Chapter 1. Introduction

"Behold I scatter and spread here and there among thy very weeds and grass growing upon the ground, other especial shining stars ... and ... thou shouldst not either plead ignorance or neglect the same, I provoke thee to regard and look thereat, as a strange wonder."

C. Plinius Secundus or Pliny, *The History of the World*, commonly called *The Natural History*, eighteenth book, c. 70 AD, translated by Philemon Holland, McGraw Hill Book Company, New York, 1962.

Introduction

Natural temperate grassland is one of the most threatened ecosystems of south eastern Australia, with <1% of its area prior to European settlement remaining (Groves and Whalley 2002, Carter *et al.* 2003, DEWHA 2008). The exotic Chilean Needle Grass *Nassella neesiana* (Trin. & Rupr.) Barkworth (Poaceae: Stipeae) is one of the more recent threats to the integrity of these grasslands. *Nassella neesiana* is a hardy, long-lived, C_3 tussock grass, native to South America, which is highly invasive in Australia and is reportedly able to out-compete temperate native grassland species (Hocking 1998, ARMCANZ *et al.* 2001, Grice 2004b, McLaren *et al.* 2004a). It has been identified as a highly significant threat to grassland biodiversity and an ongoing cause of rapid degradation of remnants (Morgan 1998d, Groves and Whalley 2002, McLaren *et al.* 2004a).

Nassella neesiana was listed as one of 20 Weeds of National Significance (WoNS) in Australia in 1999 (Iaconis 2003), based on evaluation by technical experts on six invasiveness questions, seven impact questions, potential for spread, and documentation of socioeconomic and environmental impacts (Thorp and Lynch 2000, McLaren *et al.* 2002a). Recognition as a WoNS resulted in a National Strategic Plan that required assessment of the conservation impacts of the grass, investigations of its biology and ecology, and prevention of invasions and spread (ARMCANZ *et al.* 2001). Earlier, Gardener and Sindel (1998) had advocated quantitative studies to evaluate the biodiversity impacts of *N. neesiana*, compare the impacts resulting from general degradation of land and vegetation, and evaluate the effects of *N. neesiana* management techniques on the promotion or inhibition of biodiversity. Grice (2004a) concurred with the need for such studies, noting that monitoring of biodiversity can be an important tool in evaluating a weed management strategy. The study reported here is a major contribution to the fulfilment of these objectives.

Biology of *N. neesiana*

Little appears to be known about *N. neesiana* biology in its native lands, and like many invasive species, the focused scientific studies of *N. neesiana* have very largely been undertaken in the areas of invasion, notably New Zealand from the mid 1980s (e.g. Bourdôt and Hurrell 1989a 1989b 1992, Connor *et al.* 1993, Slay 2002c), and Australia (e.g. Gardener 1998, Hocking 1998 2002 2005b, McLaren *et al.* 1998, Gardener *et al.* 2003a 2003b, Grech 2007).

The major findings of these studies include: identification of a very large potential distribution range for *N. neesiana* in Australia (Gardener 1998, McLaren *et al.* 1998, Morfe *et al.* 2003) covering most of the area with remnant temperate natural grasslands; high rates of seed production, including clandestine basal cleistogenes; large persistent soil seed banks; and adaptations that promote animal dispersal, particularly in the wool of sheep and within the digestive tracts of livestock (Gardener 1998, Gardener *et al.* 2003a 2003b). A general consensus was also reached that *N. neesiana* is extremely difficult to eradicate (Gardener 1998, Gardener and Sindel 1998, Slay 2002a). In natural grasslands, according to Kirkpatrick *et al.* (1995 p. 35), it "seems impossible to control in its early invasive stage without causing great damage to native vegetation".

Nassella neesiana tussocks are "very hardy" and long-lived (Storrie and Lowien 2003) with over 70% of plants surviving over 3 years (Gardener *et al.* 1999) and individuals having a longevity of over 20 years (Benson and McDougall 2005). Bourdôt and Hurrell (1989a) found that plants had persisted at the probable first introduction point for c. 60 years. It appears to be well adapted to seasonal dryness (Bourdôt and Hurrell 1987b) and is drought tolerant (Muyt 2001, McLaren *et al.* 2002b, Slay 2002c, Storrie and Lowien 2003). *Nassella neesiana* forms "dense thickets" (ACT Weeds Working Group 2002), "can completely overrun pastures' with canopy cover of up to 60% (Gardener 1998 p. 4) or even higher (Grech *et al.* 2005), and sometimes forms "continuous pasture" (Slay 2002c). Cover of up to 70% has been recorded in native grasslands (Stewart 1996) although monitoring by McDougall and Morgan (2005) found it never exceeded 22% at one grassland. *Nassella neesiana* possesses many environmental traits that allow it to outcompete native vegetation (Gardener and Sindel 1998), being competitive for space, light, water and nutrients (Wells *et al.* 1986), and is very competitive when mature (Cook 1999). In native grasslands it can "almost completely displace perennial native grasses" (Liebert 1996 p. 8) and reportedly excludes all other species (Kirkpatrick *et al.* 1995).

Poaceae in general have very effective dispersal mechanisms, and alien Poaceae grass species usually comprise a large proportion of the grass flora in many regions of south-eastern Australia, particularly in livestock-based agroecosystems, and the family is commonly a major contributor to environmental weed floras (Wheeler *et al.* 1990, Williams and West 2000, Milton 2004). Species of Stipeae are commonly adventive and numerous taxa have dispersed to remote islands and intercontinentally (Connor *et al.* 1993, Watson and Dallwitz 2005). On a world basis, at least 12 *Nassella* species have been reported growing outside their native range (Randall 2002, Barkworth 2006, Baeza *et al.* 2007), comprising c. 10% of the genus. *Nassella neesiana* has dispersed to, and established in, North America, Africa, New Zealand and numerous countries in Europe (Thellung 1912, Hayward and Druce 1919, Hitchcock and Chase 1971,Wells and Stirton 1982, Moraldo 1986, Wells *et al.* 1986, Bourdôt and Hurrell 1987a, Jacobs *et al.* 1989, Edgar *et al.* 1991, Vàzquez and Devesa 1996, Stace 1997, Gardener 1998, Martín Osorio *et al.* 2000, Font *et al.* 2001, Slay 2002a, Germishuizen and Meyer 2003, Weber 2003, Scholz and Krigas 2004,Verloove 2005, Barkworth 2006, Gassó *et al.* 2009). However, so far it has only become a widespread and important weed in Australia. The plant was first recorded in Australia in the Melbourne suburb of Northcote in 1934, in New South Wales at Glen Innes in 1944 (McLaren *et al.* 1998) and in the Australian Capital Territory in 1960 (Gardener 1998). There are no published estimates of the area of Australia infested (Anderson *et al.* 2002, McLaren *et al.* 2004b), but McLaren *et al.* (2002b) determined from a survey of landholders in areas known to have *N. neesiana* populations in Victoria, New South Wales and the Australian Capital Territory, that infestations occurred over an area of over 4 million ha and that the plant was still actively dispersing.

The origins, mode of entry and dates of first establishment of Australian *N. neesiana* remain unknown (Grice 2004b, McLaren *et al.* 2004a). Deliberate introductions and trials as a pasture grass have occurred (Rogers *et al.* 1979, Cook and Dias 2006) but these post-date the first records of the plant in Australia and there is no indication that escapes from such trials have resulted in established populations.

Propagule pressure, dependent on fecundity, dispersal mechanisms and the availability and incidence of dispersal agents, is an indispensable requirement for plant invasions and may be more important than any other factor in determining the success of a potential invader (Williamson and Fitter 1996, Lonsdale 1999, Levin 2006, Lockwood *et al.* 2009). Strong propagule pressure has been a major factor in the Australian *N. neesiana* invasion and the ability of the plant to maintain its infestations (Gardener 1998, Grech 2007). The panicle seeds of *N. neesiana* are classed as creeping diaspores that are able to move along the ground under the influence of humidity variations, but such movement generally results in little actual dispersal, and is more important in enabling seeds to lodge in microsites favourable for germination (Peart 1979, Davidse 1986, Connor *et al.* 1993, Gardener and Sindel 1998, Sinclair 2002). The panicle seed has exozoochorous dispersal mechanisms, and dispersal by livestock, particularly in the fleece of sheep, has been widely recognised as important (Bourdôt and Ryde 1986, Connor *et al.* 1993, Gardener 1998, Slay 2002c, Gardener *et al.* 2003a, Grech 2007). Beyond this, the panicle seeds and the aggregates they form have many morphological features that enable attachment to a wide range of objects, including vehicles and machinery, and there is general consensus that human activities are the major cause of dispersal in Australia (Gardener *et al.* 1999, Slay 2002c, Bedggood and Moerkerk 2002, Snell *et al.* 2007). The Australian distribution can be characterised as synanthropic: infestations are strongly associated with urban areas, roads, agricultural pastures and the cultural steppe (Hocking 2007, Snell *et al.* 2007). *Nassella neesiana* also possesses subsidiary panicles with cleistogamous flowers, concealed beneath leaf sheaths on culm nodes. The cleistogenes produced may be adapted for endozoochorous dispersal resulting from the consumption of stems by grazing animals, while those at the base of the plant may be adapted not to disperse but to enable regeneration after mortality of the parent plant (Dyksterhuis 1945, Bourdôt 1989, Gardener and Sindel 1998, Gardener *et al.* 2003a). Both panicle and stem seeds can be distributed and remain viable after ingestion by livestock, but usually a high proportion of seeds are digested, and the viability of those that survive gut passage is much reduced (Davidse 1986, Gardener *et al.* 2003a, Stanton 2006).

