of the issues facing managers of sites within the natural range of this species, where the distribution and local abundance of *P. undulatum* is obviously increasing.

At Morwell National Park (MORW) Victoria, a mature and presumably remnant stand of *P. undulatum* occurring along Foster’s Gully, supports more than half of the local population of the rare epiphytic orchid *Sarcochilus australis* (Lindl.) Rchb. f. (Butterfly Orchid) (Howell 1992). Managers are understandably nervous about controlling *P. undulatum* individuals that are gradually colonising adjacent drier slopes subject to altered fire regimes, as maintenance of the *P. undulatum*-*S. australis* association is an important management objective (Howell 1992). The immediate region of Foster’s Gully has been subject to major disturbances such as logging and quarrying prior to the declaration of the National Park in 1967 (Stevens 1995). It is difficult to interpret the role of these early yet significant disturbances in ‘remnant’ vegetation. It is possible that local *P. undulatum* densities may have increased in response to these and subsequent disturbances. It is further possible that *S. australis* was naturally rare and that the species has been given a reprieve through the local abundance of *P. undulatum* and consequent increase in habitat availability. This is a classic example of a situation where the status of *P. undulatum* has to be interpreted carefully and management prescriptions need to be accordingly specific to match predetermined objectives.

In this case, the managers opted to fell individual plants that had encroached onto the adjacent drier slopes. Unfortunately, the cut stumps were not treated with herbicides and vigorous coppicing was evident within months (pers. obs.). Additionally, this procedure was implemented immediately after the winter fruiting period and large quantities of pre- and post-dehiscent fruits, containing presumably viable seeds, were present on the lopped female plants. This situation is not atypical in south east Australia where environmental weed management is often implemented when a resource or funding opportunity is available, rather than at the most opportune time in the invader’s life history. Control techniques are also restricted by the same funding and resource constraints and may not always be appropriate in a given situation, despite the best intentions. Managers of vegetation communities that naturally contain *P. undulatum* probably need clearer indications of *P. undulatum* cover-abundance damage thresholds,
as a guide for intervention, than do managers of sites where the species is clearly invasive.

The felling technique applied at MORW is commonly implemented throughout Victoria although cut stumps are generally treated with herbicides (usually glyphosate). This method provides ‘instant’ results, but the consequent increase in light infiltration may create a substantial disturbance to local site conditions, which opportunistic weed species may exploit, particularly in the absence of follow-up monitoring and control. Felled individuals are generally left on-site which raises further concerns about the potential influence of allelopathic properties present in decaying leaf matter. This control approach is often recommended in the ‘grey literature’ produced by volunteer, ‘Friends of...’ and field naturalists groups who play an increasingly important role in coordinating and implementing environmental weed management programs (AACM International 1997). This approach may be the most feasible in many instances but will certainly not produce the best results in all circumstances.

A more appropriate control method for *P. undulatum* is the ‘drill and fill’ technique where herbicides are injected into the trunk and the canopy contracts over time (Mullett 1996). This reduces the disturbance associated with lopping or felling plants, but is not often implemented in *P. undulatum* control programs (pers. obs.), possibly because the results are not as ‘instant’ or visually obvious and as such, progress may be more difficult to appreciate (AACM International 1997). These latter factors may be important for the continued motivation of volunteer groups, which conduct the majority of on-ground environmental weed control works in Australia (AACM International 1997).

The ‘drill and fill’ method has been used to good effect in the Dandenong Ranges National Park, Victoria (Gillespie 1991) where the large, established volunteer group supporting the management authority (Parks Victoria) is able to apply the necessary resources to this, and other labour intensive control options. AACM International (1997) estimate that the in-kind labour provided by this volunteer group alone is approximately $0.5m per annum, which is remarkable given that Victorian government expenditure on environmental weed control in areas managed under the *National Parks Act 1975* was only $0.83m, in the 1995/96 financial year (Environmental and Natural
Resources Committee 1998). On-going monitoring and control are essential to prevent re-invasions by \textit{P. undulatum}, or other environmental weeds, but there is no guarantee this commitment can be sustained by volunteers over time (AACM International 1997).

Prescribed burning is often recommended as an effective means of controlling invasive populations of \textit{P. undulatum} as fires intense enough to kill the basal buds in the trunk are generally fatal (Gleadow & Ashton 1981; Buchanan 1989a; Narayan 1993). While this technique may be effective in reducing \textit{P. undulatum} densities, the intensities of prescribed and naturally occurring fires are controlled to the extent that this approach is rarely successful, particularly in an urban or urban-fringe context where most \textit{P. undulatum} invasions occur. Further, it may be difficult to implement fires of an appropriate intensity in areas heavily invaded by \textit{P. undulatum}, because of the dense shading and consequent changes in fuel composition and moisture content (Twentyman 1990). Mature \textit{P. undulatum} plants can recover from low-intensity fires and benefits gained from control burning may be lost in the absence of follow-up monitoring and management. For example, initial increases in species richness were recorded in the spring following a small (~3 hectare) low-intensity autumn fire in a dry open woodland community dominated by \textit{P. undulatum} at MORN (Narayan 1993), but coppicing of damaged plants and colonisation by bird-dispersed seedlings were evident in ensuing years (pers. obs.)

Prescribed burning will not be appropriate in all communities invaded by \textit{P. undulatum} and this control technique should be used with caution even in the drier forest types adapted to more frequent fires. At MORN for example, a small population of the fire-responsive environmental weed, \textit{Chrysanthemoides monilifera} ssp. \textit{monilifera} may benefit from an ecological burn implemented to reduce the density of \textit{P. undulatum}. At PORT, the same situation applies, but with a different fire-responsive environmental weed species, \textit{Genista monspessulana}, well placed to take over from \textit{P. undulatum} as the dominant weed species. The importance of anticipating the community response to the various control techniques can not be underestimated. This requires an adequate understanding of the composition, dynamics and regeneration characteristics of the invader and the invaded community (Kluge \textit{et al.} 1986; Groves 1989, 1991).
In the appropriate context, prescribed burning may be the most cost-effective and ecologically sound method of controlling *P. undulatum*. Further studies on *P. undulatum* and community response to fires may provide useful information for future application of this management technique, but the utility of this approach will be largely determined by external influences such as community attitudes and perceptions of risk (Twentyman 1990). Bush regenerators in the Sydney region were recently advised to maintain *P. undulatum* firebreaks around bushland reserves to reduce the risk of wildfire spread into adjacent human settlements (Klaphake 1994). The author further recommended that an 18 metre wide strip of *P. undulatum* be established and maintained around remnants in the urban matrix (Klaphake 1994). This recommendation is not based on any sound ecological, fire management or patch-design principles and in the majority of urban bushland reserves, a buffer strip of this size would encroach substantially into the patch interior. Other more appropriate methods of reducing the fire risk in remnant vegetation in the urban matrix are available (Adams & Simmons 1996). It is concerning that such recommendations have been published given that the expansion of *P. undulatum* populations has long been recognised as a threat to remnant vegetation in the Sydney region (Adamson & Buchanan 1974; Adamson & Fox 1982; Buchanan 1989a, 1991). This example does however exemplify the issues that may arise when conflicting management objectives are advanced. In the Sydney region, such recommendations will only contribute to the existing uncertainties relating to the management of this species (Rose 1997b).

