1. Introduction

Elton’s pivotal book, *The ecology of invasions by plants and animals* (1958), identified a need to understand the processes underlying the spread of exotic species. Since then we have observed an unprecedented expansion of invasion biology research which has been motivated by the widespread and well documented influence of invasive species on our natural systems (Vitousek *et al.* 1996, Williamson 1999). Knowledge of which species are most successful and what areas are at risk of invasion is at the heart of predicting and ultimately preventing invasion events. Lonsdale (1999) identified three factors important for invasion success; 1) ecosystem properties - ecosystem resistance and the degree of disturbance; 2) propagule pressure; and 3) properties of the exotic species. Key approaches to understanding the relative role of each of these factors have focused on either traits of the invader (Newsome and Noble 1986, Crawley 1987) or features of the invaded community (Rejmanek 1989), resulting in numerous hypotheses to explain invasion success (Elton 1958, Blossey and Notzold 1995, Davis *et al.* 2000, Keane and Crawley 2002).

Before we consider some of these hypotheses, it is necessary to define some of the terms typically used in invasion biology. An invasion can be defined as the event in which a population is moved beyond its natural range of potential dispersal through human-mediated transport (Lee 2002). Only a small proportion of introduced species will go on to become invasive (Williamson 1996) and defining at what point they can be considered invaders is critical to invasive species management globally (Richardson *et al.* 2000). Here I follow terminology proposed by Richardson *et al.* (2000). ‘Alien plants’ are those taxa whose presence in an area is due to the intentional or accidental introduction as a result of human activity. ‘Naturalised’ taxa are alien plants that reproduce consistently and sustain populations over many life cycles usually close to the parent plant. ‘Invasive’ plants produce reproductive offspring often in very large numbers at considerable distances from the parent plant. Richardson *et al.* (2000a) suggest that for seed plants this distance must be greater than 100 m in less than 50 years. Invasive species have the potential to spread over a considerable area.

Ideas concerning interactions between alien plants and native species drive some of the major hypotheses to explain invasion success. The notion that diverse native communities somehow resist invasion is an optimistic one and of prime interest to both biologists attempting to predict invasion and land managers attempting to restore
invaded areas. High species richness has long been thought to reduce the likelihood of invasion (Elton 1958, Fox and Fox 1986a), however, experimental evidence is conflicting, reporting both positive (Robinson et al. 1995) and negative relationships (Tilman 1997). Furthermore, the relationship appears highly scale dependent (Herben et al. 2004). Relationships between native and exotic species diversity are likely to reflect resource use. Invasion success may be more dependent on the availability of resources and the ability of invaders to exploit them. The ‘fluctuating resources theory of invasibility’ (Davis et al. 2000) is one of the most widely accepted ideas in invasion biology. The theory suggests that any factor which increases the availability of limiting resources, e.g. light, space, nutrients, will increase the vulnerability of a community to invasion (Davis et al. 2000). Areas of high species richness will only resist invasion if they are utilising resources fully (Tilman 1999). Inherent in this idea is that community invasibility will fluctuate temporally and spatially (D’Antonio et al. 2001) and may provide some explanation for the idiosyncratic nature of plant invasions (Nentwig 2007). The theory of fluctuating resources also accounts for the facilitating role of disturbance commonly observed (Fox and Fox 1986a, Hobbs and Huenneke 1992). Crawley (1987) ranked plant community invasibility based on the average proportion of bare ground and on the frequency and intensity of soil surface disturbance. Bare ground represents an absent niche which exotics can exploit in the absence of competition from resident native vegetation (Richardson and Bond 1991).

Comparisons of exotics in their native and novel range have helped test ideas regarding invasion success, namely the increased competitive ability (Blossey and Notzold 1995) and natural enemies (Elton 1958) hypotheses. Invaders may acquire an increased competitive ability in their introduced range via increased biomass (Jakobs et al. 2004), greater seedling survival rates (Ruthrof et al. 2003) or increased seed size (Buckley et al. 2003). However, evidence for greater competitive advantage of invaders in their new environments remains inconclusive (Hierro et al. 2005). The success of invaders may be due to advantages gained in their new environment via a release from herbivores and other natural enemies (Keane and Crawley 2002). Despite good knowledge of herbivore control on plant invaders, our understanding of population level effects by enemies is weak (Hierro et al. 2005).

A shift towards a focus on the interaction between the invader and the recipient habitat has been a major advance for invasion biology (Lodge 1993). Propagule pressure may have a much larger role in this interaction than previously thought.
(D’Antonio et al. 2001). Propagule pressure can be defined as the number of propagules entering the environment (Lonsdale 1999). In the case of plant invasions this equates to the number of seeds present. The overwhelming influence of propagule pressure in the invasion process (Lockwood et al. 2005, Von Holle and Simberloff 2005) may explain variation in the likelihood of establishment between regions (Williamson 1996). An emerging generalisation relating to propagule pressure is that the probability of invasion increases with time since introduction (Pyšek and Jarosik 2005, Richardson and Pyšek 2006). A longer residence time for a species equates to a greater propagule pool and an increased likelihood of establishment (Rejmanek et al. 2005). The interaction between propagule pressure and the ecological resistance of a community is a key component of invasion success. The positive influence of residence time is strongly linked to temporal variations in community invasibility (D’Antonio et al. 2001) as the amount of propagules required to establish a population is reduced during times of low ecological resistance, e.g. following disturbance. Understanding the role of propagule pressure as a determinant of invasion success has been described as the new frontier in invasion ecology (Richardson 2004).

Numerous case studies have provided a number of widely cited generalisations regarding invasive species and invaded areas (Lodge 1993), however, scepticism surrounds our ability to predict invasion events (Crawley 1987, Williamson 1999). In light of this, we may need to accept that a number of non native species will become established and shift our focus towards predicting the influence of invaders in order to prioritise invading organisms on the basis of the impact they pose to native communities (Byers et al. 2002). This is crucial in a field where the number of offenders is potentially infinite but the resources to manage them are well and truly finite. The impacts of exotic species can be considerable ranging from population level (Reinhart et al. 2005) to community level (D’Antonio and Vitousek 1992) effects, leading to potential declines in ecosystem services (Charles and Dukes 2007). The ability to predict invasion impacts has been deemed the ‘holy grail’ of invasion biology (Simberloff 2006). The lack of studies focused on understanding the processes behind invasion impacts has been identified as a major shortcoming of invasion research (Levine et al. 2003).

Standardised measures of the overall impact of a species are critical for ranking species and prioritising control and research effort. Parker et al. (1999) proposed a framework which incorporates three components of impact; range, abundance and per
biomass effect of the invader. Assumptions that the most invasive species, i.e. with the largest range and/or abundance, will have the greatest negative impacts on biodiversity are invalid (Ricciardi and Cohen 2007), highlighting the importance of considering all three features of impact. An additional aspect of the impact of invading organisms is their potential to change a community in order to facilitate their establishment. The ability of invaders to favour their own conspecifics (Reinhart et al. 2006) as well as other invading organisms can greatly accelerate the invasion process and increase the level of impact (Simberloff et al. 1999).

A further advance in invasion biology has been an attempt to narrow the divide with other fields within the biological sciences including successional ecology, community ecology and conservation biology (Richardson and Pyšek 2006). The establishment of an invading organism is synonymous with the colonisation of a species into a new community and hence the factors mediating the success of invaders can provide great insight into broader ecological concepts. For example, grappling with the importance of propagule pressure versus environmental conditions for the success of exotics (D’Antonio et al. 2001) is comparable with larger debates within community ecology surrounding the limitations for plant populations and the relative contributions of seed arrival and the availability of “safe” sites (Harper 1977, Crawley 1990, Eriksson and Ehrlen 1992). Consequently, information resulting from invasion studies can help us gain an understanding of the processes underlying community assembly. The idea that the absence of a functional group in a community will facilitate invasion of a species from the same functional group has been shown to apply to small mammal assemblages (Fox 1987). However applications of the rule to plant invasion have had both positive and negative results (Von Holle and Simberloff 2004, Turnbull et al. 2005). Invasion success can also be examined in the context of niche concepts, where low levels of niche opportunities due to resident species maintaining resources at low levels leads to invasion resistance of a community (Shea and Chesson 2002).

Understanding the invasion process requires recognition of the strong link between human activities and various components of the invasion pathway. Human alteration of disturbance regimes combined with the global transport of species has enhanced the opportunities for the establishment of invasive species (Hobbs and Huenneke 1992, Hobbs 2000). Invasions are associated with wider global environmental issues including climate change, habitat fragmentation and land use change (Lodge 1993, Hobbs 2000). Knowledge from invasion processes can be used to
inform conservation decisions. For example, long distance dispersal is commonly a limiting factor for rare plant species and excessive long distance dispersal greatly enhances spread rates of invasives (Richardson and Pyšek 2006). The role of dispersal has been shown to be central to dispersal versus vicariance debates in biogeography (Cowie and Holland 2006). Insights into invasion processes have provided lessons for fields as diverse as systematics (Levin 2003) and epidemiology (Mack et al. 2000).

Invasions are of particular use for understanding ecological processes because they proceed rapidly. Due to their longer generation time, we have little knowledge of tree population dynamics (Crawley 1990) and hence tree invasions provide us with a unique opportunity to uncover some of the factors mediating tree expansion.

Disturbance limited recruitment is a driving force in tree populations within forest environments (Crawley 1990) and has also been shown to have an important role in the invasion of woody species (Mazia et al. 2001). Invasive spread of trees from forestry plantations provides an ideal situation to investigate the relative role of various factors in the invasion process. Unlike most invasions where propagule pressure is difficult to measure on a landscape scale (Richardson and Pyšek 2006), tracking spread from plantations that differ in age and size enables an examination of the influence of propagule pressure on the likelihood of invasion. The location and establishment time of each plantation is known allowing an investigation of the role of residence time on the timing of invasion events. Furthermore, examining spread on a regional scale, across which environmental conditions differ, allows an examination of the correlation between environmental factors and invasion success (Richardson et al. 2004).

The Pinaceae family has 28 known invasive species and of all genera within the family, Pinus is the most invasive (Richardson and Rejmanek 2004). Several species of the genus have been planted on a large-scale outside their native range making the genus ideal to examine the invasion process (Richardson 2006). Invasions of Pinus have occurred in all countries where major commercial plantations have been established (Richardson et al. 1994). Extensive research on Pinus invasions has provided great insight into invasive plant traits within the genus (Rejmanek and Richardson 1996). One of the most invasive species is Pinus radiata which has invaded in several countries including New Zealand, South Africa, Australia, Chile and Spain (Richardson 2006). In Australia, P. radiata is the most commonly planted pine species and despite knowledge of its spread here (Burdon and Chilvers 1977, Dawson et al. 1979) it remains a low profile invader with little resources allocated to its control.
This research focuses on the invasion of *P. radiata* within Australia. Invaders tend not to receive attention until they have reached the phase of rapid spread (Ewel *et al.* 1999), a point where control becomes difficult and costly (Mack *et al.* 2000). By focussing on a species that is known to be invasive elsewhere and yet so far has received little attention here I am hoping to reverse this trend. This study considers three components of impact (Parker *et al.* 1999); documenting the geographic range of the species, quantifying typical wildling (self-sown) densities, and assessing the impacts of a single tree on native vegetation. In addition, factors that are facilitating pine spread in Australia were examined in order to assess the potential for further spread and aid the mitigation of current and future invasion events. Common examinations of community invasibility are often confounded by the fact that different areas are likely to have been exposed to invaders of varying weakness and hence the level of invasion reflects the strength of the invader present rather than an inherent resistance of the community to invasion (Mack *et al.* 2000). By studying *P. radiata* spread from multiple plantations bordering a range of vegetation types that may differ in their vulnerability to invasion this study attempts to eliminate this source of variation.

**Thesis structure and aims**

This thesis is delivered in three major sections. The first section, Pattern of invasion, aims to determine the current level of spread in Australia. The literature review (chapter 2) consolidates existing knowledge of *Pinus* invasions elsewhere and in Australia. It also provides the motivation for the main hypotheses addressed in the thesis. Chapter 3 aims to quantify the current geographic extent of *P. radiata* in NSW. The chapter reports the results of a field survey of vegetation surrounding the major plantations in the state.

The second section, Process of invasion examines some of the factors facilitating invasion. Chapter 4 uses data obtained in the previous section to address the following hypotheses;

1) High propagule pressure will increase the likelihood of invasion,
2) Dry vegetation types, e.g. dry sclerophyll forest will be more susceptible to invasion than wetter vegetation, e.g wet sclerophyll forest, rainforest,
3) Disturbed areas will be more susceptible to invasion than undisturbed areas,
4) Pine spread will be greater downwind from the seed source.
Chapter 5 examines the role of fire in the invasion process by surveying wildling populations recently subjected to fire. The following hypothesis was addressed:

1) Fire may accelerate the invasion process by providing conditions conducive to pine establishment.

Finally, the third section, **Mechanism of impact**, aims to quantify the individual level impact of *P. radiata* with a focus on the influence on the recruitment of native species. There may be multiple interacting impacts associated with pine invasion, however, I chose to address two mechanisms thought to have the most immediate impact. I acknowledge that there are likely to be further impacts on habitat features, invertebrate populations and soil properties, but was unable to address all of these in this study. By focusing on two of the major biotic changes that occur following invasion I hope to lay the groundwork for investigating further impacts on the native community. Chapter 6 reports pine litterfall rates determined from field data. Values obtained from chapter 6 were used to establish experimental manipulations of pine and eucalypt litter levels used in the following chapter. The influence of this litter and increases in canopy cover associated with pine invasion on the germination of native species and of *P. radiata* itself were examined in chapter 7. The chapter reports results from field and glasshouse studies and addresses the following hypotheses:

1) Physical and/or chemical effects of *P. radiata* litter will have a negative influence on the germination of native species,

2) The magnitude of the physical effect will increase with increasing depth/volume of litter,

3) Increased canopy cover in invaded areas will reduce germination of native species in the field.

The general discussion (chapter 8) synthesises information from all chapters, summarising the achievements of this study. I also discuss the effectiveness of the approach used during this study as a model system for quantifying the impacts of invaders. The chapter also provides management recommendations and directs future research.
AIMS OF SECTION I: PATTERN

As the project developed it became obvious that much of the information on sleeper weeds in general and *P. radiata* in particular would be anecdotal or in unpublished reports. Therefore a general review of the existing knowledge that addressed gaps in our understanding of *P. radiata* invasion was required (chapter 2). This led to a decision to focus on the level of invasion within NSW as this would provide a large number of plantations (29) across a broad environmental gradient and would be more manageable for a field survey of the current level of invasion. Chapter 3 reports the findings of this study and documents the area of land invaded and the common spatial pattern of spread from each plantation.
2. Review of *Pinus radiata* invasion in Australia

*This chapter has been published in the journal Austral Ecology.*


*Nick Ledgard, David Richardson and Carol West provided valuable comments on the manuscript.*

**Introduction**

The negative impacts of biological invasions within natural systems are well known and have been widely documented (Lodge 1993, Dukes and Mooney 1999, Pimental *et al.* 2000). Their ability to alter ecosystem structure and function (Hobbs and Mooney 1986, Vitousek *et al.* 1987) have placed them second only to loss of habitat and landscape fragmentation as a threat to global biodiversity (Walker and Steffen 1997). Too often invasive species do not receive adequate attention until it is too late, i.e. once they have spread over large areas and eradication becomes difficult and costly. This is of particular concern when the invader has the potential to become dominant within the system, as is often the case with long lived species such as trees. Invading tree populations may take several generations to reach high densities, however, once established they have the ability to impart significant impacts by transforming canopy structure and light transmission to the understorey, altering disturbance regimes and influencing site productivity (Denslow and Hughes 2004). Early recognition of naturalised species that pose serious threats to biodiversity is the key to preventing and containing future invasions.

Commercial tree plantations represent a major source of exotic invaders (Richardson 1998). Species of the genus *Pinus* are favoured for their ability to provide fast growing high quality timber products in a range of conditions and have been planted extensively across the Southern hemisphere (Richardson 1998). Invasions of *Pinus* have been reported in most countries where large plantations are grown, including New Zealand (Hunter and Douglas 1984, Ledgard 1988), Chile (Bustamante *et al.* 2003), Israel (Lavi *et al.* 2005) and South Africa (Richardson and Brown 1986). Pine spread is considered to be a major conservation issue in South Africa and New Zealand,
two countries with long histories of forestry (Richardson and Higgins 1998). Pines have successfully invaded large areas of New Zealand and are threatening environmental and aesthetic values. South Africa has suffered from extensive pine invasions which are encroaching native fynbos and grassland vegetation (Richardson et al. 1997). Dispersal of seeds by wind leads to the establishment of dense stands of self sown pines which can shade and suppress understorey vegetation. Extrapolations from plantations indicate that exotic tree species including pines can reduce water flow (Bosch and Hewlett 1982).

Australia is a major cultivator of pine plantations with almost one million hectares growing across the country. Plantations are commonly established following the clearing of native vegetation resulting in a frequent juxtaposition with native vegetation and potential for invasion of natural areas. Pines have naturalised in a wide range of habitats in all states of Australia where they are grown (Lazarides 1997, Richardson and Higgins 1998, Blood 2001, Muyt 2001) and a number of species including *P. caribea*, *P. contorta*, *P. elliottii*, *P. halepensis*, *P. jeffreyi*, *P. nigra*, *P. pinaster* and *P. radiata* are considered invasive (Richardson 2006). Despite this, pines have a low profile as invaders and are currently not listed as Weeds of National Significance. The major environmental problems that pines are creating in New Zealand and South Africa deliver a warning that cannot be ignored. Given the invasive history of pines, the impacts they have inflicted elsewhere and the considerable plantation area in Australia, it is critical that we assess the risks associated with pine spread in this country. Little is known about the total area invaded by pines, the population biology of *Pinus* species outside of plantations or their impacts on native communities in Australia. This review assesses our current knowledge of the extent of *Pinus* invasions in Australia, focussing on *Pinus radiata*, the most commonly planted pine species. Extensive research conducted in other parts of the world, particularly South Africa and New Zealand, provides us with an extremely useful insight into the ecology of invading pine populations and the potential impacts associated with pine spread (Richardson 2006). Collation of information from current literature and examining patterns of pine spread will help apply lessons learnt elsewhere to the Australian situation, identify gaps in our own understanding and guide future research.
**Pinus invasion outside Australia**

New Zealand, Chile and Australia are the major cultivators of *Pinus radiata* in the southern hemisphere with 35.7%, 34.8% and 18.67% of the global estate respectively (Lavery and Mead 1998). South Africa is a minor grower of the species cultivating 1.4% of the estate (Lavery and Mead 1998). Within these four countries a total of twenty two *Pinus* species have been observed regenerating naturally (Richardson 2006).

In New Zealand the area affected by all conifer spread has been estimated at 150,000 hectares (Ledgard 2001). *Pinus contorta* is responsible for approximately two thirds of spread and is considered more invasive than other conifers due to its very light seed and ability to cone earlier. *Pinus radiata* has been placed behind *P. nigra*, *P. contorta*, *P. sylvestris* and *P. ponderosa* in terms of its importance as an invader (Richardson and Higgins 1998). Conifer spread is a major environmental problem and in some regions of the South Island the Department of Conservation now spend more money on wildling control than on any other weed (Ledgard 2004).

Invasions of *Pinus* species are causing major concern in South Africa where they have the potential to significantly reduce stream-flow (Versfeld and Van Wilgen 1986). *Pinus pinaster* is the most widespread invasive pine invading more than 300,000 hectares, mostly in fynbos vegetation. *Pinus radiata* and *P. patula* are the next most pervasive species covering 34,000 and 17,600 hectares respectively (Richardson and Higgins 1998). Most of the research investigating the factors that facilitate pine spread have been carried out in South Africa and in particular in the Western Cape (Richardson 2006). The Working for Water Programme was initiated in 1995 in order to control invasive species within catchments with the goal of increasing water supplies. During the 2002/2003 financial year more than 2,400 hectares of land was cleared of *Pinus* species at a cost of more than 5 million Rand (Marais et al. 2004).

*Pinus radiata* is the base of industrial forestry in Chile with almost 1.4 million hectares growing (Vargas and Sandoval 1998). The species is considered ‘introduced’ but not ‘invasive’ (Kruger et al. 1989). There is some evidence for the invasion of native forest fragments disturbed by cutting and burning (Bustamante et al. 2003), however it appears that the interiors of undisturbed fragments are resistant to invasion with abiotic conditions posing constraints to seedling establishment (Bustamante et al. 2003, Bustamante and Simonetti 2005).
Other *Pinus* invasions recorded for the southern hemisphere include spread of *P. patula* in Madagascar and Malawi; *P. pinaster* in Uruguay, *P. caribaea* in New Caledonia and *P. koraiensis* and *P. luchuensis* in Japan (Richardson 2006). In Argentina, *P. contorta, P. halepensis, P. elliotti, P. monticola, P. ponderosa, P. sylvestris* and *P. taeda* have all invaded natural areas while three *Pinus* species have also successfully established in Brazil; *P. elliottii, P. kesiya* and *P. taeda* (Richardson 2006). No invasions of *Pinus* species have been recorded for Colombia or Kenya despite the presence of large pine plantations (Richardson *et al.* 1994).

**The invasion process**

Invasive spread from plantations provides us with a unique opportunity to investigate the factors that facilitate the invasion process. Plantations have been established in many locations at multiple times under a wide range of climatic conditions and soil regimes, thus exposing a variety of vegetation types that may differ in their susceptibility to invasion (Richardson *et al.* 2004). The nature of plantations where the size and location of the original seed source is known allows us to track the invasion from each plantation and examine questions regarding community invasibility.

Plantation estates represent a huge and varying propagule source which can be quantified. The canopy-held seedbank of *P. radiata* in plantations in South Australia has been estimated at between 3.6 and 8.3 million seeds per hectare with annual seed release in a 40 year old plantation at one site estimated at approximately 1 to 3 seeds/m² (van der Sommen 1978 sourcing unpublished data in Virtue and Melland 2003). However the relationship between seed production and plantation area is not likely to be constant across sites as cone production will depend on a variety of factors including the age of the trees, the season, and the growing space for the individual trees (Fielding 1947). Other site factors such as deficiencies in soil phosphorus can reduce seed yield by up to a third (Burdon and Low 1971). Predation of seed (Ordonez and Retana 2004) and loss of seed to pathogens such as pitch Canker (Dick 1998) can dramatically reduce the amount of viable seed produced by the plantation. Seed number per cone can also vary. Ledgard (2001) recorded a mean number of 914 viable seeds per tree for *P. radiata* growing in New Zealand and observed a maximum value of more than 3000 seeds per tree. However, by using a combination of area and age as a proxy for seed
production and by examining pine spread from different plantations of different sizes and ages it is possible to investigate the role of propagule pressure in invasion success.

As well as the risk from large plantations, windbreak plantings also provide a significant amount of seed and plantings in the wrong areas may lead to considerable amounts of spread. There is evidence to suggest that widely spaced and edge trees such as those in windbreaks, produce more cones than close-spaced plantation trees as they have greater access to sunlight and space so often produce more foliage (Ledgard 2004). In addition, windbreaks are typically planted in long lines which increase the boundary between the source and native vegetation and the likelihood of spread (Richardson et al. 1994).

The invasion process of wind-dispersed pines has been described as step-wise involving 1) immigration and establishment; and 2) population growth (Richardson et al. 1994). The small mass and high wing loading of *Pinus radiata* seeds makes them highly adapted for wind dispersal (Van Wilgen and Siegfried 1986). Pine wildlings can be established at distances of up to 3 km from the plantation following long distance dispersal events (Richardson and Brown 1986). While long distance dispersal events may be rare, and only represent a small proportion of total seed dispersed they can lead to orders of magnitude increases in predicted spread rates (Higgins and Richardson 1999).

Dominant wind patterns during times of seed release will govern seed distribution at a site and result in a higher propagule pressure and greater risk of invasion in areas downwind from plantations. High velocity north-westerly winds have been responsible for the distribution of *P. radiata*, *P. pinaster* and *P. contorta* wildlings to the south-east of plantations in the South Island of New Zealand (Hunter and Douglas 1984).

**Timing**

*Pinus radiata* produces cones carrying fertile seed as early as 5 to 10 years after establishment with cone production peaking between about 10 and 20 years of age (Lewis and Ferguson 1993). This period to the production of the first viable seed is the absolute minimum time from plantation establishment to the first invasion event. Patterns of invasion from the southern hemisphere indicate that pine invasion generally takes place soon after large scale plantation establishment (Richardson et al. 1994).
Evidence from a study of \textit{P. radiata} invasion in South Africa showed that first generation colonisers were able to establish from the first viable seed released from the plantation (Richardson and Brown 1986).

The timing of an invasion event will depend heavily on the resistance provided by the surrounding landscape. Factors shown to determine the resistance or susceptibility of an area to pine invasion include levels of vegetation competition and herbivory, fire regime and land use (Richardson et al. 1994). In New Zealand grazing pressure by sheep can reduce the likelihood of wildling establishment (Benecke 1967, Ledgard 1988). Prevailing climatic conditions and variations in seed production are also important determinants of the time to first establishment (Ledgard 2001). Step wise patterns of spread of \textit{Pinus contorta} in New Zealand have been attributed to variations in seed production (Cooper & Mazey 1984 cited in Ledgard 2001). Ultimately, the suitability of a site will depend on a combination of all factors, for example spread of \textit{P. contorta} is most likely to occur on ungrazed land with low vegetation density downwind of the seed source (Ledgard 2001). An absence of suitable establishment conditions combined with a lack of heavy seed fall will result in a delay between plantation maturation and natural regeneration in surrounding land. In New Zealand, wildlings are rarely observed establishing without some lag period (pers. comm. N. Ledgard 2006). Lag times in \textit{P. contorta} spread have been attributed to the grazing pressure of rabbits (Benecke 1967). Similarly, the presence of small browsing herbivores has been used to explain the low levels of invasion observed in Chile (Richardson et al. 1994).

A recent study found that at local scales propagule pressure is in fact a better predictor of pine spread than environmental variables such as climate and vegetation type (Rouget and Richardson 2003) and it has been suggested that if propagule pressure is high enough it may be able to overcome many potential barriers to invasion (Richardson et al. 1994). As the national plantation estate increases, a wider range of habitats are exposed to invasion, increasing the likelihood of successful establishment (Richardson et al. 1994). Indeed, the extent of pine invasion has been linked with the residence time of source plantations (Richardson 1989 cited in Richardson et al. 1994).
**Habitats invaded and the role of disturbance**

Disturbance has long been thought to play a major role in facilitating the invasion process (Elton 1958, Crawley 1987, Lodge 1993). The ability of disturbance to facilitate invasion is generally attributed to the production of extra resources such as light, nutrients and water which invaders require to succeed. Hence, any factor which increases the availability of limiting resources will increase the vulnerability of communities to invasion (Davis *et al.* 2000). Evidence from pine invasions in the southern hemisphere suggests that disturbance facilitates pine invasion and that severe disturbance is required for the successful invasion of forests (Richardson and Bond 1991, Richardson *et al.* 1994). Examples of disturbance include changes to grazing pressure and fire regime and the removal of vegetation. For example, naturally occurring fires in the South African fynbos region create the disturbance thought necessary for invasions to occur (Richardson and Cowling 1992). If disturbance is deemed necessary for the invasive spread of pines it follows that intact environments free from disturbance should provide a hindrance to invasion. Indigenous forests free of disturbance and adjacent to plantations in both South Africa and New Zealand appear to resist invasion (Richardson *et al.* 1994). In New Zealand no introduced conifers have established under closed canopy forests or shrubland (Ledgard 1988) with major disturbance considered a prerequisite for establishment (Ledgard 2004). *Pinus radiata* is considered a shade intolerant species (Lewis and Ferguson 1993) and canopy covers of greater than 80 % have been deemed a limiting feature for pine spread (Richardson *et al.* 1994). In Chile, interiors of forest fragments, free of disturbance with intact dense canopies have been shown to withstand invasion (Bustamante *et al.* 2003).

Vegetation types found to be most susceptible to invasion by pines include bare ground, dunes and grasslands (Richardson *et al.* 1994). Evidence from pine invasions in the southern hemisphere indicates that areas with more nutrient rich soils and a higher presence of vigorous herbs will resist invasion (Richardson *et al.* 1994). However, observations of pine spread in New Zealand suggest that completely bare ground may in fact hinder establishment by exposing seed and seedlings to predation by birds, rabbits and insects (Davis, 1996; pers. comm. N. Ledgard 2006). The success of pines in grassland environments has been attributed to a lack of competition and the fact that the dominant growth form is different from their own (Richardson and Bond 1991). Dense tussock cover can act as a nurse for pine seedlings in high altitude areas (Benecke
1967). Invasibility may also vary within grassland environments. Benecke (1967) showed that survival of *P. contorta* seedlings was greater on unimproved grasslands compared with improved (fertilized) grasslands and attributed the difference to an increase in competition from introduced grasses on improved areas. Competition with native ground layer vegetation may also be responsible for regional differences in invasion success. Observations of spread in New Zealand indicate that pines are more invasive in the dry eastern areas of the South Island whereas in the wetter areas such as the west coast of the South Island and the entire North Island vigorous native growth may be reducing opportunities for pine establishment following disturbance (pers. comm. N. Ledgard 2006). It is possible to rank areas in terms of their susceptibility to invasion based on, among other features, vegetation structure and level of disturbance, however, the ultimate success of pines will depend on an interaction between the level of disturbance, life history traits of the species and environmental features (Higgins and Richardson 1998). For example the ability of a seedling to survive in a given microsite will depend not only on the environmental features of the site, e.g. level of vegetation cover, but also on the ability of the particular species to tolerate shade.

**Role of fire**

Fires, either naturally occurring or anthropogenic have a large influence on pine success. Natural populations of *P. radiata* are dependent on high severity fires which initiate seedling establishment (Fenton 1951, McDonald and Laacke 2003). The species has been described as a fire evader due to its release of canopy stored seed which is released after high intensity fires (Fonda 2001). The cones of *P. radiata* and other pine species are able to protect seeds from fire and maintain their viability in the post fire environment (Linhart 1978).

In areas surrounding plantations fires may facilitate the invasion process. Fire stimulates the release of large amounts of seed from the serotinous cones and can create favourable conditions for germination and establishment (Richardson and Brown 1986, Richardson *et al.* 1989, Richardson *et al.* 1994). In South Africa, invasive populations of serotinous pines grow rapidly after fire (Richardson and Cowling 1994). *Pinus radiata* abundance has been found to increase after fire with areas free from fire experiencing slower rates of invasion (Richardson and Brown 1986). Pine success after fire has been attributed to a reduction in native cover and hence a lack of competition.
(Richardson and Cowling 1992). Recolonisation of a site post-fire may pose a barrier to invasion, for example the establishment of exotic grasses can prevent pine seedlings from establishing in New Zealand (pers. comm. N. Ledgard 2006).

Fire can also also be a cost-effective control tool if used properly in the right places. Small wildlings (up to 2-3m) are readily killed by grass/scrub fires in New Zealand (pers. comm. N. Ledgard 2006). Larger trees can survive fires that do not reach the canopy (De Ronde 1982) which means that the effectiveness of burns to control wildlings will depend on the size structure of the invading population. Richardson and Brown (1986) generalised that a fire interval of 9 years or less would kill all pines established since the last fire. Fires more than 9 years apart may kill adult pines, however, recruitment following the release of seeds will result in population growth and dispersal into new areas. Ultimately, the effect of fire on pine invasion will vary with fire intensity, the size and maturity of wildlings, proximity of the seed source and the vigour of other vegetation present which may invade after the fire.

**Impacts of invasion**

The majority of research investigating the impacts of pine invasion has been based on extrapolating impacts from the establishment of *Pinus* plantations. There are vital differences between areas invaded by pines and plantations which may make extrapolating impacts less appropriate in certain situations. Plantations result in total planting across an entire site whereas self-sown trees can be more site-specific in terms of their establishment resulting in comparatively reduced impacts upon biodiversity and hydrology (Ledgard 2001). Furthermore, due to the nature of the invasion process the majority of land affected by wildling spread will have very low densities of pine with reduced impacts. However, in the absence of adequate controls, wildling stands can exhibit densities higher than those of plantations and may have the potential to impose similar significant and wide ranging ecological impacts, some of which are outlined below.

Plantations have obvious differences to native forest including reduced structural and compositional diversity, reduced light levels and a continuous layer of pine needles on the forest floor (once the plantation is established) resulting in the potential for impacts upon a variety of trophic levels ranging from soil dwelling invertebrates to native mammals. In Australia, the establishment of planted stands has been associated
with reductions in vegetation structure (Smith 1997), bird diversity (Disney and Stokes 1976, Smith 1997) and mammalian and arboreal marsupial species richness (Lindenmayer et al. 2000). However, the quality of habitat provided by plantations will depend strongly on time since establishment (Suckling et al. 1976). In some cases plantations can provide good habitat for native fauna. For example bird densities in New Zealand were found to be higher in pine plantations at Kaingaroa than in native forest (Brockie 1992).

Afforestation with *P. radiata* causes dramatic reductions in the cover and density of native plants in fynbos vegetation in South Africa (Richardson and Van Wilgen 1986). Increased shade created by the closed canopy of pines can result in the local extinction of indigenous species (Richardson and Van Wilgen 1986, Richardson et al. 1989). Ethylene released by decomposing *P. radiata* can inhibit the growth and germination of some species (Lill and McWha 1976, Lill et al. 1979) and may also be responsible for negative impacts on understorey vegetation.

The higher growth rates and increased biomass that accompanies afforestation results in litter accumulation and changes to nutrient cycling and the severity of fires (Versfeld and Van Wilgen 1986). When the original vegetation is of low stature such as grasslands and shrublands, this increase in biomass is dramatic and can result in changes to ecosystem hydrology including reductions in streamflow (Van Wyk 1987). It is possible that high density invasions of similar environments (grasslands etc.) will result in comparable impacts on water supply (Kruger 1977), however as the causes of the changes to hydrology are unclear, extrapolation to the invasion situation remains difficult (Versfeld and Van Wilgen 1986). Changes to water yield will depend on previous vegetation and can vary across regions (Vertessy et al. 2003). Afforestation impacts on water quality will also depend on past land use. There is strong evidence to suggest that the conversion of farmland to plantation can result in improvements to water quality in Australia (Turner et al. 2004) and that tree planting in general is an effective strategy for salinity abatement (Vertessy 2000).

Major increases in biomass that accompany afforestation can also accelerate erosion rates. Scott and Van Wyk (1990) have shown that increased fire intensity associated with biomass increases can reduce soil wettability leading to accelerated rates of surface runoff and soil erosion. Conversely, there are many situations in New Zealand where the appropriate planting of conifers has been used to prevent erosion.
Wildlings can also improve soil quality and enhance biodiversity in degraded areas (Dyck 2004).

The establishment of coniferous vegetation has also been associated with soil acidification and reductions in nutrient availability (Miles 1985, Ogden and Stewart 1995). In contrast, Davis (1998) found evidence for increases in nutrient availability under conifers planted in the South Island of New Zealand. When acidification does occur it is typically caused by the leaching of organic acids produced in slowly decomposing pine litter (Scholes and Nowicki 1998). The impact of pines on soil properties will depend on a number of factors including soil parent type. For example, reductions in pH may be greater on poorly buffered soils with low organic matter content (Davis et al. 1996).

Further impacts of invasion include those on aesthetic and land use values. Pine invasion of treeless native grasslands and shrublands in New Zealand is seen to threaten the existing character of the landscape (Ledgard 2001). Pines are large, tall and dark, contrasting markedly with native vegetation and transforming the shape and colour of the countryside and impacting on native biodiversity (DOC 2001). Many conifer plantings, especially those in urban areas, have become such a dominant feature of the landscape in New Zealand that local residents have developed an affinity for them. A sound approach to wildling management will not require the removal of all trees, rather an assessment of the risks posed by each stand.

This review asks the following questions:

1. What is the current extent of Pinus radiata invasion in Australia?
2. Are the patterns of invasion and invasibility in Australia similar to those observed in South Africa and New Zealand?
3. How do the ecological impacts of pine invasion upon native eucalypt forest in Australia compare with those in native shrublands and grasslands of South Africa and New Zealand?
Pinus invasion in Australia

Pinus plantations in Australia

Pines are widely cultivated in Australia with almost one million hectares growing across the country. The plantation estate is expanding rapidly in response to the Australian government policy, Plantations for Australia: the 2020 Vision which aimed to treble Australia’s total plantation area, including softwood and hardwood plantations, between 1996 and 2020 (DPIE 1997). Over the past five years the annual increase in softwood plantation area has averaged almost 10,000 hectares (Parsons et al. 2006).

Pinus radiata is by far the most commonly planted Pinus species in Australia with over 740,000 hectares in cultivation. Other major species include P. elliottii (over 78,000 ha) and P. caribea (over 57,000ha) (Wood et al. 2001). The majority of P. radiata is planted in New South Wales and Victoria with a combined estate of more than 550,000 hectares (Wood et al. 2001). Smaller estates are cultivated in Western Australia, Tasmania, Australian Capital Territory and South Australia.

Current Weed Status

A number of Pinus species are considered invasive in Australia including P. caribaea, P. contorta, P. elliottii, P. halepensis, P. jeffreyi, P. nigra, P. pinaster, P. ponderosa, P. radiata and P. taeda (Richardson 2006). Two other species, Pinus canariensis and P. pinea have naturalised (Richardson 2006). Definitions proposed by Richardson et al. (2000b) were used. ‘Naturalised’ plants are those able to ‘sustain self sustaining populations for at least 10 years without direct intervention by people’. ‘Invasive’ species are those that can ‘produce offspring, often in very large numbers at considerable distances from the parent plant, and thus have the potential to spread over large distances’ (Richardson et al. 2000a). Pinus halepensis is the only species to be declared noxious in any state and no Pinus species are considered Weeds of National Significance.

Pinus radiata is considered highly invasive in south-east Australia in areas receiving >600 mm average annual rainfall (Muyt 2001). In terms of the area of land invaded, P. radiata ranks ahead of P. pinaster and P. nigra in Victoria (Carr et al. 1992). The large plantation area of Pinus radiata (74% of the softwood estate; Wood, 2001) would suggest that this position of the species as the most widely spread pine would also hold for Australia as a whole however this ranking does not reflect the
intrinsic invasiveness of the species. There is very little information on the relative invasiveness of *Pinus* species in Australia. It has been suggested that *P. halepensis* appears to have a similar invasive and competitive ability as *P. radiata* in South Australia (Virtue and Melland 2003). Minko and Aeberli (1986) suggest that *P. nigra* has a much greater reproductive potential than *P. radiata* with individuals as young as 8 and only 2.5 m tall carrying cones. Personal observations suggest that species other than *P. radiata*, e.g. *P. ponderosa* produce more cones and cone earlier in native vegetation and may pose a greater threat if left uncontrolled.

*Documentation of Pinus radiata invasion in Australia*

Records of pine spread in Australia are scarce. Observations of infestations remain largely anecdotal and quantification of wildling densities and distributions are mostly restricted to a handful of studies. Two major studies have been undertaken in the Australian Capital Territory. Chilvers and Burdon (1983) tracked an invading *P. radiata* population within a native eucalypt forest over a 14 year period. They recorded pine densities of 800 per hectare in a 20 m by 160 m transects and observed higher rates of recruitment among the pines compared to the eucalypt species present. One study undertaken in the Cotter River catchment south west of Canberra examined the factors influencing the age structure of an invading population of *P. radiata* (Dawson et al. 1979). Patterns of regeneration in the native vegetation mirrored seed production in the plantation suggesting that temporal variations in the amount of seed produced may have a strong influence on the timing of invasion.

*Pinus radiata* has been listed as a very serious threat to one or more vegetation formations in Victoria and has been observed spreading into a range of environments including heathland, lowland grasslands and grassy woodland, dry and damp sclerophyll forest and riparian vegetation (Carr et al. 1992). Quantitative work in Victoria is limited to a study by Minko and Aeberli (1986) who investigated the effects of wind, ground cover, grazing and fire on *Pinus radiata* spread at several sites. The authors recorded an average pine density of 385 individuals per hectare in unburnt sites and a maximum dispersal distance of 1.5 km. They observed higher levels of invasion downwind from plantations on exposed sites and on unburnt sites and an absence of pines in pasture areas.
In South Australia self sown wildlings are commonly observed in native vegetation and roadsides adjacent to plantations and windbreaks. *Pinus radiata* has been listed as naturalised in several regions of the state and invasions have been observed in the Mount Lofty Ranges region and Lower Eyre peninsula (Virtue and Melland 2003). Conservation areas known to be invaded include Belair NP, Deep Creek CP, Newland Head CP and Eudena Cemetery Reserve (Virtue and Melland 2003).