Extensive distribution along floodways and watercourses has led to the inference that movement of *N. neesiana* seeds in flowing water is important (Hayward and Druce 1919, Bourdôt and Ryde 1986, Cook 1999, Bedggood and Moerkerk 2002, Frederick 2002, Slay 2002b). However published information on water dispersal appears to be completely lacking. A recent technical report by Hocking (2011) confirms the association of *N. neesiana* with water-borne mechanisms of dispersal.

Ecology of temperate natural grasslands

Throughout the world temperate native grasslands have been centres of human agricultural and urban development and subjected to high levels of anthropogenic disturbance, making them generally highly prone to invasion by exotic plants (Fox and Fox 1986, Hobbs 1991, Adair 1995, Adair and Groves 1998). Consequently, all are now conspicuously invaded by weeds (Aguiar 2005). In Australia, temperate grasslands are one of the ecosystems most severely affected and heavily invaded by a wide range of exotic plant species (McIntyre and Lavorel 1994a, Groves and Whalley 2002).

The impact of *N. neesiana* in the natural temperate grasslands of south-eastern Australia is a particular concern because of the small areas of this endangered ecosystem that remain. Carter *et al.* (2003 p. 76) concluded that extant remnants represented 1.7% of the pre-1750 area (an estimated 5.8 million ha), that only a small proportion of these were in good condition, and that "few or no ... large, species rich" sites existed. Most remnants are "isolated, modified and have habitat elements missing" (Hocking 2005a). The high boundary: area ratio of the small reserves intensifies a range of edge effects and increases their susceptibility to various disturbances and to invasion by exotic plants (Morgan 1998d, Sharp 1997, Byers *et al.* 2002, Mathison 2004, Williams *et al.* 2006). In particular, large edge: area ratios increase invasion opportunities from adjacent, usually weedy habitat (Davies 1997). Native plant richness in surviving remnants is strongly related to the historical disturbance regime, particularly burning and grazing history (Kirkpatrick *et al.* 1995, Dorrough *et al.* 2004). Although DNRE (1997) considered the Victorian Basalt Plains grasslands to be floristically rich at a regional scale, Willis (1964) considered the flora to be floristically 'deficient' in comparison with other regions of the State, and these grasslands are considerably less species-diverse than some herb-rich grassy woodlands of western Victoria (Lunt 1990d).

The vascular plant floras of Australian temperate native grasslands have been relatively well described (Tremont and McIntyre 1994) although it is unclear to what extent the extant floras are representative of the pre-European situation, or even of the early historical period. Profound changes in composition due to grazing occurred across most areas after European colonisation (Wadham and Wood 1950 p. 87) and there was an almost complete "lack of adequate description before alteration occurred" (Jones 1999 p. 29). The pre-European composition is "poorly understood" (McIntyre and Lavorel 2007), "almost impossible" to determine (Lunt 1990a p. 47) or "speculative" (Lunt *et al.* 1998). But there is general agreement that the pre-European grassland was probably more diverse than current reference areas, and that many species have been eliminated or greatly depleted in most areas (Sharp 1997), as is "undoubtedly" the case for the grassy woodland remnants of south-eastern Australia (Lunt 1995b p. 239). Many of the major exotic plant components are of agricultural origin and the prevalence of exotics is strongly correlated with historical intensity of grazing (Moore 1973, Lunt *et al.* 1998).

Dominant and subdominant grasses

Temperate grassland remnants are, or once were, generally dominated by perennial tussock grasses including *Themeda triandra* Forssk., *Poa*, *Austrodanthonia* and *Austrostipa* species, with the latter two genera being more dominant in drier areas (Kirkpatrick *et al.* 1995, Sharp 1997, Lunt and Morgan 2002). *Themeda triandra* was almost certainly the most widespread and dominant grass before European occupation (Groves 1965, Mack 1989, Moore 1993, Kirkpatrick *et al.* 1995, Lunt *et al.* 1998) and it generally accounts for a very high proportion of the biomass (Groves 1965). The tussocks are mostly widely spaced (10 cm or more apart) and grass cover may be only 30-50%, so the vegetation is often relatively open, with much 'bare' ground (Sutton 1916-1917, Patton 1935, Lunt *et al.* 1998, Lunt and Morgan 2002). Except for *T. triandra* and *Bothriochloa macra* (Steud.) S.T. Blake, the major grasses have the C_3 photosynthetic pathway and grow mostly in spring and autumn (Groves and Whalley 2002).

Themeda triandra (Andropogoneae), is a C_4 (warm season), perennial tussock grass adapted to frequent fire but susceptible to eradication by introduced livestock and is a keystone species in areas it dominates (Groves and Whalley 2002, Prober and Lunt 2009). It is highly productive under suitable climatic conditions and develops high biomass in the absence of fire or grazing (Groves 1965, Morgan 1998e). In common with dominant caespitose grasses in temperate grasslands around the world, its accumulation of dead leaves and litter gradually reduces floristic richness by excluding plants of the intertussock spaces (Stuwe and Parsons 1977, McIntyre 1993, Morgan 1995b 1997b 1998b 1999b, Henderson 1999, Overbeck and Pfadenhauer 2007). Under natural conditions this biomass accumulation functions to promote burning, and frequent fire enables *T. triandra* to retain its dominance. But in the absence of fire or other biomass reduction a process of senescence can proceed, after a period of years, to a stage where a self-shading effect prevents the growth of new tillers, and eventually results in tussock death (Lunt and Morgan 1999c, Morgan and Lunt 1999). This senescence dieback has been found to remove biotic resistance and open the community to invasion by weeds including *N. neesiana* (Lunt and Morgan 2000).

Plants of the intertussock spaces

Herbs that grow in the intertussock spaces account for most of the floristic diversity (Lunt 1991, Trémont and McIntyre 1994, Sharp 1997, Carter *et al.* 2003). These are mostly geophyte or hemicryptophyte forbs except in the driest regions where they are annuals, with the exotic species mostly annuals (Morgan 1994, Trémont and McIntyre 1994, Lunt *et al.* 1998, Lunt and Morgan 2002). As with other temperate grasslands worldwide, most species are post-fire resprouting, long-lived forbs and there are few obligate seeders (Overbeck and Pfadenhauer 2007).

Early historical records indicate an abundance of lilies, orchids, daisies and other forbs (Lunt *et al.* 1998), with the predominant native families apart from Poaceae in modern times being Asteraceae and Liliaceae *sens. lat.* (Sutton 1916-1917, Patton 1935, Willis 1964, Groves 1965, Kirkpatrick *et al.* 1995, Morgan and Rollason 1995, Carr 1999). Other important families include Fabaceae, Orchidaceae, Cyperaceae and Juncaceae, with the former two now often severely depleted (Willis 1964, Trémont and McIntyre 1994, Kirkpatrick *et al.* 1995, Carr 1999, Jones 1999, ACT Government 2005, Smith *et al.* 2009). A high proportion of species occur infrequently, many occur rarely, and a disproportionately large number are threatened (McIntyre and Lavorel 1994a 1994b, Morgan 1997a, Lunt *et al.* 1998, Carr 1999). Detailed ecological knowledge exists for only a few species (Morgan 1999b).

Maintaining or enhancing the native forb component is one of the key problems in biodiversity management in native lowland grasslands (Morgan 1998b 1999b). Many species appear to have highly specific regeneration niches that now rarely occur but may be created by management practices that are often currently considered to be harmful, such as soil disturbance that mimics the activities of the native vertebrates that once inhabited these grasslands (McIntyre 1995, Robinson 2003, Reynolds 2006).