Biological control is not a feasible option for reducing densities of *P. undulatum* in south east Australia given the inherent risk of damage to natural populations of this species. Biological control of invading populations of *P. undulatum* may be appropriate in areas outside Australia and an annotated list of potential agents is included in Goodland and Healey (1997a). None of these agents directly impact upon reproductive structures although further investigation throughout the natural range of this species may reveal potential agents.

Control attempts for *P. undulatum* and indeed most environmental weed species, will have little long-term success if the underlying causes of invasion are not addressed (Humphries *et al.* 1991; Hobbs & Humphries 1995). Randall (1997) suggests that invasions by indigenous plants responding to modified disturbance regimes are best
addressed by restoring original disturbance conditions. This is often promoted as a key objective by various management agencies (Westman 1990), but is likely to be an elusive goal in most cases. Disturbance, whether endogenous, modified endogenous or exogenous, is a critical element of contemporary vegetation management, yet it is little understood or appropriately managed. Across the Australian continent as elsewhere, natural systems have been so fundamentally altered that “it is not enough to say that the original disturbance regime is the desired state” (Hobbs & Huenneke 1992, p. 333).

Achieving a balance in disturbance management, that promotes indigenous species diversity without providing a window of opportunity for invasive species (Johnstone 1986), is one of the greatest challenges of modern vegetation management. Remaining natural systems need to be actively managed because all disturbances are now fundamentally artificial, or occur in grossly altered landscapes. The concept of ‘natural’, in itself, can be considered ‘anachronistic’ (Soule 1990) given the scale of human-mediated ecosystem disruption.

The restoration of natural disturbance processes is likely to be impossible given the scale of habitat loss and fragmentation and attendant changes in ecosystem composition, structure and function (Hobbs & Hopkins 1990; Saunders et al. 1991; Haila et al. 1993). Even if natural disturbance regimes could be reinstated there is little evidence to suggest that the community would return to the pre-disturbance state (Woods 1997). Management of disturbance processes should be tailored to address specific goals (Hobbs & Huenneke 1992; Hobbs & Humphries 1995). As Randall (1997) stresses, conservation managers need to have clear management objectives. Species that pose a current or potential threat to these management objectives should be identified after the desired species composition has been determined (Randall 1997).

Saunders (1996) suggests that the ecological sustainability of agricultural landscapes is impeded by a "lack of vision" of how “we as a society want these landscapes to look like and how we want them to function” (Saunders 1996, p. 321). This impediment is equally applicable to the management of remaining natural or semi-natural ecosystems in Australia. The acclimatisation societies of the late 1800’s and early 1900’s worked towards a collective vision of a re-modeled Australian landscape characterised by introduced flora and fauna (Rolls 1964). It would seem that their vision has been
overwhelmingly realised. It is difficult to predict what the Australian landscape will look like in the future and how continued plant invasions and a multitude of other current and emerging threats will affect ecosystem functions. The continued loss of biodiversity at the genetic, species and population levels erodes the diversity and resilience of remaining ecosystems (Ehrlich & Mooney 1983; Recher & Lim 1991; Recher 1993; Wilson 1993; van Wilgen et al. 1996; Hobbs & Mooney 1998) and in some cases may provide further impetus for invasion. The development and implementation of long-term plans will indeed be essential if biodiversity values and the provision of ecosystem services are to be maintained in perpetuity. Addressing the threat posed by invasive plant species should be of paramount importance in any such strategies.

Environmental weed management in Australia suffers from the paradox that quantitative studies on the ecological impacts of invasions are needed to attract resources necessary for control initiatives, yet environmental weed research is desperately under-funded because of a lack of awareness about the severity of the issue. Without public education and subsequent community support and political pressure, the factors that impede current environmental weed management can not be expected to change. As Adair and Groves (1998, p. 3) point out, “we still do no know the attitudes and perceptions of the general Australian public to this problem”. Until we do, and these attitudes are targeted appropriately, the continued invasion of weeds, homogenisation of natural ecosystems and loss of biodiversity values will continue. At a fundamental level, notoriously invasive plant species are still commercially available from Nurseries. Recent initiatives to contain this threat are encouraging (Weeds CRC & NIAA 1999), but managing the threat posed by weedy ornamentals already scattered across the landscape may prove impossible.

Interest in environmental weed invasions is increasing and the issue is starting to emerge on the political and conservation management agendas (Humphries 1995). The first National Weeds Strategy was published in 1997 (Commonwealth of Australia 1997, 1999) and is supported by various State, Territory and regional weed management strategies (for example, New South Wales Department of Agriculture 1997; Tamar Valley Weed Management Group 1997; Department of Natural Resources and Environment 1998). Pest plants were the subjects of a Victorian parliamentary inquiry
in 1997 (Environment and Natural Resources Committee 1998) and weed education kits (Grant et al. 1996) and initiatives such as ‘weedbuster week’ have also raised community awareness and understanding of environmental weed issues (Beck et al. 1996; Vitelli et al. 1999). Greater community and political commitment to the principles of weed related policies and strategies are required if these initiatives are to be successfully implemented. The invasion by *P. undulatum* into habitats outside its natural range in Victoria was listed as a ‘potentially threatening process’ in 1994, under Schedule 3 of the Victorian *Flora and Fauna Guarantee Act 1988* (Scientific Advisory Committee 1994), but an Action Statement has not yet been developed for this listing, despite the legislative requirement that this occurs as soon as possible after the listing process (State of Victoria 1990).