In Western Australia pines have invaded *Eucalyptus marginata* forest, heath on limestone, shrublands and *Banksia* woodlands in areas receiving greater than 600 mm/yr rainfall. Spread has occurred in the southern region of the state from Perth south to Esperance and approximately 100 km inland to Narrogin (G J Keighery, unpublished data 1996 in Richardson and Higgins 1998). Pines are widespread, however, they are not considered to be invaders of major importance (G J Keighery, unpublished data 1996 in Richardson and Higgins 1998).

Pines are invading natural areas in Tasmania (Swarbrick and Skarrat 1994) however, no quantitative records of spread are maintained. Pines are spreading not only from plantations but from areas originally planted with pines to stabilise gullies as well as hedge plantings on golf courses and other urban areas. Regeneration appears to be greatest along roadsides and pines grow especially well in coastal areas (pers. comm. A. Crane 2004).

*Pinus radiata* is not grown in large cultivation in Queensland, however it has been observed spreading from windbreak trees. *P. elliottii* is a major plantation tree in the state and both species are invading moist and infertile sandy soil along the south-east coast (Swarbrick 1984).

Wildling pines have been observed spreading from plantations across New South Wales, the nation’s largest cultivator of *P. radiata*. The species is a noted invader within nature reserves in the Upper Murray region of southern New South Wales. Large pines have been recorded growing in open woodland within Kosciusko National Park at distances of more than 2 km from the plantation (pers. comm. J. Molloy 2004). Lindenmayer and McCarthy (2001) investigated pine spread in the context of forest fragmentation, comparing the level of *P. radiata* invasion in remnant patches and areas of continuous forest in the areas surrounding Bucleuch State Forest just north of Kosciusko National Park. Wildlings were present in 5.5% of 507 plots (10 x 10 m) within surveyed Eucalypt remnants, located 5-400m from the plantation, and were found to be absent from areas of continuous native forest. Plots within continuous forest
were located more than 1 km from the plantation, implying that the current distribution of wildlings is limited to within this distance of the source.

The Central West of New South Wales has over 80,000 hectares of *P. radiata*. Several large plantations lie in close proximity to National Park land in the Blue Mountains region. Wildling pines are encroaching several areas of high conservation value. Considerable invasions have occurred at Newnes and Lidsdale State Forests where wildling densities exceed 2000 per hectare and isolated wildlings more than 20 m in height can be found growing at long distances at up to 4 km from the plantation (Williams and Wardle 2005a). Other large plantations in the region have sourced invasions into Blue Mountains National Park and Kanangra-Boyd National Park, at distances of up to 1 km from the seed source (M Williams, pers. obs. 2003; pers. comm. J. Bros and C. Banffy 2004). However, intact native forest bordering large plantations in the state’s south (Bombala and Tumut regions) appear to be resistant to invasion with pine spread limited to physically disturbed areas (M. Williams, pers. obs. 2006) indicating a need to investigate the factors determining pine success across sites.

*Other Pinus species*

Several minor pine species have also become invasive in Australia. *Pinus halepensis* invades mallee and grassy woodlands in South Australia, with some spread in Victoria (Muyt 2001). *Pinus pinaster* is invasive in a wide range of habitats particularly coastal bushland in New South Wales, Victoria and South Australia. The species has invaded moist sclerophyll forests, coastal plains and heathlands in Victoria (Carr et al. 1992, Swarbrick and Skarrat 1994).

*Pinus elliottii* has become invasive on the east coast of Australia, invading open forest and woodland, Wallum heathlands, roadsides, wastelands, heath (Swarbrick and Skarrat 1994) as well as sand dunes, Melaleuca swamp forest and both dry and wet sclerophyll forest (pers. comm. M. Smith 2004). The species has been spreading from plantations into adjacent native vegetation at Coloundra, Maroochydoore and the Sunshine coast. Bushland remnants in urban areas of Coffs Harbour are also being threatened from domestic plantings, e.g. along golf courses.

*Pinus caribea* and *P. elliottii* as well as a hybrid of the two species make up the majority of the plantation estate in Queensland and all three species have been observed spreading from planted areas (pers. comm. P. Locos 2005). Other documented invasions
include that of *P. brutia* in South Australia (Virtue and Melland 2003) and *P. nigra* which has limited spread into both dry and moist sclerophyll forests in Victoria (Carr et al. 1992) and Adelaide (Swarbrick and Skarrat 1994).

**The invasion process in Australia**

While studies investigating pine spread in Australia are limited, they provide us with a starting point to investigate patterns of infestation and the factors facilitating the invasion process. Initial studies indicate that patterns of dispersal in Australia are similar to those observed elsewhere. Reduction in wildling numbers with distance from the plantation is commonly observed and is typical of wind dispersed species (Burdon and Chilvers 1977, Minko and Aeberli 1986). The majority of seeds fall within a small distance from plantation trees (Wardle et al. in prep), however, strong winds can result in the establishment of wildlings at distances of up to 4 km (Williams and Wardle 2005a). Wind direction has also been shown to have a dominating influence on the distribution of wildlings with respect to the plantation. Densities of wildlings and their distance from the plantation are often higher downwind from plantations. This pattern of invasion has been observed across the Blue Mountains region in New South Wales (pers. comm. C. Banffy 2003) and at plantation sites in Victoria (Minko and Aeberli 1986).

Birds have been responsible for the movement of pine seed into native vegetation in Queensland (*P. elliottii*) (W L Thompson, pers. comm. in Richardson and Higgins 1998), Western Australia (*P. pinaster*) (pers. comm. G J Keighery in Richardson & Higgins 1998), and in southeastern Australia (Gill and Williams 1996). Yellow-tailed black cockatoos (*Calyptorhynchus funereus*) feed on *P. radiata* cones and carry seed away (Attiwill 1970, Buchanan 1989, Gill and Williams 1996). Distinguishing between bird and wind dispersed wildlings is difficult, however the appearance of single pines more than 4 km from any potential source in Kosciusko National Park (pers. comm. M. Pettitt 2005) suggests that birds may be responsible for outlying trees. Birds are an added vector of seed dispersal in Australia which may be facilitating the invasion process. The important role of long distance dispersal in plant spread is well known (Clark et al. 1998) and the failure to incorporate rare long distance dispersal events can lead to an underestimation of spread rates (Higgins and Richardson 1999). Isolated wildlings that result from bird or long distance wind dispersal will
increase the rate of invasion as they begin to produce seed at large distances from the plantation. Wildling trees are capable of producing substantial numbers of seed (Wardle et al. in prep) and recruiting a second generation of pines (Williams and Wardle 2007) indicating that wildling populations may be self sustaining in the absence of the plantation source.

**Timing**

Propagule pressure has recently been shown to play a large role in invasion success (Green 1997, D’Antonio et al. 2001, Dullinger et al. 2003, Foxcroft et al. 2004). An investigation of the determinants of pine spread in South Africa indicated that propagule pressure is a better predictor of pine distribution at small scales, while environmental variables, particularly climate and vegetation, were better at explaining spread at large scales (Rouget and Richardson 2003). Weak correlations between pine distribution and environmental variables at small scales were attributed to the fact that pines have not yet invaded all suitable habitats suggesting that time since establishment of the source must also be considered when examining the role of propagule pressure.

Previous studies which use distance to source as a measure of propagule pressure (Rouget and Richardson 2003, Foxcroft et al. 2004) do not consider residence time of the source which may have a large influence on not only seed production but on the nature of the relationship between propagule pressure and the distribution of the invader. For example in the early stages of invasion pines may not have invaded all suitable habitats yet resulting in a weak correlation between pine distribution and environmental variables (Rouget and Richardson 2003). An alternative approach could involve using the area of a plantation and time since establishment as a proxy for propagule pressure. The extent of pine invasion has been found to increase with the residence time of source plantations (Richardson 1989 in Richardson et al. 1994). If propagule pressure is a primary determinant of invasion success then you would expect the greatest amount of spread to occur from large, old plantations with small, young plantations sourcing no or few invasions.

The non-linear relationship between tree age and seed production (Danbury 1971) must be taken into account when calculating seed yield. Additional factors including the length of the plantation margin, local topography and wind intensity will influence seed rain meaning that there may not always be an exact relationship between...
Review of *Pinus radiata* invasion in Australia

seed production within the plantation and propagule pressure in surrounding areas. For example areas surrounding plantations established on take-off sites will receive higher levels of seed rain which may lead to a shorter lag time before natural regeneration occurs.

Invasion timing and success will also be determined by the biotic resistance of the recipient vegetation. When resistance is weak even a low number of propagules is capable of establishing an invasive population (D'Antonio *et al.* 2001). However, when resistance is high propagule pressure should have a strong influence on invasive success. Temporal variations in factors that influence establishment, i.e. rainfall, presence and abundance of grazing animals, level of ground cover and fire means that the susceptibility of a site to invasion will change with time. Time lags between plantation maturation and pine spread in Australia have been attributed to the browsing activities of introduced herbivores. Pine invasion into eucalypt forest in the ACT only occurred once the browsing pressure of rabbits on pine seedlings was reduced following the introduction of Myxomatosis in Australia (Dawson *et al.* 1979). Browsing by native fauna including wallabies and possums is also capable of reducing the survival and growth of *P. radiata* (Fielding 1947, Neilsen 1981). Variations in seed production within pine plantations themselves can also have an important influence on the timing of invasion. Patterns of pine regeneration in native vegetation in the ACT were shown to match peaks in seed production in the adjacent plantation (Dawson *et al.* 1979).

Clearly, temporal variation in propagule pressure imposed by the plantation will shape the invasion pattern. However it is the interaction between environmental resistance and propagule pressure which will ultimately govern invasion timing and success.

**Habitats invaded**

*Pinus radiata* will grow in a wide range of climate and soil regimes and has been reported invading a variety of both undisturbed and disturbed environments from grassland to open woodland and riparian vegetation (ANH Specimen Information Register) but is not so likely to establish in intact, continuous native forest (Lindenmayer and McCarthy 2001). In Victoria the species has invaded a range of environments including dry and damp sclerophyll forest, cleared woodlands and heath (Carr *et al.* 1992). Although some research suggests that the species invades communities equally with similar rates of invasion (Van der Sommen 1978), evidence
from both quantitative studies and personal observations indicates that vegetation types
do differ in their susceptibility to invasion. It has been suggested that open, dry
environments are more vulnerable to invasion as they provide high light conditions
favourable for pine establishment (Chilvers and Burdon 1983), whereas moist areas
with deep soils that support wet sclerophyll forest appear to resist invasion. The results
of a more recent study by Lindenmayer and McCarthy (2001) were consistent with this
idea, showing a higher incidence of pine wildlings in drier eucalypt remnants dominated
by *Eucalyptus dives* and *Eucalyptus bridgesiana* compared with other eucalypt types.
Open eucalypt forests dominated by *E. blakelyi* in Victoria appear to resist invasion by
*Pinus radiata* (Minko & Aeberli 1986).

Observations of pine spread by various land managers appear to confirm the
idea that the risk of spread will differ among vegetation types (Richardson and Bond
1991). Environments perceived to be resistant to invasion include rainforest, closed
heath and closed eucalypt forest. There is a general belief that heavily shaded areas
inhibit seedling growth. However, *Pinus radiata* seedlings are capable of establishing
amongst ground cover with some shading from native species (Virtue and Melland
2003) and have been observed growing on damp sclerophyll forest in Victoria (Carr
*et al.* 1992). Obviously, there is still more to learn about the threshold light levels and site
circumstances needed for *P. radiata* wildlings to establish within existing vegetation in
Australia and until these are known, the risk of wildling invasion cannot be predicted
accurately.

The facilitating role of disturbance thought necessary for invasions to occur
(Richardson *et al.* 1994) has yet to be fully explored within Australian environments.
Two of the primary natural disturbances in temperate forests are treefalls (Runkle
1985), and fires. Fires are ubiquitous across southeastern Australia (Gill *et al.* 1981) and
can often be devastating in forested areas during drier summers (Gill 1975). Both
disturbance types may facilitate invasion by providing extra resources, e.g. light which
pines may then exploit. Human activities may modify the natural disturbance regime
and can increase the susceptibility of an area to invasion (Fox and Fox 1986a). Human
mediated disturbances including the constructions of roads and fire trails, selective
logging and soil dumps typically occur in areas surrounding plantations. Disturbance
such as these may reduce the resistance of areas close to the plantations to invasion and
assist the establishment of initial colonizers which may then source invasions into
undisturbed areas beyond the plantation boundary. In Australia first generation pine
wildlings have been observed growing at long distances from the plantation (Williams and Wardle 2005a) and within undisturbed forest environments (Chilvers and Burdon 1983) illustrating that *P. radiata* does have a capacity to establish in areas of intact native vegetation, despite evidence to the contrary (Lindenmayer and McCarthy 2001). Models of pine spread in South Africa indicate that while the main effect of increasing disturbance is to increase the rate of invasion (Higgins and Richardson 1998), this effect is context dependent as disturbance events such as fire and treefalls will both kill individuals and provide opportunities for establishment (Higgins and Richardson 1998). Further investigations into the role of disturbance in pine spread in Australia will require an integration of other factors including plant traits and habitat suitability.

Lack of suitable soil mycorrhizae has been proposed as a limiting factor of wildling success (Richardson et al. 2000b). Initial establishment of *P. radiata* plantations was hindered by the absence of soil mycorrhizae. Inoculating nursery soils with mycorrhizae prior to planting is common forestry practice (Bowen 1965) and can increase the growth of *P. radiata* (Theodorou and Bowen 1970, Theodorou 1971). Davis et al. (1996) observed significantly higher survival rates for *P. radiata* seedlings inoculated with the mycorrhizal fungus *Rhizopogon rubescens*, compared with untreated seedlings. An absence of suitable mycorrhizae in areas adjacent to plantations may hinder the establishment of pines in native vegetation. It has been suggested that the spread of *P. elliottii* and *P. taeda* in New South Wales on drier soils inland is limited by such an absence (Morley and Toelken 1983). Only a few studies have investigated the distribution of suitable mycorrhizal fungi outside of plantations. A sharp decline in the presence of fungal species with increasing distance from the plantations has been observed during an investigation of two sites in eastern Australia (Lamb 1979). In an area free from invasion fungal abundance declined to zero between 1 and 2 km from the plantation. At a site where *P. radiata* had naturalised, wildlings located greater than 2 km from the plantation were found to be mycorrhizal suggesting that lack of a fungal association is not responsible for any inability to spread. It is also possible that pines are exploiting mycorrhizae associated with eucalypt species (Chilvers and Burdon 1983). Furthermore, Richardson et al. (1994) proposed that mycorrhizae were no longer limiting pine success outside plantations as they are ubiquitous across the southern hemisphere. Greater knowledge of the distribution of mycorrhizae outside plantations will shed light on their role in the establishment of wildling pine populations.
Role of fire

The response of *P. radiata* to fire will have a major influence on the species’ success as an invader. Areas surrounding plantations experience frequent, low intensity burns and suppression of wildfire to protect the plantation resource. *Pinus radiata* is widely considered as a fire-sensitive species and a fire intensity of 200 kW/m is capable of killing pines up to 10 m tall (Burrows *et al.* 1989). The presence of fire has been shown to significantly influence wildling populations in Australia with lower numbers of young pines recorded on burnt sites compared with unburnt sites (Minko and Aeberli 1986). Pine response to fire will depend heavily on fire frequency. Frequent burns will typically kill the majority of seedlings below flame height. Conversely, infrequent burns may allow pines to grow above the flame height and survive fire. Pine mortality has been shown to decrease with increasing diameter (Williams 2003) and even small wildlings (2-3 m tall) can survive low intensity prescribed burns (M. Williams, pers. obs. 2005).

Large, reproductive pines that survive fire may in fact contribute to the invading population. Fire stimulates seed release from cones and high recruitment of seedlings following fire has been observed in Australia. *Pinus radiata* seedlings were recorded at densities close to 1 million per hectare following wildfires in south-east South Australia. Seedling densities of more than 1300 per hectare have been recorded in invaded Eucalypt forest in New South Wales 2 years post-fire (M. Williams, unpublished). Long term monitoring of wildling populations post-fire is needed to determine the proportion of seedlings that survive to maturity. Evidence of cone damage on wildlings in recently burned areas (M. Williams, pers. obs. 2003) suggests that cockatoos may be assisting the release of seed from cones. The ability of large pines to not only survive low intensity burns but to recruit heavily after them means that despite the perception of *P. radiata* as fire sensitive, fire may in fact facilitate invasion of the species.

Future research in Australia should examine the role of a number of factors on pine spread particularly; the level of canopy and ground cover, presence of grazing animals, fire, propagule pressure, topography and wind exposure. In addition a number of components of wildling demography are also required in order to assess the risk posed by *P. radiata* in Australia including; seed production (number of cones per tree and seeds per cone), seed viability and timing of release from cone, longevity of seed in
the soil and the factors affecting seedling establishment (climate, competition, predation).

**Impacts of invasion in Australia**

The greatest disparity between the ecology of pine invasions here and those elsewhere is the structure of the recipient vegetation. *Pinus* species have predominantly invaded low stature vegetation overseas, invading native grass and shrublands in New Zealand and fynbos and grassland vegetation in South Africa. The spread of trees into these environments represents a dramatic shift in life form dominance and the associated impacts are likely to considerable. In Australia the majority of native vegetation surrounding pine plantations is woodland and invasions typically involve the addition of an exotic tree species to an already forested system. It is likely that the impacts of this process will differ from those witnessed in grassland and shrubland environments and the accuracy of inferring impacts from plantations may be reduced.

Quantification of the impacts of pine invasion in Australia is very limited and evidence for negative effects remains largely observational. One of the major concerns surrounding invasion is the potential for harmful effects on native fauna and flora. Dense stands of pines will compete for moisture and nutrients and can adversely affect the vigour, survival and regeneration of native plants (Virtue and Melland 2003). A reduction of greater than 50% in native species number and biomass was visually observed in south east South Australia after 30 years of *P. radiata* invasion (Virtue and Melland 2003). Baker *et al.* (2006) observed compositional differences in native vegetation invaded by *Pinus radiata* compared with native vegetation free from pines. Reduced eucalypt recruitment has also been associated with pine invasion (Burdon and Chilvers 1994). Noted physical changes to the forest environment include increased deep shade caused by the canopy of mature pines and a substantial accumulation of pine needle litter (Burdon and Chilvers 1994). The authors anticipated long term changes to the forest in the absence of adequate control measures.

While the direct effect of pine invasion on fauna is yet to be quantified it has been suggested that the negative effects of plantations on native animal species richness are likely to be transferred to areas invaded by pines if they are not controlled (Gill and Williams 1996). Plantations are often criticised for their paucity of resources for native fauna (Smith 1997, Lindenmayer *et al.* 2000). One of the reasons for this is that the trees
are harvested every 30 years and do not form trunk hollows which have been shown to be critical habitat for a myriad of native species (Ray et al. 1983). If pine wildlings also fail to form hollows then it is possible that this effect could be manifested in invaded areas. However, the level of resources pine stands provide will depend on the age of the trees. An investigation of vegetation structure in Victorian *Pinus radiata* plantations of varying ages found that shrub cover was greatest in young plantations (less than 12 years old) (Suckling et al. 1976). As the pines matured to 26 years, canopy cover reached 60% and shaded out understorey species. However in plantations 46 to 50 years old mature pines had thinned out, canopy cover was reduced to 35% and a return of low levels of shrub cover was observed (Suckling et al. 1976). This change in structure with time has consequences for resident fauna. Echidnas and long nosed bandicoots are able to utilise food and shelter provided by young plantations while wombat densities were found to be higher in young plantations compared with adjacent native eucalypt forest (Suckling et al. 1976). The absence of many native mammal species from plantation areas was attributed to low vegetation diversity.

It is thought that invaders impart the greatest impact when they instigate changes to the natural disturbance regime (Mack and D’Antonio 1998). *Pinus radiata* is a canopy species and has the potential to significantly impact the local environment. The accumulation of flammable pine material has been raised as a potential threat to native vegetation. As pine numbers increase and begin to dominate the community, there is a possibility that local fire temperatures will intensify and destroy usually fire-tolerant eucalypt species (Burdon and Chilvers 1994). The potential for *P. radiata* to alter the natural fire regime is one of the invader’s greatest impacts as changes to fire timing and intensity can cause dramatic shifts in community composition.

The visual impacts of pine invasion may be minimal in Australia as the contrast of pines with native eucalypt forest is far less than that of low lying tussockland in New Zealand. However, the dark green foliage of pines does contrast to some degree with the grey green foliage of eucalypts and mature pines have been observed overtopping the native canopy resulting in a notable change to the physical appearance of the forest. In heavily invaded areas where pines dominate natives the visual impact of invasion must be considered. It is also important to realise that because the surrounding vegetation is capable of obscuring wildlings, invasions are likely to go unnoticed for longer periods of time with the potential for greater ecological impacts. Conversely, pines are more visually obvious and take longer to grow and produce seed than many faster growing
invasives, e.g. Gorse and Broom. Therefore there is a longer period to find and remove individuals before any long-term impacts eventuate.

The impacts of wildlings described above will only occur in areas where wildling densities are high, i.e. similar to plantation densities. Observations of plantation sites in New South Wales suggest that pine spread is limited to within a few hundred metres of the plantation at most sites with the highest densities occurring immediately adjacent to the source. Much of the land that can be labeled ‘invaded’ has pines at very low densities. Similar patterns of spread have been observed in New Zealand. A survey of conifer invasion in the Canterbury region of the South Island found that wildling densities were less than 50 per hectare for the majority of land affected (Belton and Ledgard 1991). Furthermore, pines growing in forested areas in New Zealand have been known to take decades to grow a few metres (pers. comm. N. Ledgard 2006). In Australia where pines are typically invading forested environments it is also possible that growth rates below the forest canopy will be much slower than those observed in plantations. Competition with existing tree species may result in a pine/eucalypt mix rather than a pine dominated forest. Studies investigating the invasibility between different forest types in Australia will help determine the risk of spread and the likely level of impact in these environments.

Research questions regarding impacts of pine invasion

1. What ecological changes accompany pine invasion in Australia?
2. What is the impact of these changes on native species recruitment?
3. Are pines capable of altering the fire regime?
4. What are the typical survival/growth rates of pines in eucalypt forest? Are they likely to eventually dominate the community?
Wildling Control

A variety of successful methods have been employed to control wildling pine populations. Physical removal is an effective technique as seedlings and saplings are easily pulled out of the ground. Ring-barking is also an effective technique. However, the removal of large trees is time consuming and can be costly. A range of chemicals are also capable of controlling young *P. radiata* individuals (Minko 1985). Spraying of low concentrations of amitrole plus ammonium thiocyanate, dicamba, fosamine ammonium, glysophosate or paraquat result in the death of pines. In New Zealand, metsulfuron (100-120g/ha) is mixed with a surfactant and either glyphosate (5kg/ha) or paraquat (5.6L/ha) to spray and kill wildlings less than 3 m tall (Ledgard 2004). Chemical treatment involves injecting wildlings with herbicide and may be preferred to mechanical removal as it requires less physical effort. Sodium chlorate is used to kill stumps of wildling pines when it is not possible to remove all live foliage (Ledgard 2004). In Australia, treatments involving mechanical cutting combined with herbicide application have enjoyed 100 percent success rates (pers. comm. N. Westman and C. Banffy). There are a number of disadvantages of chemical control. Results are often variable with some wildlings surviving poisoning. Access to wildlings is also required to administer this control, and the fact that wildlings remain standing, holding viable seed that continue to contribute to the invasion after treatment must be considered when comparing the effectiveness of control measures. Another problem with chemical control (particularly stem poisoning) is that it is more difficult to distinguish between treated and untreated trees which means that some individuals may be missed during control operations (pers. comm. N. Ledgard 2006). Untreated trees are only apparent months later by which time the person contracted to do the work has usually been paid.

In areas where infestations are considerable, physical removal or poisoning may not be possible and fire may be a cost-effective management option (Pryor 1991), particularly where fires are made use of opportunistically. Burning may be useful in areas where resources for manual removal are not available and where fire can be used in conjunction with pre planned burns. For example back burning operations during wildfires in 2003 in Kosciusko National Park in New South Wales provided a chance to destroy wildlings on a large scale. Wildlings that survived the fire were physically removed after the burn (Kasel and Meers 2004). Fire is a more appropriate form of control in the early stages of invasion when pines are yet to reach reproductive maturity.
Fires that are intense enough to cause pine death and frequent enough to prevent the production of a canopy seed source are capable of preventing the spread of pines (Gill and Williams 1996).

In areas where infestations are the most severe, frequent burning of a buffer zone will prevent further spread away from the plantation. Native diversity may be reduced in the buffer zone but it remains a trade-off for conserving diversity beyond this area (Kruger 1977). However, the ability of *Pinus* species to release large amounts of seed after burning means that the use of fire as a tool for control can potentially have very undesirable effects when the fire interval is greater than the time to maturity. Solely relying on hazard reduction burns may not be adequate to kill established wildlings and is perhaps used best following a program of felling or herbicide injection of larger adults.

Formal policies of wildling control in Australia are rare and the majority of treatment is undertaken on an ad-hoc basis. Pines are typically dealt with in conjunction with more general weed policies as species of low priority. It is also a common perception that hazard reduction burns control pine wildlings (pers. comm. S. Pollett, D. Mukhar, L. Piggott 2005). When funds are allocated to pine control, treatment typically involves a combination of mechanical removal and herbicide application. One of the few authorities to develop a control program dedicated to pines is ACT Forests. A strategy implemented in 2001 was aimed at reducing the spread and impact of wildling infestations with a focus on roadsides, traveling stock reserves and areas of high recreational, ecological or cultural/heritage significance (ACT Forests 2001). Control techniques include manual (by hand) and mechanical (chainsaw, brushcutter etc.) removal and chemical spraying of trees less than 2 metres high. Manual removal was found to be the most cost-effective form of control ($28/ha) compared with mechanical ($43/ha) and chemical treatment ($93/ha). However the cost-efficiency of various control methods will depend greatly on the density of wildlings (DOC 2001).

In New South Wales, The Department of Environment and Climate Change (DECC) conduct wildling control programs in areas of heavy infestation. Limited control has taken place within Blue Mountains National Park in the form of mechanical removal, herbicide (Glyphosate) injection and hazard reduction burns. Glyphosate was found to be ineffective due to the thickness of bark on old trees. Mechanical removal has been successful but is time consuming and costly (pers. comm. J. Bros 2005). Limited control on Forests NSW land is carried out ‘mainly in areas with particular
features of conservation significance’ (pers. comm. D. Binns 2005). Further work is being carried out by various non-government groups including Conservation Volunteers Australia and various bushcare groups. Of course, like most invasive species follow up control is crucial for the effective management of wildling populations. A long-term commitment of effort and funds is required, typically for 10 years or more (Ledgard 2004). Removal of missed seedlings should take place no more than 5 years after first round operations to ensure that they do not reach reproductive age.

The option of controlling wildling pines via biological control is being explored in South Africa (Van Wilgen et al. 2000) and New Zealand (Brockerhoff et al. 2004). There is a well known suite of insects that attack the cones and seeds of pines in their native ranges (De Groot and Turgeon 1998) that have the capacity to reduce seed production in invasive populations (Moran et al. 1999). The slow form of control via seed-attackers may be beneficial in cases where the gradual removal of trees would assist native regrowth (Neser and Kluge 1986). However, previous accidental introductions of insects have caused considerable impact to plantation trees. The wood wasp Sirex noctilio is a serious concern for *P. radiata* plantations in New Zealand and Australia (De Groot and Turgeon 1998). There is also fear that introduced insects could act as vectors for *Fusarium circinatum*, the fungus which causes pitch canker disease and represents another major threat to *P. radiata* (Moran et al. 1999, Brockerhoff et al. 2004). The potential threat that insects pose to plantation populations and seed orchards in particular is often seen to outweigh any conservation benefit provided by controlling wildling pines (Dyck 2004).

**Research questions regarding control strategies**

1. What are the most cost-effective, user-friendly and safe forms of control techniques and strategies?
2. Is fire an appropriate control strategy and if so, what is the optimal fire regime to achieve pine wildling control while maintaining native species diversity?
3. Is there an identifiable point when control becomes critical?
Discussion

The slow growth rate of pines is one of the reasons why they may have been overlooked as invaders of concern. Isolated pines initially establish at low densities at varying distances from the plantation leading to a perception that infestations are ‘sporadic’ and having comparatively little impact. In the absence of adequate control wildling populations may eventually, albeit slowly, reach levels at which irreversible damage occurs. South Africa and New Zealand have already suffered significant losses in biodiversity as a result of pine infestation. Whether or not \textit{P. radiata} poses the same threat to Australia’s vegetation is not known. However, the limited work that has been carried out on wildling populations here has provided both a preliminary understanding of their ecology and cause for concern as they are capable of spreading into intact vegetation in a variety of habitat types.

Preliminary survey work suggests that substantial pine spread will not occur in closed-canopy forests. There is a need to confirm common ideas concerning the resistance of closed canopy areas to invasion. In general forest environments are regarded as highly resistant to invasion by pines (Richardson \textit{et al.} 1994). However the relative ability of pines to establish in different vegetation types will depend on traits of the invader. For example, Higgins and Richardson (1998) showed that pines with persistent seedling banks invade forest environments more rapidly. In Australia, where eucalypt woodlands represent the majority of native vegetation bordering plantations, the relative invasibility of these forests is of great interest. Establishing which vegetation communities are most prone to invasion will not only assist the management of current invasions and help predict future invasion events but also provide insight into broader ideas of community invasibility.

This review has highlighted that our major source of information on the specific impacts of \textit{P. radiata} spread in Australia comes from our understanding of the impacts of plantations, and this may not accurately represent reality in a wildling situation. It is clear that in comparison to native forests, pine plantations form biologically impoverished elements of the landscape. The question that remains is what components of plantations are responsible for this ‘impoverishment’ and will this extrapolate to areas of invaded native forest? Areas heavily infested with \textit{P. radiata} can resemble conditions in mature aged plantations, although conifer dominance may be very slow, or even unlikely, within intact native forest communities. Whether or not the impacts of
plantations translate to invaded areas also needs to be determined in order to establish the total impact of pine invasion and assist the prioritisation of the species as an invader of concern.

The dispersal pattern of pines in the early stages of invasion complicates the quantification of the area of land invaded. If four large pines establish at 50m, 100m, 200m and 500m from the plantation, how much land should be considered invaded? The entire area of vegetation from the plantation edge up to the last pine? Or, the combined area under the canopy of the trees? Control agencies in New Zealand use stems per hectare to indicate the degree of invasion, however this does not reflect the actual area of land impacted. Part of the answer to this problem lies in a quantification of the impacts of one pine. Monocultures of pines are known to have negative impacts on soil properties and understorey species diversity, however, the area of influence of one tree is unknown. For example, how far out from the tree is there an effect on soil pH? Determining this area of impact will help quantify the area of land invaded and is important for identifying the point at which these impacts coalesce. It then becomes possible to determine pine densities at which control becomes critical. Tree invasions in comparison to many other weeds, e.g. Lantana and Broom, are slow and provide a relatively large window of opportunity to execute effective control measures. This is vital when allocating resources for invasive species management as it is not possible to control for all species at all sites. The effectiveness of control actions can be compared between sites based on improvements to biodiversity values (see Stephens 2004).

Further questions remain about P. radiata’s interaction with fire. Does fire facilitate or control invasion? In South Africa where pines are considered major threats to biodiversity, burns are commonly implemented to control pines. In Australia burns are very rarely initiated with wildling control as a primary objective. When control via fire does take place it is almost always in conjunction with pre-planned hazard reduction burns. Fire has the ability to change community composition significantly and must be implemented in a manner that will maintain native species diversity while keeping wildling populations in check. This can be difficult and will not be a priority in areas where pines are not considered a major problem. Even though low intensity hazard reduction burns may be capable of controlling young individuals, the ability of large pines to survive fire and recruit afterwards must be an important consideration when managing this species. The suggestion that pines themselves have the potential to alter the natural fire regime (Burdon and Chilvers 1994) also requires further investigation.
In heavily invaded areas this phenomenon may have permanent negative impacts on native diversity and increase fire risk to the plantation resource. Further research into the fire-pine relationship will help develop appropriate fire regimes required to adequately control wildling populations.

While control techniques (mechanical removal and chemical treatment) have been shown to be very effective at destroying pines, identifying the best strategies to prevent spread should be a priority. A number of recommendations have been made to reduce pine invasion. Preventative measures include avoiding planting spread-prone species, intensive use of land adjacent to plantations and repeated monitoring and removal of wildlings in downwind areas (Ledgard and Langer 1999). Other prevention measures include preventing plantation establishment in highly exposed sites and reducing the perimeter between plantations and native vegetation by planting few large plantations rather than many small (Richardson et al. 1994). Ledgard and Langer (1999) also suggest planting less spread-prone species around the margins of more invasive species to prevent dispersal of seed from edge trees which are thought to produce more cones. A focus on the removal of outlying individuals before they become reproductive is also critical to prevent the instigation of a new invasion front (Moody and Mack 1988). Spread of Pinus nigra in New Zealand is promoted by high distance dispersal events (Buckley et al. 2005) and the removal of reproductive pines from exposed positions where the opportunity for long distance dispersal is maximised has been highlighted as a priority.

The role of various factors in the invasion process has been shown to differ across regions (Richardson et al. 1994, Richardson et al. 2004) and is likely to differ within Australia also. Management strategies will need to reflect these differences. One of the major factors influencing range expansions of Pinus worldwide is the interaction between pine seedlings and native biota (Richardson and Bond 1991, Richardson and Higgins 1998). Grazing by sheep and rabbits is the main factor controlling invasion in the South Island of New Zealand (Richardson et al. 1994) and the manipulation of grazing pressure in areas surrounding plantations is a potential option for controlling pines (Benecke 1967, Ledgard 2001). Rabbits have also been implicated as control agents in Australia (Dawson et al. 1979) and it is possible that other larger herbivores, e.g. kangaroos and wallabies are slowing the invasion process by hindering seedling establishment. Evidence for the resistance of pasture land to invasion by pines in Australia (Minko & Aeberli 1986, M. Williams, pers. obs. 2005), suggests that

---

**PATTERN**  
**PROCESS**  
**MECHANISM**
manipulating grazing pressure and land use around plantations will be an effective management approach. Similarly, in Chile, small browsing animals may be responsible for the low occurrence of invasion (Richardson et al. 1994). In contrast the low abundance of herbivores and unsuitability of land for grazing in South Africa means that other factors such as fire are the main drivers of the invasion process (Richardson et al. 1994).

A major challenge that lies ahead for future management of invasive pine populations is the issue of genetic engineering of forestry trees. The genetic transformation of conifers is aimed at improving growth rates, wood properties and quality as well as pest and herbicide resistance (Tang and Newton 2003). Transfer of genes bred in plantation trees to invasive populations, typically takes place via pollen movement. Transgenes are usually dominant meaning that first generation hybrids between plantation and wildling trees will express the improved gene (Richardson and Petit 2005). The influence of improving characteristics such as wood quality in feral pines is difficult to determine, however increased pest and herbicide resistance and improved growth rates are likely to enhance the overall fitness of wildling pines (Richardson and Petit 2005). Conversely, there are real opportunities for genetic engineering to contribute to long term control of pines. The development of sterile pines would be in the interest of commercial foresters and conservationists alike. Plantation pines unable to produce seed would dramatically reduce the risk of spread and may also enhance plantation yields as trees no longer devote valuable resources to reproduction (Lindenmayer and McCarthy 2001).

The extent of pine invasions is likely to increase dramatically over the next few decades as the widespread planting of *Pinus radiata* across the southern hemisphere will inevitably lead to invasion of new areas (Richardson and Higgins 1998). As the Australian plantation estate expands so too will the amount of seed produced. Increases in seed production will enhance the likelihood of long distance dispersal events which will place larger areas of native vegetation at risk of infestation and lead to increased spread rates (Higgins and Richardson 1999). The quantification of long distance dispersal is difficult, but it remains crucial for the accurate prediction of invasion rates and must be a consideration during the management process (Trakhtenbrot et al. 2005).

Expansions of pine invasion will most likely be favoured by processes such as climate change and fragmentation of natural areas (Richardson and Rejmanek 2004). In addition, human mediated disturbance of forests may increase the vulnerability of
Australia’s eucalypt woodlands to invasion by pines (Richardson and Rejmanek 2004). Monitoring of existing wildling pine populations in Australia is necessary to determine if eventual dominance of invaded eucalypt forest is likely and will provide further insight into the factors facilitating pine invasion. Investigations of areas that remain free of wildlings both in Australia and in other regions may prove equally informative. For example the lack of invasion at low latitude sites such as Colombia and Kenya has been attributed to the presence of a vigorous, year-round ground cover which prevents the establishment of pine seedlings (Richardson et al. 1994). Even though the current level of invasion in Australia is low with many areas adjacent to plantations remaining invasion free, the dense infestation of several sites suggests that we may be observing a species that is leaving the lag phase of invasion and demands adequate response from agencies and policy makers.

One of the major difficulties associated with the control of pine invasions is that the target species is commercially important and that in certain areas conifer plantations are desirable. The plantation forestry industry makes a significant contribution to Australia’s economy (combined annual turnover of more than $18 billion) (Parsons et al. 2006). However, the industry is also a source of numerous invasive species (Richardson et al. 2003) requiring the development of strategies that deal with this conflict of interest. It is also crucial that we are aware of developments within the industry that may be creating new pathways for spread and that these pathways are managed (Richardson et al. 2003). During the last decade major changes to the forestry sector in Australia include increases in plantation area, increasing privatisation of plantations and increases in plantations established on farmland (Parsons et al. 2006). These changes have important consequences for the management of pine spread. An increase in the number of woodlots would see the establishment of many small estates resulting in large boundary to area ratios and a greater potential for invasion (Richardson et al. 1994). Multiple ownership of plantations may impede efforts to achieve a coordinated approach to control and management of the species. Effective management of pines outside plantation boundaries requires recognition of responsibility by land owners. Recent legislation in South Africa (CARA 1983) has placed pines in a special category of invaders that forces landowners to control spread beyond their boundaries. Since then Rouget et al. (2002) have emphasised the need to categorise areas based on their spread risk to help determine the level of action required.
by landowners. The establishment of similar policy in Australia is instrumental to the long term, widespread management of pine invasions.
3. Extent of invasion

Land manager questionnaire

In order to determine the level of knowledge of pine invasion in NSW and to identify potential field sites, a questionnaire was sent to appropriate land managers in the state (Appendix 1). Forestry NSW is the major owner of plantations in NSW. The estate is divided into four planting regions; Macquarie in the central west of the state, Monaro on the east coast, Hume in the south west and the Northern region. Forestry NSW planning managers in charge of each of these regions were surveyed as well as all Department of Environment and Conservation and Climate Change (DECC) staff who managed National Parks or Nature Reserves in close proximity to *Pinus* plantations. Participants were intitially contacted by email or post with follow up phone calls to respondents who identified that they were available for further contact. Some respondents were also contacted when initial participants forwarded the survey to colleagues. Phone surveys of relevant people in other states were also conducted opportunistically. Participants were asked to identify any sites invaded by *Pinus radiata* or areas adjacent to pine plantations and free from invasion as well as score the current and potential future threat of the species. They were requested to estimate the area of land invaded and the distance to the pine furthest from the source. A further aim of the questionnaire was to generate and confirm hypotheses regarding the factors facilitating invasion. Participants were asked to comment on the vegetation types invaded and other patterns of invasion observed to identify anecdotal evidence regarding pine spread. The questionnaire was also used as an opportunity to determine the type and effectiveness of control measures being implemented.
Results

Extent of invasion

Of the 25 people surveyed, a total of 16 responses were received including 13 from DECC staff and three from Forestry NSW staff including two planning managers (Northern and Hume regions) and an ecologist from the Hume region. Of the DECC staff, seven were located in the Macquarie region, four were located in the Hume region and two were from the Northern region. Comments from two other ecologists within Forestry NSW are also included.

Estimating the extent of spread proved to be a difficult task for many of the participants mainly due to a lack of systematic surveys and the dispersal pattern of the pines. One respondent commented that it was hard to distinguish how much land should be considered invaded; the entire area of vegetation from the plantation edge up to the last pine, or the combined area under the canopy of the trees? Nevertheless several responses included estimates of the area of land invaded and they are outlined in Table 3.1.
Table 3.1 Summary of sites identified by DECC and Forestry NSW staff as being invaded by *Pinus radiata*.