Exotic plants

Exotic plants are now present almost universally in temperate Australian grasslands, and include a wide diversity of annual, biennial and perennial forbs, and annual and perennial grasses (Trémont 1994, Kirkpatrick *et al.* 1995, Sharp 1997, Eddy *et al.* 1998, Groves and Whalley 2002, Carter *et al.* 2003, Dorrough *et al.* 2004). Lowland grassland in Victoria was considered by Carr *et al.* (1992) to be one of the weediest of the broad vegetation formations in Victoria, with 344 exotic taxa, of which 87 were considered very serious weeds. Between one quarter and one third of the flora in each of the main grassland regions consists of exotics, and weed invasion is a major problem for survival of the native flora (Kirkpatrick *et al.* 1995, Groves 2004).

Exotic invasions occurred simultaneously with the introduction of livestock and resulted from their carriage of seed, the transport of fodder and the superior adaptations for survival that these plants possessed under the new grazing regimes (Moore 1973, Mack 1989, Kirkpatrick *et al.* 1995). Invasions may have been facilitated by the disappearance or dysfunction of *T. triandra*, the various C_3 grass species, or the intertussock forbs (Groves and Whalley 2002) resulting from various forms of disturbance, with raised levels of available soil nutrients resulting from the destruction of *T. triandra* having particularly insidious effects (Wijesuriya and Hocking 1999). Since the 1930s, exotic invasions have continued, driven *inter alia* by the introduction of new pasture species and generalised fertiliser addition (Kirkpatrick *et al.* 1995).

Dynamics

Classical succession theory is an inappropriate framework for understanding the dynamics of lowland native grasslands as currently understood: there is no climax formation and the composition varies little over time (if the exotic components are disregarded), but does vary widely on a patch scale in otherwise uniform areas (Mott and Groves 1994). The compositional variation that occurs is explained in part by high rates of dormancy by many species, characterised as ‘pseudo turnover’ by Morgan (1998e). However, a type of successional change may possibly occur when *T. triandra* senescence dieback occurs. Under current conditions, weeds often invade following *T. triandra* senescence, but what happens, or once happened, when exotic plants are absent appears to be unclear. The result might have once been herb-rich formations, or dominance by other grasses.

Most of the native plant species flower and fruit mainly in spring-early summer, the major flowering period corresponding with the time that evaporation begins to exceed precipitation – a high proportion of these forb species have no living parts above ground for much of the year (Patton 1935, Willis 1964, Lunt *et al.* 1998, Groves and Whalley 2002).

The absence of a successional climax means that the longer term dynamics are best described by 'state and transition' models, with disturbance and management regimes determining the dynamics of the plant components. McIntyre and Lavorel (2007) presented such a model for temperate grassy woodlands of south-eastern Australia that exemplifies historical chains of development (Fig. 1.1). Transitions from one state to another occur as a result of specific management activity (or the lack of it). Invaded grasslands with moderate or high exotic components have been permanently altered (Mack 1989) and appear to represent a new metastable condition that does not revert to its former status (Sharp 1997). Native pasture may revert back to native grassland, but its properties and composition will have been more or less altered. "Enriched grassland" includes areas no longer cultivated or managed for grazing but which remain nutrient enriched, are largely dominated by exotic perennial pasture rosette-forming herbs and appear to be "an alternative stable state [requiring] a very high level of management to shift" (McIntyre and Lavorel 2007p. 15).

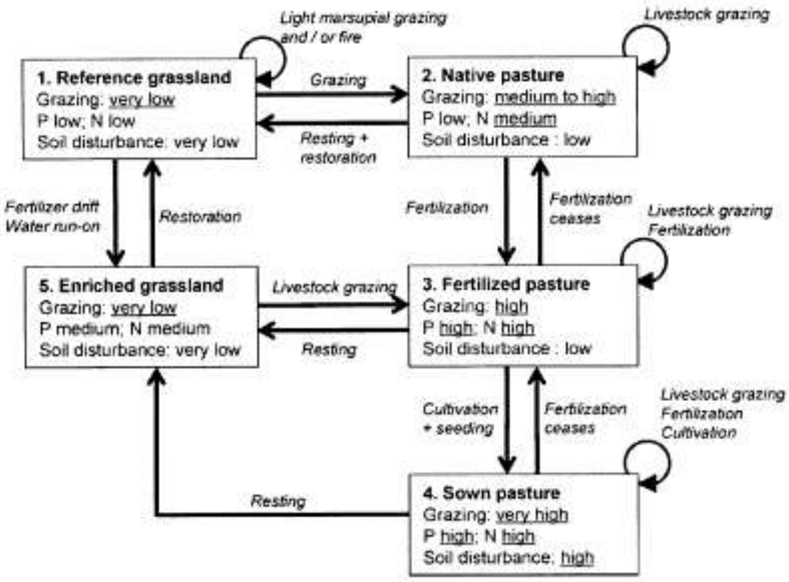

Figure 1.1. The McIntyre and Lavorel (2007 p. 14) 'state and transition model' for temperate grassy woodlands of south-eastern Australia.

Management inputs required include nutrient depletion, weed control (including the dominant grasses) and reintroduction of native species, particularly forbs. There is are pronounced variation in scientific understanding of the different states and processes, reflecting the historical agronomic approach to the study of agricultural land, and the use of floristic ecological techniques in natural grasslands. The least understood transitions are those that may be classed as restoration: from developed pastures through enriched grassland back to native grassland (McIntyre and Lavorel 2007). Transition from reference grassland to enriched grassland supposedly occurs in most cases accidentally, through nutrient enrichment from fertiliser drift or water movement.

Fauna

The grasslands of temperate south-eastern Australia were once inhabited by a marsupial megafauna which may have been important in their formation and probably disappeared due to aboriginal hunting in association with other factors (e.g. changes in climate), at some time from 26 to 15 kybp (Webb 1978, Flannery 1994, Kershaw *et al.* 2000, Johnson 2009). Before European occupation, and in early historical times, the temperate grasslands were inhabited by a diverse fauna of medium sized marsupials, which have subsequently almost entirely disappeared (Wakefield 1964a 1964b, Aitken 1983, Menkhorst 1995, Lunt *et al.* 1998, Hadden 2002, Keith 2004). The complex consequences of the loss of native grazing species, mammalian plant-predators and carnivores have only recently begun to be explored, and very little is known about the ramifications. However the removal or alteration of soil disturbance by mammals has probably had a strong negative impact on regeneration of many native forbs (Reynolds 2006), and the dispersal opportunities for many types of native plant seeds must have been radically altered.

Insects are the dominant herbivores in temperate grasslands (Tscharntke and Greiler 1995). They are a prominent feature of Australian formations and comprise the overwhelming majority of the invertebrate faunas (Yen 1999, Gibson and New 2007). Many minor and some major studies of the invertebrate faunas of Australian natural temperate grasslands have been undertaken (e.g., Melbourne 1993, Yen *et al.* 1994a 1994b 1995, Driscoll 1994, Daniell 1994, Edwards 1994, Greenslade 1994, Rowell and Crawford 1995, Hadden 1997 1998, Sharp 1997, Farrow 1999 2006, Hadden and Westbrooke 1999, New 2000, Gibson and New 2007) but this ecosystem remains among the least investigated entomologically in south-eastern Australia (Gibson and New 2007). Useful generalisations about the invertebrate fauna have not so far been possible (Yen 1995 1999) and no adequate synthesis of the scattered knowledge exists.

Aboriginal management and utilisation

In south-eastern Australia, the densest aboriginal populations were centred on permanent water sources (Gott 1993). Apart from riverine areas and the coast, extensive grasslands and open woodlands were the main ecosystems occupied (Kirkpatrick *et al.* 1995). Most of Australia, including Tasmania, was probably occupied by aboriginal people by 35,000 (Hope 1994) or 32,000 years bp, all major environments were certainly occupied by 22,000 years bp, and occupational intensities increased after c. 5,000 years bp (Kershaw *et al.* 2000). Digging of tuberous and bulbous food plants and burning of the vegetation were probably the most important aboriginal activities impacting on grassland ecology, and areas of open grassland appear to have been extended in size by aboriginal activities (Kirkpatrick *et al.* 1995, Gott 2005). Roots of numerous species were harvested for food by intensive digging, particularly Murnong, *Microseris* spp., which was stockpiled and traded, as well as Turrac (probably *Pelargonium rodneyanum*) (Gott 1983, Wigney 1994, Zola and Gott 1992, Lunt *et al.* 1998, Gott 1999 2005). Approximately one quarter of the vascular plant species recorded in the Victorian Basalt Plains were used by aboriginals, of which approximately 20% were used as food (Gott 1999). Digging would have resulted in improved aeration, water infiltration and nutrient incorporation, and increased the availability of regeneration niches for many plants (Gott 1999 2005).