Similar ecosystem-level effects to those described for *P. undulatum*, may be exerted by other densely-foliaged, fleshy-fruited woody weeds including *Ligustrum* spp. on the central coast of New South Wales (Adamson & Fox 1982; Buchanan 1989a) and *Olea europaea* in the dry forests of Adelaide (Jupp et al. 1999). The ecosystem-level effects imposed by this suite of environmental weeds are considerable and the potential for irreversible changes to occur in invaded communities is high. As discussed in Chapter 5, the development and implementation of strategies to address ecologically-damaging relationships between opportunist frugivores and fleshy-fruited weed species is likely to be controversial. Preventing the sale of such ornamental species and encouraging replacement with suitable plants may be an important first step towards addressing this issue.

It is unrealistic to assume that all invasive populations of *P. undulatum* or any environmental weed can be controlled given present resource constraints. Managers are encouraged to contain the spread of weed invasions early and direct resources into managing weeds in areas of high conservation value and in relatively intact ecosystems (Hobbs & Humphries 1995; Panetta & Lane 1996; Panetta & James 1999). This is not to say that other remnants should be abandoned to weed invasion as these provide a range of direct and indirect values, even if their ecological integrity has been compromised. Local ownership of the weed problem is an essential component of any weed management program, but may be especially important in highly fragmented urban and rural landscapes where investment of public funding to weed control is a
higher risk, given the potential for reinvansion by the same or different weeds. Greater technical and financial support will need to be supplied to volunteer groups if the onus for on-ground environmental weed management remains on the community. A commitment to monitoring, follow-up weed control and where necessary, revegetation programs, is also required.

The causes and consequences of *P. undulatum* invasion are difficult to separate and often operate in a complex and additive manner. Integrated control programs that address the underlying causes of invasion will likely be more successful and cost effective than those that are restricted to reducing densities through physical and chemical means (Kluge *et al.* 1986; Groves 1989, 1991). The restoration of processes that previously contained populations of *P. undulatum* to the wetter forest types of south east Australia will however, be impractical, if not impossible to emulate in most current cases.

The homogenisation of regional biota is an entrenched and rapidly escalating problem (Soule 1990; Humphries *et al.* 1993; Vitousek *et al.* 1997). In this context, some take the perhaps pragmatic view that most communities are now ‘synthetic’ (Bridgewater 1988, 1990) and should be managed accordingly. Areas invaded by environmental weed species still function in the sense that invasive plants bind soil, use water, transfer energy and produce oxygen (Hobbs 1992b) and may perform important functional roles in their host communities (Williams 1997).

Implicit in an acceptance of synthetic vegetation communities, however, is an acceptance of a species-impoverished and less resilient landscape. An acceptance of synthetic vegetation complexes also appears to be dangerous given our admittedly incomplete understanding of invasion ecology (Crawley 1987; Rejmanek 1996). The fallibility of models to predict invasive species (Williamson & Fitter 1986), uncertainties about the consequences of global warming on species distributions (Westman 1990; Schwartz 1997; Williams 1997) and our appreciation of the complexities associated with ‘sleeper weeds’ (Fox 1995; Groves 1999) should provide the basic impetus for rejecting this management option.
Acceptance of synthetic vegetation would also appear to conflict with at least two central tenets of Australia’s commitment to ecologically sustainable development; the precautionary principle and the issue of intergenerational equity (Council of Australian Governments 1992). Knowledge of the ecological, social, economic and political consequences of allowing further biotic homogenisation and ecosystem simplification is incomplete and there is a grave danger this transformation will occur (and be irreversible) without the full knowledge of the ramifications. Weed ecologists, let alone the public and politicians do not have a complete understanding of the issues to allow an accurate judgement to be made. Importantly, acceptance of synthetic vegetation communities and consequent biotic homogenisation effectively reduces options for future generations to choose against this approach as the simplification of remaining ecosystems may become too entrenched for remedial action. In this sense, environmental weed invasions are as much a socio-economic and political issue as an ecological issue (Hobbs & Humphries 1995; Humphries 1995; Panetta & Scott 1995).

If society chooses to allocate resources towards the conservation of biodiversity values against the opportunity cost of allocating resources to other potential benefits, then it is worth the continual and considerable investment of time, resources and labour required to control populations of *P. undulatum* in invaded communities. In the absence of control, this species will continue to expand both its range and local densities. This study has demonstrated that the ecological consequences of *P. undulatum* population expansion are substantial and contribute to fundamental changes in the composition and successional trajectory of affected communities. These processes ultimately lead to the loss and simplification of biodiversity values and the homogenisation of affected habitats. The ecological impacts documented for *P. undulatum* invasion in south east Australia and the emerging threat posed by this species in south west Australia, should provide an impetus for reviewing the current minimal allocation of resources directed towards the control of this species at the regional, State and National levels.
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Research Centre for Weed Management Systems and Nursery Industry Association of Australia, Adelaide.


APPENDICES

Appendix I. Research permits

Victoria


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<th>Year</th>
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<td>1/70/97/037</td>
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<td>1998-1999</td>
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*Permit under both Flora and Fauna Guarantee Act 1988 and National Parks Act 1975

Collection of plant material in areas managed under the provisions of the National Parks Act 1975

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<tr>
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<td>1997-1998</td>
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Permit to live-capture, retain live and release at point of capture a maximum of five Pied Currawongs (Strepera graculina) under provisions of the Wildlife Act 1975

<table>
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*Deakin University Animal Experimentation Ethics Committee Approval (A06/96)

New South Wales

Conduct research and collect plant material under provisions of the National Parks and Wildlife Act 1974

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Appendix 2. Summary of mean seasonal climatic variables selected to characterise populations sampled in this study.

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<td>990.7</td>
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<td>290.4</td>
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Appendix 3. Spearman Rank correlation matrix of mean leaf characters, geographic and climatic attributes obtained for each population sampled. Significant relationships (two-tailed test) are indicated (*P < 0.05; **P < 0.01, ***P < 0.001). Significant correlations between morphological characters and between morphological characters and environmental parameters are set in boldface. All climate variables represent mean seasonal data. Abbreviations as follows: T – Temperature (°C); Min. – Minimum; Max. – Maximum; RH – Relative Humidity.

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Appendix 4. Spearman Rank correlation matrix of mean fruit characters, geographic and climatic attributes obtained for six populations sampled in Victoria. Significant relationships (two-tailed test) are indicated (*P < 0.05; **P < 0.01, ***P < 0.001). Significant correlations between fruit characters and fruit characters and environmental parameters are set in boldface. All climate variables represent mean seasonal data. Abbreviations are as follows: T – Temperature (°C); Min. – Minimum; Max. – Maximum; RH – Relative Humidity.