<table>
<thead>
<tr>
<th>Site</th>
<th>Area invaded and density of invasion</th>
<th>Distance of furthest pine from plantation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>MACQUARIE REGION</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urban fringe Wentworth Falls to Mount Victoria (upper Blue Mountains)</td>
<td>Low 1-20 ha at many localities</td>
<td></td>
</tr>
<tr>
<td>Newnes SF</td>
<td>High ~300 ha</td>
<td></td>
</tr>
<tr>
<td>Mt Walker (Lidsdale SF)</td>
<td>High ~ 300 ha</td>
<td></td>
</tr>
<tr>
<td>Abercrombie River NP (Gurnang SF)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue Mts NP adjacent to Oberon Colong Stock Route southern sector at park entrance (Yerranderie Rd)</td>
<td>50 ha</td>
<td></td>
</tr>
<tr>
<td>Kanangra Boyd</td>
<td>700 ha (for Kanangra Boyd and Blue Mountains NP combined)</td>
<td></td>
</tr>
<tr>
<td>Mount Canobolas State Conservation Area</td>
<td>Medium less than 10ha mainly occurs as isolated individuals</td>
<td>&lt;300m</td>
</tr>
<tr>
<td>Winburndale NR, Sunny Corner SF, Copperhania NR</td>
<td>5 – 50ha</td>
<td></td>
</tr>
<tr>
<td><strong>HUME REGION</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burrinjuck NR, southern side, north of Burrinjuck dam</td>
<td>300ha</td>
<td>&lt;250m</td>
</tr>
<tr>
<td>Tallaganda NP and SCA along nth black range trail and Mulloon Ck Valley</td>
<td>Scattered individuals</td>
<td>8km</td>
</tr>
<tr>
<td>Area bounded by Mannus SF, Clarkes Hill and Bogandyera</td>
<td>6km</td>
<td></td>
</tr>
<tr>
<td>Wereboldera SCA tumut, Kosciusko NP**</td>
<td>15,000ha*</td>
<td>22km*</td>
</tr>
<tr>
<td>Murrugulderie Flora reserve</td>
<td>Low density</td>
<td></td>
</tr>
<tr>
<td>Pilot hill arboretum*</td>
<td>Low density</td>
<td></td>
</tr>
<tr>
<td><strong>NORTHERN REGION</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yabbra NP; south Yabbra rd.</td>
<td>Individuals present up to 5km along roadside</td>
<td>Up to 1km</td>
</tr>
<tr>
<td><strong>MONARO REGION</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bago SF, Yambulla SF, Wingello SF, Nlbaugh SF, Glenbog SF</td>
<td>Occasional pine</td>
<td>&gt;20km</td>
</tr>
<tr>
<td>Ben Boyd NP**</td>
<td>600 ha in northern section</td>
<td></td>
</tr>
<tr>
<td></td>
<td>200 ha in south</td>
<td></td>
</tr>
</tbody>
</table>

* not all *P. radiata*

** remnant of ex-plantation site
Two reserves in the state’s north; Ngulin NR and Nowendoc NP were known to be uninvaded despite their close proximity to large plantations at Riamukka State Forest and Nowendoc State Forest.

A variety of *Pinus* species other than *P. radiata* were also considered to be invasive. In Kosciusko National Park a number of species have spread from an ex plantation site named the Jounama plantation, including *P. contorta*, *P. ponderosa*, *P. monticola*, and *P. loricio*. Pine wildlings have been frequently recorded within 1 km of the plantation, with a decrease in wildling density at 2-5 km. However isolated individuals have also been observed at 17 km from the plantation (Leaver 1983, Spate *et al.* 1986 cited in Kasel 2004a). A survey of the 24 000 hectares surrounding the plantation in Kosciusko NP estimated a pine wildling population of approximately 16 000 trees (Kasel 2004b). *Pinus elliotti* is an increasing concern on the sunshine coast of NSW where it is invading a wide range of vegetation and soil types (pers. comm. M. Smith 2004). *Pinus ponderosa* appears to be more invasive than *P. radiata* and is known to readily establish on disturbed roadside edges (pers. comm. N. Westman 2005).

*Perception of the problem*

The perceived threat of pine invasion varied across regions that differed in their extent of spread. Infestations at Newnes State Forest and Lidsdale State Forest were allocated the highest rating of 5 (severe) by the respondents. All other sites were allocated 2; low or 3; moderate, with an average current rating of 2.5. Of the 16 respondents, 8 suggested that the potential threat of *P. radiata* will increase into the future, 7 felt that it would stay the same and one participant suggested that at Lidsdale the threat would reduce, i.e from low to zero, presumably via control.

*Patterns of invasion*

The dominant vegetation type known to be invaded is eucalypt woodland and particularly open, dry eucalypt woodland, with some invasion of grasslands in the northern region. There was general consensus that heavily shaded areas including rainforest, closed heath and closed eucalypt forest as well as wet sclerophyll forest are less susceptible to invasion. However, there was one observation of *P. radiata* invading disturbed wet sclerophyll forest in Yabbra NP. Pines have also been observed invading
frost hollow grasslands in Kosciusko NP. *Pinus elliottii* has been known to invade a wide range of vegetation types including dry sclerophyll forest, littoral rainforest, melaleuca swampland and sand dunes.

The majority of respondents mentioned long distance dispersal of seed by Yellow-tailed Black Cockatoos (*Calyptorhynchus funereus*), as well as patterns of clustering around adult trees, i.e. self-regeneration. Five participants observed higher levels of invasion downwind and two witnessed higher levels of invasion after fire.

**Field Survey**

*Study Area*

The study area encompassed 29 *P. radiata* plantation sites in NSW (Figure 3.1). Where possible, sites identified by the questionnaire were surveyed. The largest distance between two sites was 693 km, between Riamukka State Forest in the northern NSW and Bondi State Forest, near the southern border. The two closest sites were Wingello A and Wingello B; 3.2 km apart. The Monaro region was composed of six sites that are geographically disjunct. Four sites, Penrose, Belangelo, Wingello A and Wingello B occur in the Moss Vale region located approximately 140 km south west of Sydney. The remaining two sites in the region, Bondi and Coolangubra are located a further 250 km south near the Victorian border. Site attributes of the plantations are shown in Table 3.2.
Figure 3.1 Twenty nine plantation sites surveyed for *Pinus radiata* invasion in NSW.

Table 3.2 Climate and plantation attributes of the 29 plantations.

<table>
<thead>
<tr>
<th>Plantation</th>
<th>Plantation Size (ha)</th>
<th>Residence time (years)</th>
<th>Mean Annual Rainfall (mm)</th>
<th>Altitude (m)</th>
<th>Border surveyed (km)</th>
<th>% of total border surveyed</th>
<th>Area/ boundary ratio of plantation</th>
</tr>
</thead>
<tbody>
<tr>
<td>MACQUARIE REGION</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gurnang</td>
<td>11924</td>
<td>74</td>
<td>995</td>
<td>1150</td>
<td>34.7</td>
<td>22.5</td>
<td>77.3</td>
</tr>
<tr>
<td>Hampton</td>
<td>1367</td>
<td>39</td>
<td>946</td>
<td>1150</td>
<td>3.7</td>
<td>16.9</td>
<td>62.4</td>
</tr>
<tr>
<td>Jenolan</td>
<td>3929</td>
<td>77</td>
<td>967</td>
<td>1200</td>
<td>29.1</td>
<td>51.2</td>
<td>69.2</td>
</tr>
<tr>
<td>Kinross</td>
<td>467</td>
<td>20</td>
<td>870</td>
<td>1000</td>
<td>1.9</td>
<td>14.2</td>
<td>34.9</td>
</tr>
<tr>
<td>Lidsdale</td>
<td>751</td>
<td>83</td>
<td>761</td>
<td>950</td>
<td>7.5</td>
<td>58.1</td>
<td>58.2</td>
</tr>
<tr>
<td>Mount</td>
<td>9133</td>
<td>70</td>
<td>1079</td>
<td>1000</td>
<td>16.6</td>
<td>11.9</td>
<td>65.5</td>
</tr>
<tr>
<td>Mullions</td>
<td>2057</td>
<td>83</td>
<td>964</td>
<td>900</td>
<td>16.7</td>
<td>44.0</td>
<td>54.1</td>
</tr>
<tr>
<td>Newnes</td>
<td>2171</td>
<td>93</td>
<td>1072</td>
<td>1100</td>
<td>38.7</td>
<td>86</td>
<td>48.2</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>2695</td>
<td>36</td>
<td>851</td>
<td>700</td>
<td>37.3</td>
<td>81.3</td>
<td>58.7</td>
</tr>
<tr>
<td>Roseberg</td>
<td>787</td>
<td>17</td>
<td>847</td>
<td>800</td>
<td>18.4</td>
<td>100</td>
<td>42.8</td>
</tr>
<tr>
<td>Sunny Corner</td>
<td>9866</td>
<td>83</td>
<td>939</td>
<td>1100</td>
<td>27.3</td>
<td>20</td>
<td>72.3</td>
</tr>
<tr>
<td>Vulcan</td>
<td>18556</td>
<td>78</td>
<td>861</td>
<td>1200</td>
<td>7.9</td>
<td>3.4</td>
<td>85.2</td>
</tr>
<tr>
<td>HUME REGION</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bago</td>
<td>8537</td>
<td>84</td>
<td>1399</td>
<td>700</td>
<td>24.5</td>
<td>36.4</td>
<td>126.6</td>
</tr>
<tr>
<td>Blowering</td>
<td>2849</td>
<td>64</td>
<td>989</td>
<td>700</td>
<td>10.2</td>
<td>23.6</td>
<td>65.8</td>
</tr>
<tr>
<td>Bogandyera</td>
<td>1402</td>
<td>10</td>
<td>740</td>
<td>650</td>
<td>5.1</td>
<td>19.1</td>
<td>52.5</td>
</tr>
<tr>
<td>Buccleugh</td>
<td>41627</td>
<td>78</td>
<td>1300</td>
<td>800</td>
<td>44.2</td>
<td>16.4</td>
<td>154.8</td>
</tr>
<tr>
<td>Clarkes Hill</td>
<td>1681</td>
<td>22</td>
<td>740</td>
<td>900</td>
<td>2.9</td>
<td>15.1</td>
<td>87.5</td>
</tr>
<tr>
<td>Green Hills</td>
<td>11035</td>
<td>85</td>
<td>1399</td>
<td>700</td>
<td>7.5</td>
<td>12.2</td>
<td>180.0</td>
</tr>
<tr>
<td>Mannus</td>
<td>372</td>
<td>70</td>
<td>982</td>
<td>550</td>
<td>8.0</td>
<td>67.8</td>
<td>31.5</td>
</tr>
<tr>
<td>Tallaganda*</td>
<td>1732</td>
<td>37</td>
<td>748</td>
<td>1100</td>
<td>16.4</td>
<td>55.4</td>
<td>58.5</td>
</tr>
<tr>
<td>NORTHERN REGION</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hanging Rock</td>
<td>7720</td>
<td>83</td>
<td>1414</td>
<td>1100</td>
<td>45.3</td>
<td>53.8</td>
<td>91.7</td>
</tr>
<tr>
<td>Nowendoc</td>
<td>2830</td>
<td>22</td>
<td>1038</td>
<td>1200</td>
<td>27.2</td>
<td>76.6</td>
<td>79.7</td>
</tr>
<tr>
<td>Riamukka</td>
<td>3351</td>
<td>33</td>
<td>1114</td>
<td>1300</td>
<td>14.3</td>
<td>51.6</td>
<td>121.0</td>
</tr>
<tr>
<td>Belangelo</td>
<td>1052</td>
<td>87</td>
<td>876</td>
<td>650</td>
<td>8.6</td>
<td>47.8</td>
<td>58.4</td>
</tr>
<tr>
<td>MONARO REGION</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bondi</td>
<td>21116</td>
<td>77</td>
<td>970</td>
<td>900</td>
<td>67.2</td>
<td>47.2</td>
<td>148.3</td>
</tr>
<tr>
<td>Coolangubbra</td>
<td>8963</td>
<td>35</td>
<td>646</td>
<td>580</td>
<td>39.5</td>
<td>23.5</td>
<td>53.2</td>
</tr>
<tr>
<td>Penrose</td>
<td>1405</td>
<td>74</td>
<td>1017</td>
<td>700</td>
<td>23.8</td>
<td>70</td>
<td>41.3</td>
</tr>
<tr>
<td>Wingello A</td>
<td>1383</td>
<td>80</td>
<td>1093</td>
<td>650</td>
<td>51.1</td>
<td>85.0</td>
<td>23.9</td>
</tr>
<tr>
<td>Wingello B</td>
<td>109</td>
<td>40</td>
<td>707</td>
<td>650</td>
<td>4.3</td>
<td>91.5</td>
<td>23.3</td>
</tr>
</tbody>
</table>

* Tallaganda is officially considered to be part of the Monaro forestry region, however it has been included in the Hume region in this study as it is in closer geographic proximity to other sites within the region and a single vegetation database for the Hume region sites also covered Tallaganda.
Survey techniques

At each site, the level of invasion was quantified by driving the border of the plantation and scoring the level of pine infestation in the adjacent vegetation. Scoring involved allocating an ‘Infestation Index’ for each 100 m interval and calculating a mean infestation index per 100 m for each site. Each 100 m interval is referred to as a ‘sample’. Scores ranged from 0, indicating no pines present to 5, which represents mature pines overtopping the eucalypt canopy. The index is a simple tool to quickly assess the level of invasion and allow comparison between sites. Divisions were based on a combination of pine basal area and density (Table 3.3). The index needs to reflect both the length of time the invasion has been occurring, i.e. older large trees represent an old invasion, and the density of the invasion which is an indicator of the susceptibility of the vegetation to invasion. In order to distinguish between young and old invasions, areas with pines greater than 10 m tall at any density were given a score of 3 or above independent of pine density. The maximum index and proportion of border with an index greater than or equal to 3 were also calculated. In areas where it was obvious that physical removal of wildlings had taken place the score was estimated using the presence of remaining pine stumps.

Table 3.3 Infestation Index for Pinus radiata invasion.

Every 100 m interval of vegetation surveyed was assigned an infestation index.

<table>
<thead>
<tr>
<th>Infestation Index</th>
<th>Level of infestation</th>
<th>Description</th>
<th>Pine basal area m²/ha</th>
<th>Maximum Height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>None</td>
<td>No pines present</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>Very Low</td>
<td>Very few pines or few small pines</td>
<td>0-1</td>
<td>&lt;5</td>
</tr>
<tr>
<td>2</td>
<td>Low</td>
<td>Small pines at density higher than level 1</td>
<td>1-2</td>
<td>&lt;10</td>
</tr>
<tr>
<td>3</td>
<td>Medium</td>
<td>Pines at least 10m tall at any density</td>
<td>Typically 2-5</td>
<td>&gt;10</td>
</tr>
<tr>
<td>4</td>
<td>High</td>
<td>Tall pines at high pine density, typically in same density as native eucalypts</td>
<td>5-10</td>
<td>&gt;15</td>
</tr>
<tr>
<td>5</td>
<td>Very High</td>
<td>Very high pine density and basal area, i.e. lots of old trees. Greater density than native eucalypts</td>
<td>&gt;10</td>
<td>&gt;15</td>
</tr>
</tbody>
</table>
The index represents the level of invasion within the first 50 m of vegetation from the plantation. Therefore each sample refers to an area of native vegetation 50 x 100 m in size. It was assumed that areas with high levels of infestation close to the plantation also had pines growing the furthest away from the plantation and thus the greatest area of land infested. This pattern was observed visually and the assumption was tested by surveying transects placed perpendicular to the plantation in areas of high pine density. The height, diameter at breast height (dbh) and number of cones were recorded within 20 m wide transects. Transects ended when pines were no longer present or terrain prevented further survey by foot. In addition, the presence of recent recruitment in the form of seedlings (pines with whorls absent) and saplings (<2 m tall) was noted. Evidence of control measures was also recorded.

Difficult terrain, road obstructions and time restrictions meant that not all borders of all plantations were surveyed. Priority was given to borders that faced opposite compass directions in order to investigate the influence of wind direction on invasion, and to areas where native vegetation bordered the plantation. Many of the larger plantations had substantial proportions of their boundaries abutting cleared or heavily grazed land. Field observations indicate that pines very rarely establish in these areas and therefore survey effort was focused on native vegetation.

Infestation index data are displayed using boxplots. The bottom and top horizontal lines for each category indicate the lowest and highest scores respectively. The box shows the middle 50% of scores (interquartile range). The dark horizontal line within the box indicates the median score. Circles represent outliers. The area of land invaded for each site was estimated using a combination of transect data, field observations and infestation index data. For example, where transect data provided the distance of the furthest pine from the plantation this information was extrapolated to estimate the extent of invasion for this border of the plantation. In other instances, opportunistic observations while surveying allowed an estimate of the extent of invasion on certain borders. Polygons of invaded areas were plotted onto plantation maps and the total area invaded was calculated in hectares for each plantation using ArcMap 9.1 (ESRI 2005).
Results

Of the 29 plantations surveyed, 20 experienced very low levels of invasion with a mean infestation index less than 1 (Table 3.4). However most of these sites had at least a few large wildlings present with diameters reaching 70 cm. At the two most heavily invaded sites, Mannus and Lidsdale, more than 90% of the borders were heavily invaded. Wildlings were restricted to within the first 200 m from the plantation and high levels of infestation (index ≥ 3) were restricted to less than 10% of the plantation boundary at the majority of sites.

There were several cases of pines being dispersed long distances of 2 km or more at Mannus, Lidsdale, Mullions Range and Newnes (Table 3.4). The longest recorded distance was 10 km, presumably from the Mannus plantation. This observation was provided by DECC staff using aerial survey data. A map of NSW showing the invaded sites is presented in Figure 3.2 and a description of the extent of invasion in each of the forestry regions is outlined below. Evidence of pine control was observed at Lidsdale, Penrose, Gurnang and Canobolas.
Table 3.4 Mean and maximum infestation index and distance of the furthest surveyed pine from the 29 plantations. Sites are placed in order of descending level of invasion. * pines mapped from the air

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean Infestation Index (Max)</th>
<th>% surveyed border length with index ≥ 3</th>
<th>Max height (m)</th>
<th>Max diameter (cm)</th>
<th>Furthest surveyed pine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mannus</td>
<td>4.64 (5)</td>
<td>93.8</td>
<td>20</td>
<td>45</td>
<td>2 km, 10km*</td>
</tr>
<tr>
<td>Lidsdale</td>
<td>4.28 (5)</td>
<td>90.7</td>
<td>30</td>
<td>64</td>
<td>2 km</td>
</tr>
<tr>
<td>Penrose</td>
<td>3.25 (5)</td>
<td>74.4</td>
<td>18</td>
<td>40</td>
<td>200 m</td>
</tr>
<tr>
<td>Belangelo</td>
<td>2.99 (5)</td>
<td>62.8</td>
<td>18</td>
<td>50</td>
<td>230 m</td>
</tr>
<tr>
<td>Wingello B</td>
<td>2.49 (5)</td>
<td>46.5</td>
<td>20</td>
<td>50</td>
<td>100 m</td>
</tr>
<tr>
<td>Mullions Range</td>
<td>2.41 (5)</td>
<td>43.7</td>
<td>25</td>
<td>95</td>
<td>2.2 km</td>
</tr>
<tr>
<td>Jenolan</td>
<td>1.67 (5)</td>
<td>28.2</td>
<td>30</td>
<td>80</td>
<td>400 m</td>
</tr>
<tr>
<td>Newnes</td>
<td>1.47 (5)</td>
<td>28.9</td>
<td>23</td>
<td>46</td>
<td>4 km</td>
</tr>
<tr>
<td>Wingello</td>
<td>1.06 (5)</td>
<td>16.6</td>
<td>20</td>
<td>50</td>
<td>80 m</td>
</tr>
<tr>
<td>Gurnang</td>
<td>0.92 (5)</td>
<td>11.3</td>
<td>15</td>
<td>50</td>
<td>700 m</td>
</tr>
<tr>
<td>Vulcan</td>
<td>0.89 (3)</td>
<td>2.5</td>
<td>15</td>
<td>60</td>
<td>50 m</td>
</tr>
<tr>
<td>Coolangubbra</td>
<td>0.60 (5)</td>
<td>8.9</td>
<td>18</td>
<td>40</td>
<td>180 m</td>
</tr>
<tr>
<td>Green Hills</td>
<td>0.60 (3)</td>
<td>0.1</td>
<td>8</td>
<td>10</td>
<td>50 m</td>
</tr>
<tr>
<td>Mount Canobolas</td>
<td>0.58 (3)</td>
<td>7.8</td>
<td>10</td>
<td>30</td>
<td>50 m</td>
</tr>
<tr>
<td>Blowering dam</td>
<td>0.58 (4)</td>
<td>13.7</td>
<td>10</td>
<td>20</td>
<td>20 m</td>
</tr>
<tr>
<td>Bondi</td>
<td>0.52 (5)</td>
<td>4.8</td>
<td>20</td>
<td>50</td>
<td>50 m</td>
</tr>
<tr>
<td>Sunny Corner</td>
<td>0.47 (3)</td>
<td>1.8</td>
<td>20</td>
<td>70</td>
<td>200 m</td>
</tr>
<tr>
<td>Tallaganda</td>
<td>0.32 (4)</td>
<td>4.3</td>
<td>11</td>
<td>30</td>
<td>200 m</td>
</tr>
<tr>
<td>Bago</td>
<td>0.3 (4)</td>
<td>0.1</td>
<td>20</td>
<td>70</td>
<td>100 m</td>
</tr>
<tr>
<td>Buccleugh</td>
<td>0.22 (5)</td>
<td>5.6</td>
<td>20</td>
<td>80</td>
<td>500 m</td>
</tr>
<tr>
<td>Hampton</td>
<td>0.22 (2)</td>
<td>0.1</td>
<td>20</td>
<td>20</td>
<td>20 m</td>
</tr>
<tr>
<td>Hanging Rock</td>
<td>0.07 (1)</td>
<td>0.4</td>
<td>25</td>
<td>50</td>
<td>60 m</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>0.05 (1)</td>
<td>0.1</td>
<td>15</td>
<td>30</td>
<td>20 m</td>
</tr>
<tr>
<td>Riamukka</td>
<td>0.04 (1)</td>
<td>0</td>
<td>10</td>
<td>25</td>
<td>20 m</td>
</tr>
<tr>
<td>Nowendoc</td>
<td>0.03 (1)</td>
<td>0</td>
<td>5</td>
<td>3</td>
<td>20 m</td>
</tr>
<tr>
<td>Roseberg</td>
<td>0.01 (1)</td>
<td>0</td>
<td>3</td>
<td>5</td>
<td>20 m</td>
</tr>
<tr>
<td>Bogandyera</td>
<td>0 (0)</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kinross</td>
<td>0 (0)</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clarkes Hill</td>
<td>0 (0)</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.2 Twenty nine plantation sites colour coded by mean infestation index.

The estimated area of land invaded by *P. radiata* and the density of invasion varied greatly between the nine most heavily invaded sites (Table 3.5). The largest extent of invasion has occurred at Lidsdale with an estimated 1800 hectares invaded, six times the area estimated by respondents in the questionnaire. The site also experienced the highest density of invasion with basal areas of more than 50 m$^2$/ha recorded in areas adjacent to the plantation (Williams and Wardle 2005a). In general, areas with a smaller areal extent of invasion experienced lower maximum densities. Pine basal area also varied with distance from the plantation. At two sites, Jenolan and Mullions Range, peak basal area occurred at 200 m and 300 m from the plantation respectively (Figure 3.3). These peaks corresponded to mature pines overtopping the eucalypt canopy (Figure 3.4). At Mullions Range, the peak in basal area is dominated by one pine with a diameter of 95 cm and more than 100 cones present. One hundred and forty nine pine seedlings were found within a 20 m radius of the pine. The total area of land invaded for the most heavily invaded sites reached 4085 hectares. Of the remaining sites, Gurnang contributed 300 hectares while all other sites had less than 20 hectares of land invaded giving a total area of 4480 hectares across all sites.

**Table 3.5 Summary of the density and aerial extent of invasion in hectares (ha) at the nine most heavily invaded sites.**

<table>
<thead>
<tr>
<th>Plantation</th>
<th>Maximum density (per ha)</th>
<th>Maximum basal area (m$^2$/ha)</th>
<th>Area of land invaded (ha)</th>
<th>Tenure of invaded land</th>
<th>Appendix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lidsdale *</td>
<td>2425</td>
<td>56.1</td>
<td>1800</td>
<td>Crown land, SF</td>
<td>2</td>
</tr>
<tr>
<td>Newnes *</td>
<td>2825</td>
<td>38.5</td>
<td>400</td>
<td>SF</td>
<td>3</td>
</tr>
<tr>
<td>Jenolan</td>
<td>1400</td>
<td>34.5</td>
<td>200</td>
<td>SF, NP</td>
<td>4</td>
</tr>
<tr>
<td>Mullions Range</td>
<td>3375</td>
<td>18.2</td>
<td>1020</td>
<td>SF, SRA</td>
<td>5</td>
</tr>
<tr>
<td>Mannus</td>
<td>900</td>
<td>23.4</td>
<td>290</td>
<td>SF</td>
<td>6</td>
</tr>
<tr>
<td>Penrose</td>
<td>825</td>
<td>13.8</td>
<td>170</td>
<td>SF</td>
<td>7</td>
</tr>
<tr>
<td>Belangelo</td>
<td>1450</td>
<td>9.4</td>
<td>120</td>
<td>SF</td>
<td>8</td>
</tr>
<tr>
<td>Wingello B</td>
<td>1550</td>
<td>15.3</td>
<td>25</td>
<td>Crown land</td>
<td>9</td>
</tr>
<tr>
<td>Wingello A</td>
<td>1050</td>
<td>24.8</td>
<td>60</td>
<td>SF</td>
<td>10</td>
</tr>
</tbody>
</table>

* Data for Newnes and Lidsdale was collected during 2003 for an honours project
Figure 3.3 *Pinus radiata* basal area (m$^2$/ha) with increasing distance from the plantation at Mullions Range and Jenolan State Forests. Values are mean basal area calculated from replicate transects placed perpendicular to the plantation boundary.
Percentage of reproductive pines

The proportion of reproductive wildlings also varied across the nine most heavily invaded sites ranging from approximately 15 % at Jenolan to just over 85 % at Newnes (Table 3.6). Newnes also has the greatest number of cones per tree with a mean value of 34.5. There was a significant positive correlation between the number of cones on a tree and the proportion of reproductive wildlings at a site (r = 0.86; p = 0.03).
Table 3.6 Percentage of reproductive pine wildlings at the nine most heavily invaded sites. Data were collected from transects placed perpendicular to the plantation boundary.

<table>
<thead>
<tr>
<th>Plantation</th>
<th>% reproductive wildlings &gt; 5m</th>
<th>Mean no. cones per tree (SE)</th>
<th>Number of pines surveyed &gt; 5m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mannus</td>
<td>15.8</td>
<td>3.5 (0.7)</td>
<td>260</td>
</tr>
<tr>
<td>Lidsdale *</td>
<td>48.1</td>
<td>7.0 (1.4)</td>
<td>212</td>
</tr>
<tr>
<td>Penrose</td>
<td>25.2</td>
<td>2.2 (0.3)</td>
<td>151</td>
</tr>
<tr>
<td>Belangelo</td>
<td>29.5</td>
<td>3.4 (1.5)</td>
<td>88</td>
</tr>
<tr>
<td>Wingello B</td>
<td>31.7</td>
<td>9.1 (5.1)</td>
<td>60</td>
</tr>
<tr>
<td>Mullions Range</td>
<td>57.1</td>
<td>12.4 (1.3)</td>
<td>70</td>
</tr>
<tr>
<td>Jenolan</td>
<td>15.6</td>
<td>3.6 (0.6)</td>
<td>83</td>
</tr>
<tr>
<td>Newnes *</td>
<td>85.4</td>
<td>34.5 (6.9)</td>
<td>96</td>
</tr>
<tr>
<td>Wingello</td>
<td>54.3</td>
<td>6.7 (1.7)</td>
<td>35</td>
</tr>
</tbody>
</table>

* Data for Newnes and Lidsdale was collected during 2003 for an honours project

Extent of invasion within regions

Macquarie Region

Four sites in the Macquarie region exhibited high levels of invasion (interquartile ranges reaching 3 or more) and four sites had moderate to low levels of invasion with the majority of samples falling below 1 (Figure 3.5). Plantations which appear relatively free of invasion include Hampton, Kinross, Roseberg and Pennsylvania (Figure 3.5). Lidsdale was the most heavily invaded site with a mean infestation index of 4.3 and the majority of samples lying between 4 and 5. The majority of invasion has occurred in a south easterly direction towards Mount Walker on crown and state forest land (Appendix 2). The area of infestation was estimated as 300 hectares (pers. comm. D. Noble), although this survey indicates approximately 1800 hectares of land invaded. In 2003 the site was surveyed for pine wildlings. Pine densities were high in areas close to the plantation (>2000/ha) and large 20 m tall pines persisted at low densities of approximately four individuals per hectare for an estimated distance of 2 km from the plantation (Williams and Wardle 2005a).

High pine densities of more than 2000 per hectare have been recorded in areas adjacent to the plantation at Newnes (Williams and Wardle 2005a). Currently, the invasion is concentrated to the lower south-eastern edge where pines are growing at a density of 500 individuals per hectare, 450 m from the plantation. The majority of the infestation lies within State Forests land, however, Newnes State Forest is bounded by
Wollemi National Park to the north and Blue Mountains National Park to the east and further expansion of the wildling population will result in an encroachment of these areas (Appendix 3).

A significant invasion to the south of the plantation at Jenolan State Forest has also occurred with pine densities reaching 1400 per hectare in the most heavily invaded areas (Appendix 4). Jenolan State Forest is located in very close proximity to world heritage listed vegetation in Kanangra-Boyd National Park and wildlings are currently approaching the park boundary.

Mullions Range State Forest is also one of the most heavily invaded sites (Appendix 5). Large pines overtop the native eucalypt canopy at an estimated density of approximately 20 per hectare for a distance of up to 2 km from the plantation. The majority of spread has occurred on Staeforest land to the east of the plantation.

The large plantation at Gurnang State Forest is directly bordered by Kanangra-Boyd and Blue Mountains National Parks. *Pinus radiata* is known to have invaded an area of approximately 50 hectares of Eucalypt woodland in the southern section of Blue Mountains National Park, adjacent to the Gurnang plantation (pers. comm. J. Bros). This survey recorded pine densities of up to 500 per hectare with many large reproductive pines present and a total invaded area of 300 hectares. Considerable invasion of native vegetation to the south east of the plantation has also occurred. Low levels of invasion have taken place at Sunny Corner State Forest, which is bordered by Winburndale Natuer Reserve and Mount Canobolas State Conservation Area. Pines are generally limited to within 200 m from the plantation at both sites.
Figure 3.5 Level of invasion at sites within the Macquarie region.

Boxes show the middle 50% of scores (interquartile range). The dark horizontal line within the box indicates the median score. Circles represent outliers. Sites are ranked in order of decreasing level of invasion.

**Hume Region**

Very little invasion has occurred within the Hume region (Figure 3.6). The only heavily invaded site was Mannus State Forest where large mature pines overtop eucalypt canopy at an estimated density of 100 per hectare for up to 300 m from the plantation (Appendix 6). Several *Pinus* species have also spread up to 200 m from the Pilot Hill Arboretum at Bago. Plantations which remain relatively free of invasion include Clarkes Hill, Bogandyera, Buccleugh and Blowering Dam. At Tallaganda, a small amount of invasion has occurred to the south east of the plantation where pines have spread up to 120 m into the native vegetation.
Figure 3.6 Level of invasion at sites within the Hume region.

Boxes shows the middle 50% of scores (interquartile range). The dark horizontal line within the box indicates the median score. Circles represent outliers. Sites are ranked in order of decreasing level of invasion.

**Northern Region**

Very little invasion has occurred at the three northern sites; Hanging Rock, Riamukka and Nowendoc (Figure 3.7).
Figure 3.7 Level of invasion at sites within the Northern region.
The dark horizontal line indicates the median score. Circles represent outliers. Sites are ranked in order of decreasing level of invasion.

Monaro Region

Plantations situated in the northern section of the Monaro region were among the most heavily invaded with significant wildling populations occurring at all four sites (Figure 3.8). At Penrose, large pines are invading swampland surrounding the plantation, at a density of approximately 160 per hectare (Appendix 7). More than 90% of the border is invaded and a fifth of this is at the highest level; 5. Belangelo and Wingello B are also heavily invaded, however wildlings are restricted to within 230 m and 100 m from the respective plantations (Appendices 8 and 9). Pine spread at Wingello A has primarily taken place in the northern section of the site and is limited to 80 m from the plantation boundary (Appendix 10). The two most southern plantations, Bondi State Forest and Coolangubra State Forest recorded mean infestation indices less than one. However, the sites are not entirely invasion free with some invasion occurring. At Coolangubra, pines have spread up to 180 m into the adjacent Coolambooka Nature Reserve. At Bondi small clusters of pines have established in recently disturbed roadsides, e.g. next to soil dumps.
**Figure 3.8 Level of invasion at sites within the Monaro region.**

Boxes shows the middle 50% of scores (interquartile range). The dark horizontal line within the box indicates the median score. Circles represent outliers. Sites are ranked in order of decreasing level of invasion.

**Discussion**

The field survey identified several significant wildling populations and a total estimated area of land invaded of almost 4 500 hectares in NSW. This extent of spread is much less than observed in South Africa (34,000 ha; Richardson *et al.* 1994). In New Zealand *Pinus radiata* is one of the least invasive conifers. Of the 150 000 hectares of land affected by conifer spread, two thirds is composed of *P. contorta* with *P. radiata* accounting for a much smaller area (Ledgard 2001). This figure for NSW is likely to represent only one component of the total area invaded in Australia as invasion is also known to take place in the ACT and Victoria (Chilvers and Burdon 1983, Minko and Aeberli 1986). Additional spread is known to have occurred from sites that were unable to be surveyed. For example the total area invaded within Kosciusko National Park has been estimated at 15 000 ha. Although, this is likely to be taking into account the total area covered by widely dispersed individuals. Pines growing in windbreaks and
established in urban settings are also a source of invaders particularly in the Blue Mountains region of NSW (Williams 2003)

The most heavily invaded sites are located in the central west and Moss Vale regions. Wildling populations at Lidsdale and Mullions Range accounted for almost half of the total area of land invaded. The majority of sites experienced low levels of invasion suggesting that at the landscape scale *P. radiata* is yet to have a large impact. However, the presence of large wildling populations at sites such as Lidsdale and Mullions Range suggests that if the conditions are conducive to invasion, *P. radiata* can become an established invader with a dominant presence in the community.

At many of the sites pines are invading or approaching land of high conservation value. The plantation at Penrose is bordered by swampland which has been invaded by pines. The Temperate Highland Peat Swamps have recently been listed as an endangered ecological community under the Environment Protection and Biodiversity Act 1999 (EPBC Act). The swamps include three species listed under the Threatened Species Conservation Act 1995 (TSC Act) including *Eucalyptus aquatica* which only grows in the catchment between Wingello and Penrose and is listed as vulnerable (Fairley 2004) and a small population of the endangered *Gentiana wingecarribiensis* at Hanging Rock swamp near Penrose (Fairley 2004). At Sunny Corner State Forest, pines are invading vital habitat of the Bathurst Copper butterfly (*Paralucia spinifera*). The species is considered endangered in NSW and is listed on Schedule 1 of the Threatened Species Conservation Act 1995 (TSC Act). The Bathurst Copper Butterfly is also listed nationally as a vulnerable species under section 178 of the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act). Pine wildlings have been removed from areas of Sunny Corner SF as part of a recovery program for the butterfly (NPWS 2001).

The Blue Mountains region lies within the Macquarie forestry region and contains just over one million hectares of world heritage listed vegetation dominated by temperate eucalypt forest which is protected within a string of eight National Parks. The field survey identified a number of areas within the National Park estate that are undergoing threat from pine invasion. Pines are approaching the Kananga-Boyd National Park boundary and Jenolan Karst Reserve at Jenolan State Forest. Further spread from the plantation at Newnes will result in invasion of Blue Mountains National Park to the east and Wollemi National Park to the north. Isolated pines have already been recorded within Wollemi National Park boundaries. The eastern border of Blue
Mountains National Park is being invaded by pines from Gurnang State Forest. Several other infestation sites have been documented in the region including within Abercrombie National Park (pers. comm. C. Banffy 2003).

More than a third of wildlings over 5 metres in height were reproductive at most sites suggesting a high potential for further invasion from secondary seed sources. Peaks in pine density and basal area at distances of up to 300 m from the plantation at Mullions Range and Jenolan are due to clusters of large adult pines. Recruitment of seedlings was observed at Mullions Range and has also been recorded at Newnes and Lidsdale during a previous study (Williams and Wardle 2007). This pattern of invasion is consistent with spread patterns in South Africa where seedlings establish around isolated colonists at long distances from the source (Richardson and Brown 1986).

The high percentage of reproductive wildlings at Newnes can be explained by the presence of a species other than *P. radiata* which was not identified until after the survey had taken place. *Pinus ponderosa* is prevalent throughout the most heavily invaded area and is contributing to the high number of cones present. *Pinus ponderosa* is thought to be more invasive than *P. radiata* (pers. comm. N. Westman 2005) and at this site, *P. ponderosa* wildlings appears to be producing more cones. Other species including *P. contorta* are also more invasive than *P. radiata*. Within Kosciuszko National Park 60% of wildlings were *P. contorta*, a species which only made up 5% of the source plantation (Leaver 1983; Spate *et al.* 1986 in Kasel, 2004a).

The infestation index only represents the level of pine infestation in the land immediately surrounding the plantation which may be limiting the accuracy of our results. Isolated pines are known to establish at long distances from the plantation both in Australia (Williams and Wardle 2005a) and elsewhere (Richardson and Brown 1986) and are unlikely to be detected using this survey method. For this reason this technique is likely to have underestimated the area of land invaded by pines. Monitoring wildling populations from the air is possible as the crown and tone of *P. radiata* distinguishes the species from native eucalypt vegetation. Aerial surveys have been used previously to assess crown health in plantations (Sims 2007) and would be able to detect isolated pines commonly observed at long distances from the plantation and have been used to map pines in an area south west of the Mannus plantation.

Remote sensing techniques such as aerial photograph interpretation or satellite imagery is an effective technique for assessing landscape spread of alien plants. For example Landsat imagery has been successfully used to map *Acacia longifolia ssp*...
sophorae over large areas in Victoria (Emeny et al. 2006). Such techniques could easily be applied to map and monitor invasions of P. radiata and would also assist in determining the influence of topography and vegetation type on invasion success. Unfortunately, budgetary and time constraints prevented the application of this approach during this study.

Despite this limitation, the infestation index remains a useful tool for quickly assessing the level of invasion and was necessary to allow the surveying of a large number of sites. Maps of invaded plantation sites provide a snapshot representation of the current level of infestation within NSW and can help prioritise sites for control. The index itself will also be useful for assessing changes in the level of infestation over time. The first two quantitative components of impact of this species, i.e its geographic extent and a range in abundance of the invader across sites (Parker et al. 1999) have been established. While, highly invaded areas may not necessarily be inherently more invasible (Richardson and Pyšek 2006), an examination of the factors that separate invaded and uninvaded sites will help identify some of the variables influencing pine success. The influence of plantation and environmental variables on the level of invasion at each site will be investigated in the following section.
AIMS OF SECTION II: PROCESS

This section is composed of two chapters. The first chapter is delivered in four sub subsections which share an introduction and attempt to explain the pattern of invasion identified in section one. They utilise data obtained by the methods outlined in chapter 3 in order to address the following hypotheses;

1) High propagule pressure will increase the likelihood of invasion,
2) Dry vegetation types, e.g dry sclerophyll forest will be more susceptible to invasion than wetter vegetation, e.g wet sclerophyll forest, rainforest,
3) Disturbed areas will be more susceptible to invasion than undisturbed areas,
4) Pine spread will be greater downwind from the seed source.

These aims are achieved by analyzing the data on two scales, i.e. at a landscape scale (4.1) and on a local scale (4.3). Subsection 4.2 takes a closer look at the vegetation types invaded. The final subsection (4.4) synthesises information from the chapter.

The second chapter (5) examines the role of fire in the invasion process and attempts to address the following hypothesis;

1) Fire may accelerate the invasion process by providing conditions conducive to pine establishment.
4. Factors influencing invasion success

Introduction

Common approaches to understanding the factors that mediate invasion success include identifying characteristics common among invaders (Noble 1989, Rejmanek and Richardson 1996) and invadable communities (Crawley 1987, Levine and D'Antonio 1999, Symstad 2000). More recently, there has been a growing awareness of the important role of propagule pressure in the invasion process (Lockwood et al. 2005, Von Holle and Simberloff 2005). In fact a review of the progress towards a predictive understanding of invasions found that the most frequent positive result regarding the establishment of invaders is a positive influence of propagule pressure (Kolar and Lodge 2001). Despite the recognised importance of this, our understanding of the relationship between propagule pressure and invasion success is poor as propagule pressure is rarely quantified nor included in invasion research (Williamson 1996). Studies that have considered propagule pressure often find that it is a stronger predictor of the distribution of invasive species than environmental (Von Holle and Simberloff 2005) or abiotic conditions (Dullinger et al. 2003, Foxcroft et al. 2004).