Aboriginal burning of grasslands was probably frequent prior to European occupation, being used in hunting and to encourage new growth, and probably assisted in maintaining treelessness (Stuwe 1994, DNRE 1997, Jones 1999). Aborigines would have increased fire frequency above the background rate as a result of deliberate burning, accidental escapes from camp fires (Stuwe 1994) and possibly the use of fire as a weapon against invading non-indigenous people (Flannery 1994). The average fire interval may have been about 5 years and summer burning was possibly commonplace (Gott 2005). However little is known about the motives, scale and ecological significance of aboriginal fire management in Australia (Murphy and Bowman 2007) and palynological records of grasses in lake and swamp cores indicate that south-eastern Australian grasslands existed long before aboriginal occupation, and are not of anthropogenic origin (Jones 1999, Kershaw 2000); rather, aboriginal activities modified existing grassy ecosystems and shifted their boundaries (Jones 1999). Aboriginal fire regimes are “embedded” in the ecosystem and can potentially be revealed by modern studies (Gott 2005 p.1203), e.g. by palaeobotanical studies of soils or lake sediments.

Pastoral development had an immediate and devastating effect on the aboriginal population: introduced livestock destroyed their prime feeding grounds and muddied and destroyed the waterholes and soaks (Zola and Gott 1992). Diseases and other mortality had decimated aboriginal populations by the mid 1850s (Coutts 1982). The cessation of aboriginal fire regimes resulted in well-documented substantial change in vegetation structure, particularly involving increases in tree cover (Hope 1994).

Historical management

European occupation brought a novel range of exogenous disturbances that resulted in rapid, abrupt changes to Australian grasslands, initially largely due to grazing of sheep and other livestock (McIntyre and Lavorel 1994a, Dorrough *et al.* 2004). Grasslands were preferentially occupied by squatters and their livestock very early in the colonial period (Johnson and Jarman 1975, Sharp 1997, Jones 1999, Mansergh *et al.* 2006a). Thirty million sheep had been introduced to the grassy plains of Victoria and New South Wales by 1851, along with 1.7 million cattle and 32,000 horses (Lunt *et al.* 1998). Grazing rapidly caused severe degradation and ecological breakdown of the native ecosystems (Mansergh *et al.* 2006a), "permanent" changes in floristic composition (Groves *et al.* 2003) and led to the formation of vast areas which Matthews (1976) characterised as the "cultural steppe".

From the 1860s large areas of Crown land began to be alienated, cultivation of major areas commenced, particularly for cereal growing, and fencing began to be used instead of shepherding (Johnson and Jarman 1975, Powell and Duncan 1982, Scarlett and Parsons 1993). By 1910 pasture occupied c. 12 million ha in Victoria, of which <5% was sown (Mansergh *et al.* 2006a). From this period through to the 1950s closer settlement schemes led to more intensive development of most grassland areas (Powell and Duncan 1982). By 1916, Sutton (1916-1917 p. 112) observed that the Keilor Plains grasslands to the north and west of Melbourne "had been put so thoroughly to pastoral and agricultural uses that hardly any part now remains in the virgin state." Further destruction of native grasslands occurred through the use of fertilisers, particularly superphosphate, from the 1930s onwards, and the sowing of exotic grasses and herbaceous legumes which naturalised and dispersed widely (Moore 1973 1993, Groves and Whalley 2002, Cook and Dias 2006, Mansergh *et al.* 2006a). These changes resulted in P and N enrichment of the soil, facilitating the invasion of new suites of weeds, but lifted productivity "in the short term" (Keith 2004 p. 105). In Victoria, the area of native pasture dropped from c. 8 million ha in 1950-51 to c. 2 million ha in 2000-01 (Mansergh *et al.* 2006a).

Destruction of the natural grasslands by livestock followed a similar course to that in temperate grasslands on other continents that were dominated by caespitose (tussock-forming) grasses and lacked large, native, congregating, hard-hooved ungulate grazers during the Holocene (Mack 1989). Growing points and reproductive structures of the tussock grasses were more susceptible to destruction than rhizomatous grasses (Mack 1989) and the perenniality of the dominant species, which "made annual re-establishment unnecessary", meant that recruitment was poor (Evans and Young 1972 p. 231). In Australia, continuous grazing by hard-hooved livestock initially removed the more palatable and sensitive intertussock herbs and the tall C_4 grass (*T. triandra*); fire exacerbated these losses; *T. triandra* was replaced by cool-season C_3 native grasses (such as *Austrodanthonia* spp.). Further grazing favoured short cool-season grasses and eliminated or greatly reduced the remaining palatable forb components, and loss of both these functional groups led to nutrient enrichment of the soil, particularly with N, which in turn allowed invasion by alien forbs and annual grasses of European origin (Moore 1973, Mack 1989, Moore 1993, Groves and Whalley 2002, Groves *et al.* 2003). In temperate Australian grasslands, the main trends in plant composition were from summer to winter-growing grasses, from perennials to annuals and from native to introduced species (Moore 1973, Stuwe and Parsons 1977, Mack 1989, Moore 1993, Groves and Whalley 2002, Prober *et al.* 2002, Prober and Lunt 2009). Intense grazing of *T. triandra* during its reproductive phase when it is mobilising nutrients from leaves to storage organs may have been the critical factor in its extensive demise (Dunin 1999).

The appropriate management regimes for remnant natural temperate grasslands of south-eastern Australia have been a controversial topic for many years, but the main factors resulting in losses of vascular plant diversity and the management activities required to minimise such losses are clear. Grasslands dominated by *T. triandra*, the most important dominant grass in wetter areas, and a rapid accumulator of dead biomass, require regular burning at intervals of less than five years (Wong and Morgan 2007) or other forms of biomass reduction management such as grazing, mowing or slashing (ACT Government 2005). Continued intensive livestock grazing in these grasslands results in weed invasion, biodiversity losses and habitat degradation, and it is sometimes argued (e.g. Wong and Morgan 2007) that grazing is only appropriate for low-diversity areas, and as a default activity to prevent biomass build-up where burning cannot be undertaken. Grasslands dominated by other grasses, mainly C_3 *Austrodanthonia* and *Austrostipa* species, are more tolerant of grazing, but this is primarily because their composition is a consequence of a prior grazing history, and the species sensitive to grazing have already disappeared (Wong and Morgan 2007). Continued light grazing may be the most appropriate management where the grassland has been previously maintained in this way (Scarlett *et al.* 1992). Strategic grazing to achieve management purposes is often an acceptable approach (ACT Government 2005) and rotational grazing is currently used in conservation grasslands in the Australian Capital Territory to control biomass accumulation of *T. triandra*. Although the *Austrostipa*/ *Austrodanthonia* systems are not as well understood as *T. triandra* grasslands, removal of grazing is not known to advantage weeds, has no known negative effects on biodiversity, and may enable these systems to transition to new states that can be more biodiverse (Wong and

Morgan 2007). Possibly the most critical unsolved problem is how to re-establish native forbs in areas where they have been lost, and maintain their populations in the absence of natural disturbance regimes (Robinson 2003 2005, Reynolds 2006). Soil disturbance by grazing livestock may mimic that once provided by extinct native animals (Reynolds 2006) and provide regeneration niches that are absent in areas managed solely by fire. Norton (1998) and Zimmer *et al.* (2010a 2010b) for example provided evidence that rotational livestock grazing can enable the increase of native forbs.

Relationship between disturbance and exotic plant invasion

The term "disturbance" is used in this thesis following the definition of van Andel and van den Bergh (1987): "a change in conditions which interferes with the normal functioning of a given biological system". Due recognition is given to the fact that 'normal' functioning may at times be unknown or poorly described (the ecological history of these grasslands being poorly understood) and that there is a continuing risk of tautology, since a particular change in conditions can only be defined as a disturbance by measuring effects on the system.

Disturbance frequently increases the invasibility of communities (Hobbs and Huenneke 1992, Levine *et al.* 2003) and the more frequent, intense or prolonged the disturbance, the greater the invasions are likely to be (Fox & Fox 1986, Carr *et al.* 1992). Plant invasions occur generally in disturbed habitats and are less common in intact ecosystems (Ramakrishnan and Vitousek 1989, Hierro *et al.* 2006). Continuous intensive grazing of livestock in Australian temperate native grasslands resulted in invasions by exotic plants that were dispersed by livestock and in fodder and were favoured by the types of disturbance associated with hard-hooved ungulates. Numerous studies have demonstrated that exotic plant invasions in Australian temperate grasslands are enhanced by disturbance, including livestock grazing, nutrient enrichment and cultivation (Lunt 1997b). McIntyre and Lavorel (1994a 1994b) for instance found that exotic species richness in New England tablelands grasslands was enhanced by anthropogenic water enrichment and soil disturbance. However, generalisations about the relationship between particular disturbances and exotic plant invasions have remained elusive, and there is consensus that at least some weeds can invade without major anthropogenic habitat alteration (D'Antonio *et al.* 1999). It is also widely agreed that weeds with the highest impacts tend to be those that propel their own invasion through positive feedback effects: their impacts facilitate further invasion (Levine *et al.* 2003).