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</tr>
<tr>
<td>Winter Max. T</td>
<td>-0.94**</td>
<td>-0.42</td>
<td>0.77</td>
<td>-0.77</td>
<td>0.63</td>
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<td>0.65</td>
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<td>Summer 3pm RH</td>
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<td>.37</td>
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<td>Summer Max. T</td>
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<td>.78</td>
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<td>.82*</td>
<td>-.25</td>
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<td>-.65</td>
<td>.25</td>
<td>.48</td>
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Appendix 5. Correlation matrices: Interactions between four *P. undulatum* developmental stages and ‘overstorey’ at six sites in Victoria.

Significant correlations (Spearman’s Rank Correlation Coefficient – two tailed test) are indicated: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, NSNot significant $P > 0.05$.

<table>
<thead>
<tr>
<th>All sites pooled data</th>
<th>$P. u.$ juvenile</th>
<th>Overstorey</th>
<th>$P. u.$ 1-2m</th>
<th>$P. u.$ &gt;2m</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Overstorey</strong></td>
<td>0.15***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$P. u.$ 1-2m</td>
<td>0.49***</td>
<td>0.16***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$P. u.$ &gt;2m</td>
<td>-0.17***</td>
<td>-0.21***</td>
<td>-0.02NS</td>
<td></td>
</tr>
<tr>
<td>$P. u.$ seedling</td>
<td>0.57***</td>
<td>0.17***</td>
<td>0.32***</td>
<td>-0.26***</td>
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<table>
<thead>
<tr>
<th>CROA</th>
<th>$P. u.$ juvenile</th>
<th>Overstorey</th>
<th>$P. u.$ 1-2m</th>
<th>$P. u.$ &gt;2m</th>
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<tbody>
<tr>
<td><strong>Overstorey</strong></td>
<td>0.32***</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>$P. u.$ 1-2m</td>
<td>0.13NS</td>
<td>0.11NS</td>
<td></td>
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<tr>
<td>$P. u.$ &gt;2m</td>
<td>-0.05NS</td>
<td>-0.16NS</td>
<td>0.12NS</td>
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<td>$P. u.$ seedling</td>
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<td>-0.19*</td>
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<table>
<thead>
<tr>
<th>GLEN</th>
<th>$P. u.$ juvenile</th>
<th>Overstorey</th>
<th>$P. u.$ 1-2m</th>
<th>$P. u.$ &gt;2m</th>
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<tbody>
<tr>
<td><strong>Overstorey</strong></td>
<td>0.34***</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>$P. u.$ 1-2m</td>
<td>0.44***</td>
<td>0.27**</td>
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<tr>
<td>$P. u.$ &gt;2m</td>
<td>-0.28***</td>
<td>-0.22**</td>
<td>-0.11NS</td>
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<tr>
<td>$P. u.$ seedling</td>
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<td>0.40***</td>
<td>0.39***</td>
<td>-0.30***</td>
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<table>
<thead>
<tr>
<th>MORW</th>
<th>$P. u.$ juvenile</th>
<th>Overstorey</th>
<th>$P. u.$ 1-2m</th>
<th>$P. u.$ &gt;2m</th>
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</thead>
<tbody>
<tr>
<td><strong>Overstorey</strong></td>
<td>0.03NS</td>
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</tr>
<tr>
<td>$P. u.$ 1-2m</td>
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<td>-0.07NS</td>
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</tr>
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<td>$P. u.$ &gt;2m</td>
<td>-0.07NS</td>
<td>-0.26**</td>
<td>0.12NS</td>
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<td>$P. u.$ seedling</td>
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<td>0.15NS</td>
<td>0.06NS</td>
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<td>MORN</td>
<td>$P_{u.}$ juvenile</td>
<td>Overstorey</td>
<td>$P_{u.}$ 1-2m</td>
<td>$P_{u.}$ &gt;2m</td>
</tr>
<tr>
<td>-------</td>
<td>-------------------</td>
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<td>--------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Overstorey</td>
<td>0.11$^{NS}$</td>
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<tr>
<td>$P_{u.}$ 1-2m</td>
<td>0.26$^{**}$</td>
<td>-0.04$^{NS}$</td>
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</tr>
<tr>
<td>$P_{u.}$ &gt;2m</td>
<td>0.08$^{NS}$</td>
<td>0.05$^{NS}$</td>
<td>0.34$^{***}$</td>
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<td>$P_{u.}$ seedling</td>
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<td>0.12$^{NS}$</td>
<td>0.01$^{NS}$</td>
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<table>
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<th>$P_{u.}$ 1-2m</th>
<th>$P_{u.}$ &gt;2m</th>
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<tbody>
<tr>
<td>Overstorey</td>
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<td></td>
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</tr>
<tr>
<td>$P_{u.}$ 1-2m</td>
<td>0.33$^{***}$</td>
<td>0.17$^{*}$</td>
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<tr>
<td>$P_{u.}$ &gt;2m</td>
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<td>-0.01$^{NS}$</td>
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<td>$P_{u.}$ seedling</td>
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<td>0.28$^{***}$</td>
<td>-0.28$^{***}$</td>
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<table>
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<tr>
<th>PORT</th>
<th>$P_{u.}$ juvenile</th>
<th>Overstorey</th>
<th>$P_{u.}$ 1-2m</th>
<th>$P_{u.}$ &gt;2m</th>
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</thead>
<tbody>
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<td>Overstorey</td>
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<tr>
<td>$P_{u.}$ 1-2m</td>
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<td>0.26$^{**}$</td>
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<td></td>
</tr>
<tr>
<td>$P_{u.}$ &gt;2m</td>
<td>-0.01$^{NS}$</td>
<td>-0.01$^{NS}$</td>
<td>0.02$^{NS}$</td>
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<td>$P_{u.}$ seedling</td>
<td>0.52$^{***}$</td>
<td>0.25$^{**}$</td>
<td>0.23$^{**}$</td>
<td>-0.18$^{*}$</td>
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</table>
Appendix 6. List of Vascular plants censused at for sites in south east Australia (see Chapter 7)