There are two important and distinct components of propagule pressure. These are the absolute number of propagules: propagule size (not to be confused with the actual size of individual propagules) and the number of discrete release events: propagule number (Lockwood et al. 2005). For pines, the conditions that lead to dispersal events are not well understood and are difficult to predict (Lanner 1998). Many Pinus species have serotinous cones which remain closed on the tree for many years after the cones mature. Seeds are then released rapidly after fire. Pinus radiata is considered to have intermediate serotiny, where cones will also open without fire in response to high temperatures (Keeley and Zedler 1998). Despite uncertainties surrounding the timing of seed release, an estimate of the amount of seed produced by the plantation can provide a proxy for the amount of seed available. Total seed production within a site relates to the potential pool of propagules and hence larger plantations with more trees represent a higher level of propagule pressure.

In the absence of a measure of the number of release events, time since plantation establishment at a site may be used as a proxy. A greater residence time relates to higher propagule pressure and increased chance of recruitment and of
Factors influencing invasion success

establishing isolated wildlings (Rejmanek et al. 2005). The stochastic nature of community invasibility (D’Antonio et al. 2001) implies that residence time is likely to have a large influence on the likelihood of invasion. If seed has been present at a site for a long period of time it is more likely that environmental conditions will, at some point, be favourable for pine dispersal and establishment. Considering these two components of propagule pressure for plantations, I expect that sites bordering larger, older plantations will experience high levels of invasion, while younger, smaller plantations remain invasion free. The interaction between plantation size and residence time may also shed light on the relative roles of the two aspects of propagule pressure in the invasion process. If small, old plantations source invasions while large, young plantations remain unininvaded, I may conclude that residence time or the number or release events is more important than total propagule pool.

One of the factors that will influence the delivery of propagules to an area is wind. Previous studies have found denser populations (Stabb 1974 cited in Minko and Aberli 1986) and higher maximum dispersal distances (Minko and Aeberli 1986) of pines downwind from source plantations in Australia. Given similar site conditions surrounding a plantation I expect to find greater levels of invasion on downwind borders. Once seed has arrived at a site, the nature of the native vegetation will have a strong influence on establishment success (Lonsdale 1999). The intrinsic resistance of a community to invasion will ascertain how much propagule pressure is needed to establish a colonizing population (D’Antonio et al. 2001). Both abiotic and biotic forms of resistance will vary spatially and temporally. This variation may influence the relationship between propagule supply and invasion success. When resistance is weak even a low number of propagules is capable of establishing an invasive population (D’Antonio et al. 2001). Whereas, when resistance is high propagule pressure should have a strong influence on invasive success.

The environmental features that facilitate and limit pine expansion have been particularly well studied in South Africa. In short, facilitating factors include bare ground or low vegetation cover, moderate levels of disturbance, long residence times and large plantation areas with large boundary:area ratios (Richardson et al. 1994). Richardson and Higgins (1998) ranked vegetation types according to their susceptibility to pine invasion as follows: forest<<shrubland<grassland<<dunes<bare ground. Studies on pine spread in Australia suggest that dry sclerophyll forest is more susceptible to invasion than wet sclerophyll forest (Chilvers and Burdon 1983) and that
open vegetation is more vulnerable than dense vegetation types (Virtue and Melland 2003). Studies examining spread into different forest types are contradictory. Lindenmayer and McCarthy (2001) found that eucalypt remnants differed in their susceptibility to invasion while Van der Sommen (1978) observed *P. radiata* invading equally into different eucalypt communities in South Australia, however this idea is yet to be tested on a large scale.

The influence of disturbance and propagule pressure on the relative invasibility of these environments is of prime interest. This study examined the factors influencing pine distribution on a landscape scale. All instances of invasion into forest have shown that severe disturbance is necessary before recruitment and population expansion can occur (Richardson *et al.* 1994) and so I expect to find higher levels of invasion within physically disturbed forest environments. Disturbance associated with herbivory is likely to have a very different influence on pine establishment. Grazing by sheep in New Zealand (Ledgard 1988) and rabbits in Australia (Dawson *et al.* 1979) has been known to reduce wildling recruitment and so I expect to observe a lower level of invasion in grazed areas. Finally, the idea that high enough propagule pressure may be able to overcome natural barriers to invasion (Richardson *et al.* 1994) suggests that the level of infestation will be greatest in areas surrounding large, old plantations and downwind from the source.

The results are presented in three subsections. The first subsection, 4.1, describes landscape scale variation examining the role of propagule pressure, percentage wet vegetation and annual rainfall on invasion success across sites using a General Linear Model (GLM) and Classification Tree. Due to the small number of sites examined, i.e. 29, traditional methods of investigating the influence of multiple factors on the level of invasion at each site have low power. For this reason, the raw data is also presented and commented on in order to reveal patterns that the GLM may be disguising.

Subsection 4.1 investigated the influence of broad differences in vegetation type on invasion success. However, previous research suggests fine differences in vegetation composition may be an important determinant of invasibility (Lindenmayer and McCarthy 2001). The aim of subsection 4.2 is to provide a closer examination of the invasion patterns within 15 vegetation types for all sites combined and on a regional basis. Vegetation data also provided an opportunity to examine the role of physical disturbance on the likelihood of invasion.
Some factors likely to influence invasion success may be operating on a smaller scale than can be detected when individual plantations are acting as the sample unit. The dispersal of seed from the plantation into the surrounding vegetation is likely to differ across borders within individual plantations. Similarly, canopy cover and the presence of grazing is highly variable within a site. The role of propagule pressure on a local scale, i.e. the plantation compartment level, and its interaction with vegetation type and wind direction at each plantation site is investigated in subsection 4.3. The influence of canopy cover and the effect of grazing were also investigated.
4.1 Landscape scale variation: the role of propagule pressure, percentage wet vegetation and annual rainfall

Methods

Statistical Analysis

The small number of sites surveyed in this study limits the usefulness of common approaches used to examine the influence of multiple predictor variables on a response variable, e.g. multiple regression and principal components analysis. The response variable being examined is the level of invasion for each plantation represented by a mean infestation index. There are a number of factors that could be simultaneously influencing pine success across sites. Climatic variables such as rainfall and temperature and plantation characteristics i.e. plantation size and residence time can be accurately assigned to each site. However, other variables such as presence of grazing and level of disturbance will vary within a plantation and require analysis on a smaller scale. Furthermore, the total number of predictors that can be included in the analysis is limited by the number of sites. Only 29 plantations were surveyed and hence the influence of only 3 or 4 predictors could be analysed accurately (Field 2005). A division of samples within plantation sites, for example based on the direction from the plantation, would provide more replicates, however it would also result in assigning climatic variables to all divisions resulting in pseudoreplication. The non-independent nature of samples that were collected continuously during a survey of the plantation border would also reduce the validity of this approach.

Due to these limitations this analysis focused on four predictor variables which were expected to have the largest influence on invasion success between sites; annual rainfall, percentage wet vegetation, plantation size and plantation residence time. Generalised linear models (GLM) with normal distribution were used to assess and compare the relative weight of each independent variable in the model. Analyses were performed with the statistical package SPSS 15.0 (2006). Parameters were estimated using the maximum likelihood method. The goodness of fit of the model was measured using Akaike’s information criteria (AIC) (Akaike 1974) where lower values indicate a better fit of the model. Percentage wet vegetation was the only categorical variable and was converted into dummy variables with <1 % wet vegetation as the reference.
category. Differences between levels of the categorical variable were tested for using the Wald $\chi^2$ statistic. The dependent variable, mean infestation index, was square root transformed prior to analysis to improve normality.

Classification and regression trees (Breiman et al. 1984) are commonly used for exploring and modeling the relationships between a number of predictor variables and a response variable. They are rarely used in ecology despite being a simple and useful technique for understanding complex ecological data (De'ath and Fabricius 2000). Classification trees have been successfully used to screen for weedy species (Caley and Kuhnert 2006) and for invasive fish in North America (Kolar and Lodge 2002). They have a number of advantages over regression models. They are non-parametric and therefore do not make assumptions about the distribution of the data. They can also identify interactions between variables and provide an output that is easy to interpret. The tree is constructed by repeatedly splitting the data, defined by a simple rule based on a single explanatory variable. Successive splits are made until a terminal node is reached. Variables in classification tree models are selected to create splits that maximize the resulting node homogeneity, therefore the variables used in earlier splits are considered more important (Miller and Franklin 2002). Splitting is terminated when all nodes are as homogenous as possible.

While classification trees work best with a large sample size (Armstrong and Andress 1970), it was decided that, in combination with GLM this technique would be useful for examining the variables influencing the level of infestation at each of the sites. A classification tree was constructed using SAS Enterprise Miner 5.2 (2006) and investigated the influence of the same four predictor variables used in the GLM on mean infestation index for a site. The number of invaded sites present within each node was noted. Sites with a mean infestation index of more than 1 were deemed as invaded. In addition splitting criteria were imposed on the data to demonstrate the distribution of sites within each level of the variables of interest. Plantations were divided into two groups based on residence time (<40 years and $\geq$40 years), plantation size (<10 000 ha and $\geq$10 000 ha) and the amount of wet vegetation present (Dry: $\leq$10% (categories 1 and 2) and Wet: $>$10% categories 3 and 4: see below for explanation).

At a landscape scale the number of samples is low, i.e. there only 29 plantations, which reduces the power of the GLM and the classification tree. In addition, the distribution of the four factors of interest across these plantations is uneven which further reduces our ability to investigate their influence. For example, of the 5
plantations over 10,000 ha in size, four of them are characterised by wet vegetation which makes it difficult to separate the effect of plantation size and vegetation type. To address this issue the relationship between factors in the model was investigated using Pearson’s correlation coefficient. A series of bi-variate plots help illustrate some of the limitations associated with the previous analyses by presenting the data in its rawest form.

Propagule pressure

To quantify the amount of seed production for a plantation, seed output per annum was estimated using data collated from a number of sources.

\[
\text{Seed output per annum} = \text{Area of plantation} \times \text{tree density} \times \text{cones/tree} \times \text{seeds/cone}
\]

**Area:** the area of the plantation within a particular age class in hectares

**Tree density:** stocking rates in stems per hectare (Lewis and Ferguson 1993)

**Cones per tree:** ranged from 2 (Fielding 1960) to 12 (Wardle *et al.* unpublished)

**Seeds per cone:** ranged from 44 (Pederick and Brown 1976) to 200 (McDonald and Laacke 2003).

A range in seed output was calculated using minimum and maximum values for cone and seed production. For example minimum seed output for a 20 year old compartment = Area of compartment (ha) x 680 (stems per ha) x 2 cones x 44 seeds per cone. Seed output per annum was summed for all compartments to give a total maximum and minimum estimate for seed production at each plantation.

There was a highly significant positive correlation between maximum seed production and plantation area \((r = 0.982, p < 0.001)\). Therefore, seed production was excluded from the analysis and plantation size was used as a proxy. The influence of residence time, i.e. time since first planting at a site was also examined.

Percentage wet vegetation

Categorising vegetation type for all sites required a classification scheme that was consistent across the 29 plantations. This information was obtained from a state wide vegetation map (DEC 2005). Sites were categorised based on the percentage of wet
vegetation present in close proximity to the plantation where surveying took place. Wet vegetation included wet sclerophyll forests, freshwater wetlands and forested wetlands and sites were placed in four categories; <1%, 1-<10%, 10-50%, >50%. The category interval was large due to the coarse resolution of the map.

**Rainfall**

Rainfall amount and distribution has been shown to have a large influence on the productivity of *P. radiata* within plantations (Jackson and Gifford 1974, Hunter and Gibson 1984) and hence may also be expected to have an influence on the growth and abundance of pine wildlings. The mean annual rainfall for all sites were obtained from the Bureau of Meteorology (BOM 2006).

**Boundary-to-area ratio**

To investigate the influence of the boundary-to-area ratio on the extent of spread the correlation between the amount of land invaded at each site and the boundary to area ratio for each plantation was examined using Pearson’s correlation coefficient. For the heavily invaded sites values for the area of land invaded presented in the previous section were used (Table 3.5). For the remaining sites, the area of land heavily invaded was calculated by multiplying the number of samples with infestation indices greater than 2 by the area of the sample (50 m x 100 m).

**Results**

**Generalised linear model**

Residence time and annual rainfall were both highly significant (p < 0.01) predictors in the model with positive and negative influences on the level of invasion respectively (Table 4.1.1). Plantation size also had a significant negative influence (p < 0.05) while percentage wet vegetation had no influence on the level of invasion. There was no significant difference between categories of percentage wet vegetation ($\chi^2 = 0.865$, df = 3, p = 0.834). Correlation coefficients of all predictors are low suggesting that the model fails to explain much of the variation in invasion success between sites. When the interaction between percentage wet vegetation and residence time was included the AIC
increased slightly to 36.76 and the interaction term was not significant in the model ($\chi^2 = 5.02$, df = 3, $p = 0.171$).

**Table 4.1.1. Generalised linear model of mean infestation index for a plantation with plantation characteristics, annual rainfall and percentage wet vegetation as predictors.**

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>B (S.E.)</th>
<th>Wald $\chi^2$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residence Time</td>
<td>0.023 (0.003)</td>
<td>44.66</td>
<td>0.000***</td>
</tr>
<tr>
<td>Annual Rainfall</td>
<td>-0.002 (&lt;0.001)</td>
<td>12.99</td>
<td>0.000**</td>
</tr>
<tr>
<td>Plantation Size</td>
<td>-2.3e-05 (&lt;0.001)</td>
<td>6.66</td>
<td>0.010*</td>
</tr>
<tr>
<td>Percentage wet vegetation</td>
<td>0.87</td>
<td>0.834</td>
<td></td>
</tr>
<tr>
<td>1-10% wet vegetation</td>
<td>-0.046 (0.188)</td>
<td>0.06</td>
<td>0.804</td>
</tr>
<tr>
<td>10-50% wet vegetation</td>
<td>0.120 (0.220)</td>
<td>0.30</td>
<td>0.587</td>
</tr>
<tr>
<td>&gt;50% wet vegetation</td>
<td>-0.058 (0.185)</td>
<td>0.10</td>
<td>0.755</td>
</tr>
<tr>
<td>Intercept</td>
<td>1.140 (0.356)</td>
<td>10.3</td>
<td>0.001</td>
</tr>
</tbody>
</table>

* $p \leq 0.05$ ** $p \leq 0.01$ *** $p \leq 0.0001$

AIC: 35.39

**Classification Trees**

Fitting the classification tree resulted in four splits of the data and the retention of only two variables, plantation size and residence time (Figure 4.1.1). Both splits based on plantation size revealed a higher mean level of infestation within smaller sites. Six of the nine invaded sites were between 768.8 ha and 5824.5 ha in size and greater than or equal to 72 years old.
Figure 4.1.1 Classification tree of the infestation index at each site.

The explanatory variables were plantation size in hectares and plantation residence time in years. Each of the four splits (nonterminal nodes) is labeled with the variable and its values that determined the split. For each of the leaves (terminal nodes), the mean infestation index and the number of observations within the node is displayed. The number of uninvaded and invaded sites is in brackets.

A self imposed split of sites found that seven of the nine most heavily invaded sites were greater than 40 years old, less than 10 000 hectares in size and surrounded by dry vegetation (Figure 4.1.2). Mean infestation indices of the remaining terminal nodes were all less than 1. This division of plantation sites also revealed unequal sample sizes within the variables. For example all the young plantations were less than 10 000 ha in size. Within the older sites, there were more than three times as many small dry sites as small wet sites.
Figure 4.1.2 Division of sites based on residence time, plantation size and percentage wet vegetation. For each node the mean infestation index and the number of sites within the node are displayed. The number of uninvaded and invaded sites are in brackets. ‘Wet’ vegetation refers to sites with more than 10% wet vegetation present. The inset indicates the positions of the sites in relation to each other.
**Plantation size**

A negative relationship between plantation size and the level of invasion was strongly influenced by the largest site, Buccleugh (Figure 4.1.3). The correlation was not significant ($r = -0.276$, $p = 0.139$). Seventeen of the 29 sites were less than 5 000 ha in size and had mean infestation indices ranging from 0 to 4.64. All sites greater than 5 000 ha had mean indices less than 1.

![Figure 4.1.3. Relationship between plantation size and mean infestation index for the 29 plantations.](image)

Residence time

There was a significant positive relationship between residence time and mean infestation index \((r = 0.484, p = 0.008)\) and a threshold of approximately 40 years with almost no invasion occurring prior to this (Figure 4.1.4). With the exception of Wingello B, all sites with a mean infestation index higher than 1 are greater than 60 years old. However, there was very little predictability in the level of invasion for older sites with mean indices ranging from 0.3 to 4.64.

Figure 4.1.4 Relationship between residence time and mean infestation index for the 29 plantations.

Percentage wet vegetation

While there was a trend for reduced levels of invasion with an increasing percentage of wet vegetation (Figure 4.1.5), there was no significant difference in the level of invasion between groups ($F_{3,25} = 2.40, p = 0.092$), explaining its poor predictive power in the GLM. Dry sites, with less than 10% wet vegetation experienced all levels of invasion with mean infestation indices ranging from 0 to 4.64. Sites with more than 50% wet vegetation present had only 2.9% of the surveyed border heavily invaded (index $\geq 3$) while sites with less than 1% and less than 10% wet vegetation had 25% and 28.7% of their borders heavily invaded respectively. All sites with more than 50% wet vegetation present experienced low levels of invasion with a mean infestation indices ranging from 0.3 to 0.53.

![Figure 4.1.5 Mean infestation index (±SE) for sites with increasing percentage of wet vegetation.](image)

There was a non significant negative relationship between mean annual rainfall and mean infestation index at a site ($r = -0.194, p = 0.303$) (Figure 4.1.6). All sites with more than 1300 mm annual rainfall were relatively invasion free with mean infestation indices less than 1.
Figure 4.1.6 Relationship between mean annual rainfall and level of invasion at a plantation.


**Boundary-to-area ratio**

There was no significant relationship between the boundary to area ratio for a site and the area of land invaded for all sites combined ($r = 0.066, p = 0.79$)
Discussion

Previous studies examining the influence of propagule pressure on the large-scale distribution of pines have used distance to a source plantation as a measure of propagule pressure (Rouget et al. 2002, Rouget and Richardson 2003), thus assuming that propagule pressure declines with distance away from the source. This study differed from previous approaches as it examined the influence of the size and residence time of the source plantation on invasion success. Here, it was assumed that large plantations would be supplying a higher number of seeds to the surrounding area than small plantations resulting in an increased likelihood of invasion. In fact there was a negative correlation between plantation size and the level of invasion. This relationship was heavily influenced by several large sites with low levels of invasion. Three explanations might be offered for this counter-intuitive result. Firstly, the unequal distribution of sites within size classes prevented an adequate examination of the influence of very large versus small sites. The classification tree illustrated the unequal distribution of sites within factors. This reduces the power of the GLM and hence an examination of the correlation plots is also worthwhile. The two largest sites had a high presence of wet sclerophyll forest which is thought to resist invasion (Chilvers and Burdon 1983). A lack of larger, drier sites hindered our ability to examine the interaction between the presence of wet vegetation and plantation size.

Secondly, the number of seeds within a plantation may poorly correlate with the actual number of seeds that will disperse into surrounding areas. Annual seed release from a plantation can be orders of magnitude lower than annual seed output. Seed stored in the canopy of a 40 year old *P. radiata* plantation in South Australia has been estimated at 1000 seeds/m² while seed release was approximately 1-3 seeds/m²/year (van der Sommen 1978, sourcing unpublished data by R. Boardman). An absence of invasion from large plantation sites may be due to a lack of dispersal events rather than a lack of propagules within the plantation. Long term storage of seeds within serotinous cones of *P. radiata* results in the delayed release of seed following fire and extreme temperatures (Keeley and Zedler 1998). Plantation trees are protected from fire which means that seed release from plantations will rely on appropriate environmental conditions. Poor correlations between invasion events and peak seed production within plantations may be a result of delayed seed release.
Thirdly, the level of invasion in areas immediately adjacent to the plantation is likely to reflect the level of propagules within the dispersal distance of the vegetation of interest, i.e. the seed production of trees within the closest plantation compartment, and may have no relationship with the total size of the plantation. The influence of propagule pressure on a local scale will be investigated in subsection 4.3.

It was expected that the level of invasion would increase with our second component of propagule pressure; time since plantation establishment. The positive correlation between residence time and extent of invasion and the importance of residence time in the classification trees and GLM is consistent with previous observations of *Pinus* invasions in South Africa (Richardson 1989 cited in Richardson et al. 1994) and of the regional distribution of exotic plants in other regions (Pyšek and Jarosik 2005). Both large and small sites younger than 40 years experienced little or no invasion. This lag phase is consistent with observations of wildling spread in New Zealand (pers. comm. N. Ledgard 2006) and with delays in tree spread observed in Germany (Kowarik 1995). However, small populations of pines with diameters up to 30 cm and 40 cm were observed at Tallaganda (37 years old) and Coolangubra (35 years old), respectively, which indicates that the timing of wildling establishment may be much earlier. Previous studies of pine spread into eucalypt forest have observed colonization as early as 20 (Van der Sommen 1978) and 26 years (Burdon and Chilvers 1977) after plantation establishment.

Delays associated with woody invasion can be dangerous as they lead to an underestimation of invasive potential (Wangen and Webster 2006). Despite this, our general understanding of reasons for lag phases is poor (Ewel et al. 1999). The lag period between plantation establishment and invasion success observed for *P. radiata* is partially explained by the time to reproduction of plantation trees. *Pinus radiata* produces fertile cones as early as 5 to 10 years after establishment, while substantial crops are not yielded until age 15 or 20 or later in dense stands (McDonald and Laacke 2003). These results still suggest a period of more than 20 years between the time of peak cone production and extensive invasion. Evidence from plant invasions in Germany suggests that as little as 2 % of introduced woody species will establish self sustaining populations and half of these will go on to become extinct after invasion (Kowarik 1995). The ability of *P. radiata* to become a successful invader will depend on its ability to establish a self sustaining population which may take much longer than the period until first spread. Evidence for wildling recruitment from wildling
populations have been observed at two sites in NSW (Williams and Wardle 2007) and at a site in the ACT after 21 years (Burdon and Chilvers 1994). Observations in Australia are consistent with those in South Africa where *Pinus radiata* produced a second generation of invaders after only 21 years (Richardson and Brown 1986). The establishment of self sustaining populations will depend on the ability of these recruits to survive in the native vegetation.

Intervals between plantation establishment and wildling spread may also be contributing to the idea that intact continuous forest is resistant to invasion by conifers (Lindenmayer and McCarthy 2001, Ledgard 2004). Forest interiors may not in fact be intrinsically resistant to invasion, rather the invasion has not had sufficient time to progress the required distance away from the plantation. The presence of mycorrhizae has also been used to explain the relative resistance of forests to invasion. In these areas, pines will not have an advantage over native trees that are already ectomycorrhizal and have good access to nutrients (Read 1998).

The low level of predictability of invasion observed for sites older than 40 years and the lack of invasion at two of the larger, older sites, Bago and Buccleugh suggests that factors other than propagule pressure are responsible for invasion success. A significant interaction between the amount of wet vegetation present and propagule pressure might have been expected, however the interaction between the vegetation categories and residence time were not significant. Sites with more than 50 % wet vegetation present had mean infestation indices of 0.27 and less than 3 % of their borders heavily invaded. However, there was no significant difference in mean infestation index of sites between categories explaining the low influence of vegetation in the GLM. All sites receiving in excess of 1300 mm of rainfall (including Bago and Buccleugh) were relatively invasion free suggesting that communities in these areas are resistant to invasion.

A non significant influence of percentage wet vegetation in the GLM may be disguising a more subtle influence of vegetation in the invasion process. A previous study based on a single site in NSW, suggested that slight differences in forest type can have a significant influence on pine invasibility (Lindenmayer and McCarthy 2001). The current study investigated 29 sites and a much broader range of vegetation types. Investigating differences in invasibility between large numbers of forest types was not possible using the GLM. The following subsection 4.2 will attempt to build on the work
of Lindenmayer and McCarthy (2001) by reporting on the level of invasion within the 15 different forest types surrounding the study sites.

There are a number of reasons why the GLM failed to explain much of the variation in invasion success between sites. Firstly, this analysis was based on a correlative approach which relies on the assumption that the invading species is in equilibrium with the environment, i.e. is found in all suitable areas of habitat. During the early stages of invasion this assumption is likely to be invalid (Richardson et al. 2004). Twenty of the 29 plantations in our study experienced low levels of infestation with a mean index of less than one and less than 20 hectares of land invaded (chapter 3) indicating that they are still in the very early stages of the invasion process and that they are unlikely to be in equilibrium with the environment. At this phase of the process propagule pressure is more likely to constrain spread (Rouget and Richardson 2003) and the distribution of the invader will be weakly predicted by physical environmental variables. As the invasion progresses predictability should improve as suitable sites become more saturated. Wiser et al. (1998) found that the importance of distance to forest margin for explaining the spread of an exotic herb into New Zealand Beech (Nothofagus solandri var. cliffortioidesi) forest, reduced as time progressed. Eventually interiors of continuous forest were invaded. A closer examination of older sites which are more likely to be in equilibrium with the environment may provide further insight into the factors driving pine invasion.

It is highly probable that many of the factors mediating the success of pines at the landscape scale were not accounted for here. This study focused on propagule pressure and its interaction with the amount of wet vegetation present. The influence of residence time was significant, however, the large variability in infestation level among older sites clearly implies that other factors are operating. For example, high levels of rainfall appear to be restricting pine spread. Pine distribution is influenced by a range of additional site variables not considered here, including fire regime, agricultural practices and soil pH (Rouget et al. 2001). The ultimate success of pines will depend on an interaction between the level of disturbance and a range of environmental features (Higgins and Richardson 1998). A closer investigation of invasion patterns within different forest types provided in the following chapter will offer further insight into the influence of vegetation and disturbance on pine invasibility.

Annual variation in seed production within the plantation has been shown to have an important influence on the timing of pine regeneration surrounding plantations
sites in the Australian Capital Territory (Dawson *et al.* 1979). I have no knowledge of
the yearly variation in seed production for the plantations in this study and more
importantly how this may have interacted with environmental conditions. Conditions for
seed release, dispersal and seedling establishment do not always coincide (Richardson
*et al.* 1994). Long residence times may ensure good propagule supply but it does not
guarantee that events required for seedling establishment will occur. The time to a
disturbance event which may facilitate invasion will be different across sites explaining
the poor predictability of invasion level for older sites.

Another factor not considered here and commonly ignored in studies of pine
spread is the influence of variations in seed viability or tree performance between
plantation stocks. Variations in tree performance due to provenance have been observed
for *P. contorta* seedlings in New Zealand (Ledgard 1980 cited in Ledgard 2001)
suggesting natural selection for adaptation to New Zealand conditions. Superior
provenances of *P. radiata* and *P. ponderosa* introduced earlier have also been observed
in Australia (Eldridge, 1974 cited in Ledig 1998). Genetic differences between
plantation stocks across sites may be an important factor influencing invasion success.
Genotypes used in Australian plantations are a subset of the genetic diversity in
California (Moran and Bell 1987), and have been selected for economically desirable
characteristics such as rapid, straight growth and disease resistance. Improvements in
breeding with time may have resulted in genetic variation across plantations
established at different times, possibly resulting in increased growth potential among
younger plantations. Variations in pine success at the landscape scale may be heavily
confounded by differences in pine performance.

Finally, there are a number of controlling factors that remove wildlings and will
contribute to the poor level of predictability. These include fire, herbivory and control
operations. Natural and prescribed fires are capable of destroying wildlings (Gill and
Williams 1996 and see section 4.4). Not accounting for individuals that have been
eliminated by fire will result in an underestimate of the level of invasion within some
areas. The browsing pressure of herbivores can also act as a control measure. Becerra
and Bustamante (unpublished data) have shown significant declines in *P. radiata*
seedling survival following herbivory by rabbits in Chile. In Australia, Dawson *et al.*
(1979) attributed the failure of *P. radiata* to regenerate in eucalypt forests to the high
grazing pressure applied by rabbits prior to their control by myxomatosis. Human
control measures will also remove wildlings resulting in an underestimation of the
invasibility of an area. Even though some cases of control have been documented and were taken account of, it is possible that evidence of control operations were overlooked in some areas. Clearing of pines during control operations means that absence at a site may not reflect the potential occurrence of *P. radiata*. Confounding due to extrinsic factors such as these makes elucidation of the prime determinants of spread difficult (Richardson *et al.* 1992).

Despite the limitations associated with the survey methods employed, this study has provided useful insight into the role of propagule pressure in the invasion process. The relationship between propagule pressure and invasion success has been referred to as the ‘dose-response’ curve, where dose refers to propagule pressure and the response is the probability of establishment (Ruiz and Carlton 2003). Exponential or linear increases in the likelihood of establishment indicate a consistent benefit of control. Whereas, responses that include thresholds suggest that control effort becomes redundant after a certain level of propagule supply (Ruiz and Carlton 2003). A semi-threshold effect was observed. A residence time of 40 years is required before invasion occurred but it did not guarantee invasion success. The role of vegetation type, disturbance, grazing and wind in the invasion process will be discussed in the following subsections and may provide further insight into the factors driving wildling spread.
4.2 Vegetation types invaded

Methods

Vegetation type and disturbance

To examine the pattern of invasion among different forest types and to investigate the influence of disturbance, vegetation data available in GIS (Geographic Information Systems) format was obtained for the 29 sites (Appendix 11). All GIS data had a scale greater than 1: 50 000 and was interpreted from satellite imagery. Published vegetation maps were also available for some sites. As vegetation classification schemes differed between databases a broad classification was imposed across all sites to allow for comparison (Table 4.2.1).

<table>
<thead>
<tr>
<th>Vegetation Description</th>
<th>Code</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cleared</td>
<td>C</td>
</tr>
<tr>
<td>Degraded Grassland</td>
<td>DG</td>
</tr>
<tr>
<td>Dry sclerophyll forest</td>
<td>D</td>
</tr>
<tr>
<td>Disturbed dry forest</td>
<td>DDF</td>
</tr>
<tr>
<td>Disturbed dry woodland</td>
<td>DDWo</td>
</tr>
<tr>
<td>Disturbed wet forest</td>
<td>DWF</td>
</tr>
<tr>
<td>Grassland</td>
<td>G</td>
</tr>
<tr>
<td>Grassy Woodland</td>
<td>GW</td>
</tr>
<tr>
<td>Heath</td>
<td>H</td>
</tr>
<tr>
<td>Plateau complex</td>
<td>P</td>
</tr>
<tr>
<td>Remnant Bushland</td>
<td>Rm</td>
</tr>
<tr>
<td>Rock complex</td>
<td>R</td>
</tr>
<tr>
<td>Wetlands</td>
<td>WL</td>
</tr>
<tr>
<td>Wet sclerophyll forest or wet woodland</td>
<td>W</td>
</tr>
<tr>
<td>Woodland</td>
<td>Wo</td>
</tr>
</tbody>
</table>

Table 4.2.1 Codes for vegetation classes

Two types of disturbance are identified within these vegetation classes. The first is grazing which is expected to reduce the level of invasion via herbivory of seedlings by sheep and cattle. Grazing was common on Cleared areas (C) and in areas of Remnant Bushland (Rm) and for this reason I expect the level of invasion to be low on these two vegetation types. Remnant bushland referred to natural areas that have been highly
fragmented. These areas were characterised by low levels of native understorey, assumed to be due to grazing pressure, and a high level of grassy ground cover. Determining the intensity of grazing surrounding the plantations was beyond the scope of this study, therefore some variation in the level of invasion due to variation in grazing pressure within grazed areas is expected. Disturbed vegetation types refer to areas of forest that have a level of physical disturbance notable on satellite imagery, including selective logging and road and trail construction. In addition, observations of these physical disturbances and smaller levels of disturbance, e.g. soil dumps, were noted during field work and alterations to GIS vegetation data were made. These physical disturbances are expected to increase the likelihood of invasion and for this reason the three disturbed vegetation types (DDF, DWF and DDWo) are expected to have the highest level of invasion. Physical disturbance is likely on cleared land also however, I predict that the grazing pressure in these areas will reduce pine establishment and override any facilitation due to physical disturbance.

Each sample was assigned one of the 15 vegetation classes using union analysis in ArcMap 9.1 (ESRI 2005). I examined the level of invasion within vegetation classes for all sites combined. Results are displayed using boxplots. The bottom and top horizontal lines for each category indicate the lowest and highest scores respectively. The box shows the middle 50% of scores (interquartile range). The dark horizontal line within the box indicates the median score. Circles represent outliers. In order to account for the large variation in sample size all vegetation types with less than 30 samples were removed and a minimum number of cases were randomly selected from the remaining categories. Random selection was carried out using SPSS 15.0 (2006). Vegetation classes have been ordered in descending level of invasion based on mean infestation index. Significant differences in the level of invasion between vegetation types were tested using a one factor ANOVA. I repeated the analysis after removing all sites less than 40 years old as very little invasion has occurred at any of these sites. An absence of wildlings from these areas is less likely to reflect differences in the susceptibility of these communities and more likely to be due to an absence of sufficient propagule pressure.

To investigate invasion patterns further the sites were divided into forestry regions. The reason for this division is two-fold. Firstly, in most cases sites within a region experience a similar climate as they are geographically proximate to each other. By examining regions separately the influence of vegetation can be analysed.
independently of climate. Secondly, three of the regions are covered by more detailed vegetation databases with a greater number of vegetation classes. The Hume region is covered by the Forest Ecosystems South database (Thomas et al. 2000), the Monaro region is covered by the Southeast NSW database (Tozer et al. 2006) and the Northern region is covered by the Forest Ecosystems Lower North East database (NPWS 1999). Greater detail within databases allows an examination of differences within forest types. More detailed descriptions of the forest types included within each vegetation class are provided in Appendix 12. Following vegetation rankings proposed by Richardson and Higgins (1998) and incorporating knowledge of invasions in Australia I anticipated the following order of vegetation types with decreasing susceptibility to invasion:

\[ R > DDF > DDW > DWF > DG > GW > H > P = D > W > WL > Rm > C \]

**Results**

*Vegetation surveyed*

The Macquarie region was primarily composed of woodland and disturbed dry sclerophyll forest (Figure 4.2.1). The remaining three regions all had large proportions of wet sclerophyll forest present, 44%, 29.3% and 21.6% for Hume, Monaro and Northern respectively. Almost three quarters of the northern region was composed of dry sclerophyll forest. The Monaro region had the greatest diversity of vegetation present, including, Grassy woodland, Wetlands and Heath. Vegetation composition also varied considerably between sites within regions (Appendix 13).
Vegetation types invaded

Figure 4.2.1 Vegetation composition of surveyed land in the four forestry regions.

Vegetation types invaded

Combining data for all sites, the most heavily invaded vegetation types were Wetlands, Disturbed wet forest, Degraded grasslands, Disturbed dry forest and Rock complexes (Figure 4.2.2). Dry sclerophyll and Wet sclerophyll forest as well as Woodland all had very similar levels of invasion with mean infestation indices of 0.65, 0.73 and 0.77 respectively. Cleared areas, Remnant bushland and Disturbed dry woodland experienced very little invasion.
Vegetation types invaded


Sub-sampling resulted in the exclusion of five vegetation types (DG, R, H, G, DDWo). The category of Wetlands was removed as this result represents an invasion into wetlands at one site, Penrose which was considered a special case. I randomly selected the minimum number of samples from the remaining vegetation classes (113).

Sub-sampling resulted in a significant difference between vegetation classes (df = 8, F = 18.43, p < 0.0001). The order of vegetation classes from most invaded to least invaded was retained (Figure 4.2.3). The maximum infestation index for both undisturbed and disturbed forest areas reached 5, however, Disturbed dry and Disturbed wet forests were significantly more invaded than their undisturbed counterparts. The interquartile range for disturbed forests reached 4 for Disturbed wet and 3 for Disturbed dry forest. In comparison the majority of scores stayed below 1 for undisturbed forests. Grassy woodlands were significantly more invaded than intact sclerophyll forest types and Woodlands. There was no significant difference between Dry and Wet sclerophyll forest
and Woodlands. Almost no infestation occurred on Cleared areas and Remnant bushland.

**Figure 4.2.3 Boxplot of the level of invasion within subsampled vegetation classes.**

Number of 100 m samples within each vegetation class = 113. Excluded categories are Wetlands, Degraded grasslands, Rock complex, Heath, Grasslands and Disturbed dry woodland. Different lower case letters indicate a significant (p<0.05) difference between vegetation classes. DWF – Disturbed wet forest, DDF – Disturbed dry forest, P – Plateau complex, GW – Grassy woodlands, D – Dry sclerophyll forest, Wo – Woodlands, W – Wet sclerophyll forest, Rm – Remnant bushland, C – Cleared areas

**Old sites**

When sites less than 40 years old were excluded, a similar trend in the level of invasion between vegetation types was found. However, dry sclerophyll forest was significantly more invaded than wet sclerophyll forest (df = 7, F = 19.07, p < 0.0001) with mean infestation indices of 1.14 and 0.63 respectively. The highest scores reached 5 for dry sclerophyll forest while the majority of scores were below 1 for wet sclerophyll forest.
Macquarie region (12 sites)

Sub-sampling in the Macquarie region resulted in the exclusion of three categories (R, C, Rm). There was a significant difference in the level of invasion between the remaining vegetation classes (df = 5, F = 12.06, p < 0.0001) (Figure 4.2.4). Areas of Disturbed wet and Disturbed dry forest experienced the highest level of invasion with index scores ranging from 0 to 5 and mean infestation indices of 1.83 and 1.34 respectively. There was no significant difference between wet and dry sclerophyll forest.

Figure 4.2.4 Boxplot of the level of invasion within sub-sampled vegetation classes in the Macquarie Region. Number of 100 m samples within each vegetation class = 113. Rock complexes, Cleared land and Remnant bushland have been excluded due to low sample size. Different lower case letters indicate a significant (p<0.05) difference between vegetation classes. DWF – Disturbed wet sclerophyll forest. DDF – Disturbed dry forest, P – Plateau complex, D – Dry sclerophyll forest, W – Wet sclerophyll forest, Wo – Woodland.
*Hume region (8 sites)*

The Forest Ecosystems South database included 8 types of wet sclerophyll forest and 8 types of dry sclerophyll forest as well as one type of woodland. The major vegetation classes present were; Dry sclerophyll forest, Wet sclerophyll forest, Woodlands and Cleared land. The low level of invasion within the Hume region made comparisons within vegetation types difficult. However, there was a significant difference between vegetation classes (df = 16, F = 41.64, p < 0.0001). The two most heavily invaded vegetation classes were two types of dry sclerophyll forest, Western tablelands dry herb/grass forest (code number: 108. See Appendix 11) and Eastern tablelands dry shrub/grass forest (code number: 73) (Figure 4.2.5). However, the sample size of eastern tablelands forest is extremely low (n = 3). There were also three vegetation types that appeared relatively free from invasion despite large sample sizes. These include one type of dry sclerophyll forest present at Buccleugh; Western montane dry fern/grass forest (code no: 103) dominated by *E. dives*, *E. dalrympleana* and *E. robertsonii*. As well as two types of wet sclerophyll forest, Tableland acacia/herb/grass forest (code no: 104) dominated by *E. robertsonii* and *E. dalrympleana* and Eastern tablelands fern/herb/grass moist forest (code no: 55) dominated by *E. fastigata*. These vegetation types were present at Blowering Dam and Tallaganda respectively.
Vegetation types invaded

**Figure 4.2.5 Boxplot of the level of invasion within vegetation classes in the Hume region.** Codes for vegetation classes within the Forest Ecosystems South database are provided in Appendix 12. The number of 100 m samples within each vegetation class is shown on the x-axis. Each vegetation class was placed in one of the following broad categories; D – Dry sclerophyll forest, W – Wet sclerophyll forest, Wo – Woodland and C – Cleared land.

Division of vegetation types into broad classes resulted in a significant difference in the level of infestation across vegetation types ($df = 2$, $F = 50.914$, $p < 0.0001$) (Figure 4.2.6). However, differences in mean values between categories were small. Dry sclerophyll forest and wet sclerophyll forest had mean indices of 1.01 and 0.48 respectively and the interquartile range was the same for both vegetation types (0 to 1).
Northern Region (3 sites)

All three sites in the northern region experienced extremely low levels of invasion with mean infestation indices of less than 0.01 and were therefore excluded from analysis.