The presence of weeds where native plants once grew may be due to their ability to invade without disturbance or a consequence of damage to the native species by disturbance, but much of the research purportedly demonstrating detrimental impacts of invasive species fails to clearly show that the invasive organism is the cause of the supposed effects (Byers *et al.* 2002). Correlations between weed density and reduction in cover and abundance of a native plant implies a direct negative interaction; however the affected species could be reacting in an opposite way to some independent environmental factor, or to an altered disturbance regime resulting from human activity. It is generally difficult to determine if the invading species or the altered conditions are the primary cause of such changes (Weiss and Noble 1984, Huenneke *et al.* 1990, Woods 1997). If anthropogenic disturbance is the underlying cause, management should address the disturbance, rather than the weed.

Conditions suitable for perennial grass seedling recruitment in perennial grasslands are generally rare or infrequent (Lauenroth and Aguilera 1998), but disturbance is an important factor in the creation of safe sites for grass seed germination, and any disturbance that damages or kills the existing vegetation favours the survival of juvenile plants (Cheplick 1998). Numerous experimental studies have demonstrated negative effects on grass recruitment due to the presence of established grasses (Lauenroth and Aguilera 1998). Nutrient enrichment has also been identified as a major cause of alien grass invasion worldwide (Milton 2004). Invasion cannot occur in the absence of propagule pressure, but all communities dominated by indigenous plant species may be thought of as possessing biotic resistance to invasion.

Relationship between *N. neesiana* invasion and disturbance

Invasions of Australian temperate native grasslands by *N. neesiana* may be disturbance-driven, and disturbance may be the cause of perceived biodiversity changes that have been associated with the grass. However there is no agreement in the literature on the role of disturbance in *N. neesiana* invasions. Some authors recognise it as an important factor, while others argue that the plant's superior competitive abilities enable it to invade, regardless of the level of disturbance.

Weber (2003 p. 280), based on a very limited literature review, concluded that *N. neesiana* "invades mainly degraded and disturbed plant communities". In contrast, Bartley *et al.* (1990), commenting on the situation in Victoria, wrote that "prior disturbance does not appear to be necessary for invasion" of native grasslands, an opinion echoed by Kirkpatrick *et al.* (1995 p. 35), who nevertheless added that "its spread is certainly facilitated by soil disturbance". The plant survives well in its native habitats in the Rio de Plata grasslands where trampling by cattle is the main anthropic disturbance (Soriano *et al.* 1992). According to Slay (2002a p. 4) *N. neesiana* "evolved under conditions of low disturbance", and if this is the case, it is presumably well adapted to disperse and recruit under such conditions. However Gardener (Gardener 1998, Gardener *et al.* 1996a, 1999, 2003b) found that *N. neesiana* panicle seeds only germinate on bare ground, in gaps or areas bared by herbicides and other disturbances, and that seedlings only survive in bare areas. Other authors have also recognised an important role of disturbance in invasions: for example Bedggood and Moerkerk (2002) recorded regrowth in wheel tracks after treatment of infestations with herbicide, and Liebert (1996) recommended the avoidance of unnecessary soil disturbance to minimise invasion.

Bruce (2001) attempted to determine the importance of four types of 'disturbance' in determining the level of infestation in native grasslands by *N. neesiana* in the Australian Capital Territory, namely bare ground, other exotic weed populations, soil disturbance (earthworks, erosion, cultivation, animal diggings etc.) and the amount of refuse dumping (garden waste, soil, rubbish). *Nassella neesiana* had widely varying levels of abundance, from absent to dominant, where bare ground was present at low and medium levels. It had the largest range of abundances at high weed levels and the lowest at low weed levels (perhaps suggesting that *N. neesiana* facilitates "invasional meltdown" - a process in which "synergistic interactions among invaders ... lead to accelerated impacts on native ecosystems" (Simberloff and Von Holle 1999, p. 21)). Sites with medium soil disturbance were overall more highly invaded, but the single site with no soil disturbance had occasional *N. neesiana* patches, and sites with low soil disturbance had a range of infestation levels. The degree of infestation varied widely for all levels of garden waste dumping, but *N. neesiana* was observed to have established and be spreading from scattered piles of lawn clippings at one site. Proximity to urban development appeared to be the most important predisposing factor for *N. neesiana* invasion in the ACT, and use of the land as urban open space appeared to have almost guaranteed that it would become infested, probably as a result of seed dispersal by mowing (Bruce 2001). Understanding the role of disturbance in invasions clearly requires that propagule pressure be simultaneously assessed.

The predominant expert position therefore appears to recognise that dispersal and recruitment of *N. neesiana* is facilitated by anthropogenic disturbances, but that invasion may nevertheless occur in areas that are minimally disturbed.

Mechanisms of impact

Considerable research effort has been devoted to understanding the mechanisms by which invasive plants cause biodiversity impacts (Levine *et al.* 2003). Many invasive plants "integrate smoothly" (Woods 1997) into invaded systems and are recognised as having minimal impact (Kirkpatrick *et al.* 1995, Woods 1997, Grice 2006). Severe impacts may occur if the invader is a 'transformer' species – these often have a growth form not present in the invaded community and typically come to dominate by forming a high proportion of the biomass, or have disproportionate influences on ecosystem function (Henderson 2001, Grice

2006). Assessment of impact mechanisms is complicated because most Australian temperate grasslands have large inventories of alien vascular plant species, all areas have at least some exotics (Kirkpatrick *et al.* 1995) and invasion by multiple weed species, together or successively, is usual (Adair 1995).

Superior competitive abilities have often been invoked as the cause of biodiversity impact, but according to Woods (1997 p. 61) “there have been few cases where competition from invaders has been shown unambiguously to be responsible for significant alteration of communities. Most of the extensive literature suggesting such effects is based on correlative studies, historical records, or anecdotes”. In general, little quantitative information of effects on native species and ecosystem functioning has been published (Byers *et al.* 2002) and overall in Australia the mechanisms by which weeds impact on ecosystem structure and function – “how” weeds affect biodiversity – have not been widely quantified (Adair and Groves 1998, Grice 2004a, Grice *et al.* 2004, Grice 2006). Environmental weeds apparently cause fragmentation of habitat, disintegration of plant communities and extinctions, but the details of how this occurs, and what is impacted, have been scanty (Adair 1995).

An array of detrimental impacts of environmental weeds has been recognised in Australia. Nineteen of the 20 studies examined by Adair and Groves (1998 p.7) “demonstrated a decline in either species richness, canopy cover or frequency of native species”. A much more thorough review (Coutts-Smith and Downey 2006, updated by Downey and Coutts-Smith 2006) found negative impacts on 283 plant species (including algae and fungi), 63 animal species, 15 threatened populations and 71 endangered ecological communities (90% of all officially recognised endangered communities) in New South Wales alone. ‘Competition’ (as opposed to habitat degradation by weeds and weed control activity) was allegedly the main threatening factor.

Weed impacts can be harmful or beneficial (Adair and Groves 1998, Williams and West 2000, Low 2002, Richardson and van Wilgen 2004). Invasive plants potentially influence the structure, function and composition of ecosystems by impacting on growth, recruitment and survival of co-occurring species (Grice 2004a, Vidler 2004). These impacts are purportedly “overwhelmingly negative”, but positive impacts also occur (Groves 2004, Richardson and van Wilgen 2004). Weeds can provide food, fodder, building materials, nectar, shade and numerous other benefits for associated animal species (Richardson and van Wilgen 2004). Weeds can contribute to conservation of biodiversity, for example by protecting other plants from herbivores and acting as refuges. Shapiro (2002) documented the case of the city of Davis, California, where a diverse, highly valued urban butterfly fauna is largely dependent on naturalised and cultivated alien plants, and where, in consequence, efforts to control the alien species conflict with biodiversity goals. Low (2002) provided numerous Australian examples of native animals, including endangered species, benefiting from alien plant invasions. Complex, simultaneous negative and positive effects are probably usual. For example Lenz *et al.* (2003) found that the presence of annual exotic grasses on a hillside in one South Australian grassland facilitated native perennial grass growth on upper slopes but impeded it at the lowest elevations.