See Table 7-3 for an explanation of lifeform classifications

**MORN, Woods Reserve, Mornington Peninsula, Victoria.**

**PTERIDOPHYTA**

**DENNSTAEDIACEAE**

*Pteridium esculentum* (G. Forst.) Cockayne  
Austral Bracken  
Fern

**MONOCOTYLEDONAE**

**CYPERACEAE**

*Carex breviculmis* R. Br.  
Short-stem Sedge  
Hb

*Gahnia radula* (R. Br.) Benth.  
Thatch Saw-sedge  
Hb

*Lepidosperma laterale* R. Br.  
Variable Sword-sedge  
Hb

*Lepidosperma semiternes* F. Muell.  
Wire Rapier-Sedge  
Hb

*Schoenus apogon* Roem. & Schult.  
Common Bog-rush  
Hb

**LILIACEAE**

*Arthropodium strictum* R. Br.  
Chocolate Lily  
Hb

*Burchardia umbellata* R. Br.  
Milkmaids  
Hb

*Caesia parvifolia* R. Br.  
Pale Grass Lily  
Hb

*Dianella brevicaulis*  
Black-anther Flax-lily  
Hb

(Ostenf.) G. W. Carr & P. F. Horsfall  
*Thysanotus patersonii* R. Br.  
Twining Fringe-lily  
Ttcc

**ORCHIDACEAE**

*Caladenia carnea* R. Br.  
Pink Fingers  
Hb

*Chiloglottis valida* D. L. Jones  
Common Bird-orchid  
Hb

*Dipodium roseum* D. L. Jones & M. A. Clem.  
Hyacinth Orchid  
Hb

*Glossodia major* R. Br.  
Wax-lip Orchid  
Hb

*Pterostylis longifolia* R. Br.  
Tall Greenhood  
Hb

**POACEAE**

*Aira caryophyllea* L.  
Silvery Hair-grass  
Gr

*Cynodon dactylon* L.  
Couch  
Gr

*Ehrharta erecta* Lam.  
Panic Veldt-grass  
Gr

*Austrostipa rudis* ssp. *australis*  
Veined Spear-grass  
Gr
(J. Everett & S. W. L. Jacobs) S. W. L. Jacobs & J. Everett

**Austrostipa rudas** ssp. **nervosa**
Veined Spear-grass Gr

(Vickery) S. W. L. Jacobs & J. Everett

**Danthonia setacea** var. **setacea** R. Br.
Bristly Wallaby Grass Gr

**Microleana stipoides** (Labill.) R. Br.
Weeping Grass Gr

**Poa morrissii** Vickery
Velvet Tussock-grass Gr

**Poa sieberiana** Spreng.
Tussock Grass Gr

**Poa tenera** F. Muell. ex Hook. f.
Slender Tussock-grass Gr

**Themeda triandra** Forrsk.
Kangaroo Grass Gr

**XANTHRORHOEACEAE**

**Loemandra filiformis** (Thunb.) Britten
Wattle Mat-rush Hb

**Loemandra longifolia** Labill.
Spiny-headed Mat-rush Hb

**Xanthorrhoea minor** R. Br.
Small Grass Trek Hb

**DICOTYLEDONAE**

**APIACEAE**

**Hydrocotyle hirta** R. Br. ex A. Rich.
Hairy Pennywort Hb

**ASTERACEAE**

*Chrysanthemodics monilifera** ssp. **monilifera** L.
Boneseed Shr

*Hypochoeris glabra** L.
Smooth Cat's Ear Hb

*Hypochoeris radicata** L.
Cat's Ear Hb

**Cassinia aculeata** (Labill.) R. Br.
Dogwood Shr

**Euchiton involucratus** (G. Forst.) Anderb.
Common Cudweed Hb

**Lagenifera stiptata** (Labill.) Druce
Blue Bottle Daisy Hb

**Lagenifera gracilis** Steetz.
Slender Blue Bottle Hb

**Senecio quadridentatus** Labill.
Cotton Fireweed Hb

**Senecio tenuiflorus** (DC.) Sieber ex Sch.-Bip.
Narrow Groundsel Hb

**CLUSIACEAE**

**Hypericum gramineum** G. Forst.
Small St. Johns Wort Hb

**DILLENIACEAE**

**Hibbertia riparia** (R. Br. ex DC.) Hoogland
Erect Guinea-flower Shr

**DROSERACEAE**

**Drosera peltata** ssp. **auriculata**
Tall Sundew Hb

(Backh. ex Planch.) B. J. Conn

**Drosera whittakeri** Planch.
Scented Sundew Hb
EPACRIDACEAE

*Acrotriche prostrata* F. Muell.
*Acrotriche serrulata* (Labill.) R. Br.
*Epacris impressa* Labill.

Trailing Ground-berry  L-shr
Honey Pots  L-shr
Common Heath  Shr

EUPHORBIACEAE

*Poranthera microphylla* Brongn.

Small Poranthera  Hb

FABACEAE

*Bossiaea prostrata* R. Br.
*Dillwynia cinerascens* R. Br. ex Sims
*Kennedia prostrata* R. Br.

Creeping Bossiaea  L-shr
Grey Parrot Pea  Shr
Running Postman  Tc

GOODENIACEAE

*Goodenia geniculata* R. Br.

Bent Goodenia  Hb

HALORAGACEAE

*Gonocarpus tetragynus* Labill.

Common Raspwort  Hb

MIMOSACEAE

*Acacia mearnsii* De Wild.

Black Wattle  Tr

MYRTACEAE

*Eucalyptus obliqua* L'Her.
*Eucalyptus radiata* Sieber. ex DC.
*Eucalyptus viminalis* ssp. *pryoriana* (L. A. S. Johnson) Brooker & Slee
*Leptospermum continentale* Joy Thomps.

Messmate  Tr
Narrow-leaved Peppermint  Tr
Coast Manna Gum  Tr
Prickly Tea-tree  Shr

OXALIDACEAE

*Oxalis exilis* A. Cunn.

Wood Sorrel  Hb

PITTOSPORACEAE

*Billardiera scandens* Sm.
*Bursaria spinosa* Cav.
*Pittosporum undulatum* Vent.

Common Appleberry  Tc
Sweet Bursaria  Tsh
Sweet Pittosporum  Tsh

POLYGALACEAE

*Comesperma volubile* Labill.

Love Creeper  Tc


PROTEACEAE
* Banksia marginata Cav.  Silver Banskia  Tshr/st

RANUNCULACEAE
* Ranunculus lappaceus Sm.  Australian Buttercup  Hb

ROSACEAE
* Prunus sp.  Plum  Tshr/st
Acaena novae-zelandiae Kirk.  Bidgee-widgee  Hb
* Rubus sp.  Blackberry  Shr

RUBIACEAE
* Opercularia varia Hook. f.  Variable Stinkweed  Hb

THYMELAEACEAE
* Pimelea humilis R. Br.  Small Rice-flower  L-shr

VIOLACEAE
* Viola hederacea Labill.  Ivy-leaf Violet  Hb

PORT, Gora Forest, Portland, Victoria.