Monaro Region (6 sites)

The southeast NSW database includes six types of dry sclerophyll forest, four types of wet sclerophyll forest and three types of grassy woodland allowing a comparison of invasibility within the major vegetation classes. The major vegetation classes present were; Heath, Wetlands, Dry sclerophyll forest, Grassy Woodlands, Grasslands, Wet sclerophyll forest, Cleared land and Remnant vegetation. There was large variation in invasibility between different classes of wet and dry sclerophyll forest (Figure 4.2.7). Mean infestation index for the dry sclerophyll forests ranged from 0.74 (Southern Hinterland, code no. 81) to 2.54 (Sydney Montane, code no. 17). Mean infestation index
for wet sclerophyll forest ranged from 0.35 (Southern escarpment, code no. 9) to 1.45 (Southern tableland, code no. 11). There was also a large difference in invasibility between the grassy woodlands with mean indices ranging from 2.43 (Southern tablelands grassy woodlands, code no. 86) to 0.12 (Tableland clay grassy woodlands, code no. 40). The sample size of two of these categories is below 30.

Figure 4.2.7 Boxplot of the level of invasion within vegetation classes in the Monaro region. Codes for vegetation classes within the southeast NSW database are provided in Appendix 12. The number of 100 m samples within each vegetation class is shown on the x-axis. Each vegetation class was placed in one of the following broad categories; H – Heath, WL – Wetlands, D – Dry sclerophyll forest, GW – Grassy woodlands, G – Grasslands, W – Wet sclerophyll forest, C – Cleared, Rm – Remnant bushland.

Categories with 30 or less samples were removed (H, G) and examined differences between broad vegetation classes. After randomly selecting 73 cases from
the remaining vegetation types there was a significant difference between vegetation types (df = 5, F = 60.614, p < 0.0001) (Figure 4.2.8). Wetlands were the most heavily invaded with a mean index of 3.36. Dry sclerophyll forest was significantly more invaded than wet sclerophyll forest. Grassy woodlands experienced low levels of invasion similar to remnant vegetation and cleared areas.

Figure 4.2.8 Boxplot of the level of invasion within broad vegetation classes in the Monaro region. Vegetation classes from the southeast NSW database have been divided into broad categories and subsampled. The number of samples within each vegetation class = 73. Different lower case letters indicate a significant (p<0.05) difference between vegetation classes. WL – Wetlands, D – Dry sclerophyll forest, W – Wet sclerophyll forest, GW – Grassy woodlands, Rm – Remnant bushland, C – Cleared land. Heath and Grasslands have been excluded.

Considering results for all sites combined and for independent regions, Table 4.2.2 places vegetation types in decreasing vulnerability to pine invasion. In all cases Cleared areas and Remnant bushland experienced the lowest level of invasion. Dry
sclerophyll forest was more invaded than wet sclerophyll forest for all sites but this relationship was only significant in the Hume and Monaro regions and when only old sites were considered. Disturbed areas of forest were more susceptible to invasion for all sites combined and in the Macquarie region.

Table 4.2.2 Summary of invasion pattern across vegetation classes.
Vegetation classes are ordered in decreasing level of invasion based on results from subsampled data.

<table>
<thead>
<tr>
<th>Vegetation classes</th>
<th>Order of decreasing level of invasion</th>
</tr>
</thead>
<tbody>
<tr>
<td>All sites</td>
<td>observed: DWF&gt;DDF&gt;GW&gt;D≥Wo≥W≥Rm&gt;C</td>
</tr>
<tr>
<td></td>
<td>expected: DDF&gt;DWF&gt;GW&gt;D=Wo=W&gt;Rm&gt;C</td>
</tr>
<tr>
<td>Old sites</td>
<td>observed: DWF≥DDF=P≥Wo=D=W&gt;Rm&gt;C</td>
</tr>
<tr>
<td></td>
<td>expected: DDF&gt;DWF&gt;W=Wo=D&gt;W&gt;Rm&gt;C</td>
</tr>
<tr>
<td>Macquarie region</td>
<td>observed: DWF&gt;DDF=W≥D≥Wo</td>
</tr>
<tr>
<td></td>
<td>expected: DDF&gt;DWF=D=Wo&gt;W</td>
</tr>
<tr>
<td>Monaro region</td>
<td>observed: WL&gt;D=W≥GW&gt;Rm&gt;C</td>
</tr>
<tr>
<td></td>
<td>expected: D=W&gt;GW&gt;WL&gt;Rm&gt;C</td>
</tr>
<tr>
<td>Hume region</td>
<td>observed: D&gt;W&gt;C</td>
</tr>
<tr>
<td></td>
<td>expected: D&gt;W&gt;C</td>
</tr>
</tbody>
</table>

> significantly greater than (p < 0.05)  
≥ greater than but no significant difference
Discussion

Patterns of invasion across forest types generally matched our expectations. Disturbed forest environments were more invaded than their undisturbed counterparts in the Macquarie region. Our results are consistent with the idea that disturbance facilitates pine invasion (Richardson et al. 1994) and of exotics worldwide (Fox and Fox 1986a). Sites disturbed by fire or tree felling experienced higher pine colonization rates than undisturbed areas in South Australia resulting in a trebling of the rate of gap saturation (Van der Sommen 1978). The high level of disturbance in the Macquarie region may be driving the high level of invasion at sites within the region. Intriguingly disturbed wet forests experienced higher infestation levels than disturbed dry forests. All of the disturbed wet forest surveyed occurred at two sites, Jenolan and Penrose. For example at Penrose pines are invading swampland immediately adjacent to the plantation. In comparison disturbed dry forest was present at 11 sites. A higher mean level of infestation within disturbed wet forest is unlikely to represent the broader vulnerability of the vegetation type.

Wildling pines were found growing in seemingly intact areas of native forest which is consistent with observations of pine spread into eucalypt communities in South Australia (Van der Sommen 1978, Virtue and Melland 2003). In Chile invasion of P. radiata has only occurred in areas subjected to intense anthropogenic disturbance, and spread is restricted to the edges of fragments with low disturbance and dense native canopy (Bustamante et al. 2003). Similarly, in New Zealand, major disturbance is required before seedlings can establish and observations of wildling conifers in intact shrubland often results from establishment prior to shrub dominance, e.g. after a fire (Ledgard 2004). The ability of pines to establish in forest environments in Australia may be due to the open nature of the canopy, compared with closed forests of New Zealand and Chile. An ability of pines to establish in forested environments in Australia may also be due to low rainfall. In New Zealand P. radiata predominantly invades warm areas with high rainfall (Ledgard, 2001) which equates to vigorous vegetation growth which is known to hinder pine establishment (Richardson et al. 1994). In Australia lower rainfall may lead to a larger window of opportunity for establishment due to less competition from resident vegetation.

Dry sclerophyll forests experienced higher levels of invasion than wet sclerophyll forests across all sites combined and in the Monaro and Hume regions. The
trend became significant when only the older sites were considered. This finding suggests that differences in invasibility between vegetation types will manifest more strongly during the latter stages of invasion when sites are more likely to be in equilibrium with the environment (Richardson 2004). The pattern is also consistent with the idea that open, high light conditions within dry sclerophyll forests are conducive to pine establishment (Chilvers and Burdon 1983). The resistance of wet sclerophyll forest has been attributed to the shade intolerance of *P. radiata* (Chilvers and Burdon 1983). A further potential reason for the absence of wildlings within wet environments is the fact that they support microorganisms, fungi and invertebrates responsible for the decomposition of organic matter and pine seed within the litter layer (Kasel 2004a). An inability to establish under closed canopy has also been observed for conifers in New Zealand (Ledgard 2004) and for *Pinus lutchuensis* on a Pacific island (Shimizu and Tabata 1985). However, the ability of pines to establish in closed environments is clearly context dependent as positive effects of shading on the establishment of invasive *P. radiata* in xeric habitats have been observed in Chile (Becerra and Bustamante, unpublished). The resistance of wet sclerophyll forest to pine invasion may be the reason for an absence of invasion from large wet sites in the Monaro (Bondi and Coolangubra) and Hume regions (Bago, Green Hills).

Large variation in the level of invasion among types of dry sclerophyll and wet sclerophyll forest observed in the Monaro region is consistent with a study of pine spread at Buccleugh State Forest which suggested that eucalypt types differ in their susceptibility to pine invasion (Lindenmayer and McCarthy 2001). The authors observed higher pine occurrence in native remnants dominated by *Eucalyptus dives* and *Eucalyptus bridgesiana*, two drier eucalypt species. A heavily invaded area within the Brindabella ranges in the Australian Capital Territory is also dominated by *E. dives* and *E. bridgesiana* (Burdon and Chilvers 1977) suggesting that these species, or rather the habitats they dominate, are particularly susceptible to invasion. *Eucalyptus dives* and *E. bridgesiana* are both present at Lidsdale, one of the most highly invaded sites in this study while *E. dives* was also dominant at two other heavily invaded sites, Newnes (in association with *Eucalyptus sieberi* and *Eucalyptus oreades*) and Mannus (in association with *Eucalyptus macroryncha*), providing some support for the idea that these species are more vulnerable to invasion. However, an absence of wildlings from areas of continuous forest dominated by *E. bridgesiana* at Buccleugh State Forest...
observed by Lindenmayer and McCarthy (2001) and during this study suggests that intact areas of the forest type are able to resist invasion.

A survey of plantation sites in Victoria suggested that forests containing *Eucalyptus blakelyi* are somehow resistant to invasion (Minko and Aeberli 1986). Our results are consistent with this idea as areas dominated by *E. blakelyi* at Green Hills (Western slope herb/grass woodland) also experienced very low levels of invasion. However, a previous survey of Newnes and Lidsdale State Forests found no influence of eucalypt presence or species composition on the presence of the distribution of pine wildlings (Williams and Wardle 2005b) suggesting that eucalypt composition *per se* is unlikely to be responsible for any resistance to invasion. An absence of wildlings in areas dominated by *E. blakelyi* is more likely to reflect environmental conditions that simultaneously favour growth of the eucalypt and prevent pine establishment. Similarly, an absence of invasion within wet sclerophyll forest dominated by *Eucalyptus robertsonii* and *Eucalyptus dalrympleana* at Blowering Dam is unlikely to reflect an ability of these species to resist invasion because *E. dalrympleana* was also dominant at Jenolan, a site that experienced heavy invasion in some areas. In other cases the apparent resistance of vegetation types may be due to low propagule pressure from young plantations. For example, the absence of wildlings in wet sclerophyll forest dominated by *Eucalyptus fastigata* at Tallaganda may be due to the fact that the plantation was established only 37 years ago. Increases in seed production and future opportunities for establishment may result in invasion at the site.

This study has provided the first comprehensive examination of the influence of vegetation type on pine success in Australia. It builds on previous site specific studies (Van der Sommen 1978, Lindenmayer and McCarthy 2001, Williams and Wardle 2005b) and in general our findings are in support of previous ideas regarding pine invasibility in the southern hemisphere (Richardson et al. 1994). However, the ability of pines to establish in seemingly intact areas of native forest observed in this, and previous studies (Van der Sommen 1978, Chilvers and Burdon 1983) suggests that disturbance is not always required for invasion into forest environments, particularly in open, dry sclerophyll forests.
4.3 Local scale variation: the role of wind, local propagule pressure, grazing and canopy cover

Methods

Interaction between propagule pressure and vegetation

Forward stepwise binary logistic regression was used to examine the interaction between propagule pressure and vegetation type and their influence on the likelihood of invasion on a local scale, i.e. within 100 m samples. The infestation index was reduced to a binary variable because the number of samples with infestation indices of 0 far outweighed the number of samples with values from 1 to 5. To account for this inequality, samples with infestation indices of 2 or above were all considered ‘invaded’. Samples with values of 0 or 1 were coded as ‘uninvaded’ as an infestation index of 1 represented the presence of small wildlings typically located on the roadside and did not necessarily reflect the invasibility of the intact vegetation present. Analyses were performed on SPSS 15.0 (2006).

Two components of propagule pressure were examined; age of the adjacent plantation compartment and direction from the plantation. Areas downwind of plantations are likely to experience higher rates of seed rain with increased likelihood of invasion. Samples downwind from old compartments are expected to have the highest level of invasion. Information on wind intensity and direction was obtained from the Bureau of Meteorology in the form of wind roses grouped by season. The direction of the dominant winds during summer was determined for each site as this is the season during which seeds are typically released from cones (ForestrySA 2007). Every sample at a site was assigned a direction from the plantation and deemed as either upwind or downwind. Each sample was also assigned a value for the number of years since the establishment of the adjacent compartment in the plantation (until 2006). If a compartment was on second rotation, 30 years was added to the value. For example a 1998 compartment on second rotation was assigned a value of 38 years (2006-1998+30).

To examine the interaction with vegetation each sample was assigned a vegetation type using the same method outlined in subsection 4.2 (see table 4.2-1 for vegetation classes). In order to aid interpretation of the results the number of vegetation classes was reduced by excluding all categories with less than 30 cases. Categories
which were found to have similar levels of invasion in subsection 4.2 during previous
analysis were combined. Remaining vegetation categories were as follows; C –
“Cleared” a combination of Cleared areas and Remnant bushland. D – “Dry forest” a
combination of Dry sclerophyll forest and Woodland. DF – “Disturbed forest” – a
combination of Disturbed dry sclerophyll forest and Disturbed wet sclerophyll forest. W
– Wet sclerophyll forest. Vegetation categories were coded as dummy variables with
wet vegetation as the reference category.

The three predictors included in the logistic regression were residence time of
the adjacent compartment, wind (upwind or downwind) and vegetation class. Samples
will be highly spatially auto-correlated as they were collected by surveying
continuously around plantation borders. In order to reduce the influence of this auto-
correlation, 50 % of samples were randomly selected from each site. After random
sampling many sites either had too few invaded samples or vegetation categories to
analyse separately. Therefore data were combined for all sites in order to include a
larger variety of vegetation types. The analysis was also performed on all sites greater
than or equal to 40 years old. The Hosmer-Lemeshow test was used to determine the
difference between observed and predicted values (Hosmer and Lemeshow 1989). A
non significant result indicates that the observed values are not significantly different
from the predicted values and the model is a good fit of the data.

Influence of wind
In order to examine the role of wind direction on pine distribution beyond the
immediate boundary I compared the distance to the furthest surveyed pine, obtained
from transect data, with the dominant wind patterns for the nine most heavily invaded
sites. In addition, the land manager questionnaire (chapter 3) identified an area in the
Hume region where a record of pine spread was available and could contribute to the
field data. Pine trees have been mapped from the air by Department of Environment and
Conservation staff in the area between the plantations at Bogandyera and Mannus. The
distribution of these pines was examined in the context of surrounding plantations to
examine the influence of wind at a landscape scale

Influence of canopy cover
To investigate the influence of canopy cover I took opportunistic digital photographs of
the canopy at the majority of plantation sites (all sites excluding Clarkes Hill, Kinross,
Lidsdale and Vulcan). Photos were taken in groups of 4 in areas where transects were established and on different plantation boundaries. The number of pohos taken depended on the size of the plantation and ranged from 12 to 60. Photographs were analysed using Gap Light Analyzer 2.0 (Frazer et al. 1999) and a mean value of percentage canopy cover was calculated. In invaded areas I ensured photos only included eucalypt canopy. Canopy cover within invaded and uninvaded areas, for all sites combined, were compared using a two-tailed t-test assuming equal variances.

Influence of grazing

Observations of grazing, i.e presence of grazing animals, or grazed areas were made at 5 sites (Buccleugh, Gurnang, Penrose, Wingello A and Wingello B) during the survey period. Grazed areas were characterized by low understorey cover, high grassy grund cover and extensively cleared land. At each site the number of grazed polygons was often substantially less than the number of non-grazed polygons. To account for this difference grazed polygons were randomly sub-sampled to obtain an equal sample size. Significant differences in the level of invasion between grazed and non grazed areas were tested for using a two-sample t-test assuming equal variances.

Results

Logistic Regression

All three main predictors as well as the interaction between vegetation and residence time had a significant influence on the model (Table 4.3.1). However the overall model was a poor fit as it classified 96.1 % of uninvaded cases and only 38.5 % of invaded cases correctly. Examination of the Wald statistic revealed that residence time of the adjacent compartment had the largest influence on the likelihood of invasion followed by vegetation and the interaction between the two variables. Partial coefficients of vegetation were also significant (p < 0.05). Cleared areas and Dry sclerophyll forest are less likely to be invaded than Wet sclerophyll forest. Disturbed forest was the most likely to be invaded. The relative importance of wind to the model was much lower than the other predictors however it did have a significant influence with areas upwind of plantations more likely to be invaded.
Table 4.3.1 Logistic regression predicting invasion from vegetation, residence time of the adjacent compartment, wind and the interaction between vegetation type and residence time. Data is combined from all sites. Residence time is the number of years since establishment of the plantation compartment. Wet sclerophyll forest is the reference category for vegetation. Cleared vegetation includes both cleared areas and remnant vegetation. Dry includes dry sclerophyll forest and woodland. Disturbed includes disturbed wet and disturbed dry forest.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>B (SE)</th>
<th>Wald $\chi^2$</th>
<th>p</th>
<th>Lower</th>
<th>Odds Ratio (Exp B)</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residence time (res)</td>
<td>0.09 (0.12)</td>
<td>58.93</td>
<td>0.000</td>
<td>1.072</td>
<td>1.098</td>
<td>1.125</td>
</tr>
<tr>
<td>Vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleared</td>
<td>-5.83 (1.96)</td>
<td>8.86</td>
<td>0.003</td>
<td>0.000</td>
<td>0.003</td>
<td>0.136</td>
</tr>
<tr>
<td>Dry</td>
<td>-1.44 (0.57)</td>
<td>6.45</td>
<td>0.011</td>
<td>0.078</td>
<td>0.237</td>
<td>0.720</td>
</tr>
<tr>
<td>Disturbed</td>
<td>1.47 (0.69)</td>
<td>4.51</td>
<td>0.034</td>
<td>1.120</td>
<td>4.352</td>
<td>16.912</td>
</tr>
<tr>
<td>Wind</td>
<td>0.27 (1.14)</td>
<td>5.42</td>
<td>0.020</td>
<td>1.043</td>
<td>1.305</td>
<td>1.633</td>
</tr>
<tr>
<td>Vegetation x residence time</td>
<td></td>
<td>21.12</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleared x res</td>
<td>0.17 (0.06)</td>
<td>8.09</td>
<td>0.004</td>
<td>1.05</td>
<td>1.187</td>
<td>1.337</td>
</tr>
<tr>
<td>Dry x res</td>
<td>0.06 (0.02)</td>
<td>14.74</td>
<td>0.000</td>
<td>1.03</td>
<td>1.066</td>
<td>1.102</td>
</tr>
<tr>
<td>Disturbed x res</td>
<td>0.02 (0.02)</td>
<td>0.69</td>
<td>0.407</td>
<td>0.98</td>
<td>1.018</td>
<td>1.060</td>
</tr>
<tr>
<td>Constant</td>
<td>-4.90 (0.45)</td>
<td>118.49</td>
<td>0.000</td>
<td></td>
<td>0.007</td>
<td></td>
</tr>
</tbody>
</table>

Model $\chi^2 = 758.03$ R square = 0.234 (Cox & Snell) = 0.366 (Nagelkerke)

Hosmer and Lemeshow test indicates that observed values are not significantly different from predicted values $\chi^2 = 9.66$ p = 0.29

Exclusion of sites less than 40 years of age retained only three predictors (Table 4.3.2). However the Hosmer-Lemeshow test was significant indicating that the overall model was not well fitted to the observed data. Major differences to the results from when all sites are included are that wind is no longer a significant predictor and dry vegetation is not significantly different from wet sclerophyll forest.
Table 4.3.2 Logistic regression predicting invasion within sites ≥ 40 years old from vegetation, residence time of the adjacent compartment, wind and the interaction between vegetation type and residence time. Residence time is the number of years since establishment of the plantation compartment. Wet sclerophyll forest is the reference category for vegetation. Cleared vegetation includes both cleared areas and remnant vegetation. Dry includes dry sclerophyll forest and woodland. Disturbed includes disturbed wet and disturbed dry forest.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>B (SE)</th>
<th>Wald $\chi^2$</th>
<th>p</th>
<th>Lower</th>
<th>Odds Ratio (Exp B)</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residence time (res)</td>
<td>0.09 (0.12)</td>
<td>51.13</td>
<td>0.000</td>
<td>1.065</td>
<td>1.090</td>
<td>1.117</td>
</tr>
<tr>
<td>Vegetation</td>
<td>21.17</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleared</td>
<td>-6.00 (1.97)</td>
<td>9.30</td>
<td>0.002</td>
<td>0.000</td>
<td>0.002</td>
<td>0.117</td>
</tr>
<tr>
<td>Dry</td>
<td>-0.63 (0.59)</td>
<td>1.13</td>
<td>0.287</td>
<td>0.170</td>
<td>0.535</td>
<td>1.690</td>
</tr>
<tr>
<td>Disturbed</td>
<td>1.63 (0.70)</td>
<td>5.32</td>
<td>0.021</td>
<td>1.277</td>
<td>5.102</td>
<td>20.375</td>
</tr>
<tr>
<td>Vegetation x residence time</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleared x res</td>
<td>0.18 (0.06)</td>
<td>8.69</td>
<td>0.003</td>
<td>1.062</td>
<td>1.197</td>
<td>1.348</td>
</tr>
<tr>
<td>Dry x res</td>
<td>0.04 (0.02)</td>
<td>6.07</td>
<td>0.014</td>
<td>1.009</td>
<td>1.043</td>
<td>1.078</td>
</tr>
<tr>
<td>Disturbed x res</td>
<td>0.01 (0.02)</td>
<td>0.31</td>
<td>0.580</td>
<td>0.971</td>
<td>1.012</td>
<td>1.054</td>
</tr>
<tr>
<td>Constant</td>
<td>-4.471 (0.44)</td>
<td>102.1</td>
<td>0.000</td>
<td></td>
<td>0.011</td>
<td></td>
</tr>
</tbody>
</table>

Model $\chi^2= 550.55$  R square = 0.220 (Cox & Snell) = 0.324 (Nagelkerke)

Hosmer and lemeshow test indicates that observed values are significantly different from predicted values $\chi^2 = 32.95$, p < 0.0001.

**Transect data**

Transect data revealed little influence of wind direction on the distance to the furthest surveyed pine (Figure 4.3.1). There is some evidence for long distance dispersal downwind of the Jenolan plantation where pines were found 400 m to the south east. Higher levels of invasion to the south east compared to the north east were also observed at Newnes. Long distance dispersal was observed at both Lidsdale and Newnes where pines were observed growing 3 km and 4 km from the respective plantations. In many cases the presence of grazing land prevented an examination of the influence of wind. For example, at the Mannus plantation summer winds are predominantly north - north westerly, however land to the south is cleared land which is likely to exclude wildlings.
Figure 4.3.1 Infestation index and wind roses for the 9 most heavily invaded sites. Infestation roses are located to the left of the relevant wind rose. The length of arrows...
on infestation roses represents the distance of the furthest surveyed pine in that direction from the plantation. Scale: 1 cm = 100 m except for Lidsdale (N/NE: 2km; S: 800m) and Newnes (NW, 150m, SE – 500m, N 4km). Semi-circles represent the presence of cleared land.

Wind rose data was obtained from the Bureau of Meteorology. Each branch represents the wind coming from that direction. Each petal corresponds to a speed range from that direction. The length of the petal is proportional to the frequency of that wind. The thickness of the petal is used to indicate which speed range it represents.

* Data from Newnes and Lidsdale was collected during an honours project in 2003.

**Aerially mapped pines at Mannus**

Several large pines, visible by air, are present in Bogandyera Nature Reserve, to the south east of the Mannus plantation, as far as 10 km away (Figure 4.3.2). Surveying during this study also revealed high levels of infestation in the vegetation to the north of the Mannus plantation with large pines overtopping the native canopy. No invasion was recorded for Bogandyera. The first plantings for the Mannus and Bogandyera plantations occurred 70 and 10 years ago respectively.
Figure 4.3.2 Aerially mapped pines between Bogandyera and Mannus plantations. Vegetation layer is from the Forest Ecosystems South Database (Thomas et al. 2000).
Influence of canopy cover

Invaded areas had a significantly lower eucalypt canopy cover (df = 481, t = 5.49, p < 0.0001), averaging 38.9% compared with 47.1% in uninvaded areas. However, the range of cover values was very similar for uninvaded and invaded areas (28.3 - 54.2% and 28.0 - 57.0% respectively) (Figure 4.3.3).

![Canopy Cover Comparison](image)

**Figure 4.3.3** Canopy cover for invaded and uninvaded areas within 24 of the 29 sites. Error bars represent the total range of values recorded.

Influence of grazing

Grazed areas were significantly less (p < 0.005) invaded than ungrazed areas at all five sites. This difference was most pronounced at Wingello B, however the sample size here was also the smallest of all sites (Figure 4.3.4).
Figure 4.3.4 Mean infestation index (+SE) for grazed and ungrazed areas at 5 sites.

* significant (p<0.05) difference.
Discussion

Analysis of local scale propagule pressure revealed a positive influence of residence time on the likelihood of invasion. This result is consistent with previous observations by Lindenmayer and McCarthy (2001) who found a significant positive relationship between the age of the surrounding plantation compartment and the occurrence of *P. radiata* wildlings within eucalypt remnants at Buccleugh State Forest. A significant interaction with vegetation type suggests that the relationship between residence time and the likelihood of invasion will differ between vegetation types. The threshold of propagule pressure required to overcome barriers to invasion will depend on the inherent resistance of the area being invaded (D'Antonio *et al.* 2001). Areas resistant to invasion e.g. cleared and highly grazed areas, will relate differently to seed input compared with areas with low levels of resistance, e.g. disturbed forests. Reanalysing the data with only old sites resulted in a poorer model and a weaker, although still significant influence of propagule pressure. This is most likely owing to the fact that an inclusion of all sites results in the inclusion of samples adjacent to compartments below 20 years of age with no invasion which drives the positive relationship between residence time and likelihood of invasion. Once compartments reach reproductive age the relationship between compartment age and invasion success weakens as it is more dependent on other factors such as vegetation type.

Direction from the plantation had little influence on the probability of invasion and in fact when all sites were combined upwind areas were more likely to be invaded. This result is most likely an artefact of having a disproportionate number of uninvaded samples. The analysis also confirmed patterns identified in the section 4.2, notably a higher likelihood of invasion in disturbed forests and an absence of invasion from cleared areas. However neither regression models fitted the observed data well suggesting that factors other than propagule pressure and vegetation are operating.

Wind direction had little influence on the distance to the furthest pines surveyed at the heavily invaded sites. Jenolan and Newnes were the only two sites with higher levels of invasion downwind from the plantation. At Newnes, there was evidence for higher levels of invasion to the south east of the plantation. Maximum dispersal distance to the south east was 500 m compared with 150 m to the north east. However, both south-easterly and north-westerly winds are frequent at the site (BOM 2006), making interpretation of this result difficult. An isolated pine, 4km north of the plantation also
suggests either long distance wind dispersal or dispersal by Yellow-tailed Black cockatoos (Williams and Wardle 2005a). Dispersal of seed by cockatoos has been reported for other Pinus species in Australia, including P. elliottii in Queensland and P. pinaster in Western Australia (Richardson and Higgins 1998). Bird dispersed seed may be responsible for the appearance of isolated pines at long distances from the plantation.

One of the reasons for the inconsistency with previous observations of the important role of wind in Australia (Minko and Aeberli 1986), is that our measure of invasion is generally restricted to within 200 m from the border of the plantation. Wind direction may have the biggest influence on distribution of pines that have been dispersed long distances and can only be accurately tracked from the air. Aerial mapping of pines in the area to the south-east of the Mannus plantation revealed clusters of mature pines in the native vegetation at distances of up to 10 km which also sourced invasion to the north. The predominant direction of high intensity winds (>10 km/hr) in the region is north westerly at all times of the year (BOM 2007) and suggests that the pines have been sourced from the Mannus plantation, rather than the younger plantation at Bogandyera which has barely reached reproductive age. This finding is consistent with the common observation of wind dispersed conifers in New Zealand (Ledgard and Langer 1999) and highlights the importance of monitoring wildling populations from the air. Cleared areas compared with forested environments can increase the potential for seed dispersal (Nathan et al. 2002). The area in between the cluster of wildling pines and the plantation at Mannus is cleared land and may have assisted the long distance dispersal of seed.

While long distance dispersal events are inherently difficult to measure (Bullock and Clarke 2000, Cain et al. 2000), their large influence on the migration rate of plants (Moody and Mack 1988, Kot et al. 1996, Clark et al. 1998) means that failure to include them in spread models can result in gross underestimation of spread rates (Higgins and Richardson 1999) and can hinder conservation management (Trakhtenbrot et al. 2005). Small proportions of seed dispersing long distances (1-10 km) can lead to orders of magnitude increases in predicted spread rates (Higgins and Richardson 1999). The presence of isolated pines at distances of up to 10 km from the Mannus plantation indicates that long distance dispersal is occurring in Australia. Management efforts should focus on the removal of outlying individuals that can accelerate the invasion process (Moody and Mack 1988). In the case of pine spread in Australia distinguishing
between wildlings dispersed by wind and those dispersed by cockatoos will be necessary to accurately model spread rates.

**Effect of grazing**

All five sites with grazing observations had higher levels of invasion on ungrazed areas. The appearance of grazing in some instances, e.g. represented by the presence of extensively cleared land, may not necessarily equate to grazing pressure. More importantly it is not indicative of whether or not grazing animals were present at the time of seedling establishment when its influence on recruitment would be greatest. However, the absolute lack of invasion in landscapes cleared for grazing across a broad geographic range of sites is in support of observations of the controlling effect of grazing in New Zealand (Benecke 1967, Gibson 1988) and Victoria (Minko and Aeberli 1986). This result provides some explanation for the absence of spread from large plantations surrounded with a high proportion of grazing land, e.g. Buccleugh where more than 60% surveyed land was cleared.

The fate of woody seedlings colonizing meadows has been shown to be highly dependent on the intensity of grazing (Vinther 1983). High levels of grazing led to food scarcity and consumption of seedlings, while low levels resulted in vigorous growth of herbaceous ground cover and a limitation of establishment sites. Intermediate grazing levels were the most conducive to seedling establishment (Vinther 1983). Sheep grazing is the primary factor controlling pine spread in the Canterbury region of New Zealand (Belton and Ledgard 1991) and the manipulation of grazing pressure is an important control strategy in the country (Ledgard 2001). Our results indicate that similar strategies to control pine spread in Australia may be beneficial.

**Effect of canopy cover**

Areas invaded by pines had significantly lower canopy cover suggesting that more open canopies are more susceptible to invasion than closed environments. While, this is consistent with previous ideas regarding pine spread in Australia (Chilvers and Burdon 1983, Virtue and Melland 2003) and conifer establishment in New Zealand (Ledgard 2004), the range of canopy covers for invaded areas was large suggesting that canopy cover alone is not responsible for differences in invasibility.
There are several factors not considered in this study that may be causing differences in pine distribution within a plantation. *Pinus radiata* wildlings have been found in higher abundance in areas with open vegetation cover (Lindenmayer and McCarthy 2001). The level of ground cover is representative of microsite level disturbance and reflects the amount of resources available. Areas with low ground cover provide good conditions for pine establishment because competition with resident vegetation for light, water and space is minimised in these environments (Richardson and Bond 1991, Richardson *et al.* 1994). This study focused on landscape scale distribution and hence did not have the scope to account for differences in vegetation cover. It is highly likely that variation in pine densities surrounding a plantation are due to variation in microsite conditions.
4.4 **Summary of factors influencing invasion success**

Invasions are context-specific processes where the strength of processes influencing invasion success will vary between communities (D'Antonio 1993). The factors limiting pine establishment are likely to be different at each site and attempting to draw generality from a suite of plantations that differ in complex ways is difficult. Factors providing resistance to invasion at one site may not necessarily be responsible for an absence of invasion at all sites. In this study I chose to prioritise a small number of variables while documenting spread on a landscape scale, leading to an inevitable exclusion of some of the factors known to influence pine spread. These include annual variation in seed production (Dawson *et al.* 1979, Ledgard 2001), micro habitat conditions (Ledgard 2001), soil pH (Rouget *et al.* 2001) and topography (Ledgard and Langer 1999). This study has also shown that fire can have an important influence on wildling populations. Most importantly it is the interaction of all these factors that will drive the invasion process (Belton and Ledgard 1991, Higgins and Richardson 1998).

Despite these limitations this study has provided sufficient knowledge to explain the invasion patterns at a landscape scale and make a useful contribution to the management of *P. radiata* invasion. A number of risk factors can be developed which summarise the invasion process in Australia. In broad terms the factors investigated in this study can be placed in to two categories: i) ecological resistance and ii) propagule pressure, which interact to determine invasion success (Figure 4.4.1). Factors that increase propagule pressure are likely to have a positive influence on invasion success. However, in this study, the two main components of propagule pressure (residence time and size of the plantation) had opposing influences on invasion success. The negative relationship between plantation size and the level of invasion (represented by a minus sign linking “plantation size” to “propagule pressure”) observed in this study is unlikely to reflect a negative influence of propagule pressure on pine success and is more likely a result of the large influence of two larger sites that were uninvaded. At a landscape scale wind will influence the delivery of seed from the plantation. In this study, wildlings dispersed long distances were found down wind from the seed source. This is indicated by the positive interaction between “wind” and “propagule pressure” (Fig 4.4.1).

Those factors that increase ecological resistance of the surrounding vegetation have an overall negative influence on pine establishment. High rainfall and high canopy cover reduced the susceptibility of environments to pine invasion. The influence of
disturbance depended on disturbance type. Grazing reduced the likelihood of invasion by increasing “ecological resistance” while physical disturbance appeared to favour pine establishment.

Figure 4.4.1 Flow chart summarising the factors that influence pine invasion in Australia. Plus signs indicate a positive influence of the factor and minus signs indicate a negative influence. Factors that have a positive interaction with “Ecological Resistance” have an overall negative influence on invasion success. Factors that have a positive interaction with “Propagule Pressure” help to facilitate pine invasion.

In general patterns of invasion mirrored those of New Zealand and South Africa. Disturbed areas were more heavily invaded than undisturbed areas, a positive influence of wind was evident from an aerial survey at one site, and a positive influence of plantation age on the likelihood of invasion was found. At the most heavily invaded sites wildling distribution patterns were similar to those observed elsewhere. Large pines, referred to as satellite foci (Richardson and Higgins 1998) were found reproducing at long distances from the plantation to produce dense stands of wildlings. The most notable exception is the observation of pines in undisturbed forest
environments. An absence of invasion from large, old plantations surrounded by wet vegetation suggests that even very large levels of propagule pressure may not be able to overcome all barriers to invasion as previously suggested (Richardson et al. 1994) and that there are environments which may remain free from invasion. The high invasibility of wet disturbed forests however, confirms the idea that disturbance will reduce resistance to invasion and increase the rate of pine colonisation (Van der Sommen 1978, Richardson and Higgins 1998).

There was some evidence for differences in the level of invasion within vegetation type with dry sclerophyll forest often experiencing higher levels of invasion than wet sclerophyll forest. Sites with high levels of rainfall, i.e above 1300 mm, are yet to become invaded. This is consistent with ideas regarding pine invasion in Australia (Lindenmayer and McCarthy 2001, Virtue and Melland 2003) and observations in the south island of New Zealand where the majority of spread has occurred in the dry, eastern hill and high country (Ledgard 2004). The dominant vegetation type bordering the majority of plantations is eucalypt forest or woodland. In South Africa the majority of spread of *P. radiata* has occurred in fynbos vegetation (Richardson et al. 1994) and in New Zealand conifer spread is a particular problem in native treeless grasslands and shrublands (Ledgard 2001). This difference in vegetation may also explain the lower amount of land invaded in Australia as dispersal distances within forested environments are typically much lower than within more open landscapes (Nathan et al. 2002).

Correlations between components of vegetation structure and invasibility have been shown to be highly scale dependent. This study attempted to analyse the influence of a limited number of variables on pine success at a landscape scale (across 29 geographically distinct plantations) and on a local scale (within the vegetation surrounding a discrete plantation site). On a local scale, native diversity may resist invasions while this effect may be swamped by high propagule pressure at a larger scale (Levine 2000). Residence time was found to be an overriding influence and was significant at both scales. Our findings were also consistent with the idea that the physical environment may be having a greater influence on invasibility than community structure at larger scales (Reed et al. 1993), as annual rainfall was highly significant at the landscape scale while a significant influence of vegetation type was only observed on the local scale. Other factors such as the level of physical disturbance were only investigated at the local scale. An investigation of all factors at both scales may provide further insight into scale-dependent relationships with respect to pine establishment.
5. Influence of fire: a field study

Introduction

Knowledge of how invading species interact with fire is critical to their management as fire can both promote and control plant invaders (D'Antonio 2000). A number of Pinus species respond favourably to fire. Dense stands of P. halepensis establish in native vegetation after burning (Rouget et al. 2001). Fire also stimulates the release of large amounts of seed from the serotinous cones and creates favourable conditions for germination and establishment (Richardson and Brown 1986, Richardson and Bond 1991). Pines have many of the traits required to exploit the post-fire environment, i.e. fire-resilient, small seeds, low seed to wing loadings for good dispersal ability, short juvenile periods, moderate to high serotiny and poor fire tolerance as adults (Richardson et al. 1990). Fire has also been shown to increase the germination rate of P. radiata seeds (Reyes and Casal 2001).

In the fynbos vegetation of South Africa Pinus species are known to reproduce optimally after fire (Rabie 2000), however they can also establish in areas with a post-fire age of <10 years and in vegetation >30 years post-fire (Richardson and Brown 1986, Moll and Trinder-Smith 1992). Knowledge of post-fire pine recruitment in Australia is scarce. Densities of P. radiata have reached 1 million per hectare following wildfires in South Australia, however numbers thinned to approximately 1000 per hectare (Virtue and Melland 2003). At one of the sites in this study, Newnes State Forest, pine seedling densities of more than 1300 per hectare were recorded within eucalypt forest 2 years after an intense wildfire (M. Williams, unpublished). The long term survival of initially high numbers of seedlings will provide greater insight into the role of fire in the invasion process.

In Australia, wildfires are suppressed in areas surrounding plantations to protect the plantation resource. In addition, frequent low-intensity hazard reduction burns are carried out in areas surrounding the plantation to reduce the fuel load and fire risk to the plantation. Burns are typically implemented every 6-8 years with fire intervals longer than this considered dangerous (pers comm. D. Mukhar 2006). Observations of burnt and unburnt sites in Victoria (Minko and Aeberli 1986) found that young pines were highly susceptible to fire. Furthermore, pines are more sensitive to fire than native eucalypt vegetation (Pryor 1991) suggesting that there is an opportunity to dually control wildling populations while carrying out routine burning operations. Fires that
are intense enough to cause pine death and frequent enough to prevent the production of a canopy seed source are capable of preventing the spread of pines (Gill and Williams 1996). Pinus radiata mortality is directly related to scorch height which is related to fire intensity (Burrows et al., 1989) and so determining the influence of low intensity hazard reduction burns on the mortality of wildling populations will help assess their potential as a management tool. This study examined the influence of hazard reduction burns and high intensity wildfire on pine wildling mortality and recruitment. Seedling survival was compared for burnt and unburnt areas to assess the fate of large recruitment pulses following fire.

**Methods**

**Hazard reduction burns**

To investigate the influence of low intensity hazard reduction burns on pine mortality two sites known to be invaded by *P. radiata* and recently subjected to prescribed burns were surveyed. Mullions Range State Forest and the southern border of Gurnang State Forest adjacent to Kanangra-Boyd National Park were burnt in May 2004 and surveyed in July 2005 (15 months after the fire). The survey area at Mullions Range was also burnt in 1988 and 1985. At each site two transects 30 m wide and 200 m long were established in the first available native vegetation from the plantation (parallel to the plantation). Within each transect the height and diameter at breast height (dbh) and number of cones of all *P. radiata* individuals was recorded. Pines were recorded as either dead or alive with lack of green foliage signifying death.

**High intensity wildfire**

In January 2003 wildfire destroyed the majority of the Australian Capital Territory’s pine plantation estate. The intensity of the fire was extremely high, particularly in areas adjacent to plantations, killing many of the native eucalypts (Carey et al. 2003). Two areas heavily invaded by pines were surveyed in December 2005 to determine the influence of a high severity fire on the wildling population. A previous study of the area (Dawson et al. 1979) found that the majority of recruitment occurred in the years 1968-1971 making most of the wildlings present at the time of this study at least 25 years old. At Vanity’s Crossing two 20 m x 100 m transects and four 20 m by 20 m plots were surveyed. At Thompson’s Corner one 20 m by 100 m transect was surveyed giving a
total sample area across both sites of 0.76 hectares. Time restrictions and difficulties in accessing the site prevented equal sample effort at both sites. Vegetative ground cover was recorded at each site and found to be 10.0% at Thompson’s Corner and 36.7% (+6.5 SE) at Vanity’s Crossing.