In evolutionary time, the interactions of invasive species with other species in the invaded community changes selection pressures and ultimately results in evolutionary change, with new species arising (Cox 2004). Thus invasive species eventually tend to "become integrated into the new biotic community in such a way that their initial impacts are softened. Integration occurs through the processes of coevolution and counteradaptation" with the ecological adjustments tending to precede the evolutionary (Cox 2004 pp. 246-247). "Some weeds disappear naturally" (Maiden 1920 p. 16), usually due to more proximate causes, but rates of evolutionary change are still very improperly understood.

Feedback processes, in which the invasive species modifies the invaded environment or habitat for other organisms are doubtless frequently important causative processes in biodiversity impacts. The invader may increase temporal or spatial resource fluctuations and may increase the heterogeneity or homogeneity of the area invaded in a wide variety of ways (Melbourne *et al.* 2007).

Impacts on biodiversity may result in impacts on 'ecosystem services', a conceptual framework that enables economic quantification of chemical and biological reserves and cycles for such ecological processes as soil stabilisation and fertility, water quality and quantity, and biological production (Mansergh *et al.* 2006b). Biodiversity can provide direct economic benefits via provision of ecosystem services, and creates the distinctive milieu in which human cultures flourish (Saunders 1999, Mansergh *et al.* 2006b). But biodiversity can also create ecosystem "dis-services", including the negative impacts of exotic invasive species (Mansergh *et al.* 2006b p. 300). However, many processes alter ecosystem functioning, not just alterations to biodiversity, and its contribution to ecosystem services has not been adequately resolved (Aguiar 2005). Less diverse anthropogenic systems may in some circumstances provide similar or higher levels of service than those provided by diverse natural ecosystems.

Mechanisms of invasive plant impact on the invaded systems may include:

1. altered competitive interactions with other plants for light, nutrients, water, pollinators and other resources - resulting in changes in species composition, niche displacement, or replacement of another species (Weiss and Noble 1984, Adair 1995, FFG SAC 1996,

Woods 1997, Prieur-Richard and Lavorel 2000, Williams and West 2000, Levine *et al.* 2003, Vidler 2004).

2. changes in species richness or dominance patterns (Adair 1995, FFG SAC 1996,Woods 1997);
3. modifications of the physical structure and chemistry of the habitat (Adair 1995, FFG SAC 1996, Woods 1997, Williams and West 2000);
4. effects on animal health, habitats, food chains and trophic structure of communities (Williams and West 2000, Groves 2002, Low 2002, Levine *et al.* 2003);
5. altered phenology of native species (Woods 1997);
6. facilitation of invasions of other species, including other plant or animal pests and pathogens (Groves 2002);
7. genetic changes, including rates and details of evolutionary interactions, introduction of foreign genes, hybridisation and gene swamping (Carr 1993, FFG SAC 1996, Williams and West 2000, Cox 2004);
8. alterations to disturbance regimes and successional pathways (Woods 1997, Vitousek *et al.* 1997, Mack and D'Antonio 1998, D'Antonio *et al.* 1999, Prieur-Richard and Lavorel 2000);
9. changes in ecosystem function and ecosystem services (Versfeld and Van Wilgen 1986, Adair 1995, FFG SAC 1996, Prieur-Richard and Lavorel 2000, Levine *et al.* 2003, Richardson and van Wilgen 2004) including nutrient cycling (Vitousek *et al.* 1997, Rossiter *et al.* 2006), hydrological processes (Vitousek *et al.* 1997, Versfeld *et al.* 1998, Williams and West 2000), geomorphological processes including soil erosion and landform (Adair and Groves 1998, Williams and West 2000), fire cycles (D'Antonio and Vitousek 1992) and C storage (Seabloom *et al.* 2003);
10. shifts in management regimes, resulting from altered management directed against the weed (Groves 2002).

These mechanisms are usually interrelated in complex ways, often interact, and commonly are difficult to separate from natural processes of succession, climate-related change and anthropogenic effects due to global change or specific management regimes.

Plant species richness in Australian temperate lowland grasslands usually declines as the biomass increases (Lewis *et al.* 2008) and is frequently associated with competitive exclusion by dominant grasses, including *T. triandra* (Lunt and Morgan 1999c, Morgan and Lunt 1999). Increased biomass production may be driven by eutrophication, which increases productivity and the height of the tallest stratum (Hautier *et al.* 2009). McIntyre and Lavorel (1994a 1994b) found declines in total and rare native species in northern New South Wales grasslands with increasing natural fertility of the soil parent materials and water-enrichment. Competition for light is a major mechanism by which the taller growing species suppress other plants. Hautier *et al.* (2009) demonstrated that shading decreased diversity mainly by reducing recruitment of low-statured species, which failed to recruit from the seedbank or suffered higher rates of seedling mortality. In Australian temperate native grasslands Robinson (2003 2005) demonstrated that a high proportion of the native forbs that occupy the intertussock spaces require light to germinate and establish.

The only detailed study to date on the biodiversity impacts of *N. neesiana* was undertaken by Ens (2002a 2002b 2005, a BSc (Hons.) project) who compared effects on invertebrates in one invaded and one uninvaded area in each of two Sydney woodlands. She found significant quantitative impacts, with negative effects on the presence and abundance of various insect taxa and positive effects on others, attributed to the altered habitat structure and "indirect effects on the trophic hierarchy" (Ens 2002a). The study suffered from lack of replication, there was no clear description of the vegetation differences between invaded and uninvaded areas, no explanation of how *N. neesiana* had come to occupy the invaded areas and little indication that the few significant correlations detected were anything more than chance results given the very large number of possible correlations for which tests were undertaken. There was little real indication that the effects were caused by *N. neesiana*. Any area densely covered with any grass might have yielded similar results.

Detection of apparent impacts by comparison of invaded and uninvaded areas is insufficient reason to attribute causative effects to the invader. Mechanisms that explain the impacts must be demonstrated, and alternative explanations for the effects, notably prior disturbance, need to be ruled out. Investigators must not assign causation unless mechanisms that have enabled a particular invasion and which themselves could account for detected biodiversity effects have been adequately determined and understood.

Purpose and structure of the thesis

The thesis addresses some of the key research questions relating to invasion biology and invasive species impact assessment (Byers *et al.* 2002) – what changes to community composition and structure occur post-invasion, which areas experience the greatest impacts, what is the nature of the interactions with native species, and what ecological factors limit spread of the invasive organism or result in vulnerability to invasion. In particular the study has sought to improve understanding about mechanisms of invasion and mechanisms of impact (Grice 2004a 2004b 2006, Grice *et al.* 2004), which can be viewed as functional aspects of biodiversity change (Aguiar 2005). Such enhanced knowledge of ecological mechanisms and processes should enable better generalisations to be made about areas at risk, the particular biodiversity elements that may be affected, and the management techniques that may be useful to mitigate these impacts. Future impacts thus potentially become more predictable, and supposed historical impacts can be more critically evaluated. For the study reported here, evidence was gathered using a variety of botanical, zoological and other techniques, both experimental and observational, at a range of spatial and temporal scales, in a variety of grasslands with markedly different ecological histories, in a range of geographical areas. Core components of the research focused on vascular plant and invertebrate biodiversity differences between areas occupied by dense patches of the grass and matched areas dominated by native grasses.

Approaches and aims

Ecological mechanisms that enable environmental weed invasions are in general complex and poorly understood (Prieur-Richard and Lavorel 2000, Levine *et al.* 2003, Hayes and Barry 2008). Less than 5% of studies on invasive plant impacts examined by Levine *et al.* (2003) attempted to determine the processes causing the invasion. Disturbance has "unanimously been shown to favour plants invasions" (Prieur-Richard and Lavorel 2000 p. 3) but many species appear to be invasive in the absence of significant anthropogenic disturbance, their success being attributed *inter alia* to inherently faster growth rates, superior competitive abilities related to form, phenology, resource exploitation, etc., and the occupation of unfilled structural niches (Carr *et al.* 1986, Carr 1993).

The research reported in this thesis addresses the critical question of the extent to which *N. neesiana* is an 'active' invader able to outcompete the native flora, or a 'passive' occupier which follows anthropogenic disturbance and a symptom, rather than a cause, of biodiversity impacts. Hocking (1998 p. 86) argued that the biodiversity impact of *N. neesiana* in Australia was "likely to be major" in part because it was known to be "actively invading high quality grassland remnants", and various authors (e.g. Craigie 1993) have claimed that prior disturbance does not seem to be a requirement for it to invade. However major biodiversity impacts are more likely to arise from transformer species, particularly weeds with novel growth forms, rather than ecological analogues of native species already present (Grice 2004a). Hocking (1998 p. 86) also observed that "some well-managed" native grassland remnants have shown resistance to invasion, suggesting that the invasiveness of *N. neesiana* is in part dependent on the characteristics of the pre-existing community.