PTERIDOPHYTA
ADIANTACEAE
* Adiantum aethiopicum L.  Maidenhair Fern  Fern

DENNSTAEDTIACEAE
* Pteridium esculentum (G. Forst.) Cockayne  Austral Bracken  Fern

MONOCOTYLEDONAE
CYPERACEAE
* Lepidosperma laterale R. Br.  Variable Sword-sedge  Hb

LILIACEAE
* Burchardia umbellata R. Br.  Milkmaids  Hb
* Dianella brevicaulis R. Br.  Black-anther Flax-lily  Hb
ORCHIDACEAE

*Dipodium roseum* D. L. Jones and M. A. Clem. 
Hyacinth Orchid

POACEAE

*Brisa minor* L. 
Quaking Grass

Danthonia pennisetiformis (Labill.) P. Beauv. 
Slender Wallaby-grass

*Holcus lanatus* L. 
Yorkshire Fog

Microlaena stipoides (Labill.) R. Br. 
Weeping Grass

Poa labillardierei var. labillardierei Steud. 
Common Tussock-grass

Poa morrisii Vickery 
Velvet Tussock-grass

Poa sp. 1 
Tussock-grass

Poa sp. 2 
Tussock-grass

Themeda triandra Forssk. 
Kangaroo Grass

XANTHORHOEOIDACEAE

Lomandra filiformis (Thunb.) Britten 
Wattle Mat-rush

Lomandra longifolia Labill. 
Spiny-headed Mat-rush

DICOTYLEDONAE

APIACEAE

*Aptum prostratum* Labill. ex Vent. 
Sea Celery

Daucus glochidiatius (Labill.) Fisch. 
Austral Carrot

Hydrocotyle laxiflora DC. 
Stinking Pennywort

ASTERACEAE

*Cassina aceleata* (Labill.) R. Br. 
Dogwood

*Centaurium erythraea* Rafn. 
Common Centaury

*Cirsium vulgar* (Savi) Ten. 
Spear Thistle

*Hypochoeris radicata* L. 
Cat's Ear

Lagenifera stipitata (Labill.) Druce 
Common Blue Bottle

Senecio miminus Poir. 
Shrubby Fireweed

Senecio quadridentatus Labill. 
Cotton Fireweed

CLUSIACEAE

*Hypericum gramineum* G. Forst. 
Small St. John's Wort

CONVULVULACEAE

*Dichondra repens* J. R. & G. Forst. 
Kidney Weed

DILLENIACEAE
Hibbertia fasciculata var. prostrata
(Hook.) Hook. f.

Bundled Guinea-flower L-shr

EPACRIDACEAE

Acrotriche prostrata R. Br.

Trailing Ground-berry L-shr

EUPHORBIACEAE

Poranthera microphylla Brongn.

Small Poranthera Hb

FABACEAE

Bossiaea prostrata R. Br.

Creeping Bossiaea L-shr

*Genista monspessulana (L.) L. A. S. Johnson

Montpellier Broom Shr

Glycine clandestina J. C. Wendl.

Twining Glycine Ttec

Hovea linearis (Sm.) R. Br.

Common Hovea L-shr

Indigofera australis Willd.

Austral Indigo Shr

Kennedia prostrata R. Br.

Running Postman Ttec

GERANIACEAE

Geranium potentilloides L’ Her. ex DC.

Crane’s Bill Hb

Geranium solanderi Carolin

Austral Crane’s bill Hb

GOODENIACEAE

Goodenia geniculata R. Br.

Bent Goodenia Hb

Goodenia ovata Sm.

Hop Goodenia Shr

HALORAGACEAE

Gonocarpus micranthus Thumb.

Creeping Raspwort Hb

Gonocarpus tetragnus Labill.

Common Raspwort Hb

MIMOSACEAE

*Acacia longifolia var. longifolia Willd.

Sallow Wattle Tshr/st

Acacia melanoxylon R. Br.

Blackwood Tr

Acacia paradoxa DC.

Hedge Wattle Tshr/st

Acacia verticillata (L’Her.) Willd.

Prickly Moses Shr

MYRTACEAE

Eucalyptus baxteri (Benth.) Maiden & Blakely

Brown Stringybark Tr

Eucalyptus obliqua L’Her.

Messmate Tr

Eucalyptus viminalis ssp. proryiana

Coast Manna Gum Tr

(L. A. S. Johnson) Brooker & Slee
*Eucalyptus willisii*  
Lagides, Humphries & Brooker  
*Leptospermum continentale* Joy Thomps.  

**OXALIDACEAE**  
*Oxalis corniculata* L.  
*Oxalis radicosa* L.  

**PINACEAE**  
*Pinus radiata* D. Don  

**PITTOSPORACEAE**  
*Billardiera scandens* Sm.  
*Bursaria spinosa* Cav.  
*Pittosporum undulatum* Vent.  

**PLANTAGINACEAE**  
*Plantago lanceolata* L.  

**POLYGALACEAE**  
*Comesperma volubile* Labill. ex Vent.  

**RANUNCULACEAE**  
*Clematis aristata* DC.  

**ROSACEAE**  
*Acaena novae-zelandiae* Kirk.  
*Cotoneaster glaucophyllus* Franch.  
*Rosa rubiginosa* L.  
*Rubus sp.*  

**RUBIACEAE**  
*Opercularia varia* Hook. f.  

**RUTACEAE**  
*Correa reflexa* (Labill.) Vent.  

**SANTALACEAE**  
*Exocarpos cupressiformis* Labill.  

*Shining Peppermint*  
*Prickly Tea-tree*  
*Yellow Wood-sorrel*  
*Wood-sorrel*  
*Monterey Pine*  
*Common Apple-berry*  
*Sweet Bursaria*  
*Sweet Pittosporum*  
*Ribwort*  
*Love Creeper*  
*Old Man's Beard*  
*Bidgee-widgee*  
*Cotoneaster*  
*Sweet Briar*  
*Blackberry*  
*Variable Stinkweed*  
*Common Correa*  
*Cherry Ballart*  
*Tr*  
*Shr*  
*Hb*  
*Tccc*  
*Tshr/st*  
*Hb*  
*Tccc*  
*Tccc*  
*Hb*  
*Shr*  
*Shr*  
*Hb*  
*Shr*  
*Tr*
SCROPHULARIACEAE
Veronica caycina R. Br. Creeping Speedwell Hb

TREMANDRACEAE
Tetrapheca ciliata Lindl. Pink Bells L-shr

VIOLACEAE
Viola hederacea R. Br. Ivy-leaf Violet Hb

CROA, Point Hicks, Croajingolong National Park, Victoria.