**Seedling survival**

To investigate the influence of fire on seedling survival pine seedlings within recently burnt (Wildfire in December 2002) and relatively unburnt (last wildfire occurred in January 1952) eucalypt woodland invaded by *P. radiata* at Newnes State Forest were tagged. In both the burnt and unburnt areas four 20 m by 20 m plots were established with two plots located in the first available vegetation from the plantation and two plots located at a distance away from the plantation (200 m in the burnt area and 450 m in the unburnt area). Within each plot all *P. radiata* seedlings were tagged and assigned a unique number in October 2004. Seedlings were defined as having one or no whorls. All plots were censused in April 2005 (6 months after tagging), in March 2006 (17 months after tagging) and in October 2006 (24 months after tagging). Seedlings were either counted as dead or alive with a lack of green foliage signifying death. A total of 599 seedlings were tagged within the burnt plots and 811 seedlings were tagged in the unburnt plots. Differences in seedling survival were analysed using Kaplan-Meier survival curves and a logrank test to compare between unburnt and burnt plots. Analyses were performed using SPSS 15.0 (2006). The test statistic is compared with a $\chi^2$ distribution with 1 degree of freedom.

**Results**

*Hazard reduction burns*

Similar pine densities were recorded at Gurnang and Mullions Range with 300 and 254.4 pines per hectare respectively. A total of 462 pines were surveyed across both sites. Pine survival generally increased with diameter for both sites (Figure 5.1). The majority of pines with diameters greater than 10 cm survived the burns at both sites; 97.3% and 84.6% at Gurnang and Mullions respectively. Pines with diameters less than 1 cm were frequently killed by fire; 100% at Gurnang, 86.4% at Mullions.
However, many pines with diameters between 1 cm and 10 cm were able to survive the burn; 51.1% at Gurnang and 41.8% at Mullions.

Figure 5.1 *Pinus radiata* survival following hazard reduction burns at Gurnang State Forest and Mullions Range State Forest.

Pine survival also increased with height. Wildlings less than 2 m tall suffered high mortality rates; 100% at Gurnang and 84.2% at Mullions. Approximately two thirds of pines with a height greater than 3 m survived the burns; 68% and 65.6% at Gurnang and Mullions.

**High intensity wildfire**

At Vanity’s Crossing pine densities averaged 607 per hectare across the sample area. All wildlings with a diameter greater than 10 cm were killed (Figure 5.2). Densities of young pines (<1 m tall) were high, averaging 487.5 per hectare and reaching as high as 3050 per hectare in one plot. The high proportion of seedlings alive suggests that they have established after the fire with many of them clustering around large reproductive adults. The density of cones present was 315 per hectare and 1146 per hectare for Thompson’s Corner and Vanity’s Crossing respectively. Pines were more evenly distributed across all size classes at Thompson’s Corner. All surveyed pines were destroyed by the fire and no regenerating seedlings were found alive (Figure 5.2).
Figure 5.2 *Pinus radiata* survival by diameter at breast height (cm) following high intensity wildfire at Vanity’s Crossing and Thompson’s Corner. Survey area for each site was 0.56 hectares and 0.2 hectares respectively.
Seedling survival

After excluding all missing seedlings, the survival probability of the remaining seedlings was analysed, 304 in burnt plots and 562 in unburnt plots. Seedlings in burnt areas had significantly higher probability of survival \( \chi^2 \text{logrank} = 9.37, \text{df} = 1, p = 0.02 \) (Figure 5.3) than seedlings in unburnt areas. However the final probability of survival after 2 years was very similar for burnt and unburnt plots, 45 % and 37 % respectively.

Figure 5.3 Kaplan-Meier analysis for survival of Pinus radiata seedlings in burnt and unburnt areas at Newnes State Forest. Burnt plots n = 304 seedlings. Unburnt plots, n = 562 seedlings.
Discussion

This study has provided an exploratory look into the influence of fire on wildling pine populations at two sites. Even though hazard reduction burns have been considered a useful control strategy for pines (Pryor 1991), the results of this study suggest that they may only be effective in areas where the majority of wildlings are less than 3 m in height. High survival rates of pines within this height class are consistent with observations of fire effects on pines in plantations (Burrows et al. 1989). More than 80% of wildlings greater than 1 m tall survive when less than 60% of the crown height is scorched (Burrows et al. 1989). The ability of larger pines to survive these burns means prescribed fires will have a negligible impact on established wildling populations.

Hazard reduction burns in the Blue Mountains region typically consume vegetation below 0.5 m in height (James 1999). Cones can develop on wildlings as small as 2 m tall (M. Williams, pers. obs. 2006). Where flames do reach mature pine cones on wildling trees there is a risk of stimulating cone opening and seed release which may result in increased recruitment following fire.

Results from invaded areas in the ACT suggest that high intensity wildfire is capable of completely destroying wildling populations. However, high seedling numbers almost three years after the fire at one site and higher seedling survival probabilities for seedlings on burnt sites emphasises the need for follow up control. Pine seedling survival was higher in areas recently subjected to a wildfire at Newnes State Forest where 45% of seedlings survived after 2 years. Higher survival rates in burnt areas is most likely owing to an increase in light and nutrients following consumption of the canopy (Trabaud 1990) and a reduction in competitive ground cover (Richardson and Bond 1991). Removal of these seedlings during control operations would preferably take place within 5 years of the fire before the post fire cohort becomes reproductive and costly to remove. Given the scarcity of wildfires in areas surrounding plantations the necessary frequency of control action would not be great and a 5 year window to implement control should be achievable. Successful ‘cut, burn and follow up’ control strategies have been employed in South Africa (Richardson and Higgins 1998). This involves removing cones from or felling reproductive wildlings prior to the implementation of burns in order to minimize the spread of seed within the eucalypt woodland. Prescribed burns at 12-15 year intervals implemented in South Africa are considered to be ideal to control for Pinus species because very few trees reach maturity.
before the burn is implemented and all seedlings are killed by fire (Richardson and Higgins 1998). In Australia fire has been used for wildling control during the restoration of former pine plantations (Kasel and Meers 2004). A combination of mechanical removal and the opportunistic use of back-burning has effectively controlled wildling pines surrounding an ex-plantation site in Kosciusko National Park, NSW (Kasel 2004b). Van der Sommen (1978) suggested a maximum 20 year interval between fires to prevent effective seedling production by wildlings.

The absence of seedlings at Thompson’s Corner despite the presence of reproductive adults does not rule out the possibility of post-fire recruitment as the survey took place almost three years after the fire. However, it does indicate that if recruitment did occur, site conditions at the time of establishment may have hindered pine seedling survival. Time did not permit a replicated investigation of the influence of establishment conditions on post-fire recruitment, however, it is interesting to note that the major difference between sites was a considerably higher amount of ground cover at Thompson’s Corner. The presence of vigorous herb cover, especially grasses, is considered one of the major factors controlling the successful establishment and expansion of *Pinus* populations worldwide (Richardson & Bond 1991). Grasses can compete with pine seedlings (Pearson 1942, Madany and West 1983) while bare ground has been deemed the most susceptible to invasion by pines (Richardson et al. 1994). Our observation is similar to patterns observed in New Zealand, where rapid invasion of sites by exotic grasses following fire is thought to impede recruitment (Ledgard 2004). It appears that a lack of plant cover and high amount of bare ground at Vanity’s Corner may have provided the conditions thought necessary for pine establishment to occur (Richardson et al. 1994). Pine recruitment in the post-fire environment may also be dependent upon local propagule pressure, i.e. the number of cones on wildling pines exposed to the fire. A higher number of seedlings at Vanity’s Crossing compared to Thomson’s Corner is most likely due to a higher cone density at the site.

The ultimate influence of fire will depend on its timing and interaction with seed dispersal and recruitment. Seedling recruitment may follow good rainfall during a high seed crop year, or they may be the result of chance events. For example, storms and resultant high intensity winds have been responsible for initiating invasion events in New Zealand (pers. comm. N. Ledgard 2006). If prescribed burns are carried out soon after peak recruitment periods then they will have a detrimental effect on the seedling population. If however, burns take place after the majority of pines have reached 3 m,
many of them will escape flame height and low intensity burns will have little effect on the wildlings.

While recommendations of fire intervals can provide useful guidelines it is crucial that invaded areas are managed for native biodiversity as well as pine control. Increasing awareness about the importance of stochastic fire regimes suggests that consistent fire intervals may not be beneficial to the maintenance of native diversity (Morrison et al. 1995). Static fire regimes will favour some species and can lead to a reduction in diversity by continually selecting for the same species (Hobbs and Atkins 1988). For example, burning too frequently may lose obligate seeders (Fox and Fox 1986b). Any use of fire must weigh the costs and benefits associated with possible reductions in an invader and potential impacts on the native community (D'Antonio 2000). Here we have a situation where fire can both destroy adult pines and simultaneously favour recruitment. The net influence of fire on wildling populations is likely to be context specific and dependent on fire intensity, time of burning, weather conditions (D'Antonio 2000) and the age structure of the pines, making outcomes difficult to predict.

Pines may in fact increase the fire intensity of natural fires (Burdon and Chilvers 1994) and have an adverse influence on native species. This is potentially one of the largest impacts of pine invasion. The ability of invaders to disrupt disturbance regimes has been recognised as an avenue for significant impacts on ecosystem function (Mack and D'Antonio 1998). Invasion of fynbos vegetation by *Acacia* and *Hakea* in South Africa results in increased fuel loads of more than 50% and the potential for greater fire intensity under extreme weather conditions (Van Wilgen and Richardson 1985). Where pines represent a new life form they can have a large influence on fire regime (increase intensity and decrease frequency) (van Wilgen and van Hensbergen 1992). In Australia where pines are typically invading already forested systems the change in biomass following invasion will not be as great and the resultant impacts on fire intensity may not be as pronounced. However, pines are highly flammable (Fonda 2001) and dense pine stands have the capacity to burn hotter than native eucalypt vegetation. The potential for pines to fuel high intensity fires in areas surrounding a plantation provides powerful motivation for plantation owners to control wildling populations.
AIMS OF SECTION III: MECHANISM OF IMPACT

This section focuses on the impact of wildling pines once they have established in the native vegetation. Invasion of pines may result in a range of ecological impacts including changes to litter loads, light levels, soil chemistry, and soil microbial communities. Increased litter fall and increased shade caused by higher canopy cover are thought to be major drivers of community change following pine invasion in South Africa. The influence of these two biotic changes on the recruitment of native species within eucalypt woodlands was the prime focus of this study. Chapter 6 establishes the quantity of pine litter falling in an invaded eucalypt woodland and examines how this changes with the density of pines present and after fire. Spatial and temporal variation in both pine and eucalypt litterfall are also commented on.

Chapter 7 uses litterfall values obtained in chapter 6 to examine the influence of pine and eucalypt litter on native and pine recruitment in the field and glasshouse. The effect of increased canopy cover following pine invasion was also examined in the field. The following hypotheses are addressed;

1) Physical and/or chemical effects of *P. radiata* litter will have a negative influence on the germination of native species,
2) The magnitude of the physical effect will increase with increasing depth/volume of litter,
3) Increased canopy cover in invaded areas will reduce germination of native species in the field.

By including *P. radiata* in experimental treatments the ability of the species to establish under its own canopy and litter layer will determine the potential for self-facilitation of the invasion process.
6. Comparison of pine and eucalypt litterfall in an invaded eucalypt woodland

This chapter has been published in the journal Forest Ecology and Management.


Two anonymous referees provided valuable comments on the manuscript.

This chapter includes analysis of a small portion of data that were collected by myself during an honours project in 2003. The data of tallied pine counts within heavily invaded plots were used to calculate the level of clustering within each plot. All litterfall data was collected during the PhD candidature.

Introduction

Despite widespread recognition that invasive species have adverse effects on indigenous ecological communities (Vitousek et al. 1997, Mack et al. 2000), very few studies have examined the processes leading to those impacts (Levine et al. 2003). It is often difficult to attribute community changes to the effects of an invader as this requires long term monitoring of areas pre and post invasion. This is near impossible when the invader is slow growing, e.g. for tree invasions. A common approach involves a space-for-time substitution, comparing currently invaded and uninvaded sites (Greenwood and O'Dowd 2004, Hejda and Pyšek 2006, Vanderhoeven et al. 2006), with the potential for spatial confounding (Hurlbert 1984). Reductions in community composition observed in invaded areas may be due to inherent differences in the community rather than any negative influences of the invader. A better understanding of the processes that accompany invasion and how they may be altering a community is necessary to accurately predict the magnitude of impacts in order to prioritise management efforts (Parker et al. 1999) and to effectively restore invaded areas (Levine et al. 2003).
Several *Pinus* species have invaded native vegetation by spreading from adjacent commercial plantations in countries in the southern hemisphere including New Zealand (Hunter and Douglas 1984, Ledgard 1988), Chile (Bustamante *et al.* 2003), Israel (Lavi *et al.* 2005), South Africa (Richardson and Brown 1986) and Australia (Chilvers and Burdon 1983, Williams and Wardle 2005a). In Australia, a number of species including *P. caribea*, *P. contorta*, *P. elliottii*, *P. halepensis*, *P. jeffreyi*, *P. nigra*, *P. pinaster* and *P. radiata* are considered invasive (Richardson 2006). In the absence of comprehensive, long term studies of invasive pine populations, the impacts of *Pinus* spp. invasions are typically extrapolated from the plantation situation (Richardson and Van Wilgen 1986, Richardson *et al.* 1989). The assumption that self-sown (wildling) stands impart the same impacts as plantation stands may be valid in areas where wildlings exhibit densities up to and greater than that observed in plantations (Ledgard and Belton 1985, Richardson *et al.* 1989) and in areas where site preparation for afforestation is minimal, e.g. in fynbos vegetation in South Africa (Donald 1986 cited in Richardson *et al.* 1989). In Australia, where intense site preparation is often required prior to plantation establishment, the correspondence between plantation conditions and areas with pine wildlings may be reduced. The response of a eucalypt woodland, which typically produces a deep layer of persistent leaf and bark litter, to quantities of pine litter is likely to differ from vegetation types with lower levels of native litter.

Impacts associated with plantation establishment by *Pinus* are extensive ranging from reductions in stream-flow (Bosch and Hewlett 1982), extinction of native plant species (Richardson and Van Wilgen 1986, Richardson *et al.* 1989), soil acidification (Scholes and Nowicki 1998), as well as reductions in ant species diversity (Sinclair and New 2004), and soil microarthropod diversity (Springett 1976). Plantations have also been shown to have a negative influence on bird diversity (Disney and Stokes 1976, Allan 1997, Smith 1997) as well as mammalian and arboreal marsupial species richness (Lindenmayer *et al.* 2000). A combination of suppression by litterfall, shading effects and faster acquisition of resources by pines when compared with native vegetation is thought to be responsible for adverse effects on plant species in South Africa (Richardson and Van Wilgen 1986). A closer examination of these processes in invaded areas is the first step towards quantifying the impacts associated with pine invasion.

Litterfall rates within *P. radiata* plantations can exceed 4000 kg/ha/year and result in the accumulation of up to 24000 kg/ha of litter (Florence and Lamb 1973). Within areas invaded by pines, litter production is of particular interest because leaf litter can have a strong influence on the composition of plant communities by changing light and water availability.
(Facelli and Pickett 1991a), influencing nutrient supply rates (Denslow and Hughes 2004), by producing phytotoxins (Rice 1979), or providing a physical barrier to seedling emergence (Facelli and Pickett 1991a, Peterson and Facelli 1992, Myster 1994). Substantial accumulations of pine needle litter due to the establishment of a mature pine canopy have been observed in eucalypt forests invaded by pines (Burdon and Chilvers 1994) and may be partly responsible for changes to plant community composition and abundance observed in invaded areas (Virtue and Melland 2003, Baker et al. 2006). A quantification of litter production within invasive populations will help determine the potential for the negative litter effects observed in plantations to occur in invaded areas.

Rates of litterfall from wildling populations are likely to differ from plantation stands for a number of reasons. The number of whorls of branches for *P. radiata* is influenced by the intensity of solar radiation received by the tree (Fielding 1960). Wildling pines growing in more open environments may produce more foliage than close-spaced plantation trees as they have greater access to sunlight (Ledgard 2004). Wildling trees that survive beyond the age of plantation trees, which are harvested after approximately 30 years, are likely to produce more litter because needlefall increases with stand age (Cseresnyes et al. 2006). Fire is another major factor which may be responsible for differences in litterfall. At the same time as plantations are protected from fire, eucalypt woodlands surrounding plantations are commonly subjected to low intensity hazard reduction burns (Gill and Williams 1996) as well as natural wildfires. Pine material is highly flammable (Fonda 2001) and such fires are likely to destroy foliage and reduce litterfall.

The aim of this study was to provide an instantaneous examination of pine and eucalypt litterfall rates within a eucalypt woodland invaded by pines. Vegetation compositional differences and varying climatic conditions between invaded sites are likely to cause differences in litterfall rates, however, determining the relationship between pine litterfall and pine basal area and canopy cover will help gauge the capacity of wildling populations to produce litter at different stages of the invasion process. The inclusion of an area recently subjected to a high intensity wildfire provided an opportunity to quantify reductions in litterfall due to fire. Investigating the spatial and temporal distribution of litterfall within the eucalypt woodland will help quantify the area of land at risk from litter effects.
Methods

Study site

Our study took place within a dry eucalypt woodland bordering a 61 year old, 2000 hectare *Pinus radiata* plantation at Newnes State Forest (150°12 E, 33°24 S; altitude 1000–1170 m), approximately 7.5 km north east of Lithgow, New South Wales, Australia. The site is heavily invaded by *P. radiata*, with pine densities reaching more than 2000 per hectare in native vegetation close to the plantation and mature pines reaching heights of more than 20 m (Williams and Wardle 2005a). The average maximum temperature at the study site is 23.2°C in January and -0.8° C for July, which are the hottest and coldest months respectively. Average annual rainfall is 1071.9 mm. The majority of rain falls between January and March, and July and August are the driest months. Total rainfall at the site was below average for both years of the study but was considerably higher during the first year; 941.3 mm in 2004-2005 and 655.4 mm in 2005-2006.

Experimental design

Litter was collected within three distinct areas of the woodland; 1) Invaded and unburnt: Eucalypt woodland invaded by *P. radiata* to the south east of the plantation (between 50 m and 450 m from the plantation) 2) Uninvaded: Eucalypt woodland beyond the invasion front to the south east of the plantation (approximately 500 m from the plantation) 3) Invaded and burnt: Recently burnt eucalypt woodland invaded by *P. radiata* to the north of the plantation (up to 200 m from the plantation).

The vegetation to the south east of the plantation (Collection areas: ‘invaded and unburnt’ and ‘uninvaded’) is dominated by *Eucalyptus oreades* and *Eucalyptus sieberi* (Benson and Keith 1990). A previous survey of the site recorded an average eucalypt basal area of 39.3 m²/ha and a mean diameter of adult eucalypts of 33.5 cm across the collection area (Williams 2003). The diameter of adult eucalypts (greater than 10 m in height) ranged from 8.2 cm to 105.2 cm with a mean value of 33.5 cm (M.Williams, unpublished). Pine basal area averaged 8.0 m²/ha but reached 18.4 m²/ha in the most heavily invaded areas. Diameters of adult pines (greater than 10 m in height) ranged from 10.8 cm to 46.4 cm with a mean value of 25.9 cm (M.Williams, unpublished). Low intensity burning takes place in areas
surrounding the Newnes plantation every 7 to 8 years. The southeastern side of the plantation was subjected to a hazard reduction burn in 1991 and a wildfire in 1997. At the time of this study there was no evidence of reduced canopy due to fire and in order to distinguish this area from the more recently burnt vegetation it will be referred to as ‘unburnt’.

The vegetation to the north of the plantation (collection area ‘invaded and burnt’) is dominated by *E. sieberi* and *Eucalyptus piperita* (Benson and Keith 1990) and was subjected to wildfires in 1997 and December 2002. Fire scars were commonly observed at heights of 8 to 10 m on eucalypt and pine trunks and reductions in eucalypt canopy cover were estimated at up to 40% (Williams 2003). This area was previously planted with *P. radiata* until a wildfire destroyed the original trees in the 1970’s and the compartments were abandoned. Eucalypt regeneration in the area since then has been considerable. Wildling pines remain in the native vegetation and have presumably also regenerated from pine seeds released after the fire. Mean basal area for the collection area is 27.2 m$^2$/ha and 7.6 m$^2$/ha for eucalypts and *P. radiata* respectively (Williams 2003). Mean diameters for adult trees (greater than 10m in height) were 40cm for *P. radiata* and 28cm for eucalypts (M. Williams, unpublished). Despite differing site histories, pine and eucalypt densities and basal areas in the first available vegetation are similar to those in other invaded areas providing an opportunity to study the effects of fire on litterfall.

**Litter collection**

To determine the spatial and temporal distribution of litterfall, 114 litter traps were established within the eucalypt woodland. Traps measuring 1 m by 1 m were constructed from fine mesh (2 mm gaps) and were located in two transects in each of the three collection areas. Transects consisted of three 20 m by 20 m plots located 100 m apart running perpendicular to the plantation, with the first plot placed in the first available vegetation. To further investigate the relationship between litterfall and pine basal area and canopy cover, 4 extra plots were placed in the most heavily invaded areas with 2 either side of the first plot in each ‘invaded, unburnt’ transect, giving a total of 22 plots (10 in ‘invaded and unburnt’, 6 in uninvaded and 6 in ‘invaded and burnt’). Within the invaded areas, three traps were placed underneath pine canopy (approximately 1 m from the trunk of the three largest pine trees in the plot) and three traps were placed under eucalypt canopy (approximately 1 m from the trunk of the three largest eucalypt trees in the plot) in each plot giving a total of 60 traps in ‘invaded and unburnt’ areas and 34 traps in ‘invaded and burnt’ areas. In the ‘uninvaded’
areas, three traps were placed under eucalypt canopy in each plot (approximately 1 m from the trunk of the three largest eucalypt trees in each plot) giving a total of 18 traps.

Traps were established in September 2004 and litter was collected in February (5 months), June (3.5 months), September (3 months) and December (3 months) in 2005. In 2006 litter was collected in March (3 months), June (3 months) and September (3 months). Annual litterfall comprises all samples falling between October and the following September. All litter collected from traps was bagged and oven-dried at 60°C for 16 hours. Woody material, eucalypt bark, pine cones and strobili were discarded. Remaining eucalypt leaves and *P. radiata* needles were separated and weighed to the nearest 0.5g. Whilst the discarded components of litter may contribute to fuel loads and changes in light regime and ground layer structure, they would, due to their large mass, override subtle differences in mass between pine needles and eucalypt leaves. This difference was of most interest as the influence of eucalypt leaves and pine litter on native recruitment was the primary focus of studies in Chapter 7.

**Relationship with basal area/canopy cover**

In order to investigate the relationship between *P. radiata* canopy cover and pine needlefall, pine canopy cover was estimated using basal area values available for the six most heavily invaded plots to the south east of the plantation. The relationship between basal area and canopy cover is linear for open grown *P. radiata* trees (Leech 1984) and can be defined by the following equation which was used to calculate pine crown width for each of the plots;

\[
\text{Crown width} = 0.2073 \times \text{Dbh} + 0.7544
\]

(Leech 1984)

Dbh refers to diameter of the tree at breast height (1.4m). Canopy cover was determined by projecting crown widths onto previously mapped diagrams of the plots indicating the position and diameter of each tree. *Pinus radiata* basal area and canopy cover were correlated with mean annual litterfall within a plot using Pearson's correlation coefficient.

**Spatial distribution of pines and litterfall within a plot**

To determine the spatial distribution of pines within the six most heavily invaded plots the number of pines greater than 1 m tall in 16, 5 m by 5 m quadrats within the plot were tallied.
Quadrat counts of pines were then analysed using the index of dispersion (ID). The index estimates how a pattern departs from spatial randomness and is calculated as the ratio of mean to sample variance:

$$ID = \frac{\sum_{i=1}^{n} (\bar{x}_i - x)^2}{\bar{x}}$$

(Ludwig and Reynolds 1988)

A random arrangement of trees within the sixteen quadrats will have a frequency distribution similar to that of the Poisson distribution. Since the variance and mean are equal in Poisson distributions, a variance to mean ratio (ID) close to 1.0 is indicative of a random distribution (Dale 1999). Dispersion indices below 1.0 indicate a regular distribution while those greater than 1.0 suggest a clumped pattern. Dispersion indices were calculated for all plots with more than 10 pines greater than or equal to 1m tall present using the PASSAGE computer program (Rosenberg 2001). Results were compared to $\chi^2$ values to determine statistical significance at the $p = 0.025$ significance level.

To examine how the spatial distribution of pines within a plot influenced the spatial distribution of litterfall the ratio of total pine litter collected under eucalypt canopy / total pine litter collected under pine canopy (under euc:under pine) was calculated. In plots with clustered pines I expect to see high amounts of litter under the pine canopy and very little under eucalypt canopy and therefore a low under euc:under pine ratio. In plots with a uniform distribution of trees a more uniform distribution of litter and a high under euc:under pine ratio is expected.

**Statistical analysis**

To examine the influence of recent fire, collection time and litter type on litterfall rates, data from invaded areas was analysed using a 3 factor ANOVA. All three factors; burn status, time and litter type were fixed and the data were square root transformed to improve normality. Variances were found to be heterogeneous using Levene’s test, ANOVA was used to analyse the data as it is robust to heterogeneity when sample size is large ($n>6$; in this study $n >50$) (Underwood 1997). Comparisons between eucalypt litterfall within invaded and uninvaded areas, inter-annual differences and comparisons between pine and eucalypt litterfall were examined by summing total litterfall across the entire collection period and using paired t-tests assuming equal variances. Differences in litterfall between collection periods were tested separately for each litter type using a one factor ANOVA with collection time as a fixed factor. This approach was appropriate (rather than a repeated measures analysis) because all
litter was collected from the trap each collection period and thus each sample was independent with time.

**Results**

*Effect of fire on litterfall*

Mean annual pine needlefall reached 686.7 kg/ha/year in unburnt areas and was approximately 2.5 times greater than in burnt areas (Figure 6.1). This effect was less pronounced for eucalypts with the fire reducing litterfall by only 28% and by the final collection period litterfall in the burnt area exceeded litterfall in the unburnt area (Figure 6.1). There was a significant effect of burn status, collection time and litter type on litterfall ($P<0.001$) and significant interactions between all three factors. The 2002 wildfire resulted in a significant reduction of leaf shed for both species (Pine: $t = 9.37; \text{df} = 714; p < 0.001$; Eucalypt: $t = 4.17; \text{df} = 417; p < 0.001$).

*Eucalypt and Pine comparison*

Eucalypt litterfall was significantly greater than pine needlefall in both unburnt ($t = 10.29; \text{df} = 880; p < 0.001$) and burnt ($t = 14.8; \text{df} = 548; p < 0.001$) areas reaching a maximum of 1554.7 kg/ha/year in the unburnt woodland in 2005-06. Mean annual eucalypt litterfall within the invaded woodland did not differ significantly from that in the uninvaded areas ($t=1.75, \text{df} = 627; p = 0.08$) suggesting similar eucalypt basal area and canopy cover.
Pine and eucalypt litterfall

Figure 6.1 Mean annual litterfall (kg/ha) +SE for Pinus radiata and Eucalyptus within the three collection areas; ‘unburnt invaded’, ‘burnt, invaded’ and ‘uninvaded’. Annual litterfall values are the average of two years of litter collection.

Temporal variation in litterfall

A significant difference in litterfall between years was observed for both litter types in all collection areas (Table 6.1). Almost double the amount of P. radiata litter fell in the first year in the unburnt invaded woodland (Table 6.1).

Table 6.1 Pinus radiata and eucalypt litterfall by collection year for the three collection areas. p-values indicate level of significant difference between years.

<table>
<thead>
<tr>
<th>Burn status</th>
<th>Invasion status</th>
<th>Litter type</th>
<th>2004-2005 (kg/ha/yr)</th>
<th>2005-2006 (kg/ha/yr)</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burnt</td>
<td>Invaded</td>
<td>P. radiata</td>
<td>317.5</td>
<td>229.1</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Eucalyptus</td>
<td>879.7</td>
<td>1203.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Unburnt</td>
<td>Invaded</td>
<td>P. radiata</td>
<td>890.0</td>
<td>483.3</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Significant seasonal variation in litterfall was observed for both litter types 
(P. radiata: df = 6, F = 16.6, p < 0.0001; Eucalyptus: df = 6, F = 71.8, p < 0.0001).
P. radiata litterfall in the unburnt area peaked in the period from September 2004 to February
2005 with a mean value of 1179 kg/ha/year (Figure 6.2A). The same period in 2005 produced
the lowest amount of litter collected for the entire study with a mean of 226.7 kg/ha/year and
218.8 kg/ha/year for the December 2005 and March 2006 collections respectively.

Two major peaks in eucalypt litterfall occurred during the June 2005 collection period
and in March 2006 reaching a maximum of 3289.4 kg/ha/year (Figure 6.2A), a value which
represents more than half of the total litterfall for the year. Interestingly, the period of peak
eucalypt leaf-fall was also the period of lowest pine litterfall. The majority of eucalypt
litterfall occurred in the period from October to March; 59 % for burnt areas, 62 % in unburnt
areas and 64 % in uninvaded areas. In comparison, the proportion of pine litterfall during this
half of the year was much lower, 44 % in unburnt and only 31 % in burnt areas.

Seasonal patterns observed in the unburnt areas were generally mirrored in the burnt
areas (Figure 6.2B). Excluding the first collection period, pine litterfall in the burnt areas
showed a similar pattern to that observed in the unburnt areas with peaks in June and
September and very low levels of litterfall from September to March in 2005 (Figure 6.2B).
The reduction in litterfall due to recent fire was more distinct during the first collection period
with unburnt areas receiving almost six times more litter than burnt areas (Figure 6.2B).
Eucalypt litterfall in the burnt areas matched litterfall in the unburnt woodland with peaks in
June 2005 and March 2006 (Figure 6.2B.)
Figure 6.2 Mean eucalypt and *P. radiata* litterfall (kg/ha/year) + SE for A) ‘invaded and unburnt’ eucalypt woodland and B) ‘invaded and burnt’ eucalypt woodland at Newnes State Forest. Values are an average of litter collected in 1m$^2$ traps expressed in kg per hectare per year.

**Influence of the canopy**

Crown widths for pines, which were modeled from basal area, within the six plots with the highest pine basal area in the unburnt woodland, ranged from 1.1 m to 9.4m. Canopy cover ranged from 11 % to 29.5 % and in total covered 18 % of the combined plot area. This relationship is highly driven by the most heavily invaded plot which had a basal area of 18.4 m$^2$/ha and a canopy cover of 29.5 %.

The relationship between canopy cover and pine needlefall in the most heavily invaded plots was not significant (r = 0.713; p =0.111), however there was a significant positive relationship between basal area and pine litterfall (r = 0.861; p = 0.028) (Figure 6.3). The most heavily invaded plot experienced the highest level of litterfall
(maximum of 1500 kg/ha/year average across 6 traps within the plot and 1870 kg/ha/year for 3 traps under pine canopy in 2004-2005).

Figure 6.3. Relationship between *Pinus radiata* basal area and mean annual litterfall for the six most heavily invaded plots at Newnes State Forest ($r = 0.861$; $p = 0.028$).

Of the total amount of *P. radiata* litter collected in the invaded areas 71.9% fell under the canopy of wildling pines, with the remainder collected under eucalypt canopy. In the six most heavily invaded plots pine needlefall averaged 1052.5 kg/ha under pine canopy and only 530.4 kg/ha under eucalypt canopy. In contrast eucalypt litterfall was approximately equal under pine (47.7%) and eucalypt (52.3%) canopies.

*Spatial distribution of pines and litterfall within the six most heavily invaded plots*

The three plots with clumped distributions of pines all had litterfall ratios below 0.6 and the highest annual litterfall values underneath pine canopy (Table 6.2). Plot 2 had the only significant dispersion index indicating a highly clustered distribution and also had the highest level of litterfall below the pine canopy. The regular distribution of trees in Plot 5 produced
the lowest annual litterfall below the pine canopy and a litterfall ratio of 0.93 indicating an almost uniform distribution of pine needle fall within the plot. However, plot 4 also had a regular distribution of trees and had a much lower litterfall ratio of 0.46 indicating that the majority of pine litter is clustered under the pine canopy.

### Table 6.2. Dispersion indices (ID), mean annual litterfall (kg/ha) under pine canopy and under euc:under pine litterfall ratios for five heavily invaded plots*. IDs greater than 1 indicate clumping. The litterfall ratio represents the total amount of pine litter collected under eucalypt canopy within a plot divided by the total amount of pine litter collected under pine canopy. * One plot had less than 10 pines greater than or equal to 1m and was not analysed.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Mean annual pine litterfall under pine canopy (kg/ha/year)</th>
<th>ID**</th>
<th>p-value</th>
<th>Pine litterfall ratio (under euc:under pine)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3830</td>
<td>1.66</td>
<td>0.38</td>
<td>0.33</td>
</tr>
<tr>
<td>2</td>
<td>4385</td>
<td>2.27</td>
<td>0.00</td>
<td>0.59</td>
</tr>
<tr>
<td>3</td>
<td>2310</td>
<td>1.11</td>
<td>0.32</td>
<td>0.30</td>
</tr>
<tr>
<td>4</td>
<td>2110</td>
<td>0.89</td>
<td>0.61</td>
<td>0.46</td>
</tr>
<tr>
<td>5</td>
<td>1823</td>
<td>0.5</td>
<td>0.74</td>
<td>0.93</td>
</tr>
</tbody>
</table>

** Data used to calculate Dispersion indices were collected in 2003 during my honours project.

### Discussion

**Pinus radiata litterfall**

The maximum annual pine litterfall from wildlings (890 kg/ha/year in invaded and unburnt areas) represents a rate less than half that typically observed within *P. radiata* plantations in Australia (Raison *et al.* 1986: 1500-5000 kg/ha). Needle loss (death of green needles) which relates strongly to needlefall, has been shown to be positively correlated with stand basal area in *P. radiata* plantations (Raison *et al.* 1992). The average basal area of pine in invaded plots in unburnt areas was less than one third of a typical plantation stand (8.0 m²/ha) and accounts for the lower rate of litterfall. However, average litterfall for the most heavily invaded plot, with a pine basal area of 18.4 m²/ha, produced a maximum annual litterfall rate of 1500kg/ha/year which is comparable with litterfall rates for a plantation with almost double the pine basal area (Crockford, 1998: 1800kg/ha/year litterfall and 35.1m²/ha). This result indicates
that in the latter stages of invasion, wildling populations are capable of producing considerable quantities of litter and implies that the wildlings themselves are generating more litter than plantation trees. Most plantation growers aim to produce pines with a mean diameter of 50cm at a final stocking rate of 200 to 350 stems per hectare (Maclaren and Knowles 1995). However, pine diameters within most plantation compartments, stocked at rates of up to 900 stems per hectare (Lewis and Ferguson 1993) will be much less than 50cm. Eucalypt diameters within our study area are much greater, ranging from 8.2cm to 105.2cm. Total basal area between pine-invaded eucalypt forest and plantation stands may be similar, however, the presence of larger eucalypt trees indicates a wider spacing of trees in the eucalypt forest. Greater spacing between adult trees will lead to greater access to light for wildling pines which may be responsible for higher foliage production (Ledgard 2004) and higher amounts of litterfall. The difference in litterfall between plantation trees and wildlings may also be attributed to a lack of thinning processes which reduces litterfall in plantations (Harrington and Edwards 1999).

Comparison with Eucalyptus litterfall

The higher rate of eucalypt leaf-fall in comparison to pine needlefall can be explained by differences in stem density and basal area between pine and eucalypt. Mean pine basal area in the invaded, unburnt areas was less than one quarter of eucalypt basal area (8.0 m²/ha and 39.3 m²/ha respectively). However, Crockford and Richardson (1998) also observed considerably more litterfall in a eucalypt woodland compared to an adjacent P. radiata plantation with similar basal area and stem density suggesting differences in the amount of litterfall per tree between pine and eucalypt. The authors attributed this difference to the larger specific leaf area of pines which allows them to produce the same amount of photosynthetic activity with a smaller mass of needles; and the fact that pines retain senescent foliage resulting in increased leaching and reduction in mass prior to needle drop.

Relative differences in decomposition rates between pines and eucalypts will be more important than disparities in litterfall volume for determining litter impacts. Decomposition rates will influence the accumulation rate of litter on the forest floor (Florence and Lamb 1973) and will provide an indication of how long it takes the litter layer in infested areas to reach plantation levels. Pine needles decompose more slowly than sclerophyllous leaves (Madeira and Ribeiro 1995, Paul and Polglase 2004) with the slower rate attributed to a high initial lignin:nitrogen ratio (Madeira and Ribeiro 1995). Furthermore, decomposition rates of
sclerophyllous leaves are reduced in plantation litter (Springett 1976). Slower decomposition will lead to faster accumulation rates of litter which may provide a more effective barrier to the recruitment of native species.

**Role of fire**

Significant reductions in both pine and eucalypt litterfall for up to four years following fire were observed. This pattern was more pronounced for pine litter reflecting the greater flammability of pine foliage. A quicker return of litterfall for eucalypts may be explained by differences in foliage distribution within the trees. Pine trees are more conical in shape than eucalypts. Lower lateral branches of pines hold a large proportion of needles which are more exposed to fire. The removal of litter following burning can promote the germination of some species (Christensen *et al.* 1981). Conversely, litter can improve water conditions (Fowler 1986, Facelli and Pickett 1991a) and scorched pine needles in the post-fire environment can facilitate germination and establishment by reducing soil temperature variation and increasing soil moisture (Bonnet *et al.* 2005). The consequences of a delayed return of pine needles following fire will be a trade-off between the positive influences of litter in a recently burnt environment and the negative effects of a dense litter mat which may prevent recruitment.

**Seasonal trends in litterfall rates**

Seasonal trends are commonly observed in litterfall, typically with maximum rates observed during summer and minimum shed in winter. This generally results from high temperatures and lack of water during the warmer months (Ananthakrishnan 1996) and will be more pronounced in areas with strong seasonal differences in rainfall (Cromer *et al.* 1984, Turner and Lambert 2002). Strong seasonal trends in litterfall have also been recorded within *P. radiata* plantations (Versfeld 1981). Water stress is a good indicator of the timing of needle loss rather than of total litterfall (Raison *et al.* 1992). Peak pine needlefall in the summer and autumn months (September to June) was observed during the first year. Rainfall and daily maximum temperatures at the site also peaked during this period. High rates of pine litterfall during periods of high rainfall suggest that high temperatures are responsible for water stress induced needle drop. The low amount of needlefall observed during the second summer, a year when rainfall was at approximately 60% of the long term average, is inconsistent with observations of peak needlefall in drier years (Crockford and Richardson 1998).
Moisture stress also results in increased defoliation in eucalypts (Pook 1985, Burrows and Burrows 1992) and explains the peak in leaf shed during summer in the second, drier year. High litterfall during summer is consistent with patterns observed in eucalypt woodlands elsewhere in Australia (Burrows and Burrows 1992, Hart 1995). Interestingly, the maximum peak in eucalypt leaf-fall corresponded with a period of minimum pine needlefall. This observation may reflect a difference in resource acquisition capability between the two genera. Mature pines intercept more incident light (Chilvers and Burdon 1983) and more rainfall (Smith 1974, Crockford and Richardson 1990) than eucalypts.

Spatial distribution and the role of the canopy

Currently, the majority of pine litter in invaded areas is being distributed directly below the pine canopy with very little intrusion of litter into canopy gaps. In the most heavily invaded areas pine basal area reached an average of 11.3 m²/ha and combined pine canopy cover was 18% suggesting that at this stage of invasion approximately one fifth of invaded land will be subject to heavy pine litterfall. In self-sown stands, adult trees can be heavily clustered (Williams and Wardle 2007) resulting in overlapping pine canopies and an expected strong association between litterfall and canopy cover. Surprisingly, basal area was a stronger predictor than canopy cover of litterfall suggesting that it may be used as an indicator of the area of land subjected to pine litter impacts. This result also suggests that tree size is an important determinant of litterfall. Basal area may be a better predictor of litterfall because it has a closer relationship with canopy volume, than with canopy area.

The area of land at risk of litter impacts following invasion will also depend on the spatial distribution of the trees within the native vegetation. Dense wildling stands (>1000 ha) are presently limited to within 100 m from the plantation (Williams and Wardle 2005a) and to less than 10% of the plantation border length (M. Williams, pers. obs.). Within these areas the smaller scale clusters of pines means that less than 2% of land is subjected to heavy pine litter fall. Areas with a more regular distribution of trees had a lower amount of litter falling underneath pine canopy and in the case of one plot this litter was distributed evenly underneath both pine and eucalypt canopy. An uneven arrangement of pine litter in one plot with a regular distribution of trees suggests that factors other than spatial position are important determinants of litterfall distribution.