Most studies of biodiversity impacts have involved instantaneous comparisons of invaded and uninvaded areas ("space for time substitution" (Gaertner *et al.* 2009)) and prior effects have often been only superficially investigated. Impacts have been attributed to weeds by default, when efforts to detect ecological differences between invaded and uninvaded areas yield nothing of significance (e.g. McArdle *et al.* 2004). Widespread failure to adequately investigate mechanisms of invasion and impact has resulted in superficial explanations of complex ecological problems that generate simplistic 'solutions', usually specific herbicidal control of an individual weed species. This study sets out to test an 'invasion requires disturbance' hypothesis. Testing of a contrasting 'superior competitor' hypothesis is necessary, but this was judged to be too ambitious for the study reported here, and was not attempted.

The fluctuating resources theory posits that any increase in the amount of unused resources in a community increases its susceptibility to invasion (Davis *et al*. 2000), and that the invasibility of the community to a particular species is increased if these particular resources were previously limiting the recruitment, growth or survival of that species (Hobbs 1991). Continuity of the invasion requires that the gains the invader makes are not lost when resource supply contracts (Melbourne *et al.* 2007). Because resources are 'locked up' variably in space and time by the plants in any community, disturbance that kills or inhibits them and frees up resources is generally required for a successful invasion, or there must be extrinsic addition of resources at a rate faster than can be used by the native plants (Herbold and Moyle 1986, Hobbs 1991, Burke and Grime 1996, Cox 2004). 'Disturbance' can be defined as any process that creates open ground, changed habitat or altered resource availability (Hobbs 1989 1991, Mack and D'Antonio 1998, Lockwood *et al.* 2007). Disturbance is omnipresent at a range of spatial and temporal scales, so gaps in vegetation and fluctuating resource pools are always available. Under this definition, disturbance includes reduction or lack of normal disturbance to which the community is adapted, e.g. reduced fire frequency, removal of grazing, or loss of burrowing mammals can provide fluctuating resources, as native plants senesce, or seed banks decay without replacement. Elimination of perturbation in disturbance-dependent systems is one of the most serious 'disturbances' they can suffer (MacDougall and Turkington 2007).

Disturbance frequently increases the invasibility of communities (Hobbs and Huenneke 1992). Previous studies in Australian temperate native grasslands (e.g. Lunt and Morgan 2000) have indicated that disturbances that kill the existing native vegetation, particularly the dominant grasses, are an important cause of invasion. There is also strong evidence that nutrient enrichment is a major causative factor of *Nassella* invasions in temperate Australian grasslands (Wijesuriya 1999, Wijesuriya and Hocking 1999). Examination of a range of disturbance factors in relation to *N. neesiana* invasion was clearly required as part of the study reported here.

One of the most critical anthropogenic disturbances in grasslands dominated by *T. triandra* is suppression of fire. In the absence of fire, gradual build-up of dense biomass by *T.*

triandra results, after a period of years, in a self-shading effect that causes tussock death (Lunt and Morgan 1999c, Morgan and Lunt 1999). This senescence dieback has been found to remove biotic resistance and open the community to invasion by weeds including *N. neesiana* (Lunt and Morgan 2000). Examination of this question was also a clear priority.

The field experiment reported in this thesis was designed to test the hypothesis that invasions by *N. neesian*a are disturbance-driven, and to determine the extent to which the native grassland may possess biotic resistance to invasion. A range of other disturbances, including water enrichment were considered to be probably important, but were unable to be studied in the timeframe and with the resources available.

Aims

The overall aims of the research program were to examine the hypotheses that:

1. *Nassella neesiana* invasions are the result of disturbance involving the death of the dominant native grasses and nutrient enrichment;
2. management-induced disturbances, in particular senescence dieback of *T. triandra*, are a major cause of *N. neesiana* invasions;
3. rates of change in the size of *N. neesiana* infestations, and thus their biodiversity impacts, are controlled by management and disturbance factors at a local scale;
4. areas occupied by *N. neesiana* have reduced native plant and invertebrate diversity and increased exotic biodiversity, and
5. the presence of *N. neesiana* alters ecosystem properties with ongoing biodiversity impacts.

The main research studies undertaken to determine the composition of the affected biodiversity were:

1. floristic studies on invaded and uninvaded areas;
2. invertebrate sampling of invaded and uninvaded areas;
3. observations of the utilisation of *N. neesiana* by phytophagous invertebrates.

The studies were restricted to grasslands dominated by *T. triandra* in areas of >500 mm average annual rainfall. *Nassella neesiana* is also a threat in the more xeric grasslands, such as those of the Victorian Wimmera, dominated by *Austrostipa* and *Austrodanthonia* species, and the reader should recognise that findings from studies in the mesic grasslands may not necessarily be applicable to these other temperate grasslands.

Kirkpatrick *et al.* (1995 p. 35) noted that *N. neesiana* “generally grows to the exclusion of all other species” in temperate native grasslands of south-eastern Australia. In New Zealand *N. neesiana* commonly occurs in relatively “pure stands” (Bourdôt and Hurrell 1987a p. 207) that can look like cereal crops (Slay 2002c). In the grasslands studied in this thesis *N. neesiana* frequently occur in such more or less discrete patches, with relatively high foliar cover and minimal cover of other perennial grasses, and such visually distinct patches were generally the focus of investigation. The dispersion characteristics of *N. neesiana* populations *per se*, were not an object of study.

Methodology

Throughout the thesis taxonomic nomenclature for vascular plants and their native/exotic status is based on Walsh and Stajsic (2007) and Harden (1992 1993 2000 2002). Other references used for plant nomenclature included Shepherd *et al.* (2001) and Randall (2002), particularly as authorities for common names.

Latitudes and longitudes were taken with a Garmin GPS 76 Marine Navigator global positioning system device (Garmin International Inc. Kansas, USA) and are reported in the Geocentric Datum of Australia 1994 (GDA94) geographical coordinate set.

Research permits

The research undertaken required permits under various legislation. A permit issued by the Victorian Department of Primary Industries under the *Catchment and Land Protection Act 1994* allowed collection, transport and cultivation of *N. neesiana*, collection and transport of soil containing its seeds, and the spreading of seed in a grassland experiment at Iramoo Native Grassland Reserve (Permit PP-004-07). A Victorian Department of Sustainability and Environment research permit under the *Flora and Fauna Guarantee Act 1988*, the *Crown Lands (Reserves) (Nature Conservation Reserve) Regulations 2004* and the *National Parks Act 1975* allowed work in Victorian reserves, including collection of flora and invertebrate trapping (Permit No. 10004227). Permission to take protected flora under these Acts was also covered by Permit No. 10003823 issued to Iramoo Sustainable Community Centre. Licences issued by the Australian Capital Territory government Territory and Municipal Services under the *Nature Conservation Act 1980* permitted specimen collection and soil sampling in the ACT (Licence Nos. LT2007263 and LT2008312). Work at Yarramundi Reach was permitted by the National Capital Authority and at Iramoo by the Iramoo Committee of Management.

Statistical analyses

Data was entered into spreadsheets in Microsoft® Office Excel which was used for simple data analysis and chart generation. Statistical analyses throughout the thesis were undertaken using GenStat® Version 8.1 (Payne *et al.* 2005). Data were checked for normality and if not normally distributed were transformed appropriately to minimise residuals. General analysis of variance (ANOVA) was used to test for significance unless otherwise stated. Effects were considered significant at the P≤0.05 level, unless otherwise noted, and significant figures are generally highlighted in tables in bold fonts. Back-transformed means are presented where appropriate.

Data preservation

Victorian plant quadrat data has been supplied to the Flora Information System, a long term database repository for such information, managed by the Department of Sustainability and Environment.

The bulk of the invertebrate material collected will eventually be deposited in the Victorian Agricultural Insect Collection of the Department of Primary Industries. A few significant specimens have been deposited at the Museum of Victoria.

Study sites

Six major study sites were utilised in the research:

1. **Yarramundi Reach grassland** (35º 17.5' 149º 05'), Belconnen, Australian Capital Territory, 21.2 ha, 565 m altitude, located at the western end of Lake Burley Griffin, managed by the National Capital Authority, and the largest remaining remnant in Central Canberra (ACT Government 2005). The site has duplex yellow podzolic soils derived from porphyry that are sandy loams in the upper horizons and yellow clays at depth (Chan 1980). It has been described as an "extensive, but somewhat degraded" *T. triandra* grassland and "one of the more important ACT grasslands" (Frawley *et al.* 1995 p.147). The remnant vegetation consists of 16.4 ha of *Austrostipa* association and 4.8 ha of Dry *Themeda* association (ACT Government 2005). Frawley *et al.* (1995 p.147) considered this grassland to have "a fairly high incidence of weeds", of which the most important exotic grasses were *Avena* spp., *Paspalum dilatatum* Poir. and *Vulpia* spp. *Nassella neesiana* has been present at least since 1995 (Berry and Mulvaney 1995) and has gradually occupied large areas so that the grassland as a whole has recently been considered 'heavily invaded' (Cooper 2009).