PTERIDOPHYTA
DENNSTAEDTIA CEAE
Pteridium esculentum (G. Forst.) Cockayne Austral Bracken Fern

GYMNOSPERMAE
CUPRESSACEAE
Callitris rhomboidea R. Br. ex Rich. Oyster Bay Pine Tr

MONOCOTYLEDONAE
CYPERACEAE
Lepidosperma filiforme Labill. Common Rapier-sedge Hb
Gahnia sieberiana Kunth. Red-fruit Saw-sedge Hb

LILIACEAE
Dianella brevicaulis Black-anther Flax-lily Hb
(Ostenf.) G. W. Carr & P. F. Horsfall
Dianella tasmanica Hook. f. Tasman Flax-lily Hb
Liliaceae sp. 1 Lily Hb
Schelhammera undulata R. Br. Lilac Lily Hb

ORCHIDACEAE
Acianthus caudatus R. Br. Mayfly Orchid Hb
Pterostylis nutans R. Br. Nodding Greenhood Hb

POACEAE
Microlaena stipoides (Labill.) R. Br. Weeping Grass Gr
Poa poiformis var. poiformis (Labill.) Druce Beach Poa Gr
| **Poaceae sp. 1** | Tussock-grass | Gr |
| **Poaceae sp. 2** | | Gr |

**SMILACACEAE**

| Smilax australis R. Br. | Lawyer-vine | Ttcc |

**XANTHORROEAECEAE**

| Lomandra filiformis (Thunb.) Britten | Wattle Mat-rush | Hb |
| Lomandra longifolia Labill. | Spiny-headed Mat-rush | Hb |
| Lomandra multiflora (R. Br.) Britten | Many-flowered Mat-rush | Hb |

**DICOTYLEDONAE**

**APIACEAE**

| Hydrocotyle hirta R. Br. ex A. Rich. | Hairy Pennywort | Hb |

**ASTERACEAE**

| Chrysocephalum baxteri (A. Cunn ex DC.) Anderb. | White Everlasting | Hb |
| Lagenifera stipitata (Labill.) Druce | Blue Bottle Daisy | Hb |

**CASURINACEAE**

| Allocasuarina littoralis (Salisb.) L.A.S. Johnson | Black Sheoak | Tshr/st |

**CLUSIACEAE**

| Hypericum gramineum G. Forst. | Small St. Johns Wort | Hb |

**CONVOLVULACEAE**

| Dichondra repens J.R. & G. Forst. | Kidney Weed | Hb |

**ELAEOCARPACEAE**

| Elaeocarpus reticulatus Sm. | Blue Olive-Berry | Shr |

**EPACRIDACEAE**

| Monotoca elliptica (Sm.) R. Br. | Tree Broom-heath | Tshr/st |

**FABACEAE**

| Glycine clandestina J. C. Wendl. | Twining Glycine | Ttcc |
| Desmodium brachypodum A. Gray | Large Tick-trefoil | Hb |

**HALORAGACEAE**
Gonocarpus tetragynus Labill. Common Raspwort Hb

LAURACEAE
Cas Ethya glabella f. glabella R. Br. Dodder Laurel Ttcc

MIMOSACEAE
Acacia longifolia var. longifolia Willd. Sallow Wattle Tshr/st
Acacia melanoxyylon R. Br. Blackwood Tr

MYRSINACEAE
Rapanea howittiana F. Muell. Muttonwood Tshr/st

MYRTACEAE
Eucalyptus botryoides Sm. Southern Mahogany Tr
Leptospermum laevigatum (Sol. ex Gaertn.) F. Muell.
Coast Tea-tree Tshr/st

OLEACEAE
Notelaea venosa F. Muell. Mock Olive Tshr/st

PITTOSPORACEAE
Billardiera scandens Sm. Common Apple-berry Ttcc
Bursaria spinosa Cav. Sweet Bursaria Shr
Pittosporum undulatum Vent. Sweet Pittosporum Tshr/st

PROTACEAE
Banksia integrifolia L. f. Coast Banksia Tr
Banksia serrata L. f. Saw Banksia Tshr/st

RANUNCULACEAE
Clematis aristata R. Br. ex Ker Gawl. Old Man’s Beard Ttcc

RUBIACEAE
Cajroma quadrifida (Labill.) B. L. Rob. Prickly Currant Bush Shr
Opercularia varia Hook. f. Variable Stinkweed L-shr

SMILACACEAE
Eustrephus latifolius R. Br. Wombat Berry Ttcc

STYLIDIACEAE
Stylidium graminifolium Sw.  
Trigger-plant  
Hb

UTRICACEAE

Urtica incisa Poir.  
Scrub Nettle  
Hb

VIOLACEAE

Viola hederacea Labill.  
Ivy-leaf Violet  
Hb

Unidentified sp. A

Unidentified sp. B  
Hb

BODL, Lake Brou, Bodalla State Park, New South Wales

PTERIDOPHYTA

DENNSTAEDTIACEAE

Pteridium esculentum (G. Forst.) Cockayne  
Austral Bracken  
Fern

GYMNOSPERMAE

ZAMICAE

Macrozamia communis L. Johnson  
Cycad  
Cycad

MONOCOTYLEDONAE

CYPERACEAE

Carex sp.  
Hb

Lepidoperma laterale R. Br.  
Variable Sword-sedge  
Hb

Gahnia sieberiana Kunth.  
Red-fruit Saw-sedge  
Hb

Gahnia sp.  
Hb

Schoenus brevifolius R. Br.  
Bog-Rush  
Hb

Isolepis nodosa (Rottb.) R. Br.  
Knobby Club-rush  
Hb

Cyperaceae sp.  
Hb

LILIACEAE

Schelhammera undulata R. Br.  
Lilac Lily  
Hb

Liliaceae sp.  
Hb

ORCHIDACEAE

Acianthus sp.  
Hb

Chilloglottis sp.  
Hb
POACEAE

*Oplismenus hirtellus* (L.) P. Beauv. Australian Basket-grass Gr
Poaceae sp. 1 Gr
Poaceae sp. 2 Gr
*Poa* sp. 1 Gr
*Themeda triandra* Forrsk. Kangaroo Grass Gr