Implications for invasion impacts
Wildling pines are producing substantial amounts of litter, suggesting that in the absence of control, litter may accumulate to levels observed in plantations. One of the potential impacts of increased litter is increased fire risk. Pine needles are highly flammable and *P. radiata* are able to support crown fires (Fonda 2001). Dense accumulation of pine litter in plantations can increase the fire hazard (Dodge 1972, Cseresnyes *et al.* 2006). Within invaded areas the addition of pockets of highly flammable pines, and pine litter, will increase fire temperatures and pose a threat to the plantation resource. Intense fire temperatures may also destroy usually fire-tolerant eucalypts (Burdon and Chilvers 1994). Widespread wildfires that devastated 70% of the Australian Capital Territory in 2003 were the most severe within pine plantations with high severity fires also occurring in areas adjacent to the plantations (Carey *et al.* 2003). Initial observations of vegetation recovery indicate total destruction of *Eucalyptus albens* and no recovery of fire sensitive species including Alpine Ash and Black Cypress (Carey *et al.* 2003).

While the potential for adverse impacts of *P. radiata* litter on seed germination (Lill *et al.* 1979), understorey diversity (Richardson and Van Wilgen 1986), soil properties (Scholes and Nowicki 1998) and microfauna (Springett 1976) are recognized, the implications of litter addition in the context of pine invasion into eucalypt woodland are not well known. Investigation of litter impacts within this system requires a closer examination of differences between pine and eucalypt litter which will inform relative impacts on native germination and establishment. Morphological differences between pine needles and eucalypt leaves may influence light and water availability at the soil surface differentially. However, evidence which suggests that pine and eucalypt litter reduce radiation equally and observations of a positive influence of pine litter on eucalyptus establishment (Facelli and Kerrigan 1996) implies that litter accumulation in itself can not be responsible for reduced eucalypt recruitment in invaded areas.

The impact of pine invasion on the litter levels within invaded areas will ultimately depend on whether or not pines are replacing eucalypts within the woodland or simply growing amongst them. The only long term study which has investigated pine demography in eucalypt woodlands was not able to determine whether the pines were in fact taking the place of the eucalypts, although the authors did report that the pines were outgrowing their native counterparts (Burdon and Chilvers 1994). Such demographic changes are unlikely to be observed on practical timescales for study. However, they will determine total litter load. A replacement of eucalypts by pines would result in an overall reduction in litter levels as pines are producing less litter than eucalypts.
Changes to litter load may not necessarily be the primary driver of changes to native recruitment processes. The physical structure of the litter mat is vitally important in determining micro-climatic conditions for recruitment. Physical differences in the litter mat will influence biotic conditions at the soil surface and may have subsequent impacts on litter and soil fauna. Aeration, solar radiation and the amount and quality of soil organic matter are important determinants of soil microbial communities (Panikov 1999). Eucalypt leaves have high leaf area surface areas relative to pine needles and leaf-fall on to forest floors that typically have eucalypt limbs present results in a litter mat with large air spaces. In comparison, thin pine needles form a matrix of litter resulting in a ‘carpet’ effect with very little aeration. Pine invaded eucalypt woodlands are poorly studied and impacts associated with a mixed pine-eucalypt litter layer can not be extrapolated from studies on plantation effects. We currently know little about the structure of eucalypt litter, let alone how it interacts with an addition of pine needles or the subsequent influence on native recruitment. Further investigation of the combined effect of eucalypt and pine litter on litter fauna is required to assess the total impact of pine invasion.

Detecting and characterising invasion impacts remain a major challenge for invasion biologists (Parker et al. 1999). The first step towards detecting impacts is to determine the physical and biotic changes that accompany invasion. The high rate of litterfall recorded in this wildling population indicates that there is potential for considerable physical changes to the forest floor following pine invasion. Currently the biotic changes that follow these physical changes are poorly understood. It is possible that potential effects on native understorey species may only occur in the field when an increased litter layer is combined with reduced light levels caused by canopy closure. Reductions in understorey species following pine invasion in South Africa have been attributed to light extinction through the canopy (Macdonald and Richardson 1986). Wildling stands can reduce light levels in eucalypt woodlands by up to 60% (M. Williams, unpublished). Determining the effect of increased litter load, relative to other factors such as shading from increased canopy cover, is required to directly quantify the impacts of pine invasion on native species recruitment.
7. Impact of shade and litter on pine and native recruitment

Introduction

Despite the recognised urgency to predict and control the impacts of invasive species (Byers et al. 2002, Simberloff 2006), the precise mechanisms underlying these impacts have received very little attention (Parker et al. 1999, Levine et al. 2003). Negative interactions between native and exotic species are typical (Simberloff 2000) although positive interactions have also been observed (Richardson et al. 2000b, Tecco et al. 2006). Furthermore, the influence of one species on another may vary temporally with initially negative effects and a positive influence later in the life cycle (Callaway and Walker 1997). Facilitation plays an integral role in structuring native communities (Hunter and Aarssen 1988, Callaway 1995) and may also be having a large influence on the magnitude and nature of the impact of non-native species within these communities. The impacts of an invader can be accelerated if the species provides conditions which facilitate its own establishment. This can occur via several avenues including changes to the disturbance regime (D’Antonio and Vitousek 1992, Mack and D’Antonio 1998), plant-soil feedbacks (Klironomos 2002) and changes to light availability (Reinhart et al. 2005). Conversely, invading species can facilitate the growth of native species via direct and indirect interactions. Habitat modification via the creation of novel habitats or changes to abiotic conditions is the most common mechanism for facilitation (Rodriguez 2006). Given the potential for both positive and negative effects of exotics on the native community, and the importance of the role of self-facilitation, it is critical that an assessment of impact involves an examination of the effects of invasion on both the native community and the invader.

The addition of leaf litter is often recognised as a possible mechanism of impact of invasive species (MacDonald et al. 1989, Wearne and Morgan 2004). By changing the physical, chemical and biotic characteristics of the environment where seeds germinate, leaf litter can play an integral role in plant community dynamics (reviewed by Facelli and Pickett 1991a). The production of phytotoxins during leaching or decomposition of litter can negatively influence plant development (See review of allelopathy by Rice 1979). The accumulation of litter on the forest floor may also provide a physical barrier to seedlings (Persson et al. 1987, Ellenberg 1988). However,
litter can also have a positive effect on seedlings by increasing the resistance to water vapour diffusion from the soil surface and indirectly by reducing the soil temperature (Cheplick and Quinn 1987, Facelli and Pickett 1991a). For example, Facelli and Ladd (1996) found a positive influence of eucalypt litter on the establishment of eucalypt seedlings. A meta-analysis of litter effects by Xiong and Nilsson (1999) established that the influence of litter varies with litter quantity and type, ecosystem and target species.

In cases where the invader is the dominant canopy species, increased abundance can result in dramatic increases in canopy cover which can have both positive (Tecco et al. 2006) and negative (Holmes and Cowling 1997) impacts on native species. Woody species that form dense stands have been shown to reduce tree species diversity by hindering the recruitment of natives (Woods 1993, Hutchinson and Vankat 1997, Frappier et al. 2003). Of greater interest is the increase in shade relative to the native canopy that is already present. A number of exotics are known to alter light availability relative to their native counterparts including Pinus nigra (Leege and Murphy 2001) and Acer platinoides (Reinhart et al. 2006). The overall impact of increases in canopy cover will also depend on the interactions with other changes that accompany invasion.

In assessing the effects of the invasive tree, Myrica faya on its native counterpart Metrosideros polymorpha, Walker and Vitousek (1991) found that while increased shade by Myrica enhanced germination and seedling survival of the native, leaf litter from the tree physically inhibited germination. In this instance the net effect on the native tree was negative. Understanding the interactions between invasion mechanisms is necessary to quantify the overall impact of the invader and remains a challenge for invasion biology.

The relative importance of leaf litter and canopy cover may also change with time, making an understanding of their roles difficult. Litter has a large influence on micro-habitat conditions (Facelli and Pickett 1991a) which are critical for germination. Plant litter has been shown to have a stronger overall effect on plant germination than on establishment (Xiong and Nilsson 1999). Factors such as canopy cover and subsequent reductions in light availability may be more important determinants of survival in the latter stages of plant development.

A variety of species from the Pinus genus have spread from large timber plantations as well as smaller hedge plantings into areas of native vegetation across the southern hemisphere (Richardson and Higgins 1998). Impacts associated with Pinus invasions include changes to catchment hydrology (Versfeld and Van Wilgen 1986),
reductions in land use values (Ledgard 2001) and reductions in native plant species (Richardson and Van Wilgen 1986, Richardson et al. 1989). Two primary mechanisms of impact on native plant species are believed to be the reduction of light following canopy closure and suppression by litterfall (Richardson and Van Wilgen 1986, Richardson et al. 1989). Dense stands of Pinus rigida have reduced light availability by 94 % and excluded herbaceous species on the sandy shores of ponds in Masachussets (Craine and Orians 2004). Experimental manipulations of artificial shade and pine litter at the same site found that litter had the greater effect on herbaceous plants. Invasion of P. lutchuensis on the Bonin Islands in the Pacific Ocean has resulted in a reduction in the abundance of understorey individuals (Shimizu and Tabata 1985). The addition of a thick layer of pine needles and twigs was thought to be responsible for the changes observed. Comparisons of native stands composed of Pinus banksiana and Populus deltoids with non-native stands of Pinus nigra on the dunes of Lake Michigan have shown a reduction in understorey cover below the exotic pine in three of the four dune habitats studied (Leege and Murphy 2001). Reductions in cover were attributed to a reduction in light availability.

In New Zealand and South Africa, two countries where pines are considered major threats to biodiversity (Richardson 1998, Ledgard 2004), invasions typically occur on low lying shrubland (Richardson et al. 1997) or unimproved rangelands (Hunter and Douglas 1984). In Australia, where pines are predominantly invading eucalypt woodland, the impacts of adding a novel tree to an already forested system may be reduced. High pine litterfall rates (chapter 6), increased deep shade and reduced eucalypt recruitment (Burdon and Chilvers 1994) have been observed in forests invaded by Pinus radiata in Australia. The lack of native understorey in plantations themselves suggests that monocultures of pines are unsuitable habitat for native species recruitment. At the same time as changes to plant community composition in areas adjacent to pine plantations have been attributed to the addition of pine litter (Baker et al. 2006), experimental observations of positive effects of P. radiata litter on seedling establishment suggest that litter accumulation in itself can not be responsible for reduced eucalypt recruitment in invaded areas (Facelli and Kerrigan 1996).

When assessing the magnitude of impact by pines we must consider the current role of the dominant native species, i.e. eucalypts, on native recruitment. The influence of leaf litter will depend on the magnitude of chemical and morphological differences between pine and eucalypt litter. Differential effects of different litter types may be
attributable to abiotic influences such as light penetration (Facelli and Pickett 1991b). Conifers display different shading properties to broadleaved species which may account for their different effects on ground vegetation (Ellenberg 1988). Furthermore, the amount of impedance exerted by a litter mat will depend on the shape and size of the litter and compactness of the mat (Facelli and Pickett 1991a). If pines are influencing the native community in opposing directions to that of the eucalypts, then the overall impact will be a change in response of the native community. If, however, pines are influencing native recruitment in the same way as the eucalypts then the impact of pines will be reduced and the result will be an enforcement of existing recruitment patterns. Similarly, the interaction between the influence of eucalypts and the invading pine will have consequences for the establishment success of the pines themselves. If both species are having a positive influence on pine recruitment, the net result will be a facilitation of the invasion process. These processes are summarised in Table 7.1.

Table 7.1 Hypothesised interactions between the influence of pine and eucalypt litter on native recruitment and invasion success. The first column considers the influence of pine and eucalypt litter on native recruitment. If pine and eucalypt litter influence the native species equally then the existing effect of litter is reinforced. The second column examines the potential for pine and eucalypt litter to facilitate pine establishment and the invasion process. The worst case scenario is when both litter types favour pine success. + indicates an overall positive effect. – indicates a negative influence.

<table>
<thead>
<tr>
<th>Litter type</th>
<th>Expected effects on native plant establishment</th>
<th>Expected effects on pine establishment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eucalypt</td>
<td>+ – + –</td>
<td>– + – +</td>
</tr>
<tr>
<td>Pine</td>
<td>– + + –</td>
<td>– – + +</td>
</tr>
<tr>
<td>Response of added pine litter</td>
<td>Oppose existing pattern</td>
<td>Reinforce existing pattern</td>
</tr>
</tbody>
</table>

Increasing invasion success →→→→

This study examines the influence of pine and eucalypt canopy cover and litter on germination of *P. radiata* and native species. Both chemical and physical components of litter were examined. *Pinus radiata* litter is known to produce ethylene (Lill and McWha 1976) which can inhibit seed germination in some species (Lill *et al.* 1979). *Eucalyptus* species are also known to produce leachates which can prevent
germination (Padhy et al. 2000). The physical barrier provided by both litter types may also provide a barrier to seedling establishment and reduce light availability (Facelli and Pickett 1991a). A series of glasshouse experiments were conducted in order to identify the relative impact of these two aspects of litter. The results of a field experiment examining the combined effect of litter and canopy cover on native and pine germination are also reported. Simultaneously examining two potential mechanisms of invasion impact in a field context allows the net effect of the invader on the native species to be determined.

A further aim of this research is to examine the germination success of *P. radiata* in different environments. A study of *P. nigra* invasion found significantly higher densities of woody stems in invaded areas suggesting that the species may be accelerating succession to a woody community (Leege and Murphy 2001). Seedling recruitment represents a major filter to the success of invasive plants (Mazia et al. 2001). If pines recruit better under their own litter layer, or canopy, then they may be facilitating the invasion process. *Pinus radiata* is considered a shade intolerant species (Keeley and Zedler 1998) and observations of invasion events suggest that pines are unable to establish in closed canopy areas (Shimizu and Tabata 1985, Bustamante and Simonetti 2005). Examining the germination response of pine seedlings under pine and eucalypt canopy will help determine optimum establishment conditions for the species and assess invasion potential in this environment.

**Methods**

Seeds used in all of the following experiments were obtained commercially from the following suppliers: *Acacia* terminalis - AustraHort Seed Merchants in Cleveland, Queensland, *Eucalyptus* sieberi - Harvest Seeds and Native Plants in Terrey Hills, New South Wales, *Leptospermum polygalifolium* - Seedworld Australia, Nowra, New South Wales, *Pinus radiata* – Royston Petrie Seeds Pty Ltd. Mudgee, New South Wales.

**Chemical effect of litter: leachate experiment**

In order to examine the effect of pine and eucalypt leachate on germination three watering treatments were applied to seeds of four species. The treatments were: 1) *Pinus radiata* leachate 2) *Eucalyptus* leachate and 3) deionised water as a control. *Pinus radiata* needles were collected from the floor of a 26 year old compartment of a
plantation at Newnes State Forest (see field study below for location). Eucalypt leaves were collected from the native woodland adjacent to the plantation. Dominant eucalypt species in the area are *E. oreades* and *E. sieberi*. Leachates were prepared by soaking 200 g of litter in 5 litres of deionised water for 84 hours. The leachate was filtered and stored in a sealed container until used. Seeds of three locally abundant species; *Acacia terminalis*, *Eucalyptus sieberi* and *Leptospermum polygalifolium* as well as *P. radiata* were placed in petri dishes lined with two layers of No. 1 Whatman filter paper (20 seeds of pine or acacia in each dish and 30 seeds of *E. sieberi* or *L. polygalifolium*). Ten replicate dishes for each species and treatment level were established giving a total of 120 dishes. *Acacia* seeds were exposed to boiling water for 30 seconds to break physical dormancy (Clemens et al. 1977). Five mLs of leachate or water treatment were applied to each dish as needed and germination within each dish was monitored for a total of 5 weeks. Germination was deemed to have occurred when the hypocotyl appeared.

Data were analysed in SPSS 15.0 (2006) with a one factor ANOVA as I was interested in examining the leachate effect independently for each species. Data were square root arcsin transformed prior to analysis in order to achieve normality. Data for all species were found to have homogenous variances using Levene’s test.

**Physical effect of litter: glasshouse experiment**

To investigate the physical effect of litter on *Pinus radiata*, *Eucalyptus sieberi* and *Acacia terminalis*, layers of pine and eucalypt litter, simulating the field situation, were applied to seed planted in trays (33.5 x 28 cm) filled with potting mix (peat:sand = 2:3). In each tray, twenty seeds of each species were planted in rows of 10 with row position randomly allocated. Seven litter treatments were randomly applied to the trays after planting; Control of no litter (C), 30g *P. radiata* litter (LowP), 60g *P. radiata* litter (HiP), 30g *Eucalyptus* spp. litter (LowE), 60g *Eucalyptus* spp. litter (HiE), 15g *P. radiata* litter and 15g *Eucalyptus* spp. litter (LowE+P), 30g *P. radiata* litter and 30g *Eucalyptus* spp. litter (HiE+P). The high litter treatments of 60g equates to 6000kg/ha which is the approximate accumulation rate of litter in *Pinus radiata* plantations (Versfeld 1981). Low litter treatments of 30g equate to 3000kg/ha which represents approximately 3 years of litterfall in a Eucalypt woodland invaded by *Pinus radiata* (chapter 6: 1 years data – 885kg/ha pine and 1254kg/ha euc litter over 1 year). The high
and low litter treatments consisted of a litter layer approximately 6 cm and 3 cm deep respectively which is representative of thicknesses observed in the field. Each treatment was replicated four times giving a total of 28 trays. Trays were placed in an unheated glasshouse at the University of Sydney, NSW on 14 April 2006 and regularly watered and rotated. Emergence and survival of seedlings were monitored for 90 days.

To examine the effects of litter treatments, species maximum emergence data were analysed in SPSS 15.0 (2006) with a two factor ANOVA with species and litter treatment as two fixed factors. Data were square-root arcsin transformed (proportion of emerged seeds) to improve normality.

**Field experiment**

*Study sites*

The field study took place at Jenolan and Newnes State Forest; two areas of eucalypt woodland bordering large *Pinus radiata* plantations and known to be invaded by pines (Williams and Wardle 2005a, Baker et al. 2006). Jenolan State Forest is located approximately 28km south of Lithgow (150°2'E, 33°44'S; altitude = 1200m). Newnes State Forest is located approximately 7.5 km north east of Lithgow in western NSW (150°12'E, 33°24’S; altitude 1000–1170 m). The plantation compartments were 11 years old at Jenolan and 26 years old at Newnes at the time of the experiment. Dominant eucalypt species at the sites are *E. radiata* and *E. dalrympleana* at Jenolan and *E. oreades* and *E. sieberi* at Newnes. The two sites experience a similar climate although Jenolan received approximately 20 % more rain during the experimental period (Table 7.2).

*Experimental design*

To determine the effect of canopy cover on native and pine recruitment the germination success of three species was investigated, *Acacia terminalis*, *Eucalyptus sieberi* and *Pinus radiata*. At both sites, germination plots were established under three canopy treatments; 1) pine plantation 2) pine canopy within eucalypt woodland invaded by *P. radiata* immediately adjacent to the plantation 3) open eucalypt woodland. Four plots were established within each vegetation type and were located approximately 50m apart. The distance between plots in adjacent vegetation types was also approximately 50m. Plots consisted of 20 aluminium trays (18 x 11 cm) placed in triangle formation.
and filled with potting mix. Each tray was planted with 10 seeds of each species and placed flush with the ground. Sides of trays were left up to prevent loss of seed. *Acacia* seeds were subjected to heat shock treatment (30 seconds in boiling water) (Clemens *et al.* 1977) and *P. radiata* seeds were stratified in cold water for 48 hours prior to planting. Seeds were planted in three rows of ten with row position randomly allocated. To determine the effect of pine litter on germination, 12g of *P. radiata* litter was applied to half of the trays within each plot. Litter treatments were randomly allocated to the trays. Twelve grams of litter represents 6000 kg per hectare, and is equivalent to the high litter treatment used in the glasshouse experiment. Trays with litter were randomly interspersed throughout the plot. All planting was complete by 1st November 2005 and seedling emergence was monitored every two weeks for six weeks (i.e. planting began in the last month of spring and the experiment was completed at the end of the first month of summer).

In order to examine the influence of season on recruitment success, the entire experiment was repeated in the following autumn/winter. A further three litter treatments were included to compare the effects of pine litter to those of eucalypt litter. The four treatments were 1) 12g *P. radiata* litter 2) 12g *Eucalyptus* litter 3) 12g mix of *P. radiata* and *Eucalyptus* litter 4) Control of no litter. All litter was collected on site. At every plot each litter treatment was replicated six times with the exception of the control treatment which was replicated four times, increasing the total number of trays within a plot to 22. Litter treatments were randomly interspersed throughout the plot. Trays were monitored for germination at 2, 4, 6, 8, 10 and 14 weeks after planting. All field work took place between April and July 2006 (i.e. planting occurred in the second month of spring and the experiment was completed in the second month of winter). Mean monthly rainfall and maximum daily temperatures for the sites during both trials are provided in Table 7.2.

To calculate canopy cover four digital photographs of the sky were taken at each plot. The photographs were analysed using Gap Light Analyzer 2.0 (GLA) and a mean value for each plot was calculated.

<table>
<thead>
<tr>
<th>Table 7.2 Mean monthly rainfall and mean maximum daily temperature for Jenolan and Newnes during the two trials.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec-Nov 2005</td>
</tr>
</tbody>
</table>

PATTERN PROCESS MECHANISM
Impact of shade and litter on recruitment

<table>
<thead>
<tr>
<th></th>
<th>Jenolan</th>
<th>Newnes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean monthly rainfall</td>
<td>100mm</td>
<td>81.8mm</td>
</tr>
<tr>
<td>Mean maximum daily temperature</td>
<td>20.7°C</td>
<td>22.8°C</td>
</tr>
<tr>
<td></td>
<td>26mm</td>
<td>19.8mm</td>
</tr>
<tr>
<td></td>
<td>12.6°C</td>
<td>15.2°C</td>
</tr>
</tbody>
</table>

Data analysis

Data were square root arcsin transformed to meet normality assumptions. Data were analysed using a 3 factor ANOVA with plot as a random factor and canopy (plantation, invaded or open), and litter treatment (Spring/Summer trial: pine litter, no litter. Autumn/Winter: pine litter, eucalypt litter, mixed litter, no litter) as two fixed factors. Variance was commonly found to be heterogenous using Levene’s test, however ANOVA remains robust to violations of this assumption when sample size is large. In this experiment the lowest sample size within a factor was 20. Data were analysed separately for each species at each site. Student-Neuman-Keuls tests were used for posthoc pairwise comparisons if the ANOVA yielded significant differences. When a significant interaction was found between canopy and litter treatments, one factor ANOVAs were performed to examine the effect of canopy cover for each litter treatment separately. Pine data for Jenolan during the autumn/winter trial were omitted from analysis as average germination across all treatments was less than 1%.

Results

Chemical effect of litter

_Eucalyptus sieberi_ had the highest overall germination with an average of 69.9 % and _L. polygalifolium_ had the poorest germination success averaging only 13.8 % across all three treatments (Figure 7.1). _Acacia terminalis_ and _P. radiata_ also has high germination success, 48.5 % and 54.3 % respectively. There was no significant effect (p > 0.05) of either pine or eucalypt leachate on germination for any of the four species. No delay in germination was observed for any species.
Figure 7.1 Mean germination percentage (+SE) of Acacia terminalis, Eucalyptus sieberi, Leptospermum polygalifolium and Pinus radiata seeds treated with pine and eucalypt leachate and water control.

Physical effect of litter

Glasshouse Experiment

There was no significant interaction between species and litter treatment ($F_{12} = 0.891$, $p = 0.561$). Across all treatments Pinus radiata and E. sieberi (53.9 % and 56.4 %) achieved significantly greater maximum percentage emergence than A. terminalis (33.0 %) ($F_{3,6} = 20.8$, $p < 0.001$). Pine performance varied very little across treatments with the lowest proportion emerging in the HiP treatment (mean of 50 %) and the highest proportion emerging in the LowE+P treatments (mean of 57.5 %) (Figure 7.2). Acacia terminalis showed the greatest response to litter treatment with the lowest proportion of seeds emerging in trays without litter (22.5 %). Eucalyptus sieberi had the highest amount of seeds emerge in the control treatment (70 %). However, there was no significant effect of litter on maximum percentage emergence ($F_{3,6} = 1.9$, $p = 0.098$).
Figure 7.2 Mean maximum seedling emergence for *Acacia terminalis*, *Eucalyptus sieberi* and *Pinus radiata* for the seven litter treatments: C – control of no litter, LowE – low eucalypt, HiE – high eucalypt, LowP – low pine, LowE+P – low eucalypt plus pine, HiP – High Pine, HiE+P – high eucalypt plus pine. Treatment order reflects an increasing level of pine invasion from left to right. High and low litter treatments had the equivalent of 6000 kg/ha and 3000 kg/ha applied respectively.

Seedling emergence was delayed in the control treatments. No seedlings of any species emerging before day 14 (Figure 7.3). *Pinus radiata* and *E. sieberi* showed similar responses to the litter treatment with seedlings in the control treatment performing best followed by those in the LP treatment. The majority of seedlings of both species were negatively affected by the two eucalypt treatments and the high pine treatment seedlings, dying by the end of the experiment (Figure 7.3). This effect was more pronounced for *E. sieberi*. The majority of seedlings in the HiE treatment died by day 50. Seedlings of all species performed best in the LowP treatment in comparison to
the other litter treatments and in the case of *A. terminalis* seedlings treated with LowP outperformed all treatments including the no litter control.
Figure 7.3 Seedling survival for five of the seven litter treatments: C = Control of no litter. LoP and HiP = equivalent of 3000 kg/ha and 6000 kg/ha of *Pinus radiata* litter. LoE and HiE = equivalent of 3000 kg/ha and 6000 kg/ha of *Eucalyptus* litter. The mixed litter treatments have been excluded to improve presentation and aid interpretation of the figure.
Field experiment

There were considerable differences in germination success between species and between seasons. *Acacia terminalis* performed better during the spring/summer trial averaging approximately 20% emergence across both sites (Table 7.3). *Eucalyptus sieberi* performed poorly in spring/summer with only 11.3% emergence at Jenolan. However, the eucalypt achieved the highest germination success of any species during the second trial averaging almost 40% for Newnes and Jenolan combined (Table 7.3). *Pinus radiata* experienced the largest difference between seasons with greater than 30% emergence during spring/summer and less than 10% emergence in autumn/winter.

Table 7.3 Mean maximum emergence (+SE) across all treatments at Jenolan and Newnes for both trials.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spring/Summer 2005</th>
<th>Autumn/Winter 2006</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Jenolan</td>
<td>Newnes</td>
</tr>
<tr>
<td><em>A. terminalis</em></td>
<td>18.6 (1.2)</td>
<td>22.0 (1.2)</td>
</tr>
<tr>
<td><em>E. sieberi</em></td>
<td>11.3 (1.2)</td>
<td>21.1 (1.5)</td>
</tr>
<tr>
<td><em>P. radiata</em></td>
<td>38.9 (1.6)</td>
<td>30.9 (1.7)</td>
</tr>
</tbody>
</table>

Interaction between litter and canopy cover

During spring/summer there was a significant interaction (p < 0.05) between litter treatment and canopy treatment for eucalypt emergence at both sites and acacia and pine emergence at Jenolan (Figure 7.4). At Newnes, eucalypt emergence was significantly lower under the open canopy for the litter treatment (F = 7.62, p = 0.001), but there was no difference between canopy treatments for trays without litter. At Jenolan, the opposite pattern occurred. Eucalypt emergence in trays without litter was significantly less in open areas than under plantation or invaded canopies (F = 5.42, p = 0.005). There was no significant difference between canopy treatments for trays with litter. The same trend was observed for *A. terminalis* emergence at Jenolan. *Pinus radiata* germination during the spring/summer trial was significantly greater (F2,117 = 6.2, p = 0.03) under open eucalypt canopy within litter treatments, but was significantly lower (F2,113 = 7.0, p = 0.001) under open canopy in treatments without litter. During the autumn/winter trial there was no interaction between litter and canopy treatment except for pine emergence at Newnes (F2,3 = 3.2 p = 0.005) (Figure 7.4).
Figure 7.4 Mean emergence percentage (+SE) for *Eucalyptus sieberi*, *Acacia terminalis* and *Pinus radiata* under three different canopy treatments at Newnes and Jenolan. Data for the litter treatment in the autumn/winter trial is combined across the three different litter types. * indicate a significant difference (p < 0.05) between canopy treatments, within a litter treatment.
Influence of Canopy Cover

At Newnes, canopy cover in the open eucalypt woodland was significantly higher than in the plantation (62.4 %) or under the invaded canopy (71.17 %) \((F_{2,9} = 40.8, p < 0.001)\) averaging 20.75 %. There was no significant difference in cover between the invaded and plantation canopies. At Jenolan canopy cover in both the open woodland (36.8 %) and the plantation (50.3 %) were significantly lower \((F=6.4_{2,9} p = 0.019)\) than the invaded woodland (71.8 %).

Combining emergence across litter treatments resulted in a reversal of the effect of canopy cover on germination between trials for all three species (Table 7.4). *Acacia terminalis* germination was significantly lower in open eucalypt woodland at Jenolan during spring/summer \((F = 4.4_{2,237}, p = 0.013)\). However, during the second trial there was significantly greater germination in the open treatments (Jenolan: \(F = 12.4_{2,261}, p < 0.0001\). Newnes \(F = 5.7_{2,261}, p =0.004\) (Table 7.4). *Eucalyptus sieberi* responded similarly with significantly lower germination under open canopy at Newnes during the first trial \((F = 7.1_{2,237}, p = 0.001)\), and significantly higher germination under open canopy, compared to the plantation canopy during autumn/winter \((F = 4.1_{2,261}, p = 0.018)\) (Table 7.4). There was no significant difference between canopy treatments at Jenolan for either trial. *Pinus radiata* germination at Newnes also displayed this trend with significantly higher emergence under open canopy compared to the plantation treatment during spring/summer \((F = 6.8_{2,237}, p = 0.001)\). Maximum *P. radiata* emergence during autumn/winter was significantly higher \((F = 98.0_{2,261}, p < 0.0001)\) in the open woodland compared with invaded or plantation canopy at Newnes (21.7 %, 2.5 % and 1.0 % respectively).
Table 7.4 Influence of canopy cover on emergence.

Data is pooled across litter treatment and plot. Letters refer to the three canopy treatments; O: Open eucalypt woodland, I: Invaded eucalypt woodland, P: pine plantation. Asterisks indicate a significant difference in emergence between canopy treatments *p<0.05, **p<0.01. Arrows represent the direction of difference, e.g. O<P=I indicates emergence was significantly lower under open canopy and no difference between plantation and invaded canopy.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spring/Summer Jenolan</th>
<th>Spring/Summer Newnes</th>
<th>Autumn/Winter Jenolan</th>
<th>Autumn/Winter Newnes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia terminalis</td>
<td>* O&lt;P=I</td>
<td>NS</td>
<td>** O&gt;I=P</td>
<td>** O&gt;I=P</td>
</tr>
<tr>
<td>Eucalyptus sieberi</td>
<td>NS</td>
<td>** O&lt;P=I</td>
<td>NS</td>
<td>* O&gt;P; O=I;P=I</td>
</tr>
<tr>
<td>Pinus radiata</td>
<td>NS</td>
<td>** O&lt;P; O=I;P=I</td>
<td>negligible germination</td>
<td>** O&gt;P=I</td>
</tr>
</tbody>
</table>

Excluding eucalypt emergence at Jenolan in spring/summer, negative correlations were found between emergence of the two native species and canopy cover within a plot at both sites during both trials. This relationship was significant for A. terminalis at Jenolan during autumn/winter (r = -0.582, p = 0.047).

Influence of litter

During the spring/summer trial, emergence was significantly lower (p < 0.01) in control treatments compared with litter treatments for all species at both sites, when combining across canopy treatments. Emergence in the pine litter treatment ranged from 18.8 % for E. sieberi at Jenolan to 55.7 % for P. radiata emergence at the same site. In contrast, emergence in trays with no litter was below 11 % for all species at both sites except for pine emergence at Jenolan which reached 21.6 %. Trays with litter added also consistently experienced significantly higher emergence (p < 0.001) than the control treatment during the autumn/winter trial (Figure 7.5). However, there was no significant difference (p > 0.05) in emergence percentage between the litter treatments for any species at either site (Figure 7.5).
Figure 7.5 Mean emergence percentage (+SE) for A) *Acacia terminalis* B) *Eucalyptus sieberi* and C) *Pinus radiata* under four litter treatments at Newnes and Jenolan for the autumn/winter trial. Values are pooled across canopy treatments. * indicates significantly different (p < 0.01) from other litter treatments at the site.
Discussion

Experimental manipulations of the factors thought to be mechanisms of invasive impacts were conducted in a series of field and glasshouse studies. The expected impacts on native species emergence by chemical effects were not detected but support for a physical effect of litter and canopy cover on seedling survival was provided by the findings. The absence of a negative influence of leachate on germination does not rule out the possibility of a chemical impact of litter later in the life cycle or of long term impacts of pine leachate on soil properties (Scholes and Nowicki 1998). There was no evidence for the negative influence of *Eucalyptus* leachate on germination observed in previous studies (May and Ash 1990, Babu and Kandasamy 1997). Further studies using increasing concentrations of leachate may provide further insight. Where possible, investigations should be conducted in situ as chemical effects observed in the lab are often buffered by soil in the field (Schlatterer and Tisdale 1969).

No significant differences in maximum emergence between litter type in either the field or glasshouse were recorded with only the control treatments in the field experiment returning a significantly lower emergence percentage for all three species. All species responded similarly to pine and eucalypt litter and mixes of the two, suggesting that they are influencing the germination stage equally. However, variation in seedling survival between litter treatments in the glasshouse suggests that differences between litter types are generally observed in the latter stages of establishment. Initially, a facilitating effect of the litter treatments was observed with delays in emergence for the control treatment of no litter. Eventually seedlings of all species performed best in treatments without litter. This pattern suggests there is a change over in the variable influencing plant establishment. At first it appears that litter facilitates germination by maintaining soil moisture levels when the seed is first sown. As time proceeds and water is non-limiting, germination success appears to be more heavily influenced by the amount of light available.

Overall seedling survival was poorest in the high pine and high eucalypt treatments, suggesting that recruitment will be impeded by litter densities of 6000kg/ha, which is equivalent to approximately 6 years of pine litterfall in invaded areas (chapter 6). Previous studies have shown similar results with low levels of litter benefiting establishment and thicker litter layers reducing germination and establishment (Hamrick and Lee 1987). A build up of pine litter may also be accompanied by the establishment
of mycorrhizae in the litter layer. Mycorrhizal fungi forms dense mats in pine plantations and can provide a greater hinderance to seedlings than the leaf litter itself (Facelli and Pickett 1991a). The establishment of mycorrhizae in native eucalypt woodland areas could result in the formation of a layer impenetrable to native species.

Interestingly, seedlings in the low pine treatment often out-survived those in the low eucalypt treatment suggesting a difference in shading effect between the litter types. This is consistent with work by Facelli and Kerrigan (1996) who recorded a positive effect of pine litter on seedling establishment. However, the authors also showed that pine and eucalypt litter reduce radiation equally which implies that the difference in germination under the litter types is due to factors other than light availability. Differences in physical structure between the two species may also be important. Broad leaved eucalypt litter may impede recruitment by covering entire seeds. At low litter levels pine needles form a hatched matrix which may be penetrated more easily.

The difference in response between _E. sieberi_ and _A. terminalis_ to the litter treatments implies a difference in light requirement between the two species. Both pine treatments and the high eucalypt treatment strongly hindered survival of _E. sieberi_ seedlings. In comparison, _A. terminalis_ seedlings performed relatively well under the high pine and low eucalypt treatments with only the high eucalypt treatment having a strong inhibiting effect, suggesting the species is more shade-tolerant than _E. sieberi_. The result may also be reflecting the fragile nature of the eucalypt seedlings themselves. _Eucalyptus sieberi_ hypocotyls are thinner than _A. terminalis_ which may explain their vulnerability to thicker litter layers. Previous research has also shown a greater ability of large seeds to germinate under litter (Winn 1985, Peterson and Facelli 1992, Eriksson 1995, Dzwonko and Gawronski 2002). Species with small seeds e.g. _Eucalyptus_ are usually negatively affected by litter cover due to a shortage of reserves before the seedlings can reach the light (Winn 1985, Peterson and Facelli 1992). _Acacia terminalis_ and _Pinus radiata_ have similar sized seeds (approximately 5 x 4 mm) while _E. sieberi_ in comparison has a very small seed (1-2 mm). This difference may explain the poor survival of the eucalypt seedlings under the high litter treatments as they were unable to penetrate the litter and acquire sufficient light.

The addition of litter had the opposite effect in the field to that observed in the glasshouse as germination was significantly lower in trays without litter for all species at both sites and during both trials. It appears that the evaporative water loss from bare soil in the field was too great to support germination and explains the considerably
lower germination success of all species in the field compared with the glasshouse. These results concur with previous research suggesting that low levels of litter can facilitate the germination of some species (Facelli and Ladd 1996).

Effect of canopy cover

Invasion of eucalypt woodland by pines resulted in considerable increases in canopy cover with values of approximately 70% observed in the invaded areas of both sites. At Newnes the invaded canopy was not significantly different from the plantation canopy suggesting that light availability in invaded areas is similar to that of plantations. At Jenolan, canopy cover in the invaded area was significantly higher than in the plantation. The lower canopy cover in the plantation at Jenolan can be explained by the age of the compartment (only 11 years c.f. 26 years at Newnes).

The only significant difference in response was between the open eucalypt woodland and the remaining canopy treatments. The direction of this effect was heavily influenced by the timing of the experiment. A positive effect of shading during the spring/summer trial was observed with significant reductions in emergence under the eucalypt canopy despite higher rainfall during this period. Higher temperatures and subsequent increases in evaporative water loss may be responsible for this result. During the autumn/winter trial, germination of both the natives and _P. radiata_ was often significantly greater in the open woodland, suggesting that when water is in sufficient supply, greater light requirements under open canopy are responsible for high germination success. This observation is consistent with research on the establishment of invasive _P. radiata_ in Chile (Becerra and Bustamante, unpublished). The authors observed a positive effect of shading on pine germination in drier (xeric) habitats and no effect of shading in the moist (mesic) habitat. The authors attributed this trend to a consistency in soil moisture across canopy treatments in the mesic habitat indicating that soil moisture is more important than light availability.

Similarly, differences in invasion success between seasons have also been observed for invasive _Senecio_ species in Spain. In the spring, competition with resident vegetation and low water availability reduced the survival of seedlings (Cano _et al._ 2007). Whereas, seedlings transplanted in the fall enjoyed high recruitment success. The authors also found that seedling survival differed between habitats. Clearly, recruitment success of invaders and consequent impacts of invasion are context dependent. Studies
that do not consider temporal variation in environmental conditions will fail to accurately quantify invasion impacts.

The greater emergence of *P. radiata* in spring/summer suggests that conditions for pine establishment are better during warmer months of the year. This makes ecological sense as seed is typically released during warm, dry conditions (McDonald and Laacke 2003). Good habitat conditions at the time of dispersal are critical for establishment as *Pinus* seeds lose viability within a couple of years (Johnson and Fryer 1989). There was no evidence for the facilitation of pine germination by pine litter, pine leachate or increased canopy cover. In fact pine germination in the field was greatest in open areas suggesting that the shade intolerance of the species (Keeley and Zedler 1998) prevents it from establishing under its own canopy.

High pine emergence in the open eucalypt woodland during this period (59.8 % and 40 % for Jenolan and Newnes respectively) is indicative of the high capability of the species to establish in these areas. However, high emergence under plantation and invaded canopies during the first trial implies that the observed inability of *P. radiata* to colonise under closed canopy is due to poor seedling survival rather than insufficient germination. Similar findings have been observed for *P. radiata* invading native forest remnants in Chile where high germination success of the species but poor seedling recruitment and seedling densities have been recorded within the interior of the reserves (Bustamante and Simonetti 2005). The authors attributed this result to increased soil moisture in the interior which enhances germination and a shading effect of the canopy which limits pine growth. These findings highlight the importance of investigating all aspects of the establishment phase.