The area was set aside as the site for the National Museum of Australia around 1983 and temporary buildings opened in 1986 (Frawley *et al.* 1995), however construction of the Museum never proceeded. A conservation plan that proposed management burning of five zones every 3 to 5 years and winter mowing with removal of cut material was prepared in 1987, but was "not effectively implemented" (Frawley *et al.* 1995 p. 147). A 1992 ACT City Parks Management review included management prescriptions for the site and proposed mowing "only every several years, in rotation throughout the site" after discovery of a population of the Striped Legless Lizard *Delma impar* (Fischer) (Frawley *et al.* 1995 p.147). The site was then managed by ACT City Parks to protect the lizard by mowing one third of the area each year, with no burning. Previous studies of the grassland at the site include Chan (1980), Rowell (1996), Sharp (1997), Bruce (2001) and Muyt (2005).

This grassland was not grazed by livestock at least from 1965 (Frawley et al. 1995), although Chan (1980) indicated that the northern section was used as natural pasture. It was burnt by wildfires on 25 December 2001 except for a small part of the northern area, but escaped burning in the disastrous Canberra bushfires of 18 January 2003 (Emergency Management Australia 2006, Graeme Hirth, Environment ACT, pers. comm. 24 July 2008).

2. **Dudley Street grassland** (35º18.8' 149º05.5'), between Denman and Dudley Streets, Yarralumla, ACT, 580 m, a 2.2 ha remnant, consisting of 0.6 ha of *Austrodanthonia* association, 0.9 ha of Wet *Themeda* association and 0.7 ha of exotic grassy vegetation (Sharp 1997, ACT Government 2005). The site was rated in 2005 as "small fragment" of moderate botanical significance (ACT Government 2005 p. 68). The native grassland is approaching a critical threshold due to too frequent and close mowing and *N. neesiana* invasion (Cooper 2009).
The exotic vegetation has been managed by mowing (Sharp 1997) and the *T. triandra* area was deliberately burned by Environment ACT on 31 September 2008 (Jenny Connolly pers. comm. 11 November 2008).

3. **Crace Grassland Nature Reserve** (35º14' 149º08'), Lyneham, ACT, 580-620 m altitude, 136 ha, formerly used by the Department of Defence, the remainder being Australian Capital Territory land with a rural lease over 30 ha (Cooper 2009). The native grassland contains 35.9 ha of *Austrodanthonia* association, 3.1 ha of Dry *Themeda*, 22.5 ha of Wet *Themeda*, 41.1 ha of native pasture (*Austrostipa*) and 33.3 ha of exotic grassland (ACT Government 2005). The site was rated in 2005 as of moderate botanical significance - moderately altered by disturbance or land uses, with moderate to high native species diversity, but only of species tolerant to disturbance- with some areas of very low significance – i.e. highly disturbed with very low native forb cover and diversity (ACT Government 2005). The site is managed by grazing of cattle and is also grazed by a mob of over 100 Eastern Grey Kangaroos (Cooper 2009).

4. **Laverton North Grassland Reserve** (37° 45.2' 144°47.5'), Altona North, Victoria, 15 km west-south-west of Melbourne, 15-20 m altitude, is a 53 ha grassland bounded by Kororoit Creek Road and the Princes Freeway, managed by Parks Victoria. The Reserve, described as an "ex-paddock" site and a low quality "degraded, grazed remnant" by Lunt (1995c) is located at the eastern end of the Western Basalt Plain, has deeply cracking clay and clay loam soils derived from sheet flow basalt, and is almost flat (Craigie 1993). Grazing was the main land use for over 100 years prior to temporary reservation in 1983, fertiliser

was applied in some areas during the 1930s and management since reservation has been largely by fire (McDougall 1989, Craigie 1993, Morgan 1999b, Lunt and Morgan 1999a 1999b) described as intermittent, ad hoc burning by Henderson (1999).

The native vegetation is classified as Plains Grassland (Department of Sustainability and Environment 2007) and is mainly species-poor *Themeda triandra* tussock grassland with *Austrostipa* spp. locally abundant (McDougall 1987, Morgan 1999b). There was major loss of native forb diversity prior to reservation (Craigie 1993) and the soil seed bank is dominated by annual exotic species (Lunt 1995c) many of which are common in the intertussock spaces (Morgan 1999b). Many native forbs have been reintroduced since 1983 but the great majority have died out and few have prospered or spread (Morgan 1999b, Smith *et al.* 2009). *Nassella neesiana* has been present since at least 1987 (McDougall 1987) but, was rarely recorded in an extensive 1989 survey (McDougall 1989). However "aggressive invasion" was underway by the early 1990s (Humphries and Webster 1992 p. 2). Lunt (1995c p. 113) suggested that cessation of grazing resulted in its dramatic proliferation, however major *T. triandra* mortality occurred at the site when fire frequency exceeded 5 y, and when fire was finally used, plant and tiller densities of *T. triandra* were much lower than in regularly burnt grassland (Morgan & Lunt 1999, Lunt & Morgan 1999a). *Themeda triandra* senescence due to absence of fire in some areas for 5 or 6 years prior to c. 1995-96 (Colin Hocking pers. comm. 26 February 2009) may have been contributed to wide scale invasion at this site.

5. **Iramoo Wildlife Reserve** (37º 45.2' 144º 47.4'), Cairnlea, Victoria, 16.5 km WNW of Melbourne and just to the west of the Victoria University St Albans campus, 60-65 m altitude, is a 37 ha remnant Western Basalt Plains grassland reserved in 1996 to protect the largest known population of *Delma impar* (O'Shea 2005, Robinson 2005). The reserve occupies the northern section of the former (1939-89) Albion Explosives Factory site and is bounded by Jones Creek to the east and north, and otherwise by housing. Grazing with sheep was the main land use from the mid 1800s to 1991 (O'Shea 2005). *Themeda triandra* is the dominant native grass but *Nassella trichotoma* and *N. neesiana*, which had begun to invade by 1996, are dominant in substantial areas (Puhar and Hocking 1996, Hocking 2005b). The site is currently managed mainly by rotational burning of 2-4 ha management blocks. Grassland investigated included areas formerly dominated by *Nassella* spp. where *T. triandra* was re-established by Mason (2004).

6. **Woodlands Historic Park** (37º 39' 144º 52') formerly Gellibrand Hill Park is a 704 ha reserve managed by Parks Victoria, located in the City of Hume, 20 km north-west of Melbourne, immediately to the north of Melbourne Airport, Tullamarine, and on the outer fringe of the Melbourne metropolitan area (Parks Victoria 1998). The Park was progressively

established from 1975 to 1983 from former sheep and cattle grazing properties and contains significant remnant native grasslands and grassy woodlands (Parks Victoria 1998), however "almost nothing" is known about the original composition of the understorey vegetation (Robertson 1985 p. 40). The area is at the conjunction of Devonian granodiorite hills and Western Basalt Plains, with alluvial terraces along Moonee Ponds Creek (Robertson 1985, Parks Victoria 1998). The mean annual rainfall is c. 550 mm at Melbourne Airport, evenly spread through the year (McDougall & Morgan 2005). The contemporary vegetation, with grassy areas dominated by *Austrostipa* and *Austrodanthonia* spp. or *T. triandra*, and its interactions with fire and marsupial grazing were described in detail by Robertson (1985). The study site utilised (37°38.23' 144° 50.2') was in the Oaklands Common section of the Park, c 630 m north-west of the Woodlands Homestead and 100 m east of Moonee Ponds Creek, and consisted of open grasslands, fringed by *Eucalyptus camaldulensis* Dehnh., *E. melliodora* A. Cunn. ex Schauer and *E. microcarpa* (Maiden) Maiden woodlands, previously used as pasture, and to the south by pastures grazed by horses, sheep and cattle. The soil was a dark sandy loam (Mason 2004). *Nassella trichotoma* (Nees) Hack. ex Arechav. and *N. neesiana* have been recognised as an important problem at the Park, requiring "in places … urgent control" (Parks Victoria 1998 p. 15), but the latter was not considered a species of "particular importance" by Robertson (1985 p. 250). A *T. triandra* area investigated for invertebrate diversity was re-established by Mason (2004) after removal of formerly dominant *Nassella* spp. The grasslands are managed by burning and are grazed by kangaroos.