XANTHORRHOEACEAE

*Lomandra filiformis* (Thunb.) Britten Wattle Mat-rush Hb
*Lomandra longifolia* Labill. Spiny-headed Mat-rush Hb
*Lomandra sp.* Mat-rush Hb

DICOTYLEDONAE

APIACEAE

*Hydrocotyle laxifolia* DC. Stinking Pennywort Hb

ASCLEPIADACEAE

*Marsdenia rostrata* R. Br. Milk Vine Tlcc

ASTERACEAE

*Cassinia aculeata* (Labill.) R. Br. Dogwood Shr
*Cassinia longifolia* R. Br. Shiny Cassinia Shr
*Helichrysum elatum* A. Cunn. ex DC. Tall Everlasting L-shbb
*Hypochoeris radicata* L. Cat's Ear Hb
*Lagenifera stipata* (Labill.) Druce. Blue Bottle Daisy Hb
*Senecio quadridentatus* Labill. Cotton Fireweed Hb
*Senecio minimus* Poir. Shrubby Fireweed Hb

CASUARINACEAE

*Allocasuarina littoralis* (Salisb.) L. A. S. Johnston Black Sheoak Tshr/str

CLUSIACEAE

*Hypericum gramineum* G. Forst. Small St John's Wort Hb

CONVOLVULACEAE

*Dichondra repens* J. R. & G. Forst. Kidney Weed Hb

DILLENIACEAE

*Hibbertia prostrata* Hook. Bundled Guinea-flower Shr
ELAEOCARPACEAE

*Elaeocarpus reticulatus* Sm.  
Blue Olive-berry  
Shr

EPACRIDACEAE

Coast Beard-heath  
Tshb/Str

EUPHORBIACEAE

*Poranthera microphylla* Brongn.  
Small Poranthera  
Hb

FABACEAE

*Bossiaea prostrata* R. Br.  
Creeping Bossiaea  
L-Shr

*Desmodium brachypodum* A. Gray  
Large Tick-trefoil  
Hb

*Goodia lotifolia* Salisb.  
Golden Tip  
Shr

*Hardenbergia violacea* (Schneev.) Stearn  
Purple Coral Pea  
Ttec

*Hovea linearis* (Sm.) R. Br.  
Common Hovea  
L-shb

*Indigofera australis* Wild.  
Austral Indigo  
Shr

GERANIACEAE

*Geranium homeanum* Turcz.  
Geranium  
Hb

*Geranium potenilloides* L’Herm. ex DC.  
Crane’s Bill  
Hb

HALORAGACEAE

*Gonocarpus humulis* Orchard  
Shade Raspwort  
Hb

*Gonocarpus tetragnymus* Labill.  
Common Raspwort  
Hb

LAURACEAE

*Cassytha glabella* R. Br.  
Dodder Laurel  
Ttec

MENISPERMACEAE

*Stephania japonica*  
Ttec

MIMOSACEAE

*Acacia dealbata* Link.  
Silver Wattle  
Tr

*Acacia longifolia* var. *longifolia* Willd.  
Sallow wattle  
Tshr/st

*Acacia melanoxylon* R. Br.  
Blackwood  
Tr

MYRTACEAE

*Eucalyptus botryoides* Sm.  
Southern Mahogany  
Tr

*Eucalyptus maculata* Hook.  
Spotted Gum  
Tr
OXALIDACEAE
Oxalis radicosa A. Rich. Wood-sorrel Hb

PITTOSPORACEAE
Billardiera scandens Sm. Common Apple-berry Ttec
Pittosporum revolutum Dryand. Rough-fruit Pittosporum Shr
Pittosporum undulatum Vent. Sweet Pittosporum Tshr/st

PROTEACEAE
Banksia integrifolia L. f. Coast Banksia Tr
Banksia serrata L. f. Saw Banksia Tshr/st

RANUNCULACEAE
Clematis aristata R. Br. ex Ker Gawl. Old Man's Beard Ttec
Clematis microphylla DC. Small-leaved Clematis Ttec

ROSACEAE
*Rubus sp. Blackberry Shr

RUBIACEAE
Coprosma quadrifida (Labill.) B. L. Rob. Prickly Current Bush Shr
Opercularia varia Hook. f. Variable Stinkweed L-shb

SCROPHULARIACEAE
Veronica plebeia R. Br. Creeping Speedwell Hb

SMILACACEAE
Eustrephus latifolius R. Br. Wombat Berry Ttec

SOLANACEAE
Solanum prinophyllum Dunal. Forest Nightshade Hb

THYMELAEACEAE
Pimelea humilis R. Br. Common Riceflower L-shb

TREMANDRACEAE
Tetrapheca ciliata Lindl. Pink Bells L-shb

URTICACEAE
Urтика incisa Poir.  Scrub Nettle  Hb

VIOLACEAE

Viola hederacea Labill.  Ivy-leaf Violet  Hb

Unidentified sp. A  Hb
Unidentified sp. B  Hb
Unidentified sp. C  Ttcc
Appendix 7. Correlation Matrices: Relationship between *P. undulatum* and the cover-abundance of structural guilds at four sites in south east Australia Significant relationships (two-tailed test) are indicated (* P < 0.05, ** P < 0.01, *** P < 0.001) and significant relationships between *P. undulatum* and lifeform guilds are set in boldface.

<table>
<thead>
<tr>
<th>MORN</th>
<th>Graminoids</th>
<th>Herbs</th>
<th>Ttcc</th>
<th>Low shrubs</th>
<th>Shrub</th>
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<td>0.06NS</td>
<td>0.19NS</td>
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<td>Tall shrubs /small trees</td>
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<td>-0.07NS</td>
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<td>-0.14NS</td>
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<td>Trees</td>
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<td>-0.46***</td>
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<td>0.19&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.21&lt;sup&gt;*&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Tall shrubs/small trees</td>
<td>0.05&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.10&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.09&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.06&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.06&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trees</td>
<td>0.12&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.01&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.12&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.13&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.14&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.10&lt;sup&gt;NS&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td><em>P. undulatum</em></td>
<td>0.03&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.08&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.26&lt;sup&gt;**&lt;/sup&gt;</td>
<td>0.05&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.19&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.24&lt;sup&gt;*&lt;/sup&gt;</td>
<td>0.08&lt;sup&gt;NS&lt;/sup&gt;</td>
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