Interactions between canopy openness and litter addition were of prime interest in this study. The facilitating effect of litter might be expected to be greatest in the open eucalypt woodland where high light conditions are more likely to cause seed dessication. Frequent, significant interactions between the canopy and litter treatment were found in the first trial. The only instance that this response was reversed between litter treatments was for *Pinus radiata* germination at Jenolan during the spring/summer trial. Emergence within litter treatments was greater under open eucalypt canopy, while seeds without litter performed better in the invaded and plantation canopies. This pattern suggests that seeds will respond best when shading from either high canopy cover or a litter layer is able to mediate the effects of high water stress.
The combined effects of increased canopy cover and increased litter load have the potential to have a dramatic impact on native recruitment in invaded areas. In south east South Australia, reductions of greater than 50% native species number and established biomass have been observed after more than three decades of pine invasion (Virtue and Melland 2003). Addition of pines to the eucalypt community can potentially result in a doubling of the litter load (see chapter 6). This study has provided experimental evidence that increases in litter depth can lead to higher seedling mortality which may have a long term impact on recruitment. As pine densities increase and pine litter accumulates the effects recorded in this study are likely to intensify. Observed differences in the influence of pine canopy on native germination during different times of the year have implications for quantifying invasion impacts. Species that germinate during the summer months may initially benefit from the shade provided by the pines. However, only species that can survive under the pine canopy will become established resulting in a shift towards a shade tolerant community.
8. General Discussion

Achievements of this study

Attention is necessarily focused on Australia’s Weeds of National Significance (Thorpe and Lynch 2000) as they are perceived to pose the highest risk to biodiversity, but the National Weeds Strategy also highlights the need to eliminate sleeper weeds during their benign phase (Australian Weeds Committee 2006). Sleeper weeds are species that spend long periods in low population numbers and then expand rapidly (Groves 1999), often proceeding to have large impacts. Recognition of these weeds in the initial stages of invasion is necessary in order to enable early action and prevent them from becoming weeds of national importance. This requires identification of the point when naturalised species enter a higher risk and impact category. Direct knowledge of both the current distribution of the invader and the potential for negative impacts on native species is the only way to prioritise invaders yet to receive attention. This study provides a model approach for gaining this knowledge.

Key knowledge gaps for Pinus radiata as an invasive species in Australia have been addressed in this study. Firstly, the pattern of invasion at a landscape scale was established, providing an estimate of the total area of land invaded and illustrating the variation in invasion success between sites. Documenting the spatial extent of spread is the first step towards quantifying the impacts of invasion and allows comparisons of invasion success between species and between continents (Parker et al. 1999). This is of particular relevance for P. radiata, a species that has been planted widely with varying invasion success between regions and habitat types across the southern hemisphere (Richardson et al. 1994). Within site distribution patterns also have consequences for calculating the total area of impact. Pine densities were highly variable around the border of the plantation and with increasing distance away from the plantation. A distinction between heavy and light infestations is crucial for identifying and prioritising sites for control as control costs are heavily dependent on wildling densities (DOC 2001).

Knowledge of the pattern of pine spread established in section one was used to identify factors facilitating invasion in the second section, Process of invasion. A number of risk factors contributing to pine success at a landscape scale were identified including physical disturbance, dry sclerophyll forest and a residence time of more than
40 years. The relationship between the level of invasion and the time since plantation establishment confirms the increasingly recognised role of residence time in the invasion process (Richardson and Pyšek 2006).

Interactions between vegetation type and the age of the plantation suggest that the environment still has a large influence on the invasion process and that it is a combination of these factors that will ultimately drive invasion success. Time in itself is not a cause of vegetation dynamics, rather ecological processes are time dependent (Johnstone 1986). Residence time is acting as a reference for variations in the susceptibility of areas to invasion. An important aspect of residence time is how it relates to temporal variations in community susceptibility to invasion. This study has only provided a snapshot look at the level of invasion surrounding the plantations. Sites currently less than 40 years clearly may not all go on to become invaded. Similarly, older sites that are currently invasion free may, with time, become invaded. Biotic forms of resistance e.g. plant vigor or the level of disturbance, are particularly likely to be variable in time and space (D'Antonio et al. 2001) and may explain the large range in the level of invasion across the older sites in this study. Abiotic forms of resistance typically display thresholds of conditions above which there is no chance of establishment, i.e. no level of propagule pressure will result in invasion (D'Antonio et al. 2001). In this study sites that received more than 1300 mm annual rainfall experienced very low levels of invasion suggesting that high rainfall is imposing an abiotic constraint on pine spread. This finding is consistent with the idea that some vegetation communities are resilient to pine invasion (Bustamante et al. 2003, Bustamante & Simonetti 2005). Identifying areas where pines are prevented from establishing is important for predicting future distribution patterns of the species. However, abiotic resistance may vary over time and decrease the susceptibility of a site to invasion. Drier years, particularly following good seed crops may create an opportunity for pine establishment at wet sites.

Once the distribution of wildling pines across the landscape and within vegetation types had been established, the final step in quantifying the impact of *P. radiata* was to examine the level of effect per individual (Parker et al. 1999). The third section, Mechanism of impact, identified two avenues for the negative influence of pines. The addition of high levels of pine litter and dramatic increases in shade due to greater canopy cover led to reduced emergence and survival of two native species and
may lead to changes in community composition in the long term. However, the majority of pine litter was distributed directly below the canopy of the pine. The actual amount of native vegetation below the canopy of pines scattered throughout the landscape, and therefore at risk of invasion impacts, is likely to be much less than the the area of land considered invaded. Distribution patterns as well as the density of invaders must be considered when assessing the total impact of a species. To illustrate this point we can consider three potential scenarios for the invasion of a 1 hectare area of land (Figure 8.1). Calculating the area of land invaded using distances from the source population to the furthest individual will not result in an accurate estimate of the area of land subjected to invasion impacts. Clearly, if the effects of an invader are limited to the area under the canopy, then the amount of land at risk in scenario C is greater than that in scenario A. Despite B having more invaders present, the area of direct impact may be considered to be less than in C due to the clustering of individuals and potentially overlapping areas of impact. Additionally, a distinction between low (A) and high (B) density infestations is required.

![Figure 8.1 Three scenarios for the spatial distribution of invading organisms.](image)

Source of the invading population is on the left hand side. A) Low density infestation with isolated individuals at long distances from the source B) High density infestation close to the source and an isolated individual far away C) even distribution of individuals at all distances from the source.

The framework for quantifying invasion impacts proposed by Parker et al. (1999) suggests multiplying the three components of impact together;

\[ I = R \times A \times E, \]

Where \( I \) = total impact, \( R \) = range size of the invader, \( A \) = abundance in numbers and \( E \) = effect per individual.
However, it is clear that two of these components, Range and Abundance, will interact suggesting that a straight multiplication of factors will not always result in an accurate quantification of the area of land invaded. Incorporating density and spatial distribution of the invader into the framework for quantifying invasion impacts remains a challenge for invasion biologists.

Observations from germination trials in the field and glasshouse highlighted some of the intricacies involved in quantifying invasion impacts. The influence of pine litter and increased canopy shade varied between trials and sites. Trends in pine and native success below pine canopy reversed between seasons illustrating the importance of temporal replication for studies attempting to quantify invasion impacts. An examination of community level influence of pines involving a greater number of native species that differ in their germination requirements is likely to introduce further complexity.

The magnitude of pine invasion impacts will depend on the likelihood of pines establishing in and eventually dominating the native eucalypt community which will in turn depend on their ability to germinate and survive within the recipient habitat. This study observed successful germination of *P. radiata* within open eucalypt forest during spring and summer. High seedling densities were recorded within both burnt and unburnt eucalypt forest, with up to 45% of seedlings surviving after almost 4 years post-fire. The true potential for pines to become established within different vegetation types must be assessed with a comparison of seedling survival rates of both *P. radiata* and native *Eucalyptus* species. The sole study which compares growth rates of pines and eucalypts in Australia did observe a replacement of eucalypts by *P. radiata* in a relatively undisturbed forest environment (Chilvers and Burdon 1983). Suggestions that pines have a greater capacity for exploiting forest gaps than eucalypts (Van der Sommen 1978) and the discovery of a handful of sites with mature pine populations during this study indicates that given sufficient time, pines are capable of becoming dominant within the native forest.
Management implications

Recommendations to reduce the threat from *Pinus* invasions have been reported elsewhere (Richardson *et al.* 1994) and were reviewed in chapter 2. In New Zealand, guidelines that recognise a series of risk factors relating to conifer spread have been developed to educate plantation owners (Ledgard and Langer 1999) and most regional councils feature wildlings in their pest management strategies (Ledgard 2004). Recommendations include avoiding planting upwind from land types that are particularly susceptible to invasion, i.e. with light vegetation cover and light grazing. Exposure and slope are important and plantations should be avoided on sites that are highly exposed, whilst the long axis of the plantation should be situated at right angles to prevailing wind. This study has provided much of the knowledge necessary to produce a similar set of guidelines to ensure plantation establishment in Australia minimises the risk of wild pines spreading outside the plantation boundary. The classification tree is a useful tool for identifying high risk sites and some of the factors that contribute to invasion success. Avoiding planting in areas that are in close proximity to dry sclerophyll forest and minimising disturbance at plantation boundaries will help prevent pine spread. High levels of disturbance and a lack of grazing will promote invasion. The inclusion of data from sites located in other pine growing regions in Australia will help to consolidate some of the relationships identified in this study.

Increasing the buffer zone between plantation edges and native vegetation will reduce the impact of pine invasion. Across all sites the majority of wildlings occur within 200 m from the plantation. Under the Native Vegetation Act (2003) buffers of up to 40 m are required between plantations and rivers. Increasing the ‘no planting’ zone by 100 m would reduce the amount of land under the dispersal distance of pines. This is particularly pertinent in areas where the native vegetation is of high conservation value. For example at sites such as Penrose State Forest, where threatened swamplands border the plantation. Increasing the buffer zone will not only mitigate impacts but will simultaneously reduce fire risk to the plantation by enhancing the fire break. This is particularly important in areas where plantations are proximate to residential zones.

The lag period between plantation establishment and pine spread implies that monitoring for pine wildlings should be a priority as sites approach 40 years old. Monitoring on a 5 year cycle will successfully contain wildling populations. The nature of invasion lag phases means that even if no new plantations are established, the number
of invaders will increase into the future (Kowarik 1995). Control is easiest and most cost-effective in the early stages of invasion (Mack et al. 2000) and a systematic approach to wildling monitoring that integrates with existing forestry operations will go a long way towards preventing further incursions. For example, opportunistic removal of wildlings in native vegetation could take place during thinning and maintenance procedures carried out in adjacent plantation compartments.

The infestation index can be put to immediate use by directing control efforts. Table 8.1 outlines the recommended actions for areas suffering varying levels of invasion. Knowledge of the influence of fire on wildling populations reported in chapter 5 can be used to direct burning regimes within invaded areas. A consideration of the conservation value of sites is necessary to determine final priorities for site selection. The presence of threatened species or ecological communities as well as the susceptibility of these areas to invasion impacts must be taken into account.

<table>
<thead>
<tr>
<th>Infestation Index</th>
<th>Action</th>
<th>Priority</th>
<th>Use of fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-1</td>
<td>Monitor every 5 years after plantation reaches reproductive age – 20 years</td>
<td>Low</td>
<td>Prescribed burns are an effective control measure</td>
</tr>
<tr>
<td>2-3</td>
<td>Remove wildlings</td>
<td>Medium</td>
<td>Follow up control within 5 years of all fires. Fell reproductive wildlings prior to burning</td>
</tr>
<tr>
<td>4-5</td>
<td>Remove wildlings</td>
<td>High</td>
<td></td>
</tr>
</tbody>
</table>

The influence of wind did not have a strong influence on pine distribution in areas close to the plantation, however, observations from spread at the Mannus plantation and from the air at other plantation sites (pers. comm. C. Banffy 2003) suggests that areas downwind from plantations will be most at risk from spread. Where possible, plantations should be placed in landscape positions upwind from areas that are less susceptible to invasion. Vegetation downwind from the plantation, which has the highest risk of invasion should be already heavily grazed or at least, wet sclerophyll forest in order to limit wildling establishment. The Native Vegetation Act (2003) and the Plantation and Reafforestation Act (1999) prevent the clearing of native vegetation for plantation establishment. Consequently all new compartments will be established on previously cleared land. Hence the risk of spread from newly established plantations is
somewhat lower than from existing sites. However, plantations that are established within the dispersal distance of remaining native vegetation in the region will continue to act as potential seed sources and must be monitored.

The problem of pine spread in Australia was first recognised 30 years ago (Burdon and Chilvers 1977). Since then we have seen little control and next to nil development of policy to incorporate the threat of wildling pines. At the same time as conflicting interests associated with invasive spread from economically beneficial plantations can hinder control efforts (Geldenhuys 1986, Richardson et al. 2003) they can also provide an opportunity to hold the stakeholders accountable. Forestry authorities have an obligation to control for noxious weeds on their lands (Noxious Weeds Act 1993), but pines are currently absent from noxious lists and strategies specific to pine wildlings are rare. An incorporation of ecologically based knowledge into forestry practices in the past has increased the sustainability of the forestry sector and is featured in their public statement, improving the credibility of the industry. More recently, a growing awareness of climate change and the role of trees in carbon sequestration have led to increased investment in planted forests of exotic pines and eucalypt species in NSW (Forestry NSW 2007). Increasing the forest estate will result in an enhanced propagule pool. It is vital that risks of spread from newly established plantations are minimised and that in the process of solving one problem we are not creating another.

An incorporation of criteria to reduce pine spread risk into existing management practices is critical to preventing future invasion events. The Australian Forestry Standard is a certification scheme that provides forest managers and owners with a set of criteria that support the sustainable management of wood production. The scheme is voluntary although compliance of certified participants is verified via an independent third party. The spread of pines from plantations is considered in section 4.3.6;

“Forest managers managing plantations shall constrain the spread of introduced species, provenances or populations used in plantations, into adjacent native vegetation in order to protect its integrity.”

(AFNS 2003 p. 22)

Forestry NSW and several other major plantation owners in Australia are currently certified under the scheme. However, the presence of established wildling populations at several sites in NSW suggests that wildling control is not a priority. Clearly, a specific consideration of pine spread in existing legislative frameworks is
required. A system where authorities that gain financial benefit from the continual introduction of non-indigenous species take responsibility for the costs associated with invasion is possible and may increase the rigor with which species are introduced into new areas.

**Which road should we take?**

This study has established the extent of the problem and identified some of the risk factors associated with pine spread, however, we are a long way from an ability to predict pine invasions in Australia. A failure to predict invasions has led many to question the validity of current approaches to understanding the invasion process. Critical viewpoints highlight a lack of general answers explaining invasion patterns (Rejmanek et al. 2005) and argue that every case is unique (Williamson 1999). Important progress has been made regarding invasive traits (Pyšek and Richardson 2007) and the resistance of the native community to invasion (Levine et al. 2004), however, the probability of predictability is reduced as exotic species are constantly being introduced into novel areas and allowed to exploit new resources (Mooney and Hobbs 2000). Furthermore, assessment of generalisations associated with invasiveness and invasibility is difficult because they often rely on post-hoc measures such as observations and correlation rather than experimentation (Mack et al. 2000).

Others argue that the contradictory nature of hypotheses regarding invasion success is due to a failure to acknowledge that the processes driving invasions are likely to vary among different habitats and will change with time (Dietz and Edwards 2006). A partitioning of the invasion process into primary and secondary phases may provide greater insight into the relative importance of factors mediating invasions. For example, the role of propagule pressure may decline as the species establishes, while the importance of the resistance of habitats that the invader expands into may increase (Dietz and Edwards 2006). However, there have been very few quantitative studies investigating the importance of different factors at varying stages of establishment (Kolar and Lodge 2001). In the example of pines, research has shown that the inability of pines to establish within intact forest fragments in Chile under areas of high canopy cover is due to poor seedling survival rather than low germination success (Bustamante and Simonetti 2005). Examining different stages of plant development is critical for assessing invasion potential as short term seedling success does not guarantee adult
recruitment (Mazia et al. 2001). High emergence rates observed in the field in this study do not necessarily equate to pine success.

An examination of the interaction between factors that might be driving invasions has also been encouraged (Hierro et al. 2005). A commonly advocated approach is an experimental one involving manipulation of factors of interest. For example a factorial field experiment that replicates different levels of disturbance and introduces varying amounts of seed of both resident and exotic species might elucidate the relative importance of disturbance and propagule pressure in the invasion process (Hierro et al. 2005). However, this approach may only be relevant if findings can be extrapolated to the ‘real world’. Large temporal and spatial scale examinations of seed supply versus microsite limitation have almost never been attempted (Eriksson and Ehrln 1992), seemingly due to the large logistical difficulties in doing so.

It appears that there is a significant trade-off between studies that can incorporate all possible factors that may influence the level of invasion and necessarily have to be conducted on a micro-scale, and those that attempt to separate factors in the context of field studies in an arguably more biologically meaningful approach. In this study the nature of the data available resulted in unavoidable limitations. The locations of the plantations in the landscape and a multitude of extrinsic factors that are causing the likelihood of pine spread to be non random across sites meant that determining the relative importance of factors was difficult. In this instance I was motivated by a need to document the extent of invasion at the landscape scale as well as explore some of the factors mediating spread.

While an examination of pine spread in other pine growing states in Australia may shed more light on some of the factors mediating invasion in Australia, would this be a responsible use of research funds? Would the findings make a meaningful contribution to invasion biology and the eradication of pines? In the absence of predictability regarding invasion success we may need to accept that invasive species are going to establish and shift our focus towards prioritising species on the basis of their impact on native communities (Byers et al. 2002). This study covered three components of impact, delivering a map of the areas invaded, providing typical wildling densities for 6 levels of the infestation index and identifying two mechanisms of impact on native plant species. These findings raise questions about the level of data required in order to prioritise invasive species. Is mapping at coarse scales sufficient to quickly
assess the area of land invaded? Differences in densities of the invader are useful for prioritising control efforts but are they necessary to rank species on the basis of their total impact? Perhaps much more attention should be focused on quantifying the effect per individual. Current attempts to rank invaders based on their impacts on native species e.g. the WINS (Weed Impact to Native Species) assessment tool (Downey 2006) rely on existing knowledge within the literature or input from experts in the field. This information will most likely be biased towards species that have already become widespread and will lead to an underestimation of the impacts of species in the early stages of invasion. Research that focuses on the impacts of species that have naturalised but are yet to become widespread will help to reduce this bias.

The unprecedented success of invasions in recent times (Ricciardi 2007) and predictions of future increases in the numbers of invaders (Nentwig 2007) suggest that a capacity to rank species in terms of their impacts will be critical for maximising future control efforts and minimising the damage of invaders. However, invasion processes and consequent impacts are highly context dependent. Initial invasion success is spatially variable and the implications of invasion are species specific and will depend on the density and area of invasion as well as the vegetation type being invaded. Ecological research must remain at the heart of incorporating this complexity into the prioritisation process and is capable of arming policy makers with the knowledge of the real impacts of invasion.
Appendix 1. Questionnaire sent to Forestry NSW and DEC staff

1) What are the locations at which you have seen pines (Pinus spp.) invading (please be as specific as possible).

2) Name the species of pine (if possible)

3) Do you know any areas of native vegetation adjacent to pine plantations where you have had an opportunity to look which are free of pines? Name these locations:

4) How far from the plantation have you witnessed invading pines?

5) Have you noticed the invasion in any particular vegetation type, for example, Eucalypt woodland, grassland, rainforest.
6) Do you keep records of invasion? Are these records accessible?

7) Have you witnessed any of the following patterns of invasion? Please tick the appropriate boxes.

☐ Higher levels of invasion downwind from plantations

☐ High seedling recruitment after fire

☐ Long distance dispersal of seed by birds (name species if possible)

☐ Self-generation resulting in clustering of pines around reproductive adults?

8) Have you undertaken any procedures to control for pines outside plantations?

☐ Yes  ☐ No, resources/funding is too limited

☐ No, pines are not considered to be a problem

If Yes, please tick the control measures you have used
☐ Fire

☐ Mechanical Removal (Chainsawing, cutting, hand pulling etc.)

☐ Herbicide. Name:

☐ Other. Please specify:

9) Name the locations where these controls have taken place:

10) How effective are these forms of control? Do you have quantitative data on control success?

11) On a scale of 1 to 5 categorise Pinus species and P. radiata as a weed of environmental concern in your region in terms of its current and future impact.
1 = Unknown or Zero; 2 = Low; 3 = Moderate; 4 = High; 5 = Severe

<table>
<thead>
<tr>
<th></th>
<th>Current</th>
<th>Future</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1  2  3 4  5</td>
<td>1  2  3 4  5</td>
</tr>
<tr>
<td>Pinus species in general</td>
<td>□ □ □ □</td>
<td>□ □ □ □</td>
</tr>
<tr>
<td>Pinus radiata</td>
<td>□ □ □ □</td>
<td>□ □ □ □</td>
</tr>
<tr>
<td>Other Pinus species (name)</td>
<td>□ □ □ □</td>
<td>□ □ □ □</td>
</tr>
</tbody>
</table>
13) Would you like to receive a copy of the review reporting the results of this survey?

☐ Yes ☐ No

14) Are you interested in further participation in this project?

☐ Yes, I can be contacted for further information and assistance

☐ No

If you know of anyone else who may be able to assist this project can you please forward the email letter and questionnaire to them.
Appendix 2 *Pinus radiata* invasion at Lidsdale State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Eastern Bushlands; Holme, 1993).
Appendix 3 *Pinus radiata* invasion at Newnes State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Eastern Bushlands; Holme, 1993).
Appendix 4 *Pinus radiata* invasion at Jenolan State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Forest Ecosystems South Coast; Thomas *et al.* 2000 and Eastern Bushlands, Holme 1993).
Appendix 5 *Pinus radiata* invasion at Mullions Range State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Eastern Bushlands; Holme, 1993).
Appendix 6 *Pinus radiata* invasion at Mannus State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Forest Ecosystems South Coast; Thomas *et al.* 2000).
Appendix 7 *Pinus radiata* invasion at Penrose State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Southeast NSW; Tozer *et al.* 2006).
Appendix 8 *Pinus radiata* invasion at Belangelo State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Southeast NSW, Tozer *et al.* 2006).
Appendix 9 *Pinus radiata* invasion at Wingello B. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Southeast NSW, Tozer *et al.* 2006).
Appendix 10 *Pinus radiata* invasion at Wingello A State Forest. Plantation data is provided by Forestry NSW. Vegetation data is provided by Department of Environment and Conservation (Southeast NSW, Tozer et al. 2006).
## Appendix 11. Source of vegetation GIS and hard data for the 29 plantation sites.

<table>
<thead>
<tr>
<th>Region</th>
<th>Site</th>
<th>Digital</th>
<th>Vegetation Data</th>
<th>Published map</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hume</td>
<td>Batlow</td>
<td>EBD (S); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Blowering Dam</td>
<td>EBD (S); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Boganyera</td>
<td>EBD (S); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Buccleugh</td>
<td>EBD (S); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Clarkes hill</td>
<td>EBD (S); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mannus</td>
<td>EBD (S); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tallaganda</td>
<td>EBD (S); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macquarie</td>
<td>Gurnang</td>
<td>EBD (C); FES</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hampton</td>
<td>EBD (C); FES</td>
<td></td>
<td>Katoomba Map</td>
</tr>
<tr>
<td></td>
<td>Jenolan</td>
<td>EBD (C); FES</td>
<td></td>
<td>Katoomba Map</td>
</tr>
<tr>
<td></td>
<td>Kinross</td>
<td>EBD (C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lidsdale</td>
<td>EBD (C);</td>
<td></td>
<td>Wallerawang map</td>
</tr>
<tr>
<td></td>
<td>Mount Canobolas</td>
<td>EBD (C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mullions Range</td>
<td>EBD (C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Newnes</td>
<td>EBD (C)</td>
<td></td>
<td>Wallerawang map</td>
</tr>
<tr>
<td></td>
<td>Pennsylavnia</td>
<td>EBD (C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Roseberg</td>
<td>EBD (C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sunny Corner</td>
<td>EBD (C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vulcan</td>
<td>EBD (C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monaro</td>
<td>Bondi</td>
<td>EBD (S); SCIVI</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coolangubbra</td>
<td>EBD (S); SCIVI</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Belangelo</td>
<td>EBD (S); SCIVI</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wingello</td>
<td>EBD (C, S); SCIVI</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Penrose</td>
<td>EBD (S); SCIVI</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wingello B</td>
<td>EBD (C, S); SCIVI</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern</td>
<td>Hanging Rock</td>
<td>EBD (N); FELN</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nowendoc</td>
<td>EBD (N); FELN</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Riamukka</td>
<td>EBD (N); FELN</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Appendix 12. Vegetation types included in categories used for vegetation analysis.

**EBD:** National Parks and Wildlife Service Eastern Bushlands Database (N, C, S – indicates northern, central or southern polygon). **FES:** Forest Ecosystems South Coast Sub Region (Resolution of 25m).

**FELN:** Forest Ecosystems Lower North East CRA Forest Ecosystem Mapping for the Hunter sub-region (Resolution 1:100,000). **SCIVI:** Southeast NSW Native vegetation and mapping. (1:100,000).

* Remnant Bushland includes all areas of native vegetation within the plantation that have been allocated as exotic forest on the vegetation maps.


<table>
<thead>
<tr>
<th>Database</th>
<th>Code</th>
<th>Description</th>
<th>Dominant Species</th>
<th>Sites Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>EBD (N)</td>
<td>MEF</td>
<td>Moist Eucalypt Forest</td>
<td>HR, R</td>
<td></td>
</tr>
<tr>
<td>EBD (C)</td>
<td>MF-D</td>
<td>Moist forest tending to dry</td>
<td>Ba, CH, T</td>
<td></td>
</tr>
<tr>
<td>MF</td>
<td>MF-D</td>
<td>Moist forest tending to dry</td>
<td>Ba, CH, T</td>
<td></td>
</tr>
<tr>
<td>MF</td>
<td>MF</td>
<td>Moist Forest</td>
<td>Ba, Buc</td>
<td></td>
</tr>
<tr>
<td>MF</td>
<td>MFS</td>
<td>Moist forest system</td>
<td>Ma</td>
<td></td>
</tr>
<tr>
<td>MF</td>
<td>MFS</td>
<td>Moist Forest System</td>
<td>Ma</td>
<td></td>
</tr>
<tr>
<td>FES</td>
<td>55</td>
<td>Eastern tablelands fern/herb/grass moist forest</td>
<td>E. fastigata</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>56</td>
<td>Tableland and escarpment moist herb/fern grass forest</td>
<td>E. radiata/E. viminalis/ Viola spp.</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>62</td>
<td>Southern escarpment edge moist shrub/fern forest</td>
<td>E. fastigata/E. cypellocarpa</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>66</td>
<td>Eastern Tablelands shrub/grass moist forest</td>
<td>E. radiata, E. dalrympleana/Poa sieberiana/Daviesia ulicifolia</td>
<td>J, G</td>
</tr>
<tr>
<td></td>
<td>67</td>
<td>Northern Plateaux moist fern/herb/grass forest</td>
<td>E. fastigata, E. dalrympleana, Acacia melanoxyl, Pteridium esculentum</td>
<td>J</td>
</tr>
<tr>
<td></td>
<td>82</td>
<td>Western montane acacia/herb forest</td>
<td>E. viminalis/E. robertsonii/Cassinia</td>
<td>Ba, Buc, CH, GH</td>
</tr>
<tr>
<td>Database</td>
<td>Code</td>
<td>Description</td>
<td>Dominant Species</td>
<td>Sites Present</td>
</tr>
<tr>
<td>----------</td>
<td>------</td>
<td>-------------</td>
<td>-------------------</td>
<td>---------------</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>aculeata/Pteridium esculentum</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>87</td>
<td>Western escarpment moist shrub/herb/grass forest</td>
<td><em>E. delegatensis/E. dalyrmpleana/Dermentia dermentia/Stellaria pungens</em></td>
<td>Ba</td>
</tr>
<tr>
<td></td>
<td>95</td>
<td>tableland acacia moist herb forest</td>
<td><em>E. pauciflora, E. dalyrmpleana, A. dealbata, Helichrysum scorpioides</em></td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>104</td>
<td>tableland acacia/herb/grass forest</td>
<td><em>E. robertsonii, E. dalyrmpleana, A. dealbata, Platylobium formosum</em></td>
<td>Ba, Bl, G</td>
</tr>
<tr>
<td></td>
<td>124</td>
<td>Western montane wet heath/herb/grass woodland</td>
<td><em>E. pauciflora/E. stellulata/Epacris breviflora</em></td>
<td>Buc</td>
</tr>
<tr>
<td>SCI VI</td>
<td>7</td>
<td>South coast wet sclerophyll forests</td>
<td></td>
<td>W</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>Southern escarpment wet sclerophyll forest</td>
<td></td>
<td>Bon, Co, W</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>Southern tableland wet sclerophyll forest</td>
<td></td>
<td>Penr</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>Southern lowland wet sclerophyll forest</td>
<td></td>
<td>W</td>
</tr>
<tr>
<td>FEL N</td>
<td>15</td>
<td>Brown barrel gum</td>
<td></td>
<td>HR, R</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>Cool moist messmate</td>
<td></td>
<td>HR, No, R</td>
</tr>
<tr>
<td></td>
<td>81</td>
<td>Messmate</td>
<td></td>
<td>HR, No, R</td>
</tr>
<tr>
<td></td>
<td>82</td>
<td>Messmate – Mountain Gum Forest</td>
<td></td>
<td>HR, No, R</td>
</tr>
<tr>
<td></td>
<td>108</td>
<td>Open ribbon gum</td>
<td></td>
<td>No, R</td>
</tr>
<tr>
<td></td>
<td>168</td>
<td>Rainforest</td>
<td></td>
<td>HR, R</td>
</tr>
</tbody>
</table>

**Dry sclerophyll forest (D)**

<table>
<thead>
<tr>
<th>EBD (N)</th>
<th>DOF</th>
<th>Dry Open Forest</th>
<th>N, HR, R</th>
</tr>
</thead>
<tbody>
<tr>
<td>EBD (C)</td>
<td>DFS</td>
<td>Dry Forest System</td>
<td>G, H, J, N, P,</td>
</tr>
<tr>
<td>EBD (S)</td>
<td>DFS</td>
<td>Dry Forest System</td>
<td>Ba, Bo, Co, W, Buc, T</td>
</tr>
<tr>
<td></td>
<td>DFdomMF</td>
<td>Dry Forest dominant/moist forest</td>
<td>Ba, Bl, Co, W, T</td>
</tr>
<tr>
<td>FES</td>
<td>89</td>
<td>Eastern tablelands Acacia/herb/grass forest</td>
<td><em>E. dalyrmpleana /E.viminalis/Acacia melanoxylon/Stellaria pungens</em></td>
</tr>
<tr>
<td></td>
<td>73</td>
<td>Eastern tableland dry shrub/grass forest</td>
<td><em>E. pauciflora/E. dalyrmpleana/A. dealbata/helichrysum scorpioides</em></td>
</tr>
<tr>
<td>Database</td>
<td>Code</td>
<td>Description</td>
<td>Dominant Species</td>
</tr>
<tr>
<td>---------------------------</td>
<td>------</td>
<td>--------------------------------------------------</td>
<td>----------------------------------------------------------------------------------</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td>Northern Tablelands Acacia Herb/Grass Dry Forest</td>
<td><em>E. bridgesiana / Acacia dealbata / Hydrocotyle laxiflora</em></td>
</tr>
<tr>
<td></td>
<td>93</td>
<td>Western Tablelands herb/grass dry forest</td>
<td><em>E. robertsonii/Microlaena stipoides</em></td>
</tr>
<tr>
<td></td>
<td>103</td>
<td>Western montane dry fern/grass forest</td>
<td><em>E. dives/E. dalrympleana/E. robertsonii/Pteridium esculentum/Poa sieberiana</em></td>
</tr>
<tr>
<td></td>
<td>108</td>
<td>Western tablelands Dry herb/grass forest</td>
<td><em>E. macrorhyncha, E. dives, Hibbertia obtusifolia, Poa sieberiana</em></td>
</tr>
<tr>
<td></td>
<td>121</td>
<td>Western slopes grass/herb dry forest</td>
<td><em>E. macrorhyncha/E. goniocalyx, gonocarpus tetragnus/Poa sieberiana</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>SCIVI</td>
<td></td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>Sydney coastal dry sclerophyll forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>Sydney montane dry sclerophyll forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>South East Dry sclerophyll forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>Southern Tablelands Dry sclerophyll Forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>79</td>
<td>Central gorge dry sclerophyll forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>81</td>
<td>Southern hinterland dry sclerophyll forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>Diehard stringybark – New England blackbutt</td>
<td></td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>Dry grass stringybark</td>
<td></td>
</tr>
<tr>
<td></td>
<td>110</td>
<td>Open silvertop</td>
<td></td>
</tr>
<tr>
<td></td>
<td>113</td>
<td>Peppermint</td>
<td></td>
</tr>
<tr>
<td></td>
<td>132</td>
<td>Snow gum–mountain/manna gum</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wallerawang Map Sheet</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mt Walker complex: Woodland</td>
<td><em>E. dives, E. mannifera, E. bridgesiana, E. rossii</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Newnes Plateau Woodland</td>
<td><em>E. sieberi, E. oreades, E. dives</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Blue Mountains Woodland</td>
<td><em>E. sieberi, E. piperita</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sandstone Plateau</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Woodland (Wo)</td>
<td></td>
</tr>
<tr>
<td>Database</td>
<td>Code</td>
<td>Description</td>
<td>Dominant Species</td>
</tr>
<tr>
<td>---------------</td>
<td>------</td>
<td>-------------------------------------------------</td>
<td>-----------------------------------------------------------------------</td>
</tr>
<tr>
<td>EBD (C)</td>
<td>W</td>
<td>Woodland System</td>
<td></td>
</tr>
<tr>
<td>EBD (S)</td>
<td>WdomFP</td>
<td>Woodland dominant/forest present</td>
<td></td>
</tr>
<tr>
<td>FES</td>
<td>W</td>
<td>Woodland</td>
<td></td>
</tr>
<tr>
<td></td>
<td>101</td>
<td>North western montane dry shrub/herb/grass forest</td>
<td><em>E. dalrympleana</em>/<em>E. pauciflora</em>/<em>Daviesia latifolia</em>/<em>Coprosma hirtella</em>/<em>Stellaria pungens</em></td>
</tr>
<tr>
<td></td>
<td>116</td>
<td>Western slope herb/grass woodland</td>
<td><em>E. blakelyi</em>/<em>microlaena stipoides</em>/<em>Hydrocotyl laxiflora</em></td>
</tr>
</tbody>
</table>

**Disturbed dry forest (DDF)**

<table>
<thead>
<tr>
<th>Database</th>
<th>Code</th>
<th>Description</th>
<th>Dominant Species</th>
<th>Sites Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>EBD (C)</td>
<td>SD-DF</td>
<td>Severely disturbed dry forest</td>
<td></td>
<td>MW</td>
</tr>
<tr>
<td></td>
<td>SDF</td>
<td>Severely disturbed forest</td>
<td></td>
<td>N, P, Mu, G, J, K, L</td>
</tr>
<tr>
<td>EBD (S)</td>
<td>SD-DF</td>
<td>Severely disturbed dry forest</td>
<td></td>
<td>Co, Buc, W</td>
</tr>
<tr>
<td></td>
<td>Log</td>
<td>Regrowth – obvious loggind</td>
<td></td>
<td>Co</td>
</tr>
<tr>
<td></td>
<td>SDF</td>
<td>Severely disturbed forest</td>
<td></td>
<td>Penr</td>
</tr>
</tbody>
</table>

**Disturbed wet forest (DWF)**

<table>
<thead>
<tr>
<th>Database</th>
<th>Code</th>
<th>Description</th>
<th>Dominant Species</th>
<th>Sites Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>EBD (S)</td>
<td>DMF</td>
<td>Disturbed moist Forest</td>
<td></td>
<td>Buc</td>
</tr>
</tbody>
</table>

**Disturbed dry woodland (DDW)**

<table>
<thead>
<tr>
<th>Database</th>
<th>Code</th>
<th>Description</th>
<th>Dominant Species</th>
<th>Sites Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>EBD (N)</td>
<td>DW</td>
<td>Disturbed Woodland</td>
<td></td>
<td>HR</td>
</tr>
</tbody>
</table>

**Degraded Grassland (DG)**

<table>
<thead>
<tr>
<th>Database</th>
<th>Code</th>
<th>Description</th>
<th>Dominant Species</th>
<th>Sites Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>EBD (C)</td>
<td>DG</td>
<td>Degraded Grassland</td>
<td></td>
<td>MW, J</td>
</tr>
<tr>
<td>EBD (S)</td>
<td>DG</td>
<td>Degraded grassland</td>
<td></td>
<td>Penr</td>
</tr>
</tbody>
</table>

**Grassland (G)**

| SCIVI         | 46   | Temperate montane grasslands                   |                                                                       | Co, Bondi             |

**Grassy Woodlands (GW)**

<table>
<thead>
<tr>
<th>SCIVI</th>
<th>40</th>
<th>Tableland clay grassy woodlands</th>
<th></th>
<th>Co, bondi</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>45</td>
<td>Subalpine woodlands</td>
<td></td>
<td>Co</td>
</tr>
<tr>
<td></td>
<td>86</td>
<td>Southern tableland grassy woodlands</td>
<td></td>
<td>Be</td>
</tr>
</tbody>
</table>

**Plateau complex, heath and woodland (P)**

<table>
<thead>
<tr>
<th>Database</th>
<th>Code</th>
<th>Description</th>
<th>Dominant Species</th>
<th>Sites Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>EBD (C)</td>
<td>PIC</td>
<td>Plateau complex</td>
<td><em>Mix of dry sclerophyll and</em></td>
<td>N</td>
</tr>
<tr>
<td>Database</td>
<td>Code</td>
<td>Description</td>
<td>Dominant Species</td>
<td>Sites Present</td>
</tr>
<tr>
<td>----------------</td>
<td>------</td>
<td>------------------------------</td>
<td>--------------------------------------------------------</td>
<td>---------------</td>
</tr>
<tr>
<td></td>
<td></td>
<td>heath</td>
<td>Mix of dry sclerophyll and heath</td>
<td>Co, W</td>
</tr>
<tr>
<td>EBD (S)</td>
<td>PIC</td>
<td>Plateau complex</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock complex (R)</td>
<td></td>
<td>Rock Complex</td>
<td></td>
<td>N, Mu</td>
</tr>
<tr>
<td>EBD (C)</td>
<td>R</td>
<td>Rock Complex</td>
<td></td>
<td></td>
</tr>
<tr>
<td>EBD (S)</td>
<td>RO</td>
<td>Rocky outcrops</td>
<td></td>
<td>Ba</td>
</tr>
<tr>
<td>Wetlands (WL)</td>
<td></td>
<td>Montane Bogs and Ferns</td>
<td></td>
<td>Penr</td>
</tr>
<tr>
<td>SCIVI</td>
<td>55</td>
<td>(Freshwater wetlands)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>Temperate swamp forest</td>
<td></td>
<td>Penr</td>
</tr>
<tr>
<td>(Forested wetlands)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heath (H)</td>
<td></td>
<td>Montane heath</td>
<td>Allogasurina nana, Banksia ericifolia, Leptospermum attenuatum, Phylotta squarrosa</td>
<td>Co, W, N</td>
</tr>
<tr>
<td>EBD (S)</td>
<td>AH</td>
<td>Allogasurina nana heath</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SCIVI</td>
<td>32</td>
<td>Sydney Coastal heaths</td>
<td></td>
<td>W</td>
</tr>
<tr>
<td>Wallerawang Map Sheet</td>
<td>32</td>
<td>Montane heath</td>
<td>Allogasurina nana, Banksia ericifolia, Leptospermum attenuatum, Phylotta squarrosa</td>
<td>N</td>
</tr>
<tr>
<td>Remnant</td>
<td></td>
<td>Remnant Bushland</td>
<td></td>
<td>MW. SC. Be, G, K</td>
</tr>
<tr>
<td>EBD (C)</td>
<td>RB</td>
<td>Remnant Bushland</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

![Diagram showing vegetation composition across different regions](image-url)
LITERATURE CITED


Becerra PI, Bustamante RO (unpublished) Effect of habitat conditions and native trees on the recruitment of the exotic species *Pinus radiata* and *Eucalyptus globulus* in a Mediterranean ecosystem of central Chile.


Crockford RH, Richardson DP (1990) Partitioning of rainfall in a eucalypt forest and pine plantation in southeastern Australia: IV The relationship of interception and canopy storage capacity, the interception of these forests, and the effect on interception of thinning the pine plantation. Hydrological Processes. 4: 169-188.


Kasel S (2004b) Re-establishment of Native Vegetation on Former Pine Plantations: an Australian Perspective. School of Forest and Ecosystem Science, University of Melbourne, Creswick, Victoria.


Rabie PA (2000) Control of commercially important *Pinus* spp. in fynbos. Restoration and Reclamation Review. 6(5). 9 pp.


Rosenberg MS (2001) PASSAGE Pattern Analysis, Spatial Statistics, and Geographic Exegesis 1.1.1.3